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Net zooplankton and the biological pump: a comparison between the oligotrophic and mesotrophic equatorial Pacific

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Abstract—Structure and functioning of the zooplankton community and their consequences on the export fluxes of carbon, nitrogen and phosphorus were studied in two contrasting systems of the equatorial Pacific: the oligotrophic TTS (Typical Tropical Structure) to the west, and the mesotrophic HNLC (High Nutrient–Low Chlorophyll) in the central Pacific. Data were collected during the FLUPAC cruise equatorial transect (September–October 1994) of R.V. *L'Atalante* and four 6–8-day long time-series stations made between 165°E and 150°W. Along the equator, a sharp 2.5-fold increase in mesozooplankton biomass (200–2000 μm) was observed between 174° and 172°W, with a simultaneous change in surface salinity and chlorophyll concentration, corresponding to the shift between the TTS and HNLC systems. No significant zonal trend was observed within the two systems. Compared with TTS, HNLC presented a significantly greater contribution of the (500–2000 μm) size class to total mesozooplankton biomass, less diel variations, and a shallower vertical distribution. Lower metabolic rates in HNLC were accounted for by different taxonomic compositions in the two areas. Microzooplankton (35–200 μm) had a rather uniform biomass in TTS and HNLC, presented no significant diel variations in the 0–100 or 0–200 m layers, and displayed a shallower vertical distribution than the mesozooplankton. Consequences of such zooplanktonic features on the "biological pump" are assessed. Dissolved nitrogen (DN) and phosphorus (DP) active fluxes, resulting from excretion of interzonal mesozooplankton migrants were 2.1 times higher in the TTS than in the HNLC. However, dissolved inorganic carbon active fluxes were equal in the TTS and HNLC systems, due to differences in C, N, P metabolisms. Combined mesozooplankton and estimated micronekton nitrogen active fluxes represented 40% of the passive flux as measured by sediment traps in the TTS, and 9% in the HNLC. Estimates of mesozooplankton fecal production in the photic zone lead to a 2-fold increment between the oligotrophic and mesotrophic stations, and a larger contribution of the fecal production to the sinking flux. It is, therefore, concluded that the mesozooplankton role in the biological pump is mainly passive in the HNLC system, in contrast to the TTS site.

INTRODUCTION

The equatorial Pacific is known to be the main natural source of carbon dioxide to the atmosphere, and it is also a huge region of new production that uses part of the upwelled dissolved inorganic carbon. These characteristics, in fact, are attributes of the equatorial upwelling, which stretches from the east to a variable longitude in the west. Zonal variations of the equatorial upwelling are detectable by satellite remote sensing (Feldmann *et al.*, 1992; Dupouy-Douchement *et al.*, 1993; Halpern and Feldman, 1994). The area located west of the upwelling is oligotrophic, with no surface nutrients and low surface

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chlorophyll concentrations (McKey *et al.*, 1995; Radenac and Rodier, 1996). The equatorial upwelling mesotrophic area is referred to as being a high nutrient–low chlorophyll (HNLC) regime (Minas *et al.*, 1986), which is due to advection and diffusive nutrient inputs to the photic layer (Wyrtki, 1981; Carr *et al.*, 1995; Kessler and McPhaden, 1995), but with limited uptake by phytoplankton. The oligotrophic system, on the other hand, is a "typical tropical structure" (TTS), according to the definition given by Herbland and Voituriez (1979), with a nutrient-depleted surface layer and a nutrient-containing layer underneath. In this kind of structure, plankton biomass is an indirect function of the depth of the main pycnocline and associated nutricline. Although each of the two hydrological systems undergoes significant time variations (Radenac and Rodier, 1996; Murray *et al.*, 1995), they generate two different ecosystem structures and functionings. Accordingly, consequences on the import–export of carbon should be different (Michaels and Silver, 1988; Legendre and Le Fèvre, 1991). A particular issue to be addressed is the role played by net zooplankton in the carbon export of the biological pump in both the TTS and HNLC equatorial Pacific zones.

According to Longhurst (1991), zooplankton transfer carbon and other related elements from the surface to the deep ocean in two ways: the "Archimedian pump" is the sinking of fecal matter, produced by zooplankton in the photic layer, whereas the "reciprocating pump" is the process achieved by migrating animals, which ingest their food in the surface layer and release their catabolic end-products (e.g. carbon dioxide through respiration and dissolved organic carbon, nitrogen and phosphorus, ammonia and phosphate, through excretion) in the deep layers. The magnitude of each of these processes is associated with zooplankton biomass and its characteristics, i.e. its vertical distribution, size structure, taxonomic composition and metabolic rates. Because these characteristics are linked with the pelagic ecosystem structure and functioning, the zooplankton Archimedian and reciprocating pumps will likely be different in the mesotrophic (HNLC situation) and oligotrophic (TTS) equatorial Pacific.

The present study considers zooplankton features and their consequences on the "biological pump" in these two regimes. Data were collected during an equatorial transect (Fig. 1) and time-series stations made during the ORSTOM organized FLUPAC (FLUx dans l'ouest du PACifique équatorial) and PROPPAC (PROduction Pélagique du PACifique ouest) cruises. Results of EqPac (Equatorial Pacific) cruises of the U.S. JGOFS (Joint Global Ocean Flux Study) in 1992 and PROPPAC tropical stations will be utilized for comparison (Table 1).

OCEANOGRAPHIC CRUISES

FLUPAC cruise on R.V. *L'Atalante* consisted of an equatorial transect between 167°E and 150°W and two time-series stations: a 6-day TTS was studied at 167°E; and a 7-day HNLC situation was located at 150°W (Table 1). The cruise took place in September–October 1994, i.e. during the warm event (Liu *et al.*, 1995). The PROPPAC equatorial time-series stations of R.V. *Coriolis* were located in the western Pacific at 165°E: PROPPAC 1 took place during the 1986–1987 El Niño under TTS conditions, whereas PROPPAC 2 occurred during La Niña in April 1988 (Table 1) characterized by HNLC conditions. Our data are compared with EqPac time-series stations at 140°W in HNLC regime (Murray *et al.*, 1995).

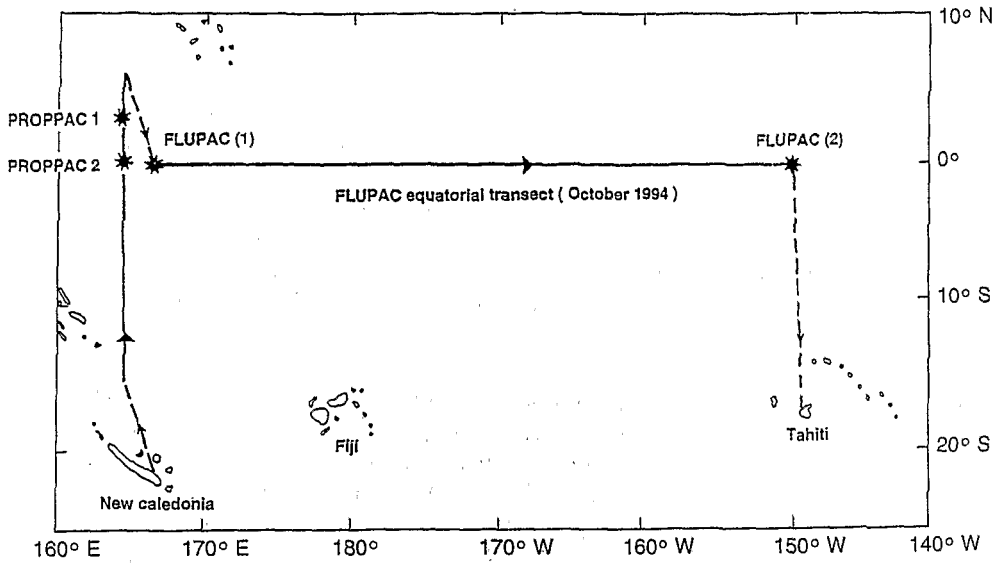

Fig. 1. Locations of equatorial time-series stations and FLUPAC cruise transect.

MATERIALS AND METHODS

Zooplankton sampling and biomass measurements

During the 6–8 day stations, two series of vertical net hauls were made every day: one in the morning and one at night, 2–3 h after dawn and dusk to avoid sampling during migration periods. Mesozooplankton (200–2000 μm) were caught by triple WP-2 nets (UNESCO, 1968; mesh size 200 μm) fitted with two T.S.K. flow-meters and, for FLUPAC only, by an Hydrobios multiple plankton sampler, MPS II (Weikert and John, 1981; mesh size 200 μm). With the MPS II, five nets were opened and closed successively, using remote

Table 1. *Positions and dates of equatorial time series stations, data of which have been used in present paper. Nitracline depth (ZNO_3 cline) is the 0.1* μM *isoline depth*

Cruise	Position	Date	ZNO_3cline (m)	Reference
HNLC stations				
PROPPAC 2	165°E–0°	12–20 April 1988	0	Le Borgne *et al.* (1992)
PROPPAC 3	165°E–5°N	26 September–3 October 1988	0	Le Borgne *et al.* (1993)
EqPac(1)	140°W–0°	23 March–10 April 1992	0	Murray *et al.* (1994)
EqPac(2)	140°W–0°	1–21 October 1992	0	Murray *et al.* (1994)
FLUPAC (2)	150°W–0°	19–25 October 1994	0	Le Borgne and Gesbert (1995)
TTS stations				
PROLIGO	173°E–15°S	16 September–7 October 1985	125	Blanchot and Gérard (1987)
PROPPAC 1	165°E–3°N	23 September–1 October1987	45	Le Borgne *et al.* (1992)
PROPPAC 4(1)	165°E–8°S	5–12 November 1989	75	Le Borgne *et al.* (1993)
PROPPAC 4(2)	165°E–15°S	17–24 November 1989	131	Le Borgne *et al.* (1993)
FLUPAC (1)	167°E–0°	3–9 October 1994	82	Le Borgne and Gesbert (1995)

controls in the shipboard laboratory, thus allowing a description of the vertical distribution of 100–0, 200–100, 300–200, 400–300 and 500–400 m. Filtered volumes were measured with Hydrobios flowmeters. Microzooplankton (35–200 μm) were sampled vertically by a triple net (Blanchot *et al.*, 1989) and sieved immediately through 200 μm metal grids. Biomass was measured on at least one net from each tow: samples were rinsed and dried (60°C, 24 h) on board and deep-frozen until being dried again and weighed for dry weight (DW) in the laboratory. Ash-free dry weight (AFDW) was measured on the same samples after they had been combusted at 550°C for 1.5 h. DW or AFDW refer to either m^3 or m^2 (i.e. integrated m^3 over the sampled water column). Mesozooplankton from the WP-2 nets was sieved through 2000 and 500 μm metal grids, thus giving two size classes: 200–500 and 500–2000 μm.

A comparison of AFDW, integrated over the 0–500 m water column, gives a good agreement between the WP-2 net and the MPS II for FLUPAC: 491 mg m^{-2} (SD = 112; $n = 12$) vs 494 (SD = 93; $n = 10$) at the first time-series station, and 1658 (SD = 254; $n = 14$) vs 1787 (SD = 293; $n = 13$) at the second station. Therefore, the results obtained with the MPS II during FLUPAC can be compared with results from the WP-2 during FLUPAC and previous cruises.

Zooplankton taxonomic composition

Countings of the major taxa were made on WP-2 net samples, preserved in buffered formaldehyde. Individuals of the whole net catch were counted except copepods, which were sub-sampled by the method of Frontier (1972). The mean individual DW of the different taxa was obtained from sorted individuals, which were weighed with a Perkin–Elmer electro-balance (precision = ± 1 μg). The wt% contribution of any taxum is the product of its number by the individual DW divided by the sum of the DW. According to Le Borgne and Roger (1983), the wt% may be considered to be the same for fresh and preserved samples, provided planktonic organisms remained in formaldehyde for a minimum of 6 months.

Zooplankton metabolic rates

During the FLUPAC cruise, metabolic rates were measured every day at the two time-series stations. Between 1 and 20 mg DW of unsorted living individuals caught with the WP-2 and 35 μm nets around 20.00 h, were pipetted into 1 l (microzooplankton) or 2 l (mesozooplankton) flasks, subsequently closed tightly, and incubated for 20 h in filtered sea water (filtration used Whatman GF/F and pressure to avoid de-oxygenation). At the end of the incubation, water was siphoned for the following analysis: dissolved oxygen (with a YSI 50B oxymeter), ammonium (Grasshoff *et al.*, 1983), orthophosphate (Strickland and Parsons, 1972), dissolved total nitrogen and phosphorus (Pujo-Pay and Raimbault, 1994). Respiration, nitrogen and phosphorus excretion rates are calculated as the differences between oxygen or nutrients concentrations measured in experimental flasks and blanks (with no animals added), expressed per mass (DW) and time (day) units. O/N and O/P ratios between oxygen uptake (O), and total nitrogen (N) and phosphorus (P) excretions are atomic ratios. Rate measurements at two different temperatures made it possible to calculate the A and B coefficients of the relationship between metabolic rates (M) and temperature (T):

$$M = AB^T$$

B^{10} is equal to Q_{10}, which is an index of zooplankton adaptability to temperature variations (see Le Borgne, 1986 for details).

C, N, P active fluxes by diel migrants

Following Longhurst *et al.* (1989), migrants are known to feed in the upper layer only at night and to transfer C, N, P during the day by their respiration and excretion in the deep levels. This applies only to the migrants and does not preclude any feeding by non-migrating zooplankton on settling particles during the day. Calculations assume a 12-h day time at the equator in October and a 100 m deep primary productivity layer at the two stations. Carbon, nitrogen and phosphorus fluxes are the product of migrants biomass, B_j, in any *j* layer, by their metabolic rates (respiration and excretion) at the day time habitat temperature, T_j. Calculations have been made in two ways:

(1) A simplified calculation, derived from Dam *et al.* (1995a), takes a mean temperature for the deep layer (i.e. 100–500 m in our case) into consideration: $T_j = 14°C$ at the two stations. Metabolic rates refering to 14°C are multiplied by ΣB_j, the 100–500 m migrants biomass to provide the active fluxes.

(2) A detailed calculation derived from Longhurst *et al.* (1989, 1990) considers the deep layer as divided into 100 m thick layers, each of them having a migrants biomass, B_j, and a metabolic rate at T_j. Total active fluxes are the sums of active fluxes calculated between 200–100, 300–200, 400–300 and 500–400 m.

Total migrants biomass, ΣB_j, is equal to the night increase in the 100–0 m layer or to the day increase in the 500–100 m layer. However, the two quantities are not equal because of sampling errors and the migration of animals living below 500 m during the day and moving up at night. Therefore, ΣB_j has been taken as the night biomass increase in the 100–0 m layer, i.e. as the difference between night and day mean values at each time-series station. In the detailed calculation, the day vertical distribution pattern of the MPS II net has been used to provide b_j, the percentage contribution of the migrants biomass, ΣB_j, in the *j* layer. The migrants biomass in the *j* layer is equal to:

$$B_j = b_j \Sigma B_j$$

B_j is multiplied by the metabolic rate at T_j to provide the active flux in the *j* layer, and the total active flux is the sum of these fluxes for the 100–500 m layer.

Zooplankton fecal production in the superficial layer

Calculations are made according to the energy budget equations as follows (see Le Borgne, 1978, for details). Fecal production (F, in mg C, N or P m^{-2} day^{-1}) can be assessed from measured metabolic end-products (excluding respiration) in the following way. F is equal to:

$$F = I - A$$

Ingestion (I) is equal to the assimilation (A) divided by the assimilation efficiency (D). A is

the sum of production (Prod.), excretion (Exc.) and respiration (Resp.). The relation between Prod and metabolic end-products is:

$$Prod = K_2(Exc. + Resp.)(1 - K_2)^{-1}$$

where K_2 is the net growth efficiency. For nitrogen and phosphorus, the above equation may be simplified since there is no respiration (Resp. = 0).

Statistical computations

For comparison between data sets, we have used the Mann–Whitney (or Wilcoxon) test (Snedecor and Cochran, 1967). In discussing our results, we use the statistical convention that the difference between groups is considered "significant" if the probability P that they come from the same population is less than 0.05 and "highly significant" if $P < 0.01$.

Standard deviations (SD) of values, which result from the product or sum/difference of two or more measured parameters (a, b, . . .), each having a SD (SD_a, SD_b,...), are equal to the square root of the product or sum, respectively, of SD_a, SD_b, . . . Such values are those presented on Table 7.

RESULTS

Mesozooplankton variability along the equatorial FLUPAC transect (167°E–150°W)

A sharp increase of zooplankton biomass along the equator can be seen between 174° and 172°W (Fig. 2). Owing to the lack of a clear trend in both sides of the "front", a mean AFDW for the two zones can be calculated: 559 mg m^{-2} (SD = 127; n = 10) in the "warm pool" (TTS) and 1425 (SD = 307; n = 12) in the HNLC situation, leading to an average 2.55-fold difference. This sudden increase of zooplankon biomass between TTS and HNLC is associated with a corresponding increase of surface salinity and chlorophyll concentrations and shoaling of the nitracline (Eldin *et al.*, 1997), but does not display any transition zone in contrast to chlorophyll and nitrate distributions.

A clear difference between the oligotrophic and mesotrophic equatorial Pacific is also evidenced in the size structure of the zooplankton community (Fig. 2). The average contribution of the 500–2000 μm size class to the total AFDW (i.e. 200–2000 μm) is smaller in the "warm pool" than in the mesotrophic system: 68% (SD = 7.0%) vs 77% (SD = 4.5%), the difference being highly significant.

Zooplankton structural and functional characteristics at equatorial time-series stations

Biomass. The HNLC situation in the central (FLUPAC 2) and western Pacific (PROPPAC 2) also generates significantly higher zooplankton biomass than the TTS (Fig. 3; Tables 2 and 3) in spite of a high variability within the two systems.

Vertical distribution.. The distribution of both micro- and mesozooplankton is highly significantly shallower in the equatorial HNLC situation than in the TTS, as shown by the higher 0–100/0–500 m biomass percentage contribution in the HNLC (Fig. 4; Tables 2 and 3). In addition, microzooplankton displays a shallower vertical distribution than mesozooplankton, although the difference is not significant between the two size fractions.

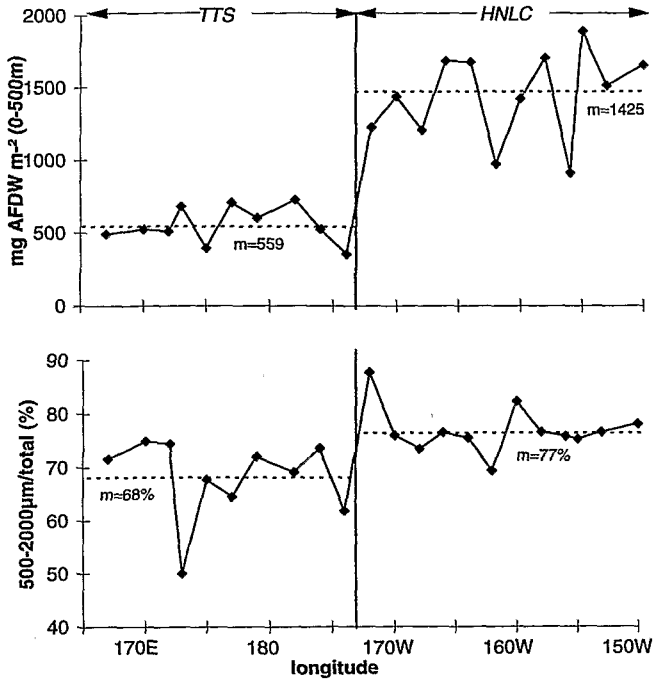

Fig. 2. Mesozooplankton ash-free dry weight (AFDW) and size structure along the FLUPAC cruise equatorial transect: TTS is the "typical tropical structure" and HNLC the "high nutrient-low chlorophyll" area. m = mean value.

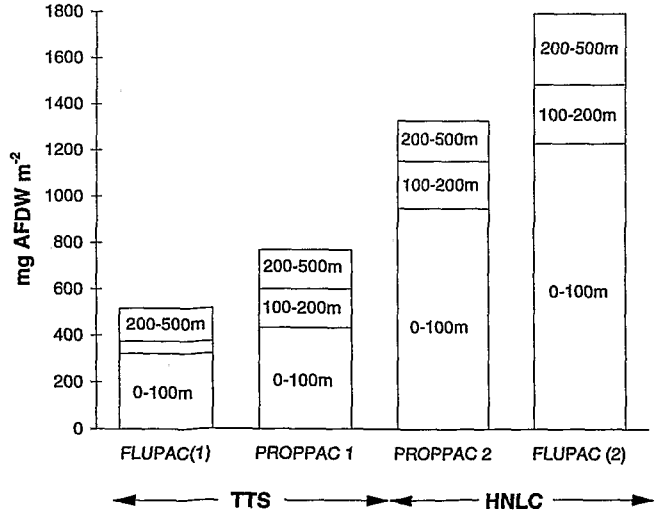

Fig. 3. Mesozooplankton ash-free dry weight (AFDW) at equatorial time series stations (see Table 2 for standard deviations and ranges of biomasses).

Table 2. Summary of mesozooplankton (200–2000 μm) AFDW data at HNLC and TTS time series stations

	HNLC		TTS	
	FLUPAC (2)	PROPPAC 2	PROPPAC 1	FLUPAC (1)
0–100 m (total)				
Avg (*n*)	1331 (13)	947 (14)	431 (16)	322 (10)
SD	213	256	152	139
Range	964–1802	636–1432	258–802	197–559
0–100 m (night)				
Avg (*n*)	1277 (6)	914 (6)	517 (8)	362(5)
SD	289	328	162	124
Range	971–1803	636–1432	311–802	204–528
0–100 m (day)				
Avg (*n*)	1192 (7)	940 (8)	347 (8)	282 (5)
SD	131	207	80	155
Range	964–1351	647–1287	258–486	197–559
0–200 m (total)				
Avg (*n*)	1486 (13)	1151 (14)	600 (16)	375 (10)
SD	259	269	131	121
Range	1060–1999	706–1564	431–880	220–570
0–200 m (night)				
Avg (n)	1565 (7)	1222 (6)	596 (8)	410 (5)
SD	324	260	143	104
Range	1060–1999	866–1558	489–880	281–559
0–200 m (day)				
Avg (*n*)	1418 (7)	1097 (8)	605 (8)	340 (5)
SD	187	280	128	137
Range	1133–1643	706–1564	431–784	220–570
0–500 m (total)				
Avg (*n*)	1790 (13)	1327 (14)	768 (16)	518 (10)
SD	293	290	155	92
Range	1169–2259	992–2120	548–1167	356–637
0–500 m (night)				
Avg (*n*)	1759 (7)	1244 (6)	848 (16)	510 (5)
SD	189	202	163	60
Range	1169–2259	1062–1596	649–1167	467–616
0–500 m (day)				
Avg (*n*)	1826 (6)	1390 (8)	688 (16)	525 (5)
SD	401	343	102	125
Range	1498–2004	992–2120	548–859	356–637

Avg: average; (*n*): sample numbers; (SD): standard deviation.

Such a result seems to indicate a closer link of microzooplankton with the photic zone and associated phytoplankton. MPS II net profiles of FLUPAC bring more details of the biomass distribution in the deep layers and evidence for the two stations, a biomass minimum between 200 and 300 m, i.e. in the oxygen minimum (Fig. 5), a result similar to that of Sameoto *et al.* (1987).

Diel variations. Clear diel variations are obvious for mesozooplankton of FLUPAC (1) in the oligotrophic situation (Fig. 5; Table 2). When average biomasses for day and night hauls

Table 3. Summary of microzooplankton (35–200 μm) AFDW data at HNLC and TTS time series stations

	HNLC		TTS	
	FLUPAC (2)	PROPPAC2	PROPPAC1	FLUPAC (1)
0–100 m (total)				
Avg (*n*)	222 (14)	183 (14)	152 (16)	192 (10)
SD	55	44	55	63
Range	149–330	131–286	81–299	115–327
0–100 m (night)				
Avg (*n*)	218 (7)	152 (6)	147 (8)	188 (5)
SD	63	25	50	51
Range	149–330	131–199	81–234	116–252
0–100 m (day)				
Avg (*n*)	225 (7)	206 (8)	157 (8)	196 (5)
SD	52	42	61	79
Range	149–300	149–286	98–299	115–327
0–200 m (total)				
Avg (*n*)	256 (14)	209 (14)	236 (16)	246 (10)
SD	60	51	101	81
Range	162–396	99–300	96–483	119–373
0–200 m (night)				
Avg (*n*)	274 (7)	182 (6)	231 (8)	234 (5)
SD	72	60	117	97
Range	162–396	99–255	116–483	119–367
0–200 m (day)				
Avg (*n*)	238 (7)	229 (8)	240 (8)	257 (5)
SD	44	35	90	69
Range	184–294	176–300	96–376	198–373

Avg: averages; (*n*): sample numbers; (SD): standard deviations.

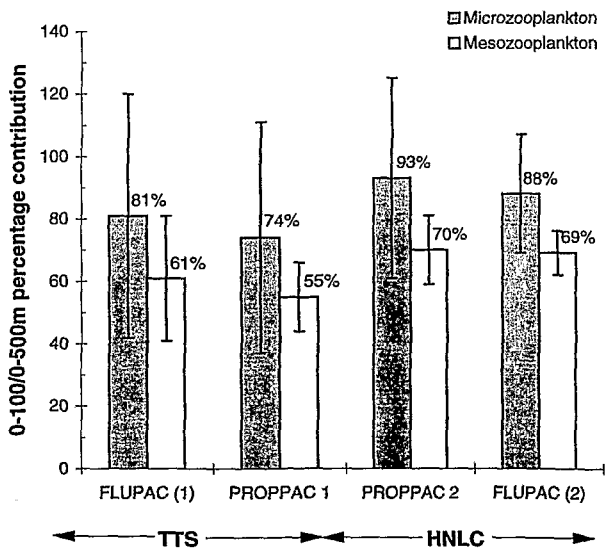

Fig. 4. Microzooplankton (35–200 μm) and mesozooplankton (200–2000 μm) ash-free dry wt (AFDW) vertical distribution: percent contributions of 0–100 to 0–500 m AFDW at PROPPAC 1 and 2 and FLUPAC (1) and (2) time-series stations.

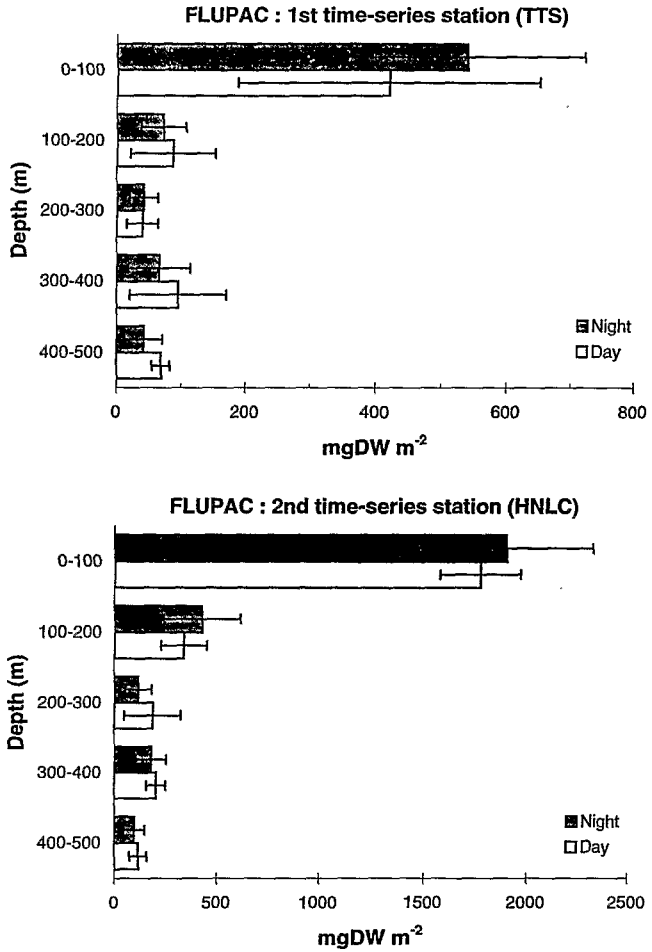

Fig. 5. Mesozooplankton DW night–day variations as observed with the MPS II net. Numbers are night–day differences (in mg DW m^{-2}). Confidence intervals are $\pm$SD. Number of hauls = five day and night samples at FLUPAC (1), and seven at FLUPAC (2).

of the time-series station are considered, DW of the upper 100 m increases by 118 mg m^{-2} during the night, which is 24% of the average value of this layer and 16% of the DW of the 0–500 m water column.

In the HNLC situation, DW also increases at night in the upper 200 m (Fig. 5) by 15% of the average 0–200 m biomass and 10% of the 0–500 m biomass. However, the sampling strategy, which involved 0–100 and 100–200 m hauls, made it impossible to bring a more accurate view of the layer involved in the night increase, which probably deals with the mixed layer depth (90–120 m).

In both situations, the night biomass increase of the upper layer is linked with a decrease in the deeper levels, which proves the upward migration at night. However, due to sampling errors and possible migration of animals living under 500 m, the night DW increase of the upper layer is not balanced exactly by a simultaneous decrease in the deeper layers (Fig. 5).

Table 4. Mean night/day ratios of the 0–100 m mesozooplankton AFDW for TTS and HNLC time series stations of the Pacific Ocean

HNLC situations	Night:day	TTS situations	Night/day
		PROLIGO	1.39
PROPPAC 2	0.97	PROPPAC 1	1.54
PROPPAC 3	1.09	PROPPAC 4 (1)	1.22
FLUPAC (2)	1.07	PROPPAC 4 (2)	1.82
		FLUPAC (1)	1.28

Data are those of Blanchot and Gérard (1987), for PROLIGO and Le Borgne *et al.* (1993), for PROPPAC 3 and PROPPAC 4).

The night/day ratio of the 0–500 m layer is very close to 1 in both TTS and HNLC stations (0.97 and 1.04, respectively), so 500 m may be considered as a fair reference depth.

Mesozooplankton diel variations, observed during FLUPAC HNLC and TTS stations, are in good agreement with observations made previously in the equatorial and western tropical Pacific (Table 4). It can be seen that the 0–100 m layer biomass undertakes much more diel variations in the TTS (night/day ratio ranging from 1.22 to 1.82) than in the HNLC (range: 0.97–1.09), the difference being significant.

Microzooplankton biomass shows no significant diel variations in both 0–100 and 0–200 m layers for either system (Table 3). A similar result is found during EqPac equatorial time-series stations for the 64–200 μm size class, night/day ratio being close to 1 (Roman *et al.*, 1995). We, therefore, conclude that microzooplankton do not participate in the reciprocating pump.

Zooplankton size structure. Total biomass increase from TTS to HNLC stations may be interpreted primarily as an AFDW increase of the largest size fraction (Fig. 6). In contrast, microzooplankton remains quite constant (209–256 mg AFDW m^{-2}) whatever the regime, and the 200–500 μm data present no clear trend. It follows that the percentage contribution of the largest size class is significantly higher for the mesotrophic than the oligotrophic situation (62–68% vs 46–48%). According to observations made by White *et al.* (1995) during the EqPac surveys, increase in the contribution of the 500–2000 μm would be due to the > 1000 μm size class. Thus, when zooplankton biomass increased between March and October 1992 from 5°N to 5°S during EqPac, the proportion of the > 1000 μm biomass increased, although no significant variation was observed for the 500–1000 μm size class.

Taxonomic composition. The dominant organisms in mesozooplankton populations for both regimes are copepods, which contribute 50–80% of total DW (Table 5).

Foraminiferans and, to a lesser extent Radiolarians, unusually account for a high percentage of the total weight at the FLUPAC HNLC station (Table 5): 16.6% (SD = 4.27; $n = 6$) and 4.8% (SD = 2.01; $n = 8$), respectively. Such large amounts of calcareous and siliceous protists in the mesozooplankton do not seem to be a permanent feature of the equatorial HNLC situation, since it was not recorded at PROPPAC 2 and 3 stations (Table 5) or by Roman *et al.* (1995) during the EqPac equatorial time-series stations. Similarly, Tumantseva (1981) observed in the eastern Pacific equatorial upwelling that combined Radiolaria and Foraminifera represent less than 8% of the < 500 μm wet weight. Significant

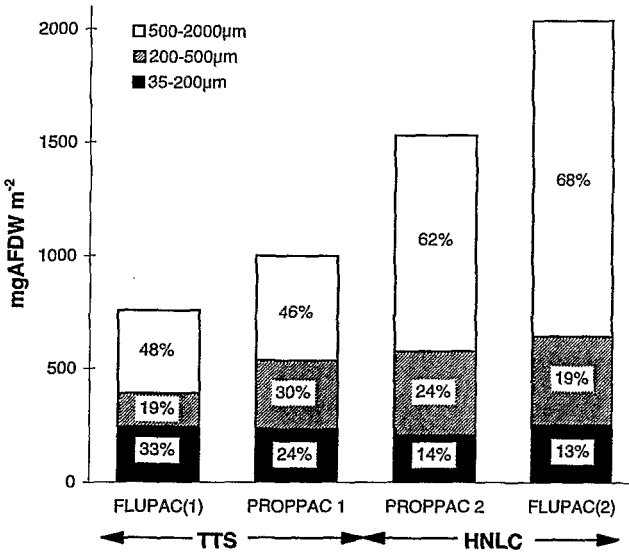

Fig. 6. 0–500 m zooplankton size structure at equatorial time-series stations: AFDW and percent contribution of the three size classes.

amounts of Radiolaria and Foraminifera at FLUPAC HNLC may have consequences for the passive sinking flux (Archimedian pump). This is in agreement with the presence of significant proportions of shelled protists in drifting sediment traps (Rodier and Le Borgne, 1997).

Metabolic rates. Respiration and total nitrogen and phosphorus excretion rates measured at the FLUPAC oligotrophic station are greater than at the mesotrophic one (Table 6). Thus, in spite of the small number of replicates (four), it appears confidence intervals of

Table 5. Weight percentage contributions of the major taxa for the 0–500 m water column of equatorial and tropical time series stations (cruise references on Tables 1 and 2)

	HNLC			TTS				
	PROPPAC2	PROPPAC3	FLUPAC(2)	PROPPAC1	PROPPAC4(1)	PROPPAC4(2)	PROLIGO	FLUPAC(1)
Number of samples	3	4	3	7	4	3	3	3
Noctiluca spp.	0.4	0.38	0.4	1.3	3.03	4.05	0.48	0.35
Radolarians/Acantharians	0.07	0.29	4.83	0.42	2.61	2.88	0.4	1.5
Foraminiferans	0.87	3.24	16.58	0.31	6.71	2.75	0.42	1.19
Total protists	*1.34*	*4.15*	*23.23*	*2.47*	*13.02*	*11.94*	*1.55*	*4.17*
Copepods	72.45	80.29	51.17	77.26	53.07	49.9	57.61	66.39
Ostracods	0.94	1.66	7.06	5	8.26	6.24	6.17	6
Larval euphausiids	2.79	1.58	3.32	1.84	3.55	4.77	17.13	4.82
Pteropods	0.3	1.47	0.33	0.5	2.92	2.07	2.77	1.78
Larvaceans	3.7	1.94	1.96	1.64	3.09	8.27	0.64	1.55
Total particle-feeders	*80.87*	*88.02*	*66.42*	*87.09*	*71.96*	*73.01*	*85.85*	*82.58*
Siphonophores	3.37	1.86	0.66	1.63	2.52	2.61	1.9	3.6
Chaetognaths	11.96	4.04	6.35	2.59	4.88	5.82	5.91	6.39
Amphipods	0.6	0.68	1.17	0.58	0.72	0.82	1.14	0.26
Total carnivores	*17.63*	*7.46*	*10.13*	*9.68*	*14.21*	*12.49*	*12.51*	*11.81*

Table 6. Mesozooplankton metabolic rates (µgat O, N, P mg DW^{-1} day^{-1}) and Q_{10} during FLUPAC time series stations (mean values±SD; four replicates for each temperature and station)

	Temperature (°C)	Respiration	Q_{10}	Total nitrogen excretion (NT)	Q_{10}	Total phosphorus excretion (PT)	Q_{10}
TTS	20.5	12.804±2.152		4.12±0.375		0.211±0.041	
(167°E)	30.5	49.036±4.001	3.829	10.837±0.161	2.630	0.549±0.053	2.602
HNLC	22.5	13.486±2.590		2.773±0.418		0.168±0.038	
(150°W)	28.2	26.660±1.280	3.305	5.04±0.500	2.852	0.278±0.005	2.420

metabolic rates measured at close temperatures (30°5–28°2 and 20°5–22°5C, for the TTS and HNLC stations, respectively) are clearly distinct ($P<0.05$) for the two stations. Although such differences could originate from slight temperature differences, an explanation that works at 28°2–30°5C but not at 20°5–22°5C, they may be related to variations in the taxonomic composition and size structure (see above), which are known to influence metabolic rates. The average contribution of ammonium to total nitrogen excretion is 40.2% at the first site and 54.0% at the second. Therefore, the other half of nitrogen is transferred as dissolved organic nitrogen (DON). Q_{10} values for total N and P excretion rates are lower than for respiration (Table 6), indicating a different effect of temperature on metabolic rates as already reported by Le Borgne (1986).

Zooplankton and the biological pump at FLUPAC 167°E and 150°W stations

Carbon, nitrogen and phosphorus transfers by diel migrators (i.e. "reciprocating pump" or "active flux") have been calculated only for the mesozooplankton, because no significant diel variations were evidenced for microzooplankton of the 0–100 m layer. Both calculation methods of the fluxes, described in "Material and Methods", provide close C, N, P flux values (Table 7): the average difference between the two results is 3% at the TTS station and 10% at the HNLC one. Data issued from the simplified calculation will be used from now on.

In spite of similar DW for migrating zooplankton at the two time-series stations, active total nitrogen (DN) and phosphorus (DP) fluxes due to inter-zonally migrating zooplankton excretion are higher (2.1 times) at the TTS station (Table 7) because metabolic rates and vertical distributions are different. But they are not statistically different due to the high standard deviations.

In contrast to nitrogen and phosphorus active fluxes, amounts of oxygen respired in the deep layers during the day by migrating mesozooplankton are similar at the two sampling sites (the ratio between TTS and HNLC is equal to 1.0). Such differences between respiration and excretion fluxes may be explained by a different effect of temperature on metabolic rates, and by the DW vertical distributions at the two sites. As a result, the average O/N and O/P ratios in the 100–500 m layer are distinct between HNLC and TTS situations. The mean atomic O/N ratio of diel migrants is equal to 2.5 at the oligotrophic site vs 5.1 at the mesotrophic one. The O/P ratio is equal to 48 and 95 at the two sites, respectively. Changes in O/N or O/P ratios can be explained by different kinds of oxidized substrate being involved in catabolic processes and linked to different zooplankton populations, feeding regimes and starvation effects during the day time (Le Borgne, 1986).

Table 7. Amounts of O, N, P consumed or released during day time (12 h in October) by zooplankton migrants in the deep layers during FLUPAC cruise

	Bj	Tj	Resp.j	Exc.NTj (μgat O, N, P m^{-2} day^{-1})	Exc.PTj
TTS (167°E)					
(1) Simplified calculation					
Total 500–100 m	118 (297)	14	315.6 (319)	129.6 (56)	6.67 (5.9)
(2) Detailed calculation					
500–400 m	29	9	39.6	19.7	1.02
400–300 m	41	11	73.3	33.7	1.74
300–200 m	15	14	40.1	16.5	0.85
200–100 m	34	18	155.6	55.0	2.82
Total 500–100 m	118		308.6	124.8	6.43
HNLC (150°W)					
(1) Simplified calculation					
Total 500–100 m	132 (471)	14	322.1 (610)	62.8 (99)	3.30 (9.4)
(2) Detailed calculation					
500–400 m	18	9	24.2	6.1	0.46
400–300 m	32	11	54.6	12.8	0.67
300–200 m	29	13	62.8	12.9	0.67
200–100 m	53	18	208.7	36.4	1.88
Total 500–100 m	132		350.2	68.3	3.68

For a given layer (j), Bj, Tj, Resp.j, DNj and DPj are the DW of migrants, mean temperature, oxygen uptake, dissolved nitrogen and phosphorus release by diel migrants, respectively. Calculations have been made in two ways: (1) considering the DW of the 500–100 m layer and a mean metabolic rate at 14°C; (2) considering the different DW of the 100 m thick layers between 500 and 100 m and corresponding metabolic rates and temperatures (see details in Materials and Methods). SD in parentheses.

At the TTS station, a clear proteolytic metabolism is obvious from the low observed O/N ratio, so that the respiration quotient (RQ = released CO_2/taken up O_2) should be closer to 0.8. At the HNLC site, however, a higher O/N ratio indicates that more carbohydrates are catabolised, and RQ value should be between 0.8 and 1.

The choice of a correct RQ to convert consumed O_2 by migrants into released CO_2 is crucial. If we take RQ = 1, as did Dam *et al.* (1995b) in their Bermuda study, we would get an equal ratio for the active CO_2 flux and O_2 respiration between our FLUPAC TTS and HNLC sites (ratio = 1.0). However, if RQ = 0.8 (for a proteolytic metabolism) in the TTS and ~1 in FLUPAC HNLC, the active CO_2 fluxes due to diel migrants would be equal to 126 μM C m^{-2} day^{-1} ($315.6 \times 0.8 \times 0.5$) in the former and 161 μM C m^{-2} day^{-1} ($322 \times 1 \times 0.5$) in the latter case, thus leading to a larger difference (ratio = 0.8) between the two FLUPAC sites as observed for N and P fluxes.

The production of fecal material by mesozooplankton was tentatively assessed for the upper 100 m of the two FLUPAC stations (Table 8): it is about twice as much at the HNLC station. Since zooplankton size structure is different in the two situations (there are more larger animals at the HNLC station), fecal material is likely made of larger particles that sink more quickly at the mesotrophic station. Thus, transfer by sinking fecal particles would probably be more than twice as much at the HNLC station.

Table 8. Mesozooplankton nitrogen fecal production in the 0–100 m layer at FLUPAC time-series stations

	TTS (167°E)	HNLC (150°W)
0–100 m biomass (mg DW m^2), B	480 (208)	1947 (317)
Total nitrogen excretion rate (mgN mg^{-1} DW day^{-1}), exc. NT	0.152 (0.002)	0.071 (0.007)
Net growth efficiency for N, $K_{2,N}$*	0.489	0.489
Nitrogen production (mg m^2 day^{-1}), $Prod_N$	69	131
Nitrogen assimilation (mg m^2 day^{-1}), A_N†	145	269
Nitrogen ingestion (mg m^2 day^{-1}), I_N	203	384
Nitrogen fecal production (mg m^2 day^{-1}), F_N	61	115

See Materials and Methods for calculations. SD in parentheses.
*From Le Borgne (1982).
†Using D = 0.7 for organic matter (Conover, 1966).

DISCUSSION

The equatorial TTS and HNLC situations can be characterized by two zooplankton regimes with different properties summarized in Table 9. The two regimes are dependent on phytoplankton biomass, composition (Blanchot *et al.*, 1992; Campbell and Vaulot, 1993; Blanchot and Rodier, 1996) and associated size structure (Le Bouteiller and Blanchot, 1991; Le Bouteiller *et al.*, 1992), which in turn are linked to nutrient availability in the photic layer. In oligotrophic structures, with deep NO_3, phytoplankton biomass is largely dominated by prochlorophytes and generates small mesozooplankton biomasses and a low contribution of large sizes, whereas in NO_3-containing waters the contribution of large phytoplankton cells is greater and is associated with more large sizes in the mesozooplankton community (Fig. 6). Such observations of zooplankton size structure are valid for the equatorial zone and the whole intertropical area as well (Fig. 7). Although a correlation coefficient cannot be calculated because the proportion of the small or large fractions in the total AFDW is not

Table 9. Summary of zooplankton main features in equatorial TTS and HNLC situations and consequences on the biological pump

	TTS		HNLC
Biomass	Small	(1%)	Larger
Size structure	More small sizes	(1%)	More larger sizes
Vertical distribution	Deeper	(1%)	Shallower
Diel variations (0–100 m)	Greater	(5%)	Not significant
Metabolic rates	Higher	(5%)	Smaller
DN active flux by migrants	Greater	(n.s.)	Smaller
DIC active flux by migrants	Smaller	(n.s.)	Greater
DN active/passive flux	Greater	(n.s.)	Smaller
Fecal production in photic zone	Small		Larger
Fecal passive flux	Small		Larger

Significance levels of statistical tests applied to data of the present study in parentheses, n.s.: not significant.

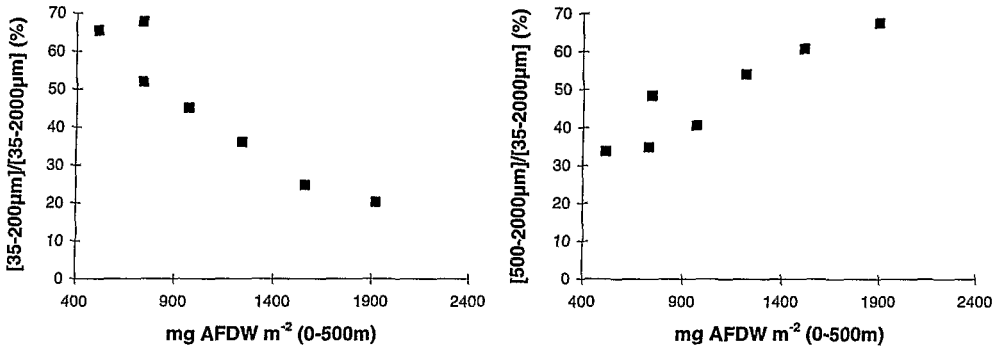

Fig. 7. Percentage contribution of (35–200 µm) or (500–2000 µm) zooplankton size classes to (35–2000 µm) AFDW at tropical and equatorial time-series stations, referenced in Table 4. Equations of the regression lines are the following: $y = -0.023X + 54$ for the percentage contribution of (35–200 µm) to total AFDW vs AFDW, and $Y = 0.025\ X + 21$ for the percentage contribution of (500–2000 µm).

independent of the total AFDW, equations of linear regression lines may be presented as a first approximation (Fig. 7):

$$y = -0.023x + 54 \tag{1}$$

y being the percentage contribution of the 35–200 µm size class to total (i.e. 35–2000 µm) AFDW, and x being the total biomass (in mg AFDW m^{-2}), and:

$$y' = 0.025x + 21 \tag{2}$$

with y' being the 500–2000 µm size class contribution to total AFDW (x being the same as in Eqn. (1)). Surprisingly, the microzooplankton biomass does not increase much from oligotrophic to mesotrophic areas (Fig. 6). This may be interpreted as a consequence of more larger individuals in the HNLC mesozooplankton if we consider them to have larger developmental stages, not sampled in the microzooplankton fraction.

As an example of the link between zooplankton and phytoplankton features, although the trophic relation between the two may be weak in most instances, we note that the zonal distributions in the equatorial HNLC are uniform for both phytoplankton (Le Bouteiller and Blanchot, 1991) and zooplankton (this paper; Vinogradov, 1981, between 122° and 155°W). Such a uniform zonal distribution of phytoplanktonic and zooplanktonic features makes it possible to extrapolate a few observed or calculated values of the biological pump to most of the HNLC equatorial Pacific.

Other properties of the zooplankton compartment are also conditioned by phytoplankton biomass and size (Table 9), which is so for the vertical distribution. In HNLC systems, large phytoplankton cells are abundant from the bottom of the photic layer to the surface, so that mesozooplankton may be more dependent on phytoplankton. Accordingly, animals have a shallower vertical distribution. In the TTS, on the other hand, NO_3 is deeper and the system generates a smaller proportion of large phytoplankton cells. In this kind of ecosystem, net zooplankton is very likely not feeding on phytoplankton and, therefore, less linked to the photic zone. As a result, its biomass is less concentrated in the photic layer. Finally, diel migrations between the photic zone and the deeper layers are less

extensive in the equatorial HNLC than in the TTS systems, an observation that might be accounted for by strong physical dynamics in the former case.

Effects of the above characteristics of the mesozooplankton community on the biological pump are now considered. The active fluxes for total nitrogen of the present paper (Table 7) are in the same range as those presented by Longhurst and Harrison (1988) and Longhurst *et al.* (1989): 28.6–207μM N m^{-2} day^{-1} (except for their high value for the Celtic Sea) and in good agreement with their data for the Panama Basin, stations at 10° and 21°S in the Indian Ocean, and the Costa Rica Dome. The values from Longhurst and Harrison (1988) were calculated from published data on mesozooplankton and nekton biomasses and total nitrogen (DN) excretion rates, while Longhurst *et al.* (1989) used direct measurements of dissolved inorganic nitrogen (DIN). Dam *et al.* (1995a) found a mean DIN active flux of 135μM N m^{-2} day^{-1} at the Bermuda time-series station, which is higher than our DN fluxes at both TTS and HNLC stations, and due to greater migrating zooplankton biomass (Table 10).

In greater detail, differences in zooplankton contributions to the biological pump between the TTS and HNLC are expected. Thus, Longhurst *et al.* (1989) established a positive relationship between the active/passive fluxes (i.e. reciprocating/Archimedian pumps) and the depth of the photic layer, which is related to plankton density: $Y = -16.4 + 0.47\,X$, where Y is the active/passive flux ratio (%), and X the photic layer depth (1% light level). This relationship was obtained from calculated and measured zooplankton and nekton DN active flux and calculated passive flux (at a 100 m depth, using the depth of the photic layer and level of primary productivity). Zooplankton DIN excretion data of Dam *et al.* (1995a) at the Bermuda station fit this relation. If we apply the model of Longhurst *et al.* (1989) to FLUPAC data of the photic zone depth (1% light level), we find $Y = 29.7\%$ at the TTS station ($X = 98$ m), and $Y = 17.9\%$ ($X = 73$ m) at the HNLC station. These Y values can be compared with the calculated active/passive flux ratios of FLUPAC stations using DN

Table 10. *Migrating zooplankton biomass and temperature range in deep layers: a comparison with other studies. Nitrogen biomass of Longhurst et al. was converted into DW assuming a factor of 10, and carbon biomass of Dam et al., a factor of 2.8*

Cruise	References	Migrating mesozooplankton DW (mg m^{-2})	Temperature range
EASTOPAC	Longhurst *et al.* (1989)	93	
BIOSTAT	Longhurst *et al.* (1989)	664	
DOME	Longhurst *et al.* (1989)	360	
Panama Basin (August)	Longhurst *et al.* (1989)	504	
id. (November)	Longhurst *et al.* (1989)	202	
CLIMAX (1972)	Longhurst *et al.* (1989)	160	
CLIMAX (1969)	Longhurst *et al.* (1989)	500	
Indian Ocean (10°S)	Longhurst *et al.* (1989)	420	
Indian Ocean (21°S)	Longhurst *et al.* (1989)	220	
Celtic Sea	Longhurst *et al.* (1989)	800	
NFLUX	Longhurst *et al.* (1989)	90	18°C (200–525 m)
BATS	Dam *et al.* (1995a)	534	18.5°C (150–250 m)
FLUPAC TTS	Present study	118	9–18°C (100–500 m)
FLUPAC HNLC	Present study	132	9–18°C (100–500 m)

fluxes of the present paper and sinking rates of Rodier and Le Borgne (1997). However, our active flux refers to mesozooplankton DN flux and should be corrected for macroplankton and micronekton DN flux. According to Roger (1988), excretion by animals of the 0.5–10 cm size class represents an average 5% of mesozooplankton nitrogen or phosphorus excretion in the upper 400 m of the western tropical Pacific Ocean. Since this size class is hardly present in the photic layer during the daytime and concentrates in the upper layer at night, we may infer that its day time excretion in the deep layers would be ~2.5% of total mesozooplankton excretion. During FLUPAC, nitrogen excreted by migrants (Table 7) was equal to 2.4 and 0.8% of total mesozooplankton excretion for the TTS and HNLC stations, respectively. If the 2.5% value for macroplankton–micronekton is applied equally to the two stations, our DN flux values for mesozooplankton (Table 7) should be multiplied by 2.04 ((2.4+2.5)/2.4) at the TTS station and 4.1 ((0.8+2.5)/0.8) at the HNLC station, in order to get the total zooplankton and micronekton DN flux. At the TTS station, DN active flux comes to 3.70 mg N m^{-2} day^{-1} (129.6 × 2.04 × 14) and it is 3.60 at the HNLC station. If these values are divided by nitrogen passive fluxes obtained at the 0.1% light level by Rodier and Le Borgne (1997) on sediment traps (i.e. 9.24 mg N m^{-2} day^{-1} at 144 m for the TTS station and 39.80 mg N m^{-2} day^{-1} at 122 m for the HNLC station), the active/passive flux ratio is equal to 40 and 9% at the TTS and HNLC stations, respectively. The two values are rather distinct from those predicted by the model of Longhurst *et al.* (1989), and they are over for the TTS (40 vs 29.7%) and under for the HNLC (9 vs 17.9%). Reasons for the discrepancy deal with values of both active and passive fluxes that have been used in our study and that of Longhurst *et al.* (1989). First, macroplankton–micronekton excretion was supposed to make the same contribution in the two systems (i.e. 5% of mesozooplankton excretion), an hypothesis that cannot be proved because there are no data for HNLC systems. However, if we extraplolate present observations on zooplankton size structure to macroplankton and micronekton there should be more of these large organisms in the HNLC than in the TTS, thus leading to an increase of our nitrogen active flux value in the former case and/or a smaller one in the TTS. Consequently, our active/passive flux ratios would approach the Longhurst *et al.* model. A second explanation deals with the day habitat temperature of diel migrants, which is lower in the equatorial Pacific than cited in literature (Table 10). Since our Q_{10} values (Table 6) are in the same range as those used by Longhurst *et al.* (1989, 1990) for ammonium excretion (2.3–2.4, between 26–27°C and 16–17°C) and respiration (1.4–2.5, same temperature range), it can be predicted that zooplankton nitrogen excretion during the day (which is the active flux) is lower in the equatorial HNLC than in other regions considered by Longhurst *et al.* or Dam *et al.* (1995a) in Table 10. Finally, the passive flux direct measurements may bring a different view than the data provided by the model used by Longhurst *et al.*, incorporating the depth of the photic zone and level of primary productivity. Nevertheless, present results agree with the idea proposed by Longhurst and Harrison (1988), that the more oligotrophic the area the more the sinking particulate flux should be corrected for the active flux by migrants when the export production is to be compared with new production.

As for nitrogen, transport of dissolved carbon by migrants should be added to the passive sinking organic carbon flux in order to calculate the export production. According to Longhurst *et al.* (1990), the migrants carbon active flux represents 5–20% of the passive flux, whereas Dam *et al.* (1995a) report a percentage varying between 18 and 70% at Bermuda station. Combining our mesozooplankton CO_2 active flux with organic carbon passive flux values provided by Rodier and Le Borgne (1997), we obtain much lower values for active/

passive flux ratio: 3.7–4.6% in the FLUPAC TTS and 1% in the HNLC, depending on RQ used in the conversion of O_2 consumption into CO_2 production. If we take correction factors for migrating macroplankton and micronekton, as we did for nitrogen excretion (i.e. 2.04 and 4.1), active/passive flux ratios are still very low: 7.5–9.4%, respectively for RQ = 0.8 and 1 and 4.2% at the TTS and HNLC sites, respectively.

The nitrogen and carbon reciprocating pumps, as we have shown in this paper, are paradoxically not very different in the oligotrophic and mesotrophic studied sites (Table 7) due to different structures and functioning of the pelagic ecosystem. The question remains about the zooplankton contribution to the sinking rate by the Archimedian pump in the two systems. Thus, as presented on Table 8, fecal production in the upper layer is nearly twice as high in the HNLC as in the TTS. Actually, most of the fecal production in the surface layer would be consumed before it sinks (Longhurst, 1991), thus entering the coprophagous filter (Gonzales and Smetacek, 1994). Assuming sinking particles collected in the traps have a fecal origin, Dam *et al.* (1995b) estimate that at most 30% of the fecal production of the photic layer would be exported below at the equator. A similar calculation using the sinking fluxes and mesozooplankton nitrogen fecal production of Rodier and Le Borgne (1997) (Table 8) leads to 15% at FLUPAC TTS site and 35% at the HNLC. Even if these two percentages represent an upper limit, because fecal particles are not the only constituents of the trap samples (Rodier and Le Borgne, 1997), they support the view that the zooplankton Archimedian pump is more efficient at the HNLC site than at the TTS. This may be ascribed to larger sinking fecal particles at the HNLC station. Moreover, since the zooplankton fecal production doubles between the two systems as seen before, it may be concluded the role of mesozooplankton in the passive export is much higher at the HNLC station.

In conclusion, the contrast between biological pumps of HNLC and TTS systems is obvious for the Archimedian pump and would be, however, more important without the compensation of the reciprocating pump in the TTS.

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