

# Summer zooplankton metabolism and its relation to primary production in the Western Mediterranean

Zooplankton  
Metabolism  
Vertical migration  
Western Mediterranean  
Thermal stratification

Zooplankton  
Métabolisme  
Migration verticale  
Méditerranée occidentale  
Stratification thermique

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## ABSTRACT

Oxygen consumption and excretion rates for ammonia and soluble reactive phosphorus (SRP) by mesozooplankton were studied at a series of stations located along a transect between the islands of Mallorca and Menorca during July 1983. As in a previous cruise also made during the summer stratification period (July 1982), vertical profiles of zooplankton biomass showed the existence of a zooplankton maximum, coinciding with the chlorophyll, phytoplankton and  $^{14}\text{C}$  fixation maxima. The mean zooplankton excretion in the euplankton layer can provide 13.7-16.8 % of the N (as ammonia) and 67.2-76.6 % of the P (as SRP) requirements for primary production, assuming a mean carbon-to-nitrogen assimilation ratio (C/N) of 6.65, equal to the mean C/N ratio of the particulate matter in the cruise, and a C/P assimilation ratio of 183.7 (equivalent to the mean composition ratio of phytoplankton). According to the rate of oxygen consumption by the zooplankton, the maintenance of its metabolic activity required 20-23 % of the primary production. Due to nyctemeral migration, zooplankton maintained a day-night rhythm in the nutrient supply to the surface layers. The night/day ratio of the excreted nutrients averaged 1.5 in the 0-50 m depth layer.

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## RÉSUMÉ

Le métabolisme du zooplancton en relation avec la production primaire pendant la période estivale dans la Méditerranée occidentale

Les taux de respiration et d'excrétion (ammonium et phosphore) du mésozooplancton ont été étudiés le long d'une radiale allant de Barcelone au canal séparant Majorque de Minorque en juin-juillet 1983. Comme lors d'une mission précédente, réalisée aussi pendant la période de stratification thermique (PEP-82, juillet 1982), la distribution verticale de la biomasse du zooplancton a montré l'existence d'un maximum en coïncidence avec les maxima de chlorophylle, phytoplancton et fixation de  $^{14}\text{C}$ . L'excrétion moyenne due au zooplancton dans la couche épiplanctonique peut fournir 13,7-16,8 % de l'azote (sous forme d'ammonium) et 67,2-76,6 % du phosphore (sous forme de phosphore réactif soluble) nécessaire à la production primaire, si l'on considère un rapport d'assimilation C/N de 6,65, égal au quotient C/N correspondant à celui de la matière organique particulaire trouvée pendant la mission et un rapport d'assimilation C/P de 183,7, égal au rapport C/P moyen du phytoplancton. En ce qui concerne le taux de respiration, l'activité métabolique du zooplancton correspondrait à 20-23 % de la production primaire. La migration verticale du zooplancton a pour conséquence un rythme journalier d'apport de sels nutritifs par excrétion dans les couches supérieures, le rapport nuit/jour étant voisin de 1,5 dans les 50 premiers mètres.

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## INTRODUCTION

Zooplankton feeding and excretion are of special interest in the study of the factors controlling planktonic production in marine ecosystems (Cushing, 1975). The ratio of primary production supported by the nutrients excreted by zooplankton has been reported to be negligible or very low in coastal and estuarine areas (Smith, 1978 *a*; *b*), but in oceanic zones, or when the vertical upward transport of nutrients has been reduced by density stratification, zooplankton excretion can be one of the most important sources of nutrients in the photic layer (Jawed, 1973; Holligan *et al.*, 1984). In some cases it can even supply all the requirements in N (Verity, 1985) and P (Martin, 1968; Eppley *et al.*, 1973) of the phytoplankton.

During summer stratification in the Western Mediterranean, planktonic production is strongly influenced by the development of deep chlorophyll and zooplankton maxima (DCM and DZM, respectively). Their characteristics were studied throughout a series of cruises (PEP-82, July 1982; PEP-83, June-July 1983; PEP-84, May 1984) sponsored by the Comisión Asesora de Investigación Científica y Técnica (CAICYT) and the Instituto de Ciencias del Mar de Barcelona (CSIC), on board the R/V *García del Cid*, in the area between Barcelona and the islands of Mallorca and Menorca. The purpose of the present paper is to study the oxygen consumption and nitrogen (ammonia) and phosphorus (soluble reactive phosphorus, SRP) excretion rates by zooplankton, as well as their contribution to primary production during the PEP-83 cruise (30 June-18 July 1983). The structure of phytoplankton populations, chlorophyll distribution, and primary production in relation to the vertical structure of the water column in the same area, have been discussed by Margalef (1985) and Estrada (1985 *a*; *b*), and the vertical distribution of zooplankton biomass and the relationship between the DZM and the DCM have been described by Alcaraz (1985) and Alcaraz *et al.* (1985).

## MATERIAL AND METHODS

The area sampled during the PEP-83 cruise (30 June-18 July 1983) comprised a transect from Barcelona to beyond the channel between Mallorca and Menorca (Fig. 1). As in a previous cruise (PEP-82, July 1982), the survey included two series of stations, "hydrographic" and "biological". In the biological stations, which lasted for 12 to 24 hours, six depths were chosen according to the profiles of temperature, salinity,  $O_2$ , underwater irradiance,  $NO_3-N$ ,  $NO_2-N$ ,  $NH_4-N$ ,  $PO_4-P$ ,  $SiO_4-Si$  and chlorophyll *a*. The parameters considered were spectrophotometric chlorophyll *a*, zooplankton (mesoplankton) biomass,  $^{14}C$  phytoplankton uptake, and zooplankton respiration and excretion rates. More details concerning the sampling strategy and methodology can be found in Estrada (1985 *a*; *b*), Margalef (1985), Alcaraz (1985) and Alcaraz *et al.* (1985). Zooplankton biomass

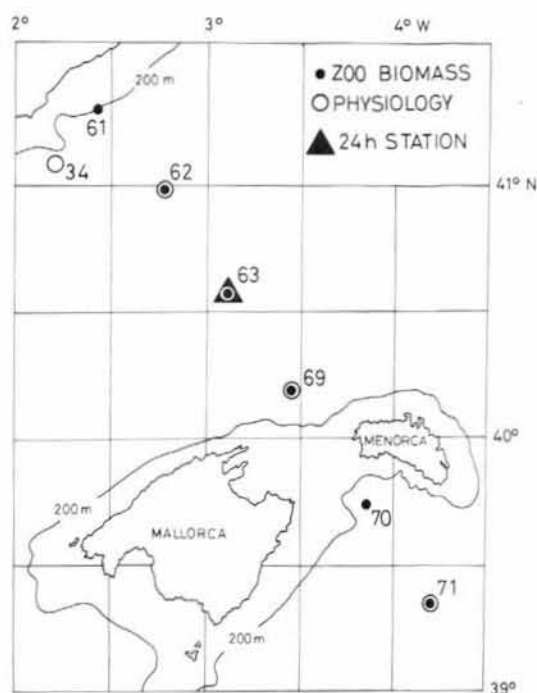


Figure 1  
Position of the stations during the PEP-83 cruise.

was estimated as described by Alcaraz (1982; 1985) and Alcaraz *et al.* (1985): 30 l water samples, taken by means of Van Dorn metacrilate bottles, were filtered through 200  $\mu m$ -mesh nylon netting, and the material retained was transferred onto pre-combusted Whatman GF/C glass fibre filters, dried and stored until analysis. The analyses of the organic C and N contents of the filters were carried out with a Perkin-Elmer model 240 CHN analyzer as described in Fraga (1976). The sample volume was considered to give an acceptable estimation of the mesoplankton biomass in view of the coefficient of variation obtained during the PEP-82 cruise, corresponding to five repeated casts at the same depth ( $Cv = 18.9\%$ , Alcaraz, 1985). Biomass has been expressed in  $\mu g \text{ at.N.l}^{-1}$  as particulate organic N is more closely related to living matter than particulate organic C, due to the significant fraction of carbon-rich detrital particulate matter which is retained by the 200  $\mu m$  filters (Holligan *et al.*, 1984; Alcaraz, 1982; 1985; Alcaraz *et al.*, 1985) in this area.

According to the position of the DCM, which was determined by means of fluorimetric analysis of samples taken at intervals of 10 m between the surface and 120 m depth, six zooplankton samples were obtained from surface to 90 m in order to estimate its vertical distribution. One sample coincided with the DCM, and two more were 10 m above and under the DCM.

The day-night changes in the vertical distribution of zooplankton biomass were studied at station 63 by means of profiles made at approximately 4-hour intervals throughout a period of 24 hours.

Respiration and excretion rates of zooplankton at the stations — shown in Figure 1 — were estimated simultaneously by the difference in oxygen, ammonia and

phosphate concentration in experimental and control bottles.

Experimental organisms (mixed zooplankton) were collected by means of a 200  $\mu\text{m}$  WP-2 net with a non-filtering cod end, hauled from 100 m depth to the surface. Zooplankton samples were immediately transferred to several 1 l jars and diluted with sea water from the DCM, previously filtered through GF/C glass fibre filters. The zooplankton was allowed to acclimatize for one hour at the experimental temperature and in dim light. One to five ml aliquots of the diluted samples, depending on the abundance of zooplankton, were introduced into 250 or 500 ml acid-rinsed beakers filled with filtered sea water (the same as that used to dilute the samples). Bottles with

and without zooplankton were stoppered avoiding the trapping of air bubbles, covered with aluminium foil, and incubated from 12 to 24 hours at 15 °C.

The samples for  $\text{O}_2$ , ammonia and SRP analysis from experimental and control flasks were taken by means of a syphon fitted with 200  $\mu\text{m}$  nylon netting in order to retain the organisms in the flasks. After sampling, zooplankton was transferred by filtration on to pre-combusted GF/C glass fibre filters and analysed as in the case of zooplankton biomass. The concentration of zooplankton in the experimental flasks was from 6 to 60 times greater than that observed in the deep zooplankton maximum (DZM). Oxygen concentration was analysed by means of the Winkler method, using a Metrohm E 425, E 473 automatic titrator fitted with a platinum electrode and a silver-silver chloride reference electrode to detect the end point, which corresponded to 333 mV.

Ammonia was analysed after Koroleff (1970), and soluble reactive phosphorus (SRP) with a Technicon autoanalyzer following the procedure of Strickland and Parsons (1972). The results were expressed as  $\mu\text{gat O}_2\text{-O}$ ,  $\mu\text{gat NH}_4\text{-N}$ , and  $\mu\text{gat PO}_4\text{-P}$  per  $\mu\text{gat N}_{200}$  per day.

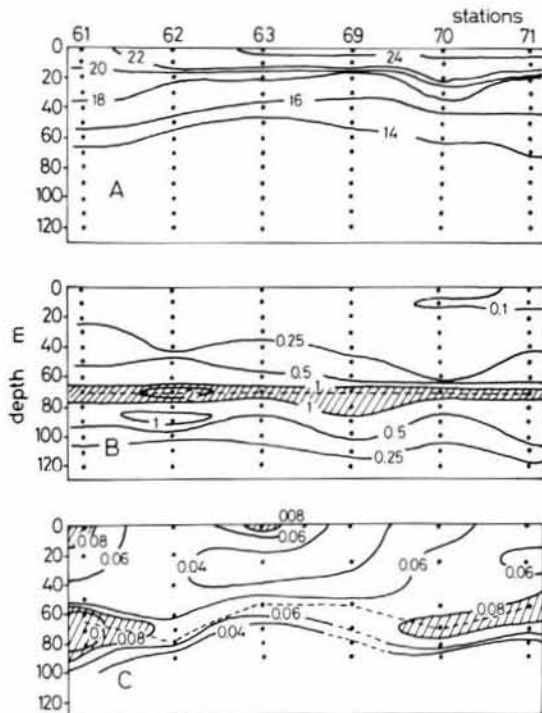


Figure 2  
Isopleths of A: Temperature (°C); B: Chlorophyll a ( $\mu\text{g l}^{-1}$ ) and C: Zooplankton biomass ( $\mu\text{gat N}_{200} \text{ l}^{-1}$ ) during the PEP-83 cruise. Shaded areas indicate concentrations above 1  $\mu\text{g chl a l}^{-1}$  and 0.08  $\mu\text{gat N}_{200} \text{ l}^{-1}$  respectively.

## RESULTS

### Zooplankton biomass and taxonomic composition

The general conditions of thermal stratification and vertical distribution of chlorophyll a (Fig. 2) during the PEP-83 cruise were in good agreement with those of the previous cruise (PEP-82, Alcaraz, 1985), as were the mean zooplankton biomass, the main features of its vertical distributions and the general taxonomic composition, although during PEP-82 DCM and DZM were between 10 and 20 m deeper. The values of zooplankton biomass along the transect (Tab. 1) showed a minimum at stations 63 and 69 (Fig. 2), at the same location where the lowest values were found during PEP-82 (station 19, Alcaraz, 1985).

Near the Catalan coast (station 34), gelatinous zoo-

Table 1

Zooplankton biomass, metabolic rates and contribution of ammonia and SRP to primary production in the Western Mediterranean. Zooplankton biomass in  $\mu\text{gat N}_{200} \text{ l}^{-1}$ ; metabolic rates in  $\mu\text{gat O}_2\text{-O}$   $\mu\text{gat N}_{200}^{-1} \text{ d}^{-1}$ ,  $\mu\text{gat NH}_4\text{-N}$   $\mu\text{gat N}_{200}^{-1} \text{ d}^{-1}$  and  $\mu\text{gat PO}_4\text{-P}$   $\mu\text{gat N}_{200}^{-1} \text{ d}^{-1}$ .  $\text{NH}_4\text{-N}$  and  $\text{PO}_4\text{-P}$  excreted by zooplankton, and N and P required by phytoplankton in  $\text{mg m}^{-2} \text{ d}^{-1}$ . Values corresponding to 15 °C.

Station	Zoo- plankton biomass	Metabolic rates			$\text{NH}_4\text{-N}$ excreted	$\text{N}^+$ required	% contri- bution	$\text{PO}_4\text{-P}$ excreted	$\text{P}^*$ required	% contri- bution
		$\text{O}_2\text{-O}$	$\text{NH}_4\text{-N}$	$\text{PO}_4\text{-P}$						
34	0.0880	0.874	0.117	—	13.05	—	—	—	—	
62	0.0514	2.910	0.083	0.0150	5.40	32.17	16.8	2.15	3.14	68.5
63	0.0448	2.560	0.061	0.0098	3.43	39.54	8.7	1.22	3.86	31.6
69	0.0457	1.920	0.107	0.0295	6.16	35.48	17.4	3.76	3.46	108.6
71	0.0581	0.835	0.077	0.0169	5.64	46.76	12.1	2.74	4.56	60.1
$\bar{X}$	0.0576	1.819	0.089	0.0178	6.74	38.48	13.7	2.46	3.75	67.2
$\sigma$	0.0178	0.950	0.023	0.0083	3.67	6.28	4.1	0.92	0.53	27.5

\* Calculated according the carbon fixation rates by phytoplankton and assuming the C : N and C : P assimilation ratios to be equal to the composition ratios of phytoplankton. C : N = 6.65 (this cruise, unpublished data); C : P = 183.7 (Mayzaud, Martin, 1975).

plankton (doliolids and siphonophores) were numerically dominant, followed by chaetognaths and copepods (small *Clausocalanus* sp.); in the stations located in the central zone of the transect, zooplankton populations were almost exclusively composed of copepods (small and large *Clausocalanus*, *Calanus*, *Lucicutia*, *Candacia*, etc., at station 62, and large copepods such as *Eucalanus*, *Calanus*, *Clausocalanus*, *Rhincalanus*, etc. at station 63). Again near the coast of the Balearic islands (station 69), doliolids, chaetognaths and salps were the dominant groups, followed by radiolarians and small copepods. Beyond the channel between the islands (station 71), the samples included mainly radiolarians and siphonophores and, as minor component, copepods.

The pattern of day-night changes in the depth of the zooplankton maximum at station 63 are shown in Figure 3. During daylight hours, zooplankton and phytoplankton maxima coincided at 60-70 m depth, while at night zooplankton ascended, its maximum becoming located at the surface. The partitioning of the 0-90 m depth biomass in two layers, one between the surface and 50 m depth (above the DCM) and another between 50 and 90 m depth (including the DCM), corresponding to day and night hours, has been summarized in Table 2. During the day, two-

thirds of the zooplankton biomass were concentrated in the 50-90 m layer, while during the night a similar proportion was found between the surface and 50 m depth.

### Respiration and excretion rates

Oxygen consumption and ammonia and SRP excretion rates at 15 °C by mixed zooplankton in the different stations of the transect are shown in Table 1. Although respiration and excretion do not seem to be related, the specific excretion rates corresponding to ammonia and phosphorus show similar trends. The mean specific respiration rate was 1.819  $\mu\text{gat O}_2\text{-O } \mu\text{gat N}_{\text{zoo}}^{-1} \text{d}^{-1}$  (range: 0.835-2.910  $\mu\text{gat O}_2\text{-O } \mu\text{gat N}_{\text{zoo}}^{-1} \text{d}^{-1}$ ). The lowest values were found at stations 34 and 71, respectively coastal and beyond the channel between the islands (Fig. 1), and the highest rates at stations 62 and 63.

Ammonia excretion averaged 0.089  $\mu\text{gat NH}_4\text{-N } \mu\text{gat N}_{\text{zoo}}^{-1} \text{d}^{-1}$  (range: 0.061-0.177  $\mu\text{gat NH}_4\text{-N } \mu\text{gat N}_{\text{zoo}}^{-1} \text{d}^{-1}$ ); as regards phosphorus, the mean excretion rate was 0.0178  $\mu\text{gat PO}_4\text{-P } \mu\text{gat N}_{\text{zoo}}^{-1} \text{d}^{-1}$  (range: 0.0098-0.0295  $\mu\text{gat PO}_4\text{-P } \mu\text{gat N}_{\text{zoo}}^{-1} \text{d}^{-1}$ ). In both cases, the lowest rates were found at stations 62 and 63.

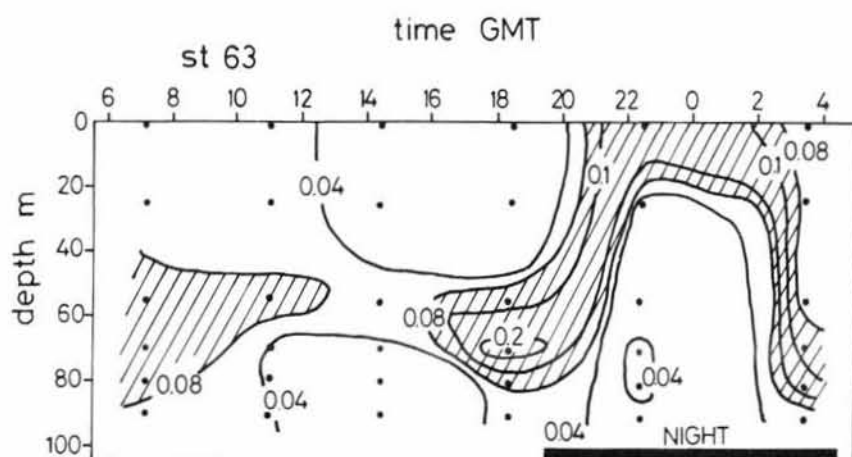


Figure 3  
Changes during a 24-hour period in the vertical distribution of zooplankton biomass at st. 63 during the PEP-83 cruise. Shaded area indicates concentrations above 0.08  $\mu\text{gat N}_{\text{zoo}} \text{l}^{-1}$ .

Table 2

Mean contribution of zooplankton excretion to the N and P requirements of phytoplankton in the 0-50 m depth layer, above the DCM: a) taking into account the effect of vertical migration; b) in the hypothetical case of lacking vertical migration. Data corresponding to 15 °C.

	Day (14 h)	Night (10 h)	Total (24 h)
a) Zoo biomass (%)	31.2	63.6	44.7
N excreted ( $\text{mg NH}_4\text{-N m}^{-3} \text{d}^{-1}$ )	0.0245	0.0357	0.0602
P excreted ( $\text{mg PO}_4\text{-P m}^{-3} \text{d}^{-1}$ )	0.00895	0.0130	0.0219
N required ( $\text{mg N m}^{-3} \text{d}^{-1}$ )	—	—	0.359
P required ( $\text{mg P m}^{-3} \text{d}^{-1}$ )	—	—	0.0350
Contribution of N excretion (%)	—	—	16.8
Contribution of P excretion (%)	—	—	62.8
b) Zoo biomass (%)	31.2	31.2	31.2
N excreted ( $\text{mg NH}_4\text{-N m}^{-3} \text{d}^{-1}$ )	0.0245	0.0175	0.0420
P excreted ( $\text{mg PO}_4\text{-P m}^{-3} \text{d}^{-1}$ )	0.00895	0.0064	0.0152
N required ( $\text{mg N m}^{-3} \text{d}^{-1}$ )	—	—	0.359
P required ( $\text{mg P m}^{-3} \text{d}^{-1}$ )	—	—	0.0350
Contribution of N excretion (%)	—	—	11.7
Contribution of P excretion (%)	—	—	43.6

N:P, O:N and O:P atomic ratios were calculated according to the  $O_2$ -O consumption,  $NH_4$ -N and  $PO_4$ -P excretion rates. The variability between stations (Tab. 3) was lower for N:P than for O:N and O:P ratios. The highest values were found at stations 62 and 63, specially in the case of O:N and O:P ratios, which showed a threefold increase in comparison with the other stations.

Table 3  
Values of the atomic ratios corresponding to  $O_2$  consumption,  $NH_4$ -N and  $PO_4$ -P excretion rates.

Station	N:P	O:N	O:P
34	—	7.4	—
62	5.5	34.9	194.4
63	6.2	43.5	230.5
69	4.5	17.9	65.1
71	3.6	10.8	49.4
Mean	4.9	22.9	144.8
$\sigma$	1.1	15.6	105.9

### Zooplankton metabolism and primary production

Nitrogen and phosphorus requirements of phytoplankton were deduced from data on  $^{14}C$  fixation rates (Estrada, 1985 b). The C:N and C:P assimilation ratios of the phytoplankton were considered to be equivalent to the mean C:N atomic composition ratio of the less than 200  $\mu m$ -size particulate matter collected during the cruise (C:N = 6.69, unpublished data), and to the mean C:P atomic composition ratio of phytoplankton given by Mayzaud and Martin (1975), C:P = 183.7.

The percentages of nitrogen and phosphorus which entered into the system via mesozooplankton excretion of ammonia and SRP in the 0-90 m depth layer have been summarized in Table 1. On average, ammonia and SRP excreted at 15 °C accounted respectively for 13.7 % of the N and 67.2 % of the P required by the phytoplankton.

The day-night changes in the position of the zooplankton maximum determined an increase in the ammonia and SRP excreted in the 0-50 m depth layer during the night. The total amount of N and P excreted (at 15 °C) above the phytoplankton maximum supplied 16.8 % of the N and 62.8 % of the P required by phytoplankton (Tab. 2), according to data on primary production in the 0-50 m depth layer given by Estrada (1985 b).

An estimate of the percentage of primary production

Table 4  
Percentage of the primary production needed to maintain the routine metabolism of zooplankton. Estimations have been made according to the mean  $O_2$  consumption rates, mean C fixation rates and considering 1 ml  $O_2$  = 0.5 mg C. Data corresponding to 15 °C.

Q $O_2$ rate ( $\mu l O_2$ -O $\mu g$ at $N_{zoo}^{-1} d^{-1}$ )	20.4
Q $O_2$ 0-90 m (ml $O_2$ -O $m^{-2} d^{-1}$ )	105.9
C respired (mg C $m^{-2} d^{-1}$ )	52.9
Primary production (mg C $m^{-2} d^{-1}$ )	258.0
% Primary production required by Zoo	20.5

which is "respired" by the zooplankton is given in Table 4. According to data on  $O_2$  consumption rates by zooplankton (Tab. 1) and to C fixation rates by phytoplankton (Estrada, 1985 b), and assuming that 1 ml  $O_2$  is equivalent to 0.5 mg C, zooplankton "respired" 20.5 % of the primary production at 15 °C.

## DISCUSSION

### Metabolic activity and atomic ratios

The changes in the metabolic rates observed along the transect can be attributed to differences in taxonomic composition such as the proportion of gelatinous zooplankton (Verity, 1985) or the size of the organisms (Ikeda, 1985).

The mean specific respiration and excretion rates for mixed zooplankton are slightly lower than those reported by Le Borgne (1973) in the Mauritanian upwelling at 14-18 °C (3.1  $\mu g$ at  $O_2$ -O  $\mu g$ at  $N_{zoo}^{-1} d^{-1}$ ; 0.231  $\mu g$ at  $NH_4$ -N  $\mu g$ at  $N_{zoo}^{-1} d^{-1}$ ; 0.021  $\mu g$ at  $PO_4$ -P  $\mu g$ at  $N_{zoo}^{-1} d^{-1}$ ), Ketchum (1962) in Long Island Sound (2.8  $\mu g$ at  $O_2$ -O  $\mu g$ at  $N_{zoo}^{-1} d^{-1}$ ; 0.364  $\mu g$ at  $NH_4$ -N  $\mu g$ at  $N_{zoo}^{-1} d^{-1}$ ; 0.021  $\mu g$ at  $PO_4$ -P  $\mu g$ at  $N_{zoo}^{-1} d^{-1}$ ) and Verity (1985) in the Sargasso Sea (0.162  $\mu g$ at  $NH_4$ -N  $\mu g$ at  $N_{zoo}^{-1} d^{-1}$ ), although Verity's data correspond to higher temperatures (21 to 29 °C). More similar are the ammonia and SRP excretion rates given by Martin (1968) in Narragansett (0.035-0.338  $\mu g$ at  $NH_4$ -N  $\mu g$ at  $N_{zoo}^{-1} d^{-1}$ ; 0.0112-0.0294  $\mu g$ at  $PO_4$ -P  $\mu g$ at  $N_{zoo}^{-1} d^{-1}$ ), Eppley *et al.* (1973) in the North Pacific central gyre (0.026-0.181  $\mu g$ at  $NH_4$ -N  $\mu g$ at  $N_{zoo}^{-1} d^{-1}$ ; 0.007  $\mu g$ at  $PO_4$ -P  $\mu g$ at  $N_{zoo}^{-1} d^{-1}$ ), Harrison *et al.* (1983) in the middle Atlantic bight (0.05-0.119  $\mu g$ at  $NH_4$ -N  $\mu g$ at  $N_{zoo}^{-1} d^{-1}$ ) and Jawed (1973) off the Columbia river (0.057-0.064  $\mu g$ at  $NH_4$ -N  $\mu g$ at  $N_{zoo}^{-1} d^{-1}$ ). These metabolic rates per dry weight have been converted to rates per  $\mu g$ at  $N_{zoo}$  considering 1 mg dry weight to be equivalent to 7  $\mu g$ at  $N_{zoo}$  (Margalef, Vives, 1967).

The deviations of the O:N, O:P and N:P atomic ratios from the theoretical ones (Redfield *et al.*, 1963) are similar to those obtained by other authors. These differences can have an experimental origin, related for example to the duration of the incubation and concentration of organisms in the experimental flasks. Le Borgne (1979) reported changes in total N and SRP excretion rates during 24 h of incubation, while respiration and  $NH_4$ -N excretion rates were constant, and Nival *et al.* (1974) observed temporal differences in the variability of excretion rates according to the concentration of organisms in the flasks. Other sources of variability can be the feeding condition of the organisms (starvation, proportion of herbivores and carnivores, *etc.*, Ikeda, 1977). The high O:N and low N:P values found during the PEP-83 cruise ( $NH_4$ -N and SRP) suggest a predominance of fat and carbohydrate-oriented metabolism (Le Borgne, 1979; Skjoldal *et al.*, 1984) which is typical of a predominance of herbivores in the zooplankton (Ikeda, 1977).

### Zooplankton metabolism and primary production

According to the zooplankton respiration and primary production rates measured during our cruise, 20 to 23 % of the carbon assimilated by phytoplankton is required for the routine metabolism of zooplankton. When considering some of the reported values of the respiration: ingestion ratio (0.5, Conover, 1956; 0.23, Martin, 1968), it can be concluded that the percentage of the primary production consumed by zooplankton during the PEP-83 cruise should be important.

The estimated contribution of the nutrients excreted by the mesozooplankton to primary production during our cruise corresponded to metabolic rates measured at 15 °C. If data were corrected for the observed 0-90 m depth mean temperature (16.4 °C), taking  $Q_{10} = 1.9$  (Ikeda, 1985), the contribution to primary production would be 16.8 % for  $\text{NH}_4\text{-N}$  and 76.6 % for  $\text{PO}_4\text{-P}$ . These results seem to be low in comparison with data from other oligotrophic areas. In the North Pacific central gyre, the nutrients released by zooplankton (mesoplankton) could account for 40 to 50 % of the nitrogen and 110 to 140 % of the phosphorus required by phytoplankton (Eppley *et al.*, 1973), and in the Sargasso Sea the remineralization rate of ammonia by zooplankton was sufficient to support 100 % of the estimated primary production (Verity, 1985).

When the upward transport of nutrients has been reduced by thermal stratification, the flux of nutrients through the nutricline can supply 50 % of the nutrients required in the DCM (Fasham *et al.*, 1985), while

above the DCM, primary production can be almost entirely supported by zooplankton excretion (Eppley, Peterson, 1979). In the Western Mediterranean, the proportion of regenerated production in surface layers should be higher than the figures obtained for mesozooplankton  $\text{NH}_4\text{-N}$  and SRP excretion. Additional sources of nutrients could be organic compounds (urea and aminoacids), which can account for 16 to 78 % of the excreted N (Mayzaud, 1973; Le Borgne, 1973; Smith, 1978 *a*; *b*) and the contribution of microzooplankton excretion (Glibert, 1982).

The day-night changes in the vertical distribution of zooplankton biomass due to nyctemeral migration is another factor which has important consequences regarding primary production in surface layers. The average contribution of regenerated nutrients to the phytoplankton requirements above the DCM during our cruise (23.8 % of the N and 86.2 % of the P at 18.8 °C, the mean 0-50 m depth temperature), increased 1.5 times during the night due to the higher zooplankton biomass, thus contributing to the enhancement of the primary production and partially counteracting the downward transport of nutrients trapped within sedimenting phytoplankton cells and particles.

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