

Feeding and metabolism of mesozooplankton in the equatorial Pacific high-nutrient, low-chlorophyll zone along 180°

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Received 30 November 2000; revised 19 September 2001; accepted 22 November 2002; published 13 November 2003.

[1] Feeding, respiration, and excretion rates (ammonium and phosphate) of mesozooplankton from the equatorial Pacific upper water column (0–100 m) were measured along the 180th meridian at different stations between 8°S and 8°N, and more repeatedly, at two time series stations, located at 3°S (TSS1) and the equator (TSS2). Only particles of size $>8 \mu\text{m}$ were grazed by the organisms used for the experiments. Grazing rates were higher at TSS1. Ammonium excretion was also maximum at TSS2, resulting in lower O/N values. This suggests that food particles were richer in terms of protein content at the equator, as is also indicated by the lower C/N ratio of particles and the higher proportion of heterotrophic protozoans. Some variations in mesozooplankton specific composition (more carnivorous copepods being present in the equatorial samples) could also explain these O/N differences. Diel variations were observed. Significantly higher grazing, respiration (only at TSS1), and excretion rates were recorded during the day, suggesting that feeding activity was related to the daytime increase of primary production. Using the grazing rates determined under experimental conditions, the grazing pressure on the stock of food particles $>8 \mu\text{m}$ was very low ($<1\%$) and the daily food intake (2.7–3.1% of the zooplankton body carbon), was far from compensating for respiration losses (22% of the body carbon). We conclude that the experimentally measured feeding activity was underestimated because of methodological problems. More realistic values were obtained from energy balance considerations, using measured respiration rates as an indication of minimal carbon requirement and extrapolating to ingestion using literature coefficients for assimilation efficiency (0.7) and net growth efficiency (0.4). According to these calculations the daily food carbon intake necessary to sustain both secondary production and respiration needs would be equivalent to 63% of the mesozooplankton body carbon, and the grazing pressure on $>8\text{-}\mu\text{m}$ food particles would reach 14% of the standing stock d^{-1} . **INDEX TERMS:** 4855 Oceanography: Biological and Chemical: Plankton; 4817 Oceanography: Biological and Chemical: Food chains; 4231 Oceanography: General: Equatorial oceanography; 9355 Information Related to Geographic Region: Pacific Ocean; 4806 Oceanography: Biological and Chemical: Carbon cycling; **KEYWORDS:** mesozooplankton, feeding, respiration, excretion, Pacific, HLNC

Citation: Gaudy, R., G. Champalbert, and R. Le Borgne, Feeding and metabolism of mesozooplankton in the equatorial Pacific high-nutrient, low-chlorophyll zone along 180°, *J. Geophys. Res.*, 108(C12), 8144, doi:10.1029/2000JC000743, 2003.

1. Introduction

[2] Because of its large surface area and to the persistence of upwelling conditions favoring the new production along its variable longitudinal extension, the equatorial Pacific plays a major role in global marine new production [Chavez and Barber, 1987; Chavez and Toggweiler, 1995]. Paradoxically, however, primary production is relatively low considering the concentrations of nitrate and phosphate, which remain above uptake saturating concentrations. Such

observations led Minas *et al.* [1986] to define the high-nutrient, low-chlorophyll (HNLC) concept. Among the possible factors controlling primary production in HNLC areas, the role of zooplankton grazing has been advanced by Walsh [1976], Cullen *et al.* [1992] and Frost and Franzen [1992] among other authors. To rigorously evaluate this mechanism, we need good assessments of the biomass and production of organisms constituting the primary and secondary levels of the food chain. It is also necessary to quantify matter and energy exchanges related to feeding processes (e.g., food intake and excretory and respiratory losses).

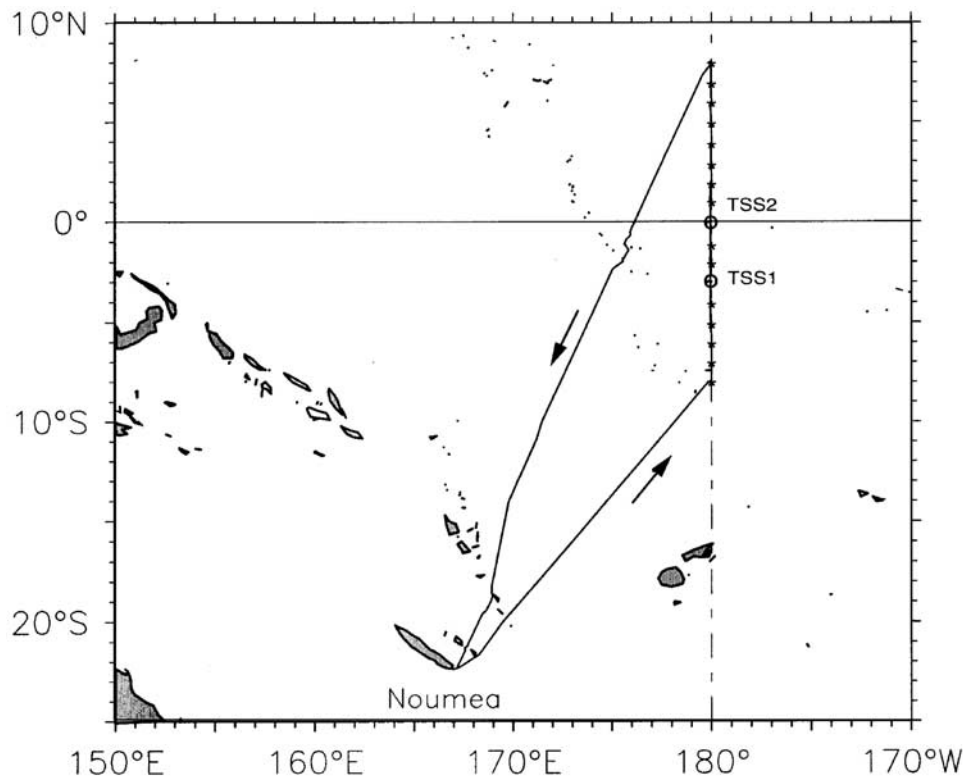


Figure 1. Map of the EBENE cruise with the location of the stations.

[3] Feeding processes also need to be assessed at the different relevant size scales of interacting predators and prey. Picoplankton constitute the main producers in mesotrophic waters of the HNLC equatorial Pacific, but they are consumed mainly by microzooplankton, principally heterotrophic nanoflagellates [Fenchel, 1987; Landry *et al.*, 1995; Calbet and Landry, 1999]. Except for some taxa, such as larvaceans [Diebel and Lee, 1992; Gorsky *et al.*, 1999], mesozooplankton filter feeders (200–2000- μm sized organisms) [United Nations Educational, Scientific, and Cultural Organization (UNESCO), 1968] are unable to retain picoplankton cells on their coarse filtering appendices [Nival and Nival, 1976; Conover, 1982]. Rather, they consume nanophytoplankton or even larger prey [Sherr *et al.*, 1986]. In addition to the different size categories of prey, the roles of mesozooplankton versus smaller consumers are often distinguished by whether he can (meso) or cannot (micro) undertake significant vertical migrations on a daily cycle.

[4] Understanding the role of grazing in regulating primary production in the equatorial Pacific zone was one of the main objectives of the studies conducted on the EBENE cruise, in October–November 1996 along the 180th meridian. During this cruise, we conducted shipboard experiments of mesozooplankton feeding, respiration and excretion to assess latitudinal variations in these rate parameters across an equatorial transect (8°S to 8°N) and day-night variations at two time series station. From these measurements and contemporaneous biomass determinations from *Le Borgne et al.* [2003], we evaluate the grazing pressure exerted by the mesozooplankton upon the stock of food particles. Complementary evaluation of the grazing

role of microzooplankton consumers is presented by *Landry et al.* [2003].

2. Material and Methods

[5] Food ingestion and metabolic rates were measured at stations 1° of latitude apart from 8°S to 8°N (except excretion rates were not measured south of 3°S) (Figure 1). Experimental rate determinations were also made during two 48-hour diel variation studies at time series stations at 3°S (TSS1) and the equator (TSS2). During these diel studies, experiments were conducted every 6 hours, around 0100, 0700, 1300 and 1900 (local time).

2.1. Experimental Design and Set Up

[6] The mesozooplankton used for experiments were sampled between 100 m and the surface, a layer which includes nearly 75% of the 0–400 m biomass at TSS1 and TSS2 [Le Borgne *et al.*, 2003]. Plankton hauls were made vertically with a triple WP-2 net equipped with 200 μm Nitex mesh [UNESCO, 1968]. Incubated mesozooplankton were unsorted except for gelatinous animals (thaliaceans, siphonophores), which were eliminated because of the difficulty of keeping them alive during the course of the experiments. Obvious predators, such as chaetognaths or large crustacean larvae, were also discarded. Two types of flasks were used for incubations: 300-mL erlenmeyers and 1-L cylindrical bottles in order to assess the effect of container volume on rate determinations. Using gentle siphon flow, the containers were filled either with unfiltered surface seawater or seawater previously filtered through a 0.45 μm Gelman fiberglass filter.

Table 1. Values (Mean \pm Sd) of Grazing, Respiration, Ammonium and Phosphate Excretion Rates, and of O/N, O/P, and N/P Atomic Ratios^a

Latitude	Grazing, $\text{mm}^3 \text{g}^{-1} \text{h}^{-1}$		Respiration, $\text{mL O}_2 \text{g}^{-1} \text{h}^{-1}$		NH ₄ Excretion, $\mu\text{M g}^{-1} \text{h}^{-1}$		PO ₄ Excretion, $\mu\text{M g}^{-1} \text{h}^{-1}$		O/N (Atomic Ratio)		O/P (Atomic Ratio)		N/P (Atomic Ratio)	
	UFW	FW	UFW	FW	UFW	FW	UFW	FW	UFW	FW	UFW	FW	UFW	FW
8°S	1.67 \pm 1.05	3.41 \pm 0.50	6.01 \pm 0.46											
6°S	1.26 \pm 0.40	9.38 \pm 1.90	4.91 \pm 0.95											
5°S	1.16 \pm 0.87	5.17 \pm 0.90	6.93 \pm 2.99											
3°S	1.19 \pm 0.25	8.00 \pm 1.12	9.49 \pm 1.09	127.8 \pm 44.50	253 \pm 21.5				7.62 \pm 2.71	3.01 \pm 0.13				
3°S	0.88 \pm 0.80		5.51 \pm 1.24											
<i>Time Series Station 1</i>														
3°S	1.42 \pm 1.12	5.27 \pm 0.60	5.04 \pm 0.61	83.7 \pm 26	33.1 \pm 10.8				4.57 \pm 1.29	6.25 \pm 1.91	15.96 \pm 6.30	115.08 \pm 40.87	18.59 \pm 3.70	18.59 \pm 3.70
3°S	0.86 \pm 0.21	8.94 \pm 2.3	8.04 \pm 1.49	99.2 \pm 19.6	88.8 \pm 19	5.77 \pm 1.35	5.43 \pm 0.69	7.74 \pm 0.98	5.77 \pm 1.35	9.02 \pm 1.17	138.86 \pm 11.59	144.13 \pm 45.13	18.52 \pm 4.57	15.38 \pm 1.57
3°S	1.02 \pm 0.18	5.97 \pm 2.70	5 \pm 2.27	73.4 \pm 16.8	46.4 \pm 22.9	3.03 \pm 1.38	4.23 \pm 1.77	7.66 \pm 1.56	3.03 \pm 1.38	13.23 \pm 5.28	199.03 \pm 50.50	150.88 \pm 81.22	18.93 \pm 6.31	15.48 \pm 3.30
3°S	2.23 \pm 0.90	8.14 \pm 11.60	7.22 \pm 2.28	80.1 \pm 33.1	41.7 \pm 28.1	3.97 \pm 1.99	7.36 \pm 2.48	9.99 \pm 2.27	3.97 \pm 1.99	22.09 \pm 9.74	194.18 \pm 99.29	109.61 \pm 35.66	11.71 \pm 4.66	12.88 \pm 1.96
3°S	0.94 \pm 0.64	5.53 \pm 1.90	5.96 \pm 0.78	69.2 \pm 10.8	69.8 \pm 19.6	6.07 \pm 0.26	4.99 \pm 0.24	8.50 \pm 3.32	6.07 \pm 0.26	8.13 \pm 1.53	90.23 \pm 12.52	121.38 \pm 51.54	14.32 \pm 2.14	11.51 \pm 3.29
3°S	1.56 \pm 0.53	11.90 \pm 3.30	6.19 \pm 3.80	88.1 \pm 36.9	125 \pm 34.8	4.81 \pm 0.49	6.42 \pm 1.85	11.97 \pm 3.64	4.81 \pm 0.49	10.8 \pm 1.03	282.23 \pm 86.79	183.6 \pm 47.28	16.13 \pm 4.80	25.86 \pm 6.12
3°S	1.81 \pm 0.93	5.38 \pm 1.90	6.46 \pm 1.91	75.7 \pm 13.9	90.6 \pm 6.18	10.06 \pm 2.45	4.61 \pm 0.62	6.99 \pm 0.95	10.06 \pm 2.45	7.68 \pm 0.99	70.73 \pm 13.31	115.28 \pm 24.24	16.40 \pm 1.74	9.46 \pm 3.05
3°S	1.86 \pm 0.95	5.94 \pm 1.10	4.34 \pm 0.75	88.1 \pm 15.9	83.5 \pm 13.2	7.88 \pm 5.75	3.32 \pm 1.87	6.16 \pm 1.42	7.88 \pm 5.75	4.18 \pm 0.01	64.40 \pm 43.19	199.56 \pm 86.35	36.38 \pm 24.34	15.39 \pm 10.29
3°S	2.76 \pm 1.12	6.28 \pm 1.50	5.78 \pm 0.88	92.6 \pm 23.5	101.1 \pm 3	5.24 \pm 0.25	5.83 \pm 1.12	5.83 \pm 1.12	5.24 \pm 0.25	27.75 \pm 5.51	98.70 \pm 4.66	100.92 \pm 31.63	17.04 \pm 2.89	18.97 \pm 0.78
3°S		6.08 \pm 1.37	5.78 \pm 2.31	86.3 \pm 20.6	105.8 \pm 51.7	6.34 \pm 1.80	6.18 \pm 1.96	6.34 \pm 2.24	6.34 \pm 1.80	5.3 \pm 0.88	84.32 \pm 21.18	90.77 \pm 35.80	14.22 \pm 1.73	15.98 \pm 3.62
<i>Time Series Station 2</i>														
0°	0.69 \pm 0.11	5.48 \pm 2.10	6.87 \pm 2.27	74.3 \pm 34.9	54.3 \pm 15.4	2.67 \pm 1.41	5.25 \pm 0.77	9.77 \pm 5.81	2.67 \pm 1.41	11.17 \pm 3.61	275.62 \pm 163.15	97.8 \pm 11.59	12.44 \pm 5.14	23.19 \pm 7.46
0°	1.28 \pm 0.31	5.78 \pm 1.40	4.17 \pm 1.02	92.7 \pm 41.5	74.3 \pm 20.8	3.48 \pm 1.16	5.30 \pm 2.66	6.15 \pm 1.69	3.48 \pm 1.16	4.98 \pm 0.63	110.66 \pm 22.59	111.45 \pm 35.46	18.18 \pm 3.89	22.19 \pm 3.54
0°	0.81 \pm 0.18	6.55 \pm 1.30	5.79 \pm 0.74	111.5 \pm 13.1	93 \pm 8	5.05 \pm 0.47	6.23 \pm 0.49	5.46 \pm 0.63	5.05 \pm 0.47	5.57 \pm 0.74	102.14 \pm 6.66	97.97 \pm 15.64	17.90 \pm 1.64	18.55 \pm 2.35
0°	0.51 \pm 0.36	5.18 \pm 1.10	6.19 \pm 2.30	164.4 \pm 17	170.2 \pm 43.9	5.13 \pm 1.37	4.81 \pm 0.81	2.73 \pm 0.39	5.13 \pm 1.37	3.27 \pm 0.85	10.32 \pm 34.09	96.26 \pm 27.06	34.80 \pm 5.97	33.43 \pm 6.24
0°	0.48 \pm 0.21	4.94 \pm 1.50	5.76 \pm 1.61	109.2 \pm 20.6	82.4 \pm 20.3	2.19 \pm 0.92	4.35 \pm 0.95	6.87 \pm 1.45	2.19 \pm 0.92	6.70 \pm 2.82	253.07 \pm 69.13	97.77 \pm 32.83	25.56 \pm 3.93	29.29 \pm 8.77
0°	0.80 \pm 0.32	8.06 \pm 2.90	6.48 \pm 1.79	112.6 \pm 59.6	60.8 \pm 20	7.33 \pm 1.18	4.28 \pm 1.67	7.07 \pm 1.15	7.33 \pm 1.18	10.02 \pm 2.79	78.72 \pm 15.18	189.28 \pm 78.62	27.29 \pm 13.45	8.31 \pm 2.83
0°	1.39 \pm 0.15	7.55 \pm 1.30	4.66 \pm 1.15	117 \pm 24.6	85.8 \pm 29.9	4.32 \pm 0.79	5.45 \pm 4.03	6.31 \pm 1.21	4.32 \pm 0.79	5 \pm 0.91	97.82 \pm 24.29	204.32 \pm 167.12	30.11 \pm 18.44	19.72 \pm 4.53
0°	1.30 \pm 0.64	8.92 \pm 2.40	6.25 \pm 1.08	131.9 \pm 27.2	91.9 \pm 24.4	4.70 \pm 0.97	6.06 \pm 0.98	6.03 \pm 0.86	4.70 \pm 0.97	6.27 \pm 1.21	119.64 \pm 13.00	134.38 \pm 30.12	21.78 \pm 3.03	19.86 \pm 5.31
0°	0.69 \pm 0.29	7.58 \pm 1.30	4.59 \pm 1.39	101.5 \pm 16.2	98.9 \pm 19.8	4.80 \pm 0.99	4.92 \pm 1.07	6.60 \pm 1.39	4.80 \pm 0.99	4.13 \pm 0.88	86.16 \pm 21.94	138.75 \pm 41.09	20.82 \pm 1.61	20.70 \pm 1.71
2°N	0.81 \pm 0.19	4.53 \pm 0.90	4.13 \pm 1.40	52.7 \pm 14.9	47.7 \pm 18.1	5.08 \pm 0.90	3.79 \pm 0.26	8.67 \pm 2.57	5.08 \pm 0.90	8.68 \pm 5.18	71.6 \pm 29.01	112.4 \pm 15.20	13.57 \pm 3.66	8.77 \pm 2.16
5°N	2.56 \pm 0.83	6.96 \pm 4.80	7.89 \pm 1.16	54.1 \pm 51	112.7 \pm 42.1	8.11 \pm 2.85	6.47 \pm 4.86	14.37 \pm 10.56	8.11 \pm 2.85	7.05 \pm 2.77	98.52 \pm 28.14	161.47 \pm 214.01	11.90 \pm 8.31	15.33 \pm 7.21
8°N	1.15 \pm 0.22	10.89 \pm 6.14	9.87 \pm 2.22	34.5 \pm 17.5	49.9 \pm 14.1	2.61 \pm 0.57	1.99 \pm 1.32	30.95 \pm 1.24	2.61 \pm 0.57	19.6 \pm 8.42	267.45 \pm 22.84	573.5 \pm 200.61	18.45 \pm 6.12	18.20 \pm 2.11
8°N	1.31 \pm 0.34	11.97 \pm 4.10	8.92 \pm 1.65	142.3 \pm 124	153.4 \pm 17.5	4.53 \pm 1.95	7.09 \pm 0.88	7.69 \pm 3.33	4.53 \pm 1.95	10.35 \pm 1.13	258.25 \pm 49.99	152.73 \pm 54.54	20.33 \pm 3.75	26.60 \pm 4.78

^aUFW, incubation in unfiltered water (5 data per experiment); FW, incubation in filtered water (8 data per experiment).

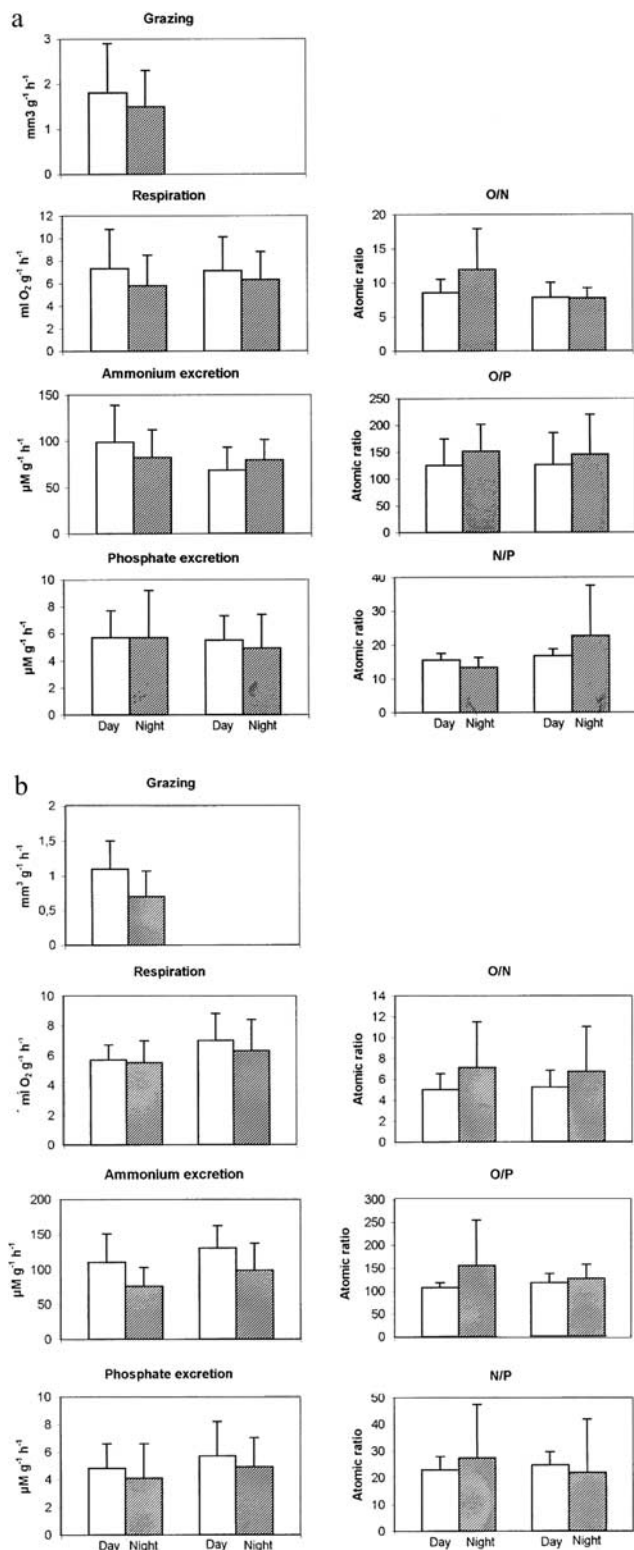


Figure 2. Specific rates of grazing, respiration, ammonium and phosphate excretion, and values of O/N, O/P, and N/P atomic ratios during the day and during the night (mean \pm sd) in mesozooplankton collected at the two time series stations, after 6-hour incubation time in unfiltered (UFW) or filtered (FW) seawater: (a) TSS1 (3°S) and (b) TSS2 (equator).

[7] For each series of experiments, eight 300-mL flasks were filled with filtered water (FW) for respiration and excretion and 8 others were filled with unfiltered water (UFW) for grazing and respiration rates of feeding animals. Within each set, three flasks were used as controls while aliquots of the zooplankton sample (23–90 individuals per flask) were added to the 5 others. The 300-mL flasks with unfiltered water were attached to a vertically rotating wheel (3 rpm) to avoid sedimentation of the particles. The 1-L flasks were used only for respiration and excretion measurements with one control and three experimental flasks (115–247 individuals per flask). After filling, the flasks were closed tightly, without air spaces. The incubation temperature (28°–29°C) was maintained by conducting experiments in a temperature-regulated room or deck incubator with circulating surface seawater. The flasks were incubated in the dark for six hours, the minimum incubation time to obtain stable levels in zooplankton physiological rates [Le Borgne *et al.*, 1998]. At the end of the incubation period, the mean concentration of oxygen in experimental flasks averaged 83% (extreme values: 74 to 93%) of the control concentrations, and the particle concentrations had been reduced to 64% (extreme values 42 and 85%) of initial values. This 6-hour incubation time was also chosen so that we could perform four successive experiments per 24 hours for the study of diel variations. Results of experiments starting at 0700 and 1300 were averaged for day rate estimates, and 1900 and 0100, for night rates.

2.2. Respiration and Excretion Rates

[8] After the 6-hour incubations, 30 mL of seawater were siphoned from each flask for dissolved oxygen measurement with a temperature and salinity compensated YSI 58 oxymeter. In each flask, two other 30-mL subsamples were analyzed for N-NH₄ and P-PO₄, using a Technicon autoanalyzer. The rest of the water was concentrated on 200-μm mesh to collect the incubated zooplankton. The animals were examined briefly to check their vitality, then laid on preweighed GF/C filters, rinsed with distilled water and dried at 60°C for 24 hours. The dried filters were kept in a desiccator until weighing at the land laboratory (Mettler 530 electrobalance, precision: ± 10 μg). Respiration and excretion rates were calculated from the differences between oxygen, ammonia or phosphate concentrations in control and experimental bottles, taking the incubation time and the dry weight of incubated zooplankton into account. O/N, O/P and N/P atomic ratios were calculated from the estimates in respiration (O), ammonium (N) and phosphate (P) excretion rates in individual flasks. As no significant difference appeared between the rates obtained in 300 and 1000-mL flasks, the mean metabolic values were calculated from all available data for each series of experiments.

2.3. Grazing Rate Assessments

[9] After incubation, 200 mL of each of the 300-mL flasks used for grazing experiments, was sieved through a 200-μm filter and kept in plastic flasks with 12 drops of filtered (0.2 μm) buffered formalin. These flasks were maintained in a dark refrigerator until the particle concentrations were measured, within 24–48 hours. Particle concentrations [in volumes] were measured with a Coulter Counter multisizer (256 size channels) equipped with a

Table 2. Comparison of the Day and Night Values for Grazing, Respiration, Excretion (NH₄, PO₄), and Atomic Ratios (O/N, O/P, and N/P) at the Two Time Series Stations^a

Parameter	Incubation Water	Mean		Number of Data		Value of t	Significance
		Day	Night	Day	Night		
<i>TSS1 (3°S)</i>							
Grazing, mm ³ g ⁻¹ h ⁻¹	UFW	1.8	1.5	28	15	1.14	ns
Respiration, μL O ₂ g ⁻¹ h ⁻¹	UFW	7.3	5.8	25	25	1.91	P < 0.05
	FW	7.1	6.3	46	31	1.28	ns
NH ₄ excretion, μM NH ₄ g ⁻¹ h ⁻¹	UFW	98.9	68.4	17	11	1.78	P < 0.05
	FW	82.2	79.5	35	23	1.51	ns
PO ₄ excretion, μM PO ₄ g ⁻¹ h ⁻¹	UFW	5.7	5.7	15	13	0.48	ns
	FW	5.5	4.9	35	23	1.2	ns
O/N	UFW	8.5	11.9	18	12	1.28	ns
	FW	7.8	7.7	36	23	0.07	ns
O/P	UFW	124.3	151.4	17	12	0.75	ns
	FW	128.8	144.9	36	23	1.13	ns
N/P	UFW	15.5	13.3	17	12	0.9	ns
	FW	16.7	22.6	35	21	1.68	ns
<i>TSS2 (Equator)</i>							
Grazing, mm ³ g ⁻¹ h ⁻¹	UFW	1.1	0.7	19	21	2.15	P < 0.01
Respiration, μL O ₂ g ⁻¹ h ⁻¹	UFW	5.7	5.5	20	23	0.38	ns
	FW	7	6.3	30	38	1.45	ns
NH ₄ excretion, μM NH ₄ g ⁻¹ h ⁻¹	UFW	110.2	75.5	20	22	3.09	P < 0.01
	FW	129.8	98.2	23	28	3.34	P < 0.01
PO ₄ excretion, μM PO ₄ g ⁻¹ h ⁻¹	UFW	4.8	4.1	20	22	1.45	ns
	FW	5.7	4.9	23	28	1.44	P < 0.05
O/N	UFW	5	7.1	20	22	2.49	P < 0.01
	FW	5.2	6.7	23	28	2.01	P < 0.05
O/P	UFW	107	155	20	22	2.01	P < 0.05
	FW	116.9	126.2	22	28	0.7	ns
N/P	UFW	22.9	27.3	20	22	2.01	P < 0.05
	FW	24.6	21.8	23	28	1	ns

^aUFW, unfiltered water; FW, filtered water; and ns, nonsignificant.

70-μm orifice tube, allowing the detection of particles ranging between 3 and 35 μm of ESD (Equivalent Spherical Diameter). The animals incubated in each flask were collected on the 200-μm mesh, then processed for dry weight measurements as described above. Food ingestion rates were calculated from the differences in particle concentrations between controls and experimental flasks summed for all size channels between 3 and 35 μm ESD. Weight specific feeding rates were calculated for each bottle by dividing total ingestion rates by the incubation time and the dry weights of incubated organisms.

3. Results

3.1. Metabolic Rates in Filtered and Unfiltered Water

[10] Table 1 presents the results of the 28 series of experiments carried out at the different latitudes. No significant differences were found between respiration rates in incubations with FW (6.65 ± 1.88 mL O₂ g⁻¹ h⁻¹) and UFW (6.22 ± 1.52 mL O₂ g⁻¹ h⁻¹): $t = 0.05$, $P < 0.20$. Similarly, neither ammonium excretion (92.8 ± 29.6 and 85.3 ± 34.3 μM g⁻¹ h⁻¹; respectively, $t = 0.8$, $P < 0.21$) nor phosphate excretion (5.14 ± 1.94 and 5.17 ± 1.26 , respectively; $t = 0.05$, $P < 0.48$) displayed difference between filtered and unfiltered treatments.

3.2. Diel Variations

[11] Day (0700 and 1300) and night (1900 and 0100) incubation data during the two time series stations were pooled for statistical comparisons. Figure 2 shows the average day-night values, and Table 2 presents the result

of the comparison tests (t' tests for unequal variance) [Sokal and Rohlf, 1981]. At TSS1, the rates of grazing, respiration, NH₄ and PO₄ excretion were slightly higher during the day. Atomic ratios O/N and O/P were higher during the night and N/P during the day. Nevertheless, most of these differences were not significantly different at $P < 0.05$. At TSS2, rates of grazing and NH₄ excretion were respectively 1.6 and 1.5 times higher during the day than during the night. PO₄ excretion increased also during the day, but the difference was significant only in filtered water. In contrast, respiration rates were almost the same during the day and night. O/N, O/P and N/P ratios were significantly higher during the night for incubations with UFW, while, for the FW treatment, the nocturnal increase was significant only for the O/N ratio.

3.3. Latitudinal Variations

[12] The particle spectra were very similar at the different latitudes (Figure 3). The smallest particles (ESD < 4 μm) were the most numerous, but a peak was also noted for the medium size particles (ESD around 15 μm) while larger particles (ESD over 30 μm) were scarce. In the measured size range, the total particle concentration varied from 0.22 to 0.64 PPM and the ingestion of particles, between 0.5 and 2.8 mm³ g⁻¹ h⁻¹ (Table 1). Lowest ingestion rates were observed at TSS2 (Table 1). Compared to the other time series station, the difference in the means was significant (Table 3). Respiration rates of zooplankton incubated in FW or UFW were close (5.7 – 6.8 mL g⁻¹ h⁻¹) and did not show any latitudinal differences (Figure 4). In UFW the rates of ammonium excretion (around 80 μM h⁻¹ g⁻¹) were similar

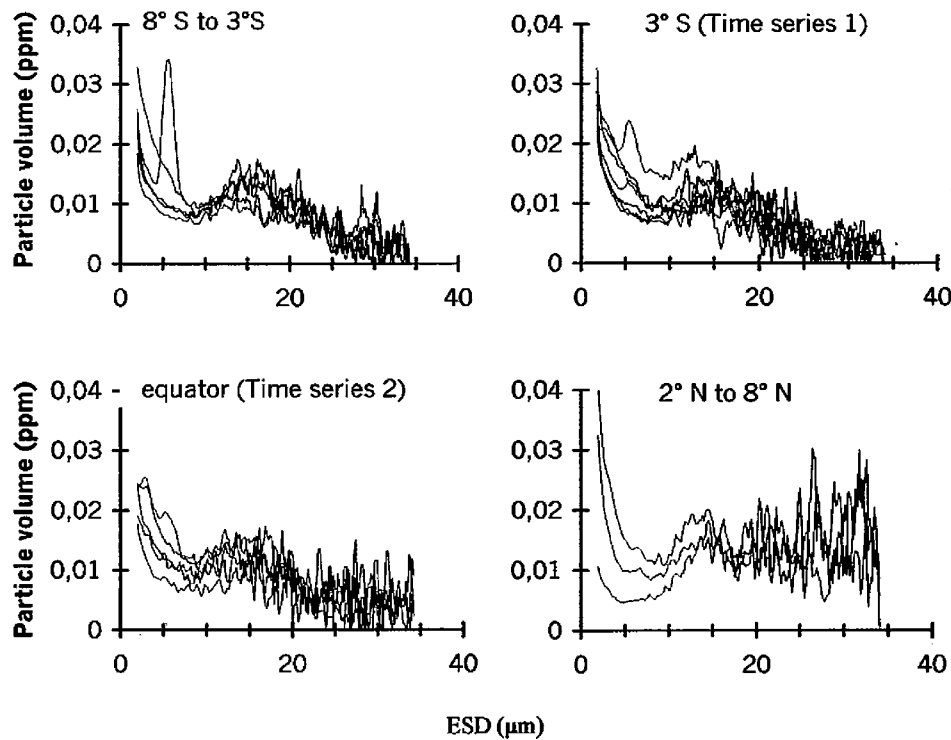


Figure 3. Shape of the particle size spectra recorded at different latitudes (one line per series of experiments) and during the two time series stations (one line per every 6-hour experiment).

at the two time series stations and also along the northern part of the transect. Conversely, in incubations with FW, the rates were markedly higher at the equator ($113 \mu\text{M h}^{-1} \text{g}^{-1}$) than at 3°S or at the northern transect stations. The difference in ammonia excretion rates in filtered water between the two time series stations was highly significant (Table 3). PO_4 excretion rates were similar at the time series stations and in the northern part of the transect, and no differences were found between the FW and UFW series nor between the two time series. All of the PO_4 excretion rate estimates ranged between 4.8 and $5.9 \mu\text{M g}^{-1} \text{h}^{-1}$.

[13] In UFW as well as in FW, average values of O/N were lower at the equator (6.1 and 6.5 respectively) than at 3°S (7.7 and 9.8) or at the northern stations (17.7 and 11.4) (Figure 4). For FW incubations, O/P ratios varied little (range 130–142) among the two time series stations and at the northern transect. For UFW treatments, however, the range of variations was wider, with a minimum average value of 114 at the equator and a maximum (mean: 174) at the northern stations (Figure 4). Average N/P ratios were similar at TSS2 in filtered and unfiltered water (20 and 24, respectively) where they exceeded the values found at TSS1 (18.3 and 16.6) and at the northern stations on the transect (16.1 and 17.1). Comparison tests for the two time series (Table 3) showed that the latitudinal differences between O/N and N/P were significant. This was also the case for the O/P ratios but only with incubations in UFW.

3.4. Grazing Pressure

[14] For the calculation of the grazing pressure, the specific grazing rates obtained in the successive experiments performed during each time series stations were averaged, for day or night periods, then multiplied by the

mean 0–100 m zooplankton biomass [Le Borgne *et al.*, 2003]. The particle density (in volume units) determined at the surface by counter measurements was extrapolated to the 0–100 m water column assuming a homogeneous vertical distribution of particles. This assumption was supported by particle load inferences from transmissometry data [Le Borgne *et al.*, 1998] which showed a good correspondence between surface concentrations and mean of the 100-m water column. (Ratio surface/water column = 1.005 at TSS1 and 1.04 at TSS2). In addition, the lack of a significant difference between day and night values of the particle load ratio allowed us to use a mean ratio for the full 24-hour day. Comparing zooplankton-grazing rates to the particle standing stocks led to an average daily intake of 0.58% of the 8–35 μm particles at 3°S and 0.52% at the equator. At both time series, although higher specific grazing rates were recorded during the day, the grazing pressure was slightly higher during the night than during the day period (night-day ratio of 1.4 at TSS1 and 1.1 at TSS2). This was the consequence of a slightly greater abundance of zooplankton during the night [Le Borgne *et al.*, 2003] and a 5–50% increase of particles biomass during the day.

4. Discussion

4.1. Influence of Experimental Conditions on Metabolic and Feeding Rates

[15] Many experimental results for various copepod species show a direct effect of food ingestion upon respiration [Conover, 1956; Gaudy, 1974; Kiørboe *et al.*, 1985]. This is particularly true with respect to the richer conditions (algal cultures), which are generally used in laboratory experiments. In our case, the similarity of the metabolic rate

Table 3. Comparison of the Values of Grazing, Respiration, Excretion (NH_4 , PO_4), and Atomic Ratios (O/N, O/P, and N/P) at the Two Time Series^a

Parameter	Incubation Water	Mean		Number of Data		Significance
		TSS1	TSS2	TSS1	TSS2	
Grazing, $\text{mm}^3 \text{g DW}^{-1} \text{h}^{-1}$	UFW	1.7	0.9	43	45	$P < 0.01$
Respiration, $\text{mL O}_2 \text{gDW}^{-1} \text{h}^{-1}$	UFW	6.5	5.7	50	47	ns
	FW	6.8	6.8	77	75	ns
NH_4 excretion, $\mu\text{M NH}_4 \text{gDW}^{-1} \text{h}^{-1}$	UFW	78.7	89.4	30	46	ns
	FW	83.7	113.4	59	55	$P < 0.05$
PO_4 excretion, $\mu\text{M PO}_4 \text{gDW}^{-1} \text{h}^{-1}$	UFW	4.93	4.77	24	45	ns
	FW	5.4	5.1	59	55	ns
O/N	UFW	9.82	6.47	30	46	$P < 0.01$
	FW	7.7	6.1	58	55	$P < 0.01$
O/P	UFW	149.7	114.2	25	44	ns
	FW	132.4	130.4	58	57	ns
N/P	UFW	16.6	20.4	24	45	$P < 0.01$
	FW	18.3	24	59	55	$P < 0.01$

^aUFW, unfiltered water; FW, filtered water; and ns, nonsignificant.

estimates for fed and unfed animals could reflect either the lack of food effect (UFW versus FW), as demonstrated previously for excretion rate measurements by *Miller and Landry* [1984], or the fact that the animals were feeding at a low rate on the food particles available in the bottles. It is likely that each animal had a limited volume of water to search for a finite number of potential prey, compared to its natural ability to explore larger volumes for more suitable prey and for areas of richer food concentration [Dagg, 1977]. It could be expected that the high concentration of animals in a close volume could lead to a rapid depletion of food concentration. Nevertheless, no severe decrease in particle abundance appears after 6 hours of incubation, implying that feeding activity was low. As shown by Figure 3, only particles over $8 \mu\text{m}$ were grazed. The inability of copepods to feed on small particles is well documented [Nival and Nival, 1976], and large sized particles are presumably preferred [Poulet, 1973; Cowles, 1979]. In our experiments, no special tendency to such a preference was observed, but the greater proportion of large particles in the TSS2 particulate matter could have implications on the quality of food eaten by the mesozooplankton.

[16] As a consequence of the low feeding activity, it could be supposed that the metabolic rate estimates may be a little lower than they might have been if the animals were actively feeding at normal rates. Table 4 shows that our calculated respiration and excretion values are in good agreement with most published data at comparable temperatures. This means that even if feeding activity was low for the reasons advanced before, life conditions were well tolerated by organisms during the time of the experiments, despite their elevated density in the bottles which is necessary to obtain significant differences of O_2 , NH_4 , and PO_4 concentrations between control and test bottles in a short time (6 hours). Thus metabolic rates appear as reliable values because these incubation experiments were relatively short (6 hours), the measured rates might reasonably reflect the physiological condition of the animals prior to collection (i.e., quality of the food eaten, day-night cycle, or latitudinal variations).

4.2. Diel Variations

[17] Significant diel variations in grazing and nitrogen excretion were observed at the equator, with more particle

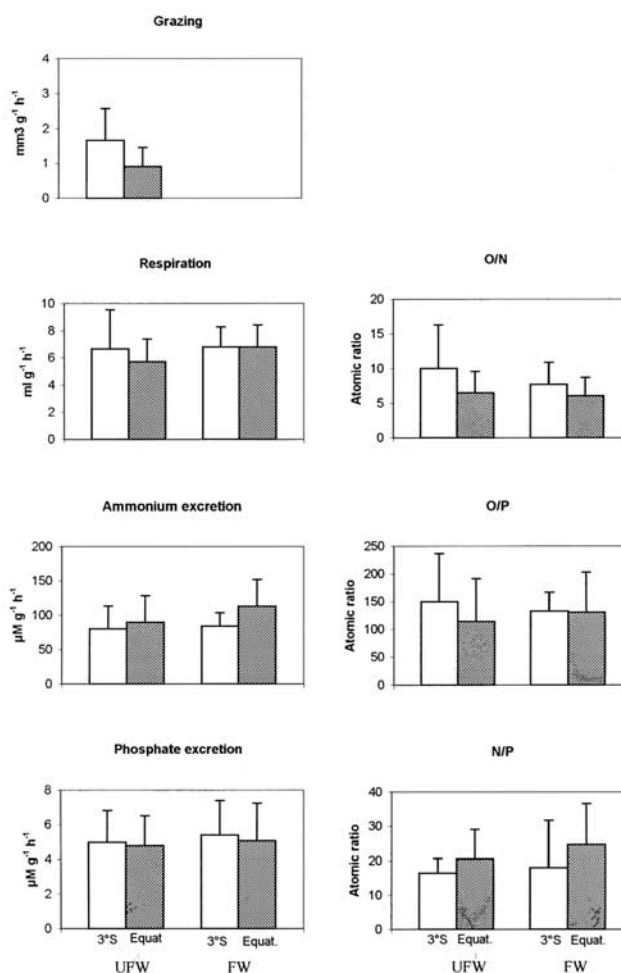


Figure 4. Specific rates of grazing, respiration, ammonium and phosphate excretion, and values of O/N, O/P, and N/P atomic ratios (mean \pm sd) in mesozooplankton collected at the two time series stations (3°S and equator), after 6-hour incubation time in unfiltered (UFW) or filtered (FW) seawater.

Table 4. Comparison of Our Data With Some Published Values of Mesozooplankton Respiration and Excretion Under Equatorial Thermal Conditions

Source	Area	Temperature	Respiration, mL O ₂ g DW ⁻¹ h ⁻¹	NH ₄ Excretion, μM g DW ⁻¹ h ⁻¹	PO ₄ Excretion, μM g DW ⁻¹ h ⁻¹
From Ikeda's [1985] polynomial equations	Atlantic, Pacific and Indian Oceans (various latitudes)	29	3.9	17.5	0.9
From Ivleva's [1980] equation	Atlantic Ocean (equator)	29	9.7		
Gaudy and Boucher [1983]	Indian Ocean (equator)	28.5	4.1–7.5	41–77	5.1–9.6
Le Borgne [1977]	Atlantic Ocean (equator)	28	8.5	84.6	3.4
Le Borgne et al. [1989]	Pacific Ocean (Tikehau atoll)	29.5	10.2	81.2	7.4
Our results (mean values)	Pacific Ocean (–3°S-equator)	29	6.5	91.4	5

material being ingested and more ammonium excreted during the day than during the night. At 3°S, the daytime values in grazing and ammonium excretion also exceeded nocturnal values, although not significantly. Considering diel variations in grazing, our result contrasts with most published works showing that feeding activity increases during the night [see Peterson et al., 1990]. Although Dam et al. [1995] showed the classical nocturnal maximum in zooplankton gut content was not the rule in the equatorial Pacific Ocean at 140°W during March–April 1992: in half of their observations [Dam et al., 1995, Figure 3], grazing rates were 3 to 4 times higher during the day than during the night. Roman and Gauzens [1997] obtained a similar result in the same area on the basis of feeding rate estimates using radioisotope labeled particles.

[18] In our incubation experiments, the difference between day and night (factor of 1.6) ingestion estimates was lower than those of Dam et al. [1995] values. This could be due to the difference between ingestion determination from total particle consumption in our case, versus gut fluorescence in Dam et al. [id.]. Such an interpretation is supported by gut fluorescence measurements made during EBENE [Champalbert et al., 2003] that show much higher night-day differences (N/D ratio: 5.8 and 6.3, at TSS1 and TSS2, respectively) for mesozooplankton collected at the surface, in agreement with those of Dam et al. [1995]. Such a difference in the kind of ingestion rate which is measured, may indicate that mesozooplankton grazing degactivity on algae is differentially stimulated by plant production during the day. Alternatively, it could mean that, during the day, a greater fraction of the chlorophyll deg-containing cells is in the size range that can be effectively captured by mesozooplankton.

4.3. Latitudinal Variations

[19] The lack of significant variation in mesozooplankton respiration along the EBENE transect was expected, considering the relative constancy of sea surface temperature (29°C) and particulate load. In contrast, latitudinal variations were found for grazing and ammonium excretion rates. Particle ingestion was higher at 3°S than at the equator in spite of the presence of similar particle concentration (0.37 ± 0.14 ppm at TSS1 and 0.34 ± 0.12 ppm at TSS2) and greater pigment concentrations at 0° [Neveux and Dupouy, 1999; Brown et al., 2003]. The difference observed in grazing activity between the two time series could result from changes of food quality or differences in mesozooplankton composition, as discussed further. As the respiration was similar at the two time series stations, the higher nitrogen excretion at the equator resulted in a lower

O/N ratio, compared to 3°S. Since O/N is generally considered as a good index of the nature of metabolized food [Le Borgne, 1986], differences in O/N between 3°S and the equator could result from (1) the food quality for general suspension-feeding zooplankton or (2) a greater occurrence of carnivorous animals at the equator.

[20] Testing the first hypothesis (1), it appears that surface chlorophyll *a* concentration was higher at the equator (0.15 ± 0.03) than at 3°S (0.11 ± 0.01) [Neveux and Dupouy, 1999; Brown et al., 2003]. Le Bouteiller et al. [2003] also showed that primary production was highest among all transect stations at the equator. These results would theoretically favor a more herbivorous zooplankton diet at the equator, but the abundance of algae of suitable size to be retained by filtration appendices was probably too low to influence the feeding strategies of mesozooplankton. On the other hand, the average sestonic C/N ratio between 0 and 80 m depth, was slightly, but significantly ($t = 1.99$, $P = 0.025$) lower, at the equator (7.4 ± 0.9) than at 3°S (7.7 ± 0.8). In addition, the ratio of numbers of heterotrophs to autotrophs in the >8-μm size fraction was higher at the equator (1.3) than at 3°S (0.8) [Brown et al., 2003]. These results suggest that the food consumed at the equator was richer in terms of protein, perhaps explaining the higher nitrogen excretion rates [Anderson, 1992] and the lower O/N ratios [Le Borgne, 1986] measured at the equator compared to 3°S.

[21] The second cause (2) could be the effect of latitudinal changes in the proportion of carnivorous animals within the zooplankton since carnivores display higher nitrogen excretion rates and therefore lower O/N values [Le Borgne, 1986]. Obvious predators, such as chaetognaths or siphonophores, were discarded in our experiments, but the remaining animals may have displayed differing degrees of carnivory. Four copepod taxa (*Undinula darwini*, *Clausocalanus* spp., *Euchaeta marina*, and *Scolecithrix danae*) represented a large proportion of both the number of animals and the biomass, because of their large individual size. From previous information about their feeding behavior [Itoh, 1970; Gaudy and Boucher, 1983], the two former are preferentially herbivorous while the latter two are mainly carnivorous. The general composition of the zooplankton assemblage was almost the same throughout the investigated area (Table 5), but, looking at the abundance of species in more detail, it appears that the numbers of *Undinula vulgaris* and *Clausocalanus* spp. were almost twice as high at 3°S and to the south of the transect, than at the equator or to the north. Conversely, while *Euchaeta marina* did not show any significant latitudinal variations, *Scolecithrix danae* was considerably more abundant at the

Table 5. Average Density of Total Copepods and Percentage Distribution of Species to the Total Number of Copepods on Different Parts of the 8°S–8°N Transect Along 180°

	South	TSS1	TSS2	North
Abundance, individuals m ⁻³	88.1	666.4	732.5	393.1
<i>Calanus gracilis-robustior</i> , %	1.93	3.56	2.29	1.47
<i>Calanus minor</i> , %	6.47	3.62	3.98	3.65
<i>Canthocalanus pauper</i> , %	1.73	0.43	2.16	4.33
<i>Undinula darwini</i> , %	21.06	29.07	13.56	15.55
<i>Mecynocera clausi</i> , %	0.81	0.00	0.00	0.00
<i>Paracalanus</i> spp., %	2.78	16.16	10.25	16.73
<i>Clausocalanus</i> spp., %	30.79	14.48	7.16	9.15
<i>Calocalanus</i> spp., %	0.31	0.50	0.34	4.75
<i>Scolecithrix danae</i> , %	0.61	2.95	10.23	2.15
<i>Euchaeta marina</i> , %	9.28	9.46	10.67	2.94
<i>Pleuromamma</i> spp., %	0.19	0.00	0.27	0.49
<i>Centropages</i> spp., %	1.40	0.77	1.02	0.83
<i>Candacia</i> spp., %	0.45	0.34	0.47	0.00
<i>Acartia</i> spp., %	0.35	0.57	0.38	0.49
<i>Pontella</i> spp., %	3.83	0.00	0.24	0.75
<i>Pontellina plumata</i> , %	0.27	0.09	0.12	0.00
other calanoid, %	0.35	0.09	0.30	1.32
<i>Corycaeus</i> spp., %	7.72	5.17	11.28	12.09
<i>Oncaea</i> spp., %	8.14	11.00	23.64	18.84
<i>Oithona</i> spp., %	1.21	1.53	1.05	3.69
<i>Clytemnestra</i> spp., %	0.18	0.00	0.30	0.15
<i>Copilia</i> spp., %	0.14	0.09	0.27	0.64

equator and the northern transect stations. Therefore the greater proportion of *Scolecithrix danae* and the lower proportion of *Undinula darwini* and *Clausocalanus* spp. in the experimental mesozooplankton at the equator could explain the lower O/N ratio found at TSS2. In summary, differences in food composition and feeding habit of dominant species may both have contributed to the observed differences in nitrogen excretion rates and O/N ratios at the two long-term stations.

4.4. Trophic Relations Between Mesozooplankton and Its Particulate Environment

4.4.1. Diel Variations of the Mesozooplankton Grazing Pressure

[22] The daily grazing pressure exerted on the particle stock (0.58% of the particle load at 3°S and 0.52% at the equator) was very low but showed limited diel variations. The nocturnal value was 1.6 times the diurnal value at TSS1 while it was 0.8 at TSS2. These variations are comparable to those observed by *Champalbert et al.* [2003] at the same stations but using the gut fluorescence technique: their night-day ratio of the grazing pressure exerted on chlorophyll by the zooplankton inhabiting the 0–100 m water column was 1.5 at TSS1 and 1.2 at TSS2. In both cases, maximum impact was observed during the night. These differences between night and day grazing impacts in the HNLC zone are comparable to the ratio (1.6) reported by *Roman et al.* [1988] for oligotrophic Gulf Stream rings and contrast with the value (4.8) found for the richer Cheseapeake Bay plume by the same authors.

4.4.2. Mesozooplankton Carbon Demand and Metabolic Cost

[23] Considering an average POC concentration of 5 μM (60 mg C m⁻³) and assuming an even distribution of particulate C within the whole particle size spectrum, the average C/particulate volume ratio was calculated. Daily carbon ingestion of particles calculated from our incubation

experiments would account for only 3.4% of the body carbon at 3°S and 2.7% at the equator. Such percentages may be compared to the zooplankton respiratory needs expressed in carbon units. Thus, considering a respiratory quotient of 0.85 [*Omori and Ikeda*, 1984], the mean measured respiration rate during EBENE (6.3 mL g⁻¹ h⁻¹) would be equivalent to 94 mg C g DW⁻¹ d⁻¹ or, using a carbon to DW ratio of 0.36 for mesozooplankton [*Le Borgne et al.*, 2003], 264 mg C (g body C)⁻¹ d⁻¹. Such a value (26.4% of body carbon d⁻¹) is in the usual range for copepods and similar to data of *Pavloskaya and Zesenko* [1985] for the equatorial Indian Ocean. Therefore the carbon ingestion, as estimated from our experiments was insufficient to balance respiration losses. Similar unbalanced budgets between experimentally calculated ingestion rates and respiratory expenses have been determined in many previous studies considering different areas, such as the North Sea [*Baars and Franz*, 1984], the southern Benguela Current [*Peterson et al.*, 1990], the western Mediterranean [*Thibault et al.*, 1994], the equatorial Indian Ocean [*Pavloskaya and Zesenko*, 1985], and the Kerguelen region [*Razouls et al.*, 1998].

[24] Although some inflation of the metabolic rates due to postcapture stress of the experimental animals is possible, we believe that the imbalance between ingestion and metabolic rates came largely from underestimations of ingestion. The limited volume of the incubation vessels may have disrupted the natural feeding behaviors of the mesozooplankton, which came into repeated contact with the container walls. In addition, each animal had a limited volume of water to search for a finite number of potential prey, compared to its natural ability to explore large volumes for more suitable prey and for zones of richer food concentration [*Dagg*, 1977].

[25] Although ingestion rates were clearly underestimated in our experiments, we can compute their likely magnitude from carbon budget considerations (Table 6). Accordingly, ingestion rates must be balanced by production, metabolic losses via respiration, and nonassimilated matter (i.e., feces). Using an average K₂ (net growth efficiency) of 0.4 from average data of *Vinogradov et al.* [1976] and *Le Borgne* [1982] for the equatorial region and an assimilation efficiency of 0.7 [see *Mauchline*, 1998], carbon must be ingested and assimilated at factors of 2.4 and 1.7 times measured respiratory losses, respectively. Since respiration accounted for 26.4% of the body C d⁻¹ in the present experiments, the daily rate of food assimilation would be equivalent to 44% of body C and the ingested food to 63%. The latter value is in the typical range for pelagic copepods [*Schnack*, 1983; *Mauchline*, 1998].

Table 6. Estimates of Zooplankton Carbon Production (PC) From the Respiration Rate (R), the Mesozooplankton Carbon Biomass (BC), *Le Borgne et al.* [2003], and the Net Growth Efficiency (K₂, C) for the 0–100 m Water Column^a

	R, mg C g C ⁻¹ d ⁻¹	BC, mg C m ⁻²	K ₂ , C	PC, mg C m ⁻² d ⁻¹
TSS1	191	468	0.4	60
TSS2	191	518	0.4	66

^aPC = R BC K₂ C / (1 - K₂, C). TSS1 and TSS2 are the two time series made at 3°S and the equator during EBENE.

[26] Using this indirectly calculated rate of ingestion, the grazing pressure on particles $>8 \mu\text{m}$ would come to 14% of standing stock d^{-1} at TSS1 and 14.5% d^{-1} at TSS2. Mesozooplankton grazing impacts of this magnitude are insufficient to control the biomass of particles $>8 \mu\text{m}$ which show high production rates in the equatorial region. For example, nanophytoplankton and microphytoplankton have growth rates on the order of 0.8 to 1 d^{-1} [Chavez *et al.*, 1991; Landry *et al.*, 1995], and the microzooplankton of tropical oceans can display daily P/B values up to 100 to 230% [Vinogradov *et al.*, 1976; Le Borgne, 1982]. For the $>8 \mu\text{m}$ plankton that remain at more or less steady state levels, they must obviously suffer other losses, because of senescence, cell sinking, and consumers, such as microzooplankton, not considered in the present experiments.

[27] In this latter regard, it should be noted that the present experiments largely involved the more advanced development stages of copepods and therefore did not account for some components of the mesozooplankton community that could potentially contribute to the grazing impact on the larger phytoplankton and heterotrophic protists. Appendicularia and salps, for example, were excluded from the incubations but are known to display rapid growth rates [Hopcroft and Roff, 1995] sustained by high rates of filtration on particles across a broad size spectrum [Alldredge, 1981; Madin *et al.*, 1997; Gorsky *et al.*, 1999]. However, these taxa were relatively scarce within the 0–100 m depth range during EBENE, accounting for less than 3–5% of total abundance and about 3.5% of DW [Le Borgne *et al.*, 2003]. Perhaps more importantly, small copepod species or larval stages such as nauplii were poorly sampled with the net used (200 μm mesh). These are generally very abundant in the equatorial region and display higher specific ingestion rates than medium or large sized species [White and Roman, 1992]. In addition to underestimating the biomass contribution of small taxa and stages to the mesozooplankton community, our calculations of the food intake needed to balance the metabolic losses of the community could be low because these organisms, with higher weight-specific rates of metabolism [e.g., Le Borgne *et al.*, 1995], were excluded from respiration experiments.

4.4.3. Regeneration of Nitrogen by Zooplankton

[28] New and total productions were measured at TSS1 and TSS2 during the EBENE cruise by Le Bouteiller *et al.* [2003], which makes it possible to estimate the regenerated production, generally assimilated to ammonium uptake by phytoplankton. Therefore measured zooplankton ammonium excretion of the present paper lends itself to a comparison with the regenerated production in order to assess the contribution of the mesozooplankton. Considering the average zooplankton NH_4 excretion rate at TSS1 and TSS2 (80 and 100 $\mu\text{M gDW}^{-1} \text{h}^{-1}$, respectively) and the corresponding average zooplankton biomass (13.9 and 14.7 mg DW m^{-3}) of Le Borgne *et al.* [2003], the daily ammonium regeneration comes to 378 and 490 $\mu\text{g N-NH}_4 \text{m}^{-3} \text{d}^{-1}$, respectively, which is equivalent to 27 and 35 $\mu\text{M N-NH}_4 \text{m}^{-3} \text{d}^{-1}$. Le Bouteiller *et al.* [2003] provide values of 699 and 774 $\text{mg C m}^{-2} \text{d}^{-1}$ for total primary production of the 0–100 m water column at TSS1 and TSS2, respectively. These values may be converted into nitrogen units by using a Redfield ratio of 6.6 (in atoms) and expressed per

cubic meter: 0.0883 and 0.0977 $\text{mM N m}^{-3} \text{d}^{-1}$. Nitrate uptake, or new production, is equal to 1.40 and 3.56 $\text{mM N m}^{-2} \text{d}^{-1}$ in the 0–100 m layer [Le Bouteiller *et al.*, 2003], equivalent to 0.0140 and 0.0356 $\text{mM N m}^{-3} \text{d}^{-1}$. The regenerated production is the difference between total and new productions and comes to 0.0743 and 0.0621 $\text{mM N m}^{-3} \text{d}^{-1}$ at TSS1 and TSS2, respectively. Now, the percent contribution of zooplankton NH_4 excretion to the regenerated production is equal to 36.3 and 56.4% for the two time series stations and the contribution of NH_4 excretion to the total primary production nitrogen demand equals 31 and 36%. Such contributions are in the range of the maximum values given by Smith [1978] during a bloom off Peru (25%), by Ikeda and Motoda [1978] in the Kuroshio region (11–44%), and by Le Borgne [1977] in the Atlantic equatorial area (57% in March and 17% during the upwelling period, in August) and are comparable to the estimation of 40–50% of the nitrogen demand in the nutrient-depleted subtropical gyre of the northern Pacific ocean [Eppley *et al.*, 1973]. In another oligotrophic zone, the Sargasso Sea, ammonium regeneration by zooplankton supports 100% of the estimated primary production [Verity, 1985]. Conversely, lower contributions of zooplankton excretion are presented by Zhang *et al.* [1995] for the central tropical Pacific during the EqPac study: 4–15% of primary production in February–March and 3–17% in August–September. Such contributions are based on modeled values of zooplankton excretion and may be underestimated as those of Dam *et al.* [1995], in the same region: mesozooplankton excretion would only support less than 7% of the nitrogen demand of phytoplankton. Nonetheless, all the contributions presented above are less than 100%, a result that points out the role played by microzooplankton excretion in addition to that of the mesozooplankton, as noted earlier by Le Borgne [1977].

4.4.4. Composition of the Mesozooplankton Diet

[29] The grazing estimates of Zhang *et al.* [1995] and Dam *et al.* [1995] were based on plant food (chlorophyll) utilization. However, considering the scarcity of medium or large sized cells in the equatorial zone compared to picoplankton, Zhang *et al.* [1995] calculated that the mesozooplankton carbon ingestion from phytoplankton represented only 21 to 48% of the carbon demand. Similarly, Dam *et al.* [1995] observed that metabolic losses were not covered by the energy intake from plant food. They concluded that more than 80% of the carbon ingested by mesozooplankton was not phytoplankton and that a significant fraction of the microzooplankton production probably passed through mesozooplankton. Pavloskaya and Zesenko [1985] drew a similar conclusion about the dietary content of copepods of the Indian Ocean, suggesting that living animals or detritus comprised the missing portion of the animals' nutrition.

[30] The present experiments indicated that mesozooplankton only impacted particles $>8 \mu\text{m}$. In another EBENE study, Champalbert *et al.* [2003] found low grazing pressure on the total chlorophyll stock, confirming previous finding on the limited role of mesozooplankton in regulating the picoplankton-dominated phytoplankton of the equatorial Pacific. Microzooplankton grazing must therefore represent the main process of phytoplankton consumption, as previously pointed out by Dam *et al.* [1995], Roman and Gauzens [1997], and Landry *et al.* [1995, 2000]. This was confirmed for the EBENE cruise by Landry *et al.* [2003]

who demonstrated that grazing by microzooplankton accounted for an average of 69% of phytoplankton production. Microzooplankton must be used, in turn, by mesozooplankton as their main food resource for satisfying metabolic and production needs. Such a link is also suggested by the low general level of O/N ratios (6–10) in our study, which indicates that the food consumed by mesozooplankton must contain a relatively high proportion of protein and therefore come from a carnivorous/omnivorous diet. According to *Van Wambeke et al.*'s [1996] study in the NW Mediterranean, such O/N values (6–10) characterized the feeding of mesozooplankton on microzooplankton in a low chlorophyll ($0.1\text{--}0.2\ \mu\text{g L}^{-1}$) environment, while values around 28 corresponded to the use of plant food under richer chlorophyll conditions ($1.9\ \mu\text{g L}^{-1}$).

[31] Finally, comparison of mesozooplankton production as estimated on Table 6, with phytoplankton production measured by the ^{14}C method [*Le Bouteiller et al.*, 2003] stresses the need for at least one intermediate level between the two trophic categories. C production values of *Le Bouteiller et al.* [2003] were from 24-hour incubations and may therefore be considered close to net production, i.e., comparable to mesozooplankton production. Primary production was equal to 700 and 800 $\text{mg C m}^{-2}\ \text{d}^{-1}$ at TSS1 and TSS2, respectively. The ratios between production of the two trophic levels, 0.03 for both stations, are far below the expected ecological efficiencies for the transfer of energy between adjacent trophic levels [*Slobodkin*, 1968; *Conover*, 1978; *Pace et al.*, 1984]. They are also much lower than mesozooplankton gross growth efficiency (K_1) which may be considered close to ecological efficiency in stable ecosystems [*Pomeroy*, 1979]. A K_1 estimate of 0.28 can be calculated from K_2 (0.4) and the assimilation efficiency, D (0.7) (i.e., $K_1 = D K_2$). Although this is a crude estimate, it implies 2 to 3 intermediate levels of consumer between phytoplankton and mesozooplankton. This would be consistent with recent analyses of microbial food web structure in the tropical Pacific [*Landry and Kirchman*, 2003].

[32] In summary, the copepod-dominated mesozooplankton are unable to feed on most of the small particles ($<8\ \mu\text{m}$) which make the bulk of the phytoplankton stock in the HNLC zone. Since microphytoplankton ($>8\ \mu\text{m}$) is scarce, mesozooplankton must fulfill their nutritional needs for maintenance and production by feeding also on microzooplankton, as indicated by their relatively high nitrogen excretion. Consequently, copepod grazing impact on phytoplankton is low and proceeds mainly through their regulating action on herbivorous microzooplankton stocks. Grazing by other taxa, however, may be significant and deserves additional studies to assess grazing pressure of noncrustacean organisms such as pteropods, appendicularians or salps which are able to retain also the smallest particles. Although the specific grazing rate of mesozooplankton is enhanced during the day, its grazing impact on particle $>8\ \mu\text{m}$ remains relatively stable with time, as a consequence of the nocturnal increase of mesozooplankton biomass. Finally, latitudinal differences, although of low amplitude, appear to be related to more or less carnivorous oriented character of mesozooplankton feeding. Such features depend on variations in their specific composition or in the kind of particulate food.

[33] **Acknowledgments.** We thank Martine Rodier, Philippe Gérard, and Laurent Vayseyre for nutrient concentration analysis, and the crew of the *R/V l'Atalante* for their assistance during the cruise. We are grateful to Mike Landry for its useful comments on a draft version of this paper.

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