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## Zooplankton of Tikehau atoll (Tuamotu archipelago) and its relationship to particulate matter

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### Abstract

The standing stock and taxonomic composition of zooplankton ( $>200\ \mu\text{m}$ ) were monitored in the lagoon of Tikehau atoll from April 1985 to April 1986. These data were supplemented by two 10 d studies on the variability, structure and functioning of the pelagic ecosystem. The biomass of animals  $>200\ \mu\text{m}$  comprised 50% of the total biomass of all organisms from 35 to  $>2\ 000\ \mu\text{m}$ . The zooplankton populations were characterized by successive blooms of copepods, larvaceans, pteropods and salps, probably arising from the periodic input of detritus from the reef during windy periods. As a result, the ecosystem was not in a steady state and the data for the fluxes of organic matter are presented separately for April 1985 and April 1986. Using the C:N:P ratio method, net growth efficiencies,  $K_2$ , were calculated for total mesozooplankton, mixed copepods, and two planktonic species, *Undinula vulgaris* and *Thalia democratica*. Combined with nitrogen and phosphorus excretion rates, these  $K_2$  values enabled the assessment of production rates. On a 24 h basis, P:B ratios (%) were close to 100 for the total zooplankton and 54, 34 and 800 for mixed copepods, *U. vulgaris* and *T. democratica*, respectively. These ratios are 5.7 times lower than that recorded for phytoplankton. High productivity may be ascribable to the high density of seston, the high temperature ( $29.5^\circ\text{C}$ ), and the kind of organisms present. Zooplankton production equalled 38 and 30% of  $^{14}\text{C}$  uptake during April 1985 and April 1986, respectively. Ingestion of animals  $>35\ \mu\text{m}$  was calculated by means of assimilation efficiencies and amounted to 17 and 7% of particulate organic carbon, 100 and 38% of living carbon, and 64 and 140% of primary production during the two periods, respectively. Finally, inorganic excretion was 32 and 18% of phytoplankton nitrogen and phosphorus requirements. A model based on the dimensional structure of the pelagic food-web, has been drawn to illustrate the biomass and carbon, nitrogen and phosphorus fluxes in the study area. The lagoon appears to export part

of its planktonic biomass, which is 4.2 times lower one sea mile outside the main pass connecting the lagoon to the open ocean.

### Introduction

Compared to the surrounding open ocean, the pelagic environment of Tikehau Atoll displays three striking characteristics: (1) its particulate organic matter is four times denser, (2) it contains an important amount of detritus, and (3) phytoplankton constitutes but a minor part of its standing crop (Charpy 1985). The fate of this particulate matter and the level of efficiency of utilization by consumers are two aspects which are of primary importance to an understanding of the functioning of the atoll pelagic food-web. Is seston consumed mainly by pelagic animals in the water mass, or by benthic ones once it has sunk to the bottom? Do they give rise to a significant predator biomass or is the efficiency of energy transfer between food and consumers low? In order to provide some answers to these questions, the role played by that part of the zooplankton which is comprised of particle-feeders has been studied. The amounts and composition of the particulate matter have been described by Blanchot et al. (1989); the present study examines the following aspects: the rate of grazing by zooplankton on organic particles; the amounts of nitrogen and phosphorus regenerated by zooplankton excretion which contributes to primary production; the amount of zooplankton production, quantification of which enables the assessment of the potential yield of zooplanktivores and the calculation of the transfer efficiency between organic particles and the zooplankton. The results are part of the ATOLL program of the ORSTOM Centre in Papeete (Tahiti); they were collected during two 10 d periods in April 1985 and April 1986 and are supplemented by weekly samples made between the two periods.

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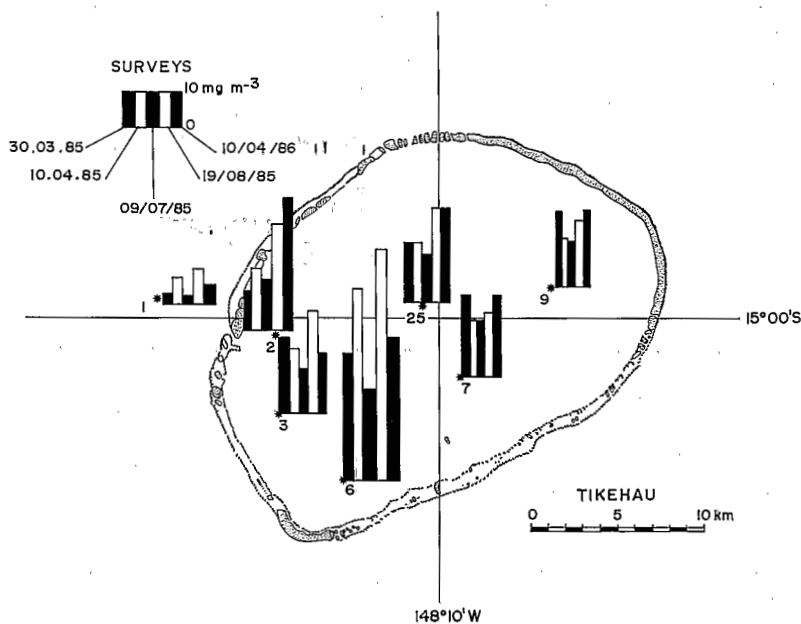


Fig. 1. Mesozooplankton. Distribution of dry weights at six stations inside and one station outside lagoon of Tikehau atoll during surveys (presented alternately in black and white) on 30 March, 10 April, 9 July, 19 August 1985 and 10 April 1986. Asterisks and numbers refer to station locations described in "site" section

### Site and general features of study

Tikehau atoll lies on the western end of the Tuamotu archipelago, and has a mean diameter of 25 km (Fig. 1). Its lagoon is connected with the open ocean by one main pass, the minimum depth of which is 3.7 m, and by a great number of shallow passes, which are only several decimeters deep, even at high tide (Intes 1984, Harmelin-Vivien 1985). Plankton hauls were made either over a six-station network inside the lagoon, plus one station 1 sea mile outside the main pass at different times (Fig. 1), or at Station 6, considered to be representative of the lagoon as a whole by Charpy (1985). The latter station was studied intensively for variability of biomasses and excretion measurements in April 1985 and 1986 and regularly between them for biomass and plankton composition. The data on excretion and production, presented here, deal with seston and zooplankton assemblages of various size-classes: 0.7 to 35  $\mu\text{m}$ , 35 to 200  $\mu\text{m}$ , 200 to 2 000  $\mu\text{m}$ , > 2 000  $\mu\text{m}$ , since not only metabolic rates of zooplankton are size-dependent but also predator-prey relationships in general. These data were complemented by microscopic examination of the zooplankton populations to determine the proportions of feeding types present. Biomass and flux data are presented as carbon, nitrogen and phosphorus, such units being applicable to all size-classes. The method used to assess zooplankton production ( $P$ : growth, moults and eggs) and ingestion ( $I$ ), is based upon the measurement of the release rate of metabolic end-products ( $T$ ) through respiration and excretion, and upon calculations of net growth ( $K_2$ ) and assimilation ( $D$ ) efficiencies, according to the following equations:

$$K_2 = P/P + T \Leftrightarrow P = T \cdot K_2 (1 - K_2)^{-1}, \quad (1)$$

$$D = P + T/I \Leftrightarrow I = (P + T)/D. \quad (2)$$

Since  $T$  was measured on natural assemblages, a holistic method was chosen for the assessment of  $K_2$  (C:N:P ratios

method: Corner and Davies 1971, Le Borgne 1978).  $D$  was assessed using the method of Conover (1966), based on the comparison of organic constituents of the faeces and seston, assuming that organic matter alone is assimilated.

### Materials and methods

#### Sample collection

Particles < 35  $\mu\text{m}$  were sampled with a 5-liter Niskin bottle at four or five depths along the water column, and 500 to 1 000 ml thereof were filtered on Whatman GF/F fibreglass filters (25 mm diam) for carbon, nitrogen and phosphorus analyses.

Microzooplankton (35 to 200  $\mu\text{m}$ ) was collected by vertical hauls from the bottom to the surface, in two different ways. In April 1985, a small net of 30 cm mouth diam sampled the water column downwards and upwards, but its short length (1 m) was deemed to provide poor filtration efficiency and hence poor estimates of the biomass. However, sampling with this net was considered satisfactory for determining the composition of the fauna. In April 1986, a longer net (3.55 m) with a mouth diameter of 33.5 cm was used, which collected filtered volumes close to theoretical values, indicating a filtration efficiency of  $\sim 100$ . During both periods, the plankton was sieved through a 200  $\mu\text{m}$  metal grid.

Mesozooplankton (200 to 2 000  $\mu\text{m}$ ) was sampled by a WP-2 net (UNESCO 1968) hauled vertically from the bottom to the surface, the filtered volume being measured with a TSK (Tsurumi-Seiki-Kosalusho Co.) mechanical flowmeter. Plankton was subsequently sieved through a 2 mm metal grid, which retained an upper fraction, the macroplankton.

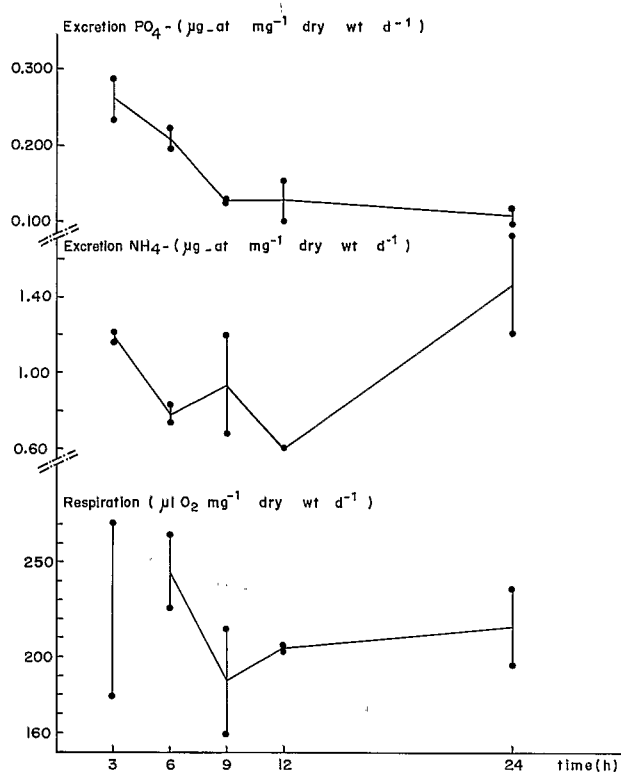


Fig. 2. *Undinula vulgaris*. Influence of duration of incubation (abscissa) on respiration and excretion rates at 29.5°C (Series No. 3)

#### Chemical composition of seston and zooplankton

Carbon, nitrogen and phosphorus were analysed from fibreglass filters or from diluted homogenates of zooplankton after drying and weighing (measuring precision to the nearest 1 µg), according to the methods of Le Borgne (1975). Carbon and nitrogen analysis were performed by means of a Hewlett-Packard 185B analyser, at 720°C to minimize carbonate interference (Telek and Marshall 1974) for seston, and at 1100°C for zooplankton. Similar samples were used for phosphorus analysis according to the method of Menzel and Corwin (1965). In all cases, fibreglass filters were rinsed with 0.1 N HCl and burnt at 500°C for 4 h to remove any organic matter before filtration.

Zooplankton ash-free dry weight was calculated as the difference between zooplankton dry weight (60°C, 24 h) and ash weight, after samples had been burnt for 1.5 h at 550°C.

#### Zooplankton respiration and excretion measurements: influence of duration of incubation

Excretion and respiration rates and atomic ratios between respiration (O), nitrogen (N) and phosphorus (P) excretions were determined from incubation experiments using non-filtered seawater, according to the methods described by Le

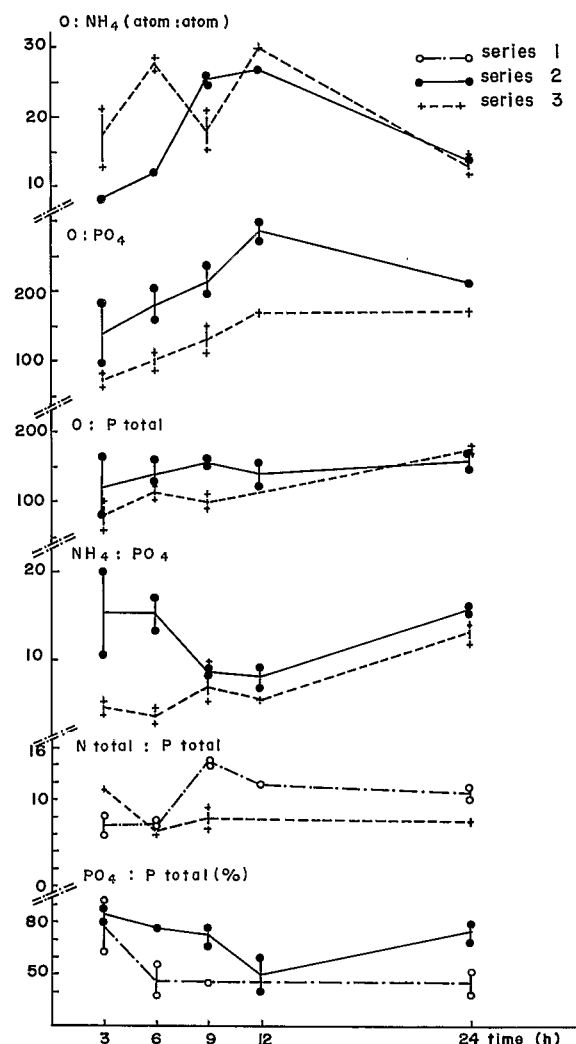


Fig. 3. *Undinula vulgaris*. Influence of duration of incubation (abscissa) on atomic ratios between respiration (O), and excretion of ammonium ( $\text{NH}_4$ ), phosphate ( $\text{PO}_4$ ), total nitrogen ( $\text{N}_{\text{total}}$ ) and phosphorus ( $\text{P}_{\text{total}}$ ).  $\text{PO}_4:\text{P}_{\text{total}}$ : percent contribution of inorganic phosphorus to total phosphorus; all other ratios are atom:atom

Borgne (1979). Since the length of incubation is known to influence the results, three sets of experiments of increasing duration were performed. The seawater medium was analysed 3, 6, 9, 12 and 24 h after the introduction of individuals of *Undinula vulgaris* (Figs. 2, 3). The phosphate excretion rate decreased over the initial 9 h, and then attained a steady state (Fig. 2 shows Series 3 only, the dry weights of the copepods being unknown in the other two series, making calculation of the rates impossible). Respiration and ammonium excretion rates varied so strongly, that it is impossible to draw any conclusions about changes as a function of time. These results agree well with those of Le Borgne (1979) for mixed plankton of the Atlantic equatorial upwelling over a temperature range of 20° to 23°C (compared to 29.5°C in Tikehau atoll). The kinetics of the metabolic rates may be

**Table 1.** Relative contributions (%) of various size classes to total zooplankton dry weight (DW), ash-free dry weight (AFDW), carbon (C), nitrogen (N) and phosphorus (P) at Station 6, in the lagoon

Size class	April 1985					April 1986				
	DW	AFDW	C	N	P	DW	AFDW	C	N	P
Microzooplankton 35–200 $\mu\text{m}$	11.0	3.7	8.0	5.3	29.0	48.7	23.9	35.7	25.5	35.0
Mesozooplankton 200–500 $\mu\text{m}$	15.8	55.5	66.5	64.7	45.6	27.7	76.1	35.5	41.8	37.6
500–2 000 $\mu\text{m}$	42.3					23.7				
Macrozooplankton > 2 000 $\mu\text{m}$	31.4	40.8	25.5	30.0	25.4	0	0	0	0	0
Total wt ( $\text{mg m}^{-3}$ )	46.4	23.3	8.35	1.70	0.217	30.6	15.4	10.82	2.26	0.242

also considered in the time evolution of the O:N, O:P and N:P ratios between respiration and excretion (Fig. 3). For example, it appears that the proportion of inorganic phosphorus decreased whereas the ratio between total nitrogen and total phosphorus excretions ( $N_t:P_t$ ) remained steady between 3 and 24 h after incubation began. Such variations, when they do occur, are related to starvation, stress due to handling, and to bacterial activity (Le Borgne 1986). Since the variability of the results decreased with time and the rates achieved a steady state at 9 h, we selected incubations of 10 h for this study.

Zooplankton net growth ( $K_2$ ) and assimilation ( $D$ ) efficiencies in terms of C,N,P

Net growth efficiency was calculated for nitrogen and phosphorus using C:N:P ratios of zooplankton body constituents, metabolic end-products, assimilation efficiencies and food (particulate matter), but could not be determined for carbon because its release through respiration (as  $\text{CO}_2$ ) and excretion (soluble organic compounds) had not been measured. Therefore, carbon production rates have been calculated from nitrogen and phosphorus production rates using zooplankton constituent C:N or C:P ratios, since production ratios must be equal to body-constituent ratios. The following N:P ratios were defined:  $a_1$  (particulate ratio),  $a_2$  (zooplankton excretion),  $a_3$  (zooplankton body constituents) and  $a_4$  (zooplankton assimilation efficiencies, i.e.,  $D_N:D_P$ ). Net growth efficiencies therefore equal:

$$K_{2,N} = a_3 \cdot K_{2,P} \cdot (a_1 \cdot a_4)^{-1}, \quad (3)$$

$$K_{2,P} = (a_1 \cdot a_4 - a_2) \cdot (a_3 - a_2)^{-1}. \quad (4)$$

Calculation of the assimilation efficiency ( $D$ ) required determination of the organic C, N and P content of the faeces (Eq. 2). Individuals of *Undinula vulgaris* (April 1985) or mixed copepods (April 1986) were left in a Becher dish for ~1.5 h, their faeces were then pipetted-out, transferred into "CHN" boats and weighed before analysis of C,N,P contents.

## Results

### Zooplankton biomass and composition

#### Relative contributions of different size-classes and taxonomic composition

The 200 to 2 000  $\mu\text{m}$  size-fraction comprised more than half the dry weight of particles >35  $\mu\text{m}$  (Table 1). Micro- and macroplankton, however, displayed different distributional patterns between sampling periods: In April 1985, microzooplankton, which may have been underestimated for this period (see "Material and methods") contributed less to the total zooplankton biomass than in April 1986, whereas macrozooplankton was more abundant during the first period due to a swarm of the salp *Thalia democratica*, which constituted 63% of the dry weight of the whole macrozooplankton fraction (Le Borgne and Moll 1986). Subsequent weekly sampling revealed this swarm to be of temporary nature, but it was followed by others – larvaceans in July–August, pteropods (*Creseis chierchiae*; L. Newman, personal communication) at the end of August, and copepods (*Undinula vulgaris*) in December 1985 (Fig. 4). Since no phytoplankton bloom was observed (Charpy unpublished data), these planktonic swarms may have resulted from inputs of detrital material from the reef or from shallow depths through wind-mixing of the water mass. Apart from these short events of quasi-monospecific zooplankton swarms, four major holoplanktonic taxa prevailed in the weekly samples: copepods (nauplii and copepodids), larvaceans, pteropods (*C. chierchiae*) and chaetognaths.

The relative contributions of the different zooplankton size-classes differed as a function of weight unit used – dry or ash-free dry weight, carbon, nitrogen or phosphorus (Table 1). These differences may have been due to the different chemical compositions of the various taxa. It is more likely however, that variations in the amount of detritus in the samples and resulting variations in the organic and inorganic fractions were the cause. The relative proportion of detritus in each sample was assessed by Blanchot and Moll

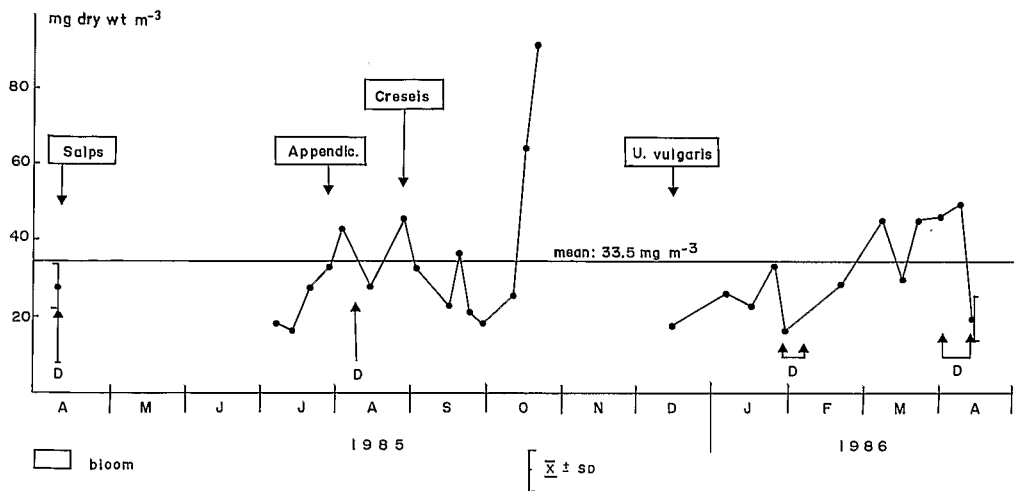


Fig. 4. Mesozooplankton. Variations in dry weight from April 1985 to April 1986 at Station 6 in the lagoon. Blooms of *Thalia democratica* (Salps), appendicularians (Appendic.), the pteropod *Creseis chierchiae*, and the copepod *Undinula vulgaris* are shown. "D" indicates large amounts of detritus

Table 2. Relative contributions (%) of main taxa to total zooplankton biomass at Station 6. Percent contribution of non-living organisms (detritus) to total dry weight is also shown (from Blanchot and Moll 1986 and Blanchot et al. 1989)

Size class	Taxa	% total biomass	% detritus
April 1985			
Microzooplankton 35–200 ( $\mu\text{m}$ )	nauplii	39.2	70
	copepods	30.6	
	bivalve larvae	19.8	
	polychaete larvae	10.4	
Mesozooplankton 500–2 000 ( $\mu\text{m}$ )	copepods	68.4	14
	chaetognaths	19.3	
	salpids	8.8	
Macrozooplankton > 2 000 ( $\mu\text{m}$ )	salpids	63.2	0
	copepods	22.8	
	chaetognaths	1.8	
April 1986			
Mesozooplankton 200–2 000 ( $\mu\text{m}$ )	copepods	73.8	3, 10, 49 <sup>a</sup>
	larvaceans	5.0	
	brachyuran larvae	8.7	
	chaetognaths	5.6	

<sup>a</sup> Three samples of mesozooplankton were measured in April 1986

(1986) and Blanchot et al. (1989) by sorting out the zooplankters, and weighing these and the remainder of the samples separately (Table 2). The proportion of detritus decreased from the smallest to the largest zooplankton size-fraction (70% for microzooplankton, 0% for macrozooplankton), and was not constant over time. In the mesozooplankton weekly samples, detritus was observed in only three samples between April 1985 and April 1986 (August, January and February). In April 1985, the proportion of detritus in the mesozooplankton sample was 14%; in April 1986 it ranged from 3 to 49% (Table 2), providing a good example of its variability. Diving observations in the lagoon revealed that in April 1985 macrodetritus occurred during rough weather conditions. It had a flaky appearance and may have included setae of the diatom *Chaetoceros* sp.

Table 3. Mesozooplankton. Mean and variance:mean ratios ( $\text{mg m}^{-3}$ ) of dry weights (DW) and ash-free dry weights (AFDW) at Station 6 in April 1986

Time of day (hrs)	(n)	DW		AFDW	
		$\bar{x}$	$s^2:m$	$\bar{x}$	$s^2:m$
Morning (10.00)	(10)	15.7	0.73	9.2	0.38
Evening (17.00)	(10)	22.9	1.98	14.2	1.21
Night (21.00)	(6)	43.2	3.14	32.4	2.35
Morning + evening	(20)	19.4	2.09	11.7	1.42

(Blanchot and Moll 1986). However, it is usually difficult to determine of what exactly the macrodetritus consists, since in both the natural environment and in plankton nets, suspended particles are aggregated by mucus.

#### Temporal variations

Variations in the dry weight of the mesozooplankton were monitored as regularly as possible at Station 6, and displayed two maxima in October 1985 (65 and 92  $\text{mg dry wt m}^{-3}$ ). The annual mean was 33.5  $\text{mg m}^{-3}$  (Fig. 4), a value higher than those recorded during the 10 d periods in April 1985 (26.8) and 1986 (19.4  $\text{mg m}^{-3}$ ). Short-term variability was noted during both periods (Figs. 5, 6), but no long-term changes emerged as a function of time. However, the variance to mean ratio  $s^2:m$ , a distribution index, was high: 3.95 in 1985 and 2.09 in 1986 for mesozooplankton, and 3.21 for microzooplankton in 1986. This variability in dry weight may be ascribable to vertical migrations and to mineral matter associated with the detritus. The diel variations are shown in Table 3, from which it is evident that ash-free dry weight (AFDW) displays a lower  $s^2:m$  ratio than dry weight (DW). A similar result was obtained for the microzooplankton:  $s^2:m$  of 3.21 for DW and 0.59 for AFDW (data not tabulated).

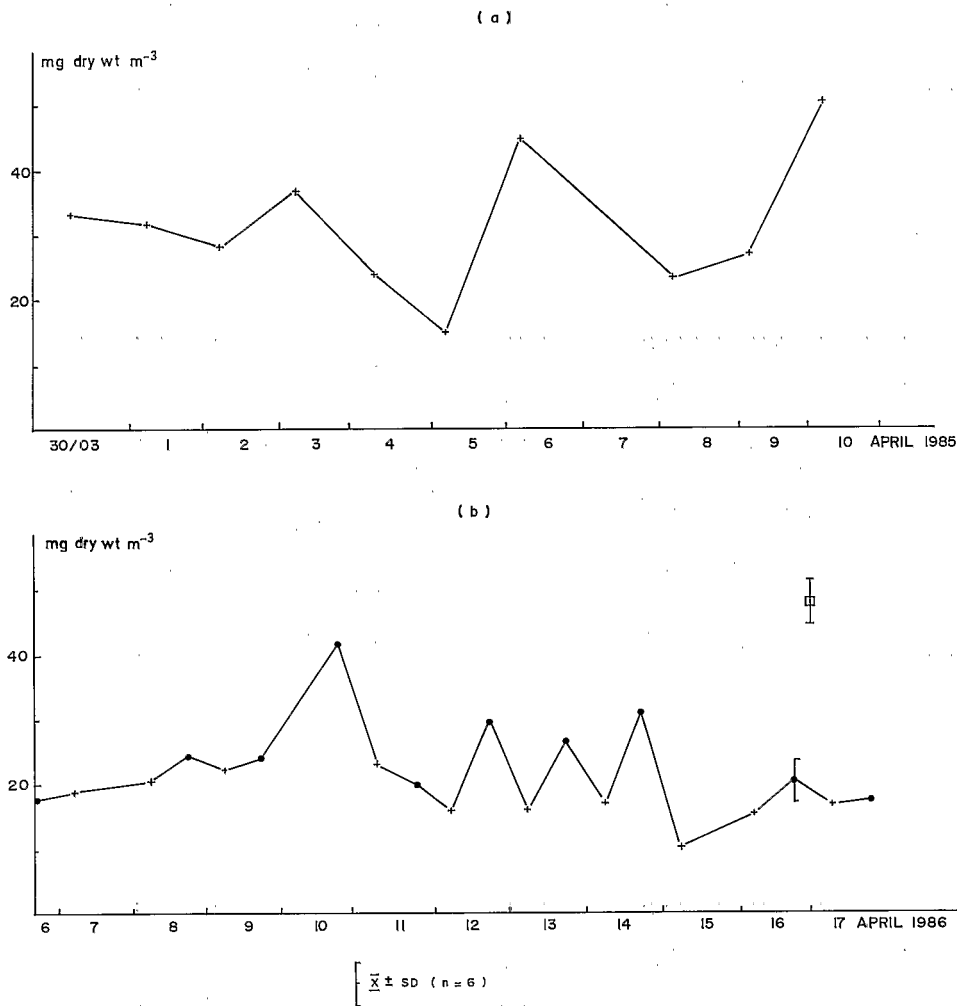


Fig. 5. Mesozooplankton. Variations in dry weight from 30 March to 10 April 1985 (a) and April 1986 (b) at Station 6, during hauls made at 10.00 hrs (+), 17.00 hrs (●) and 21.00 hrs (□).

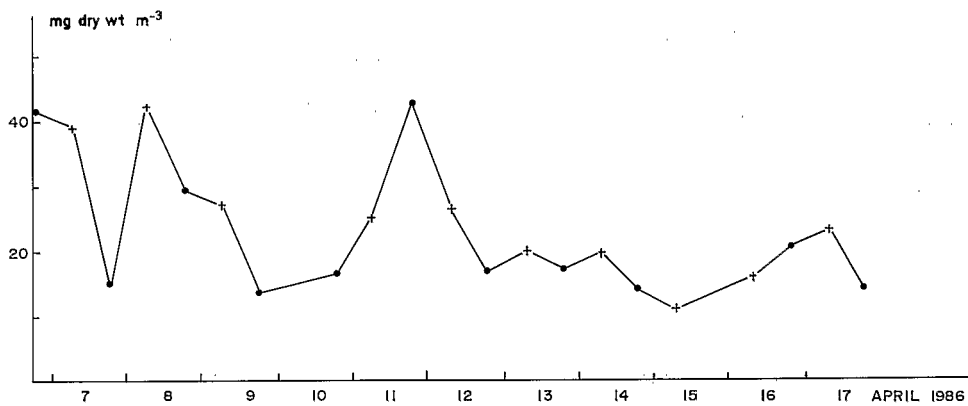


Fig. 6. Microzooplankton. Variations in dry weight during April 1986 at Station 6 at 10.00 hrs (+) and 17.00 hrs (●).

#### Geographical distribution and comparison of biomasses inside and outside lagoon

Zooplankton dry weight at Station 6 was 2.3 times as rich as at the other six stations within the sampling network of the lagoon (Fig. 1). However, no such difference is evident when the mean values of the 10 d periods at Station 6 are compared with those of the other stations (Table 4). Charpy

(1985) reported no difference in the chlorophyll *a*, carbon, nitrogen or phosphorus content of particulate organic matter in the lagoon; these displayed no spatial distribution, probably because of strong mixing of the water column, in which no thermal gradient could be observed.

The mean mesozooplankton dry weight in the lagoon was 22.7 mg m<sup>-3</sup> ( $n = 30$  stations, including Station 6) and only 5.4 mg m<sup>-3</sup> one sea-mile out of the pass in a similar

**Table 4.** Mesozooplankton. Dry weight ( $\text{mg m}^{-3}$ ) in Tikehau lagoon and one nautical mile outside the main pass (Station 1). Data were obtained during five surveys (dates shown), or from 10 d measurements in April 1985 and 1986 (all values for daytime)

Area	1985:				1988:	$\bar{x}$
	30 Mar.	10 Apr.	9 July	19 Aug.	10 Apr.	
Lagoon (except Station 6)	17.5	16.7	14.0	23.2	22.6	18.8
Station 6 alone						
surveys	33.7	50.4	25.8	64.8	37.9	42.5
10 d periods	—	26.8	—	—	15.7	21.3
Offshore (Station 1)	2.7	6.6	2.5	10.2	5.0	5.4

**Table 5.** Zooplankton. Rates of respiration ( $\mu\text{l O}_2 \text{mg}^{-1} \text{dry wt d}^{-1}$ ) and excretion ( $\mu\text{g-at mg}^{-1} \text{dry wt d}^{-1}$ ) at Station 6 in April 1985 and 1986 at 29°C. (n): no of replicates. nd: no data

Size class/species	(n)	O <sub>2</sub> respir.	Excretion of:			
			NH <sub>4</sub> -N	total N	PO <sub>4</sub> -P	total P
April 1985						
Microzooplankton	(7)	153	1.892	2.215	0.116	0.156
Mesozooplankton	(4)	245	1.948	1.930	0.177	0.226
<i>Undinula vulgaris</i>	(2)	238	0.950	1.300	0.127	0.166
<i>Thalia democratica</i>	(12)	110	0.706	1.210	0.095	0.175
April 1986						
Microzooplankton	(6)	282	nd	3.274	0.203	0.262
Mezozooplankton	(10)	259	nd	1.772	0.161	0.211

water column (30 m). The difference (4.2 times) would probably have been even greater if other stations located further from the pass had been considered, since part of the biomass at Station 1 originates from the lagoon, which is considered to export organic matter (Charpy-Roubaud et al. 1989). Similar differences between the lagoon and the outer water were observed for particulate matter; chlorophyll *a* concentrations were 3.45 times higher and ATP concentrations 4.75 times higher inside the lagoon (Charpy-Roubaud et al. 1989).

#### Zooplankton respiration and excretion

Respiration and excretion rates of the three size-classes of zooplankton were measured in April 1985 and 1986 (Table 5), together with those of the copepod *Undinula vulgaris* and of *Thalia democratica*, two species which are easily recognized and periodically abundant. These rates were from zooplankters caught during the daytime, and are possibly lower than night-times values, as demonstrated by Gerber and Gerber (1979) for copepods of Enewetak atoll, although these authors did also report that the respiration rate of the pteropod *Creseis acicula* was lower at night.

In accordance with the general rule of decreasing metabolic rate with increasing weight, the rates for micro-

zooplankton were higher than those for mesozooplankton in April 1986. Similarly, respiration and excretion rates of salps were lower than those of mesozooplankton. However, no such decrease in rates with increasing weight was apparent for the microzooplankton in April 1985. This probably resulted from differences in the classes of organisms incubated (up to 20% of some samples consisted of larval bivalves, and the metabolic rates are based on dry weights which include the shells) and also from the detritus introduced into the flasks together with the living organisms. Comparison of respiratory values with those for N and P excretion, by means of atomic ratios of O:N, O:P and N:P (Table 6) provided information about zooplankton physiology and allowed net growth efficiency  $K_2$ , to be calculated (Table 7). For micro- and mesozooplankton, most of the excreted nitrogen and phosphorus compounds appeared to be inorganic (e.g. ammonium and phosphate). The values for PO<sub>4</sub>:P<sub>i</sub> as a function of time (Fig. 3), indicated that the amount of inorganic excretion was not overestimated during the 10 h incubations. Other atomic ratios for micro- and mesozooplankton were similar between years.

The O:NH<sub>4</sub> ratio recorded was rather low for the zooplankton (Table 6), a result which indicates a partially proteic catabolism. However, the O:NH<sub>4</sub> ratios of *Undinula vulgaris* and *Thalia democratica* were high, suggesting a carbohydrate- and lipid-based catabolism.

**Table 6.** Zooplankton. Metabolic atomic ratios and contribution of inorganic excretion to total excretion (%) at Station 6. O: O<sub>2</sub> respired; NH<sub>4</sub>, N<sub>t</sub>, PO<sub>4</sub>, P<sub>t</sub>: ammonia, total nitrogen, phosphate and total phosphorus excreted. nd: no data

Size class/species	O:NH <sub>4</sub>	O:N <sub>t</sub>	O:PO <sub>4</sub>	O:P <sub>t</sub>	NH <sub>4</sub> :PO <sub>4</sub>	N <sub>t</sub> :P <sub>t</sub>	NH <sub>4</sub> :N <sub>t</sub>	PO <sub>4</sub> :P <sub>t</sub>
April 1985								
Microzooplankton	7.2	6.9	144	104	12.1	11.1	85.4	74.4
Mesozooplankton	10.8	10.8	119	92	11.4	8.6	100.0	76.5
<i>Undinula vulgaris</i>	18.4	13.2	132	100	7.9	7.9	48.2	43.1
<i>Thalia democratica</i>	15.5	8.1	103	56	7.4	6.9	58.3	54.3
April 1986								
Microzooplankton	nd	7.7	124	96	nd	12.5	nd	77.5
Mesozooplankton	nd	7.1	144	110	nd	8.4	nd	76.3

**Table 7.** Zooplankton. Net growth efficiencies ( $K_2$ ) in terms of nitrogen and phosphorus for total populations and sorted species or taxa, calculated from N:P ratios of particles ( $a_1$ ), zooplankton excretion ( $a_2$ ), and body constituents ( $a_3$ ). Number of replicates in parentheses. Data for Station 6

Size class/species	$a_1$	$a_2$	$a_3$	$K_{2,N}$	$K_{2,P}$
1985					
Mesozooplankton (9–10 Apr.)	13.9 (25)	8.6 (4)	15.0 (2)	0.894	0.828
<i>Undinula vulgaris</i>	13.9 (25)	7.9 (2)	25.7 (2)	0.623	0.337
<i>Thalia democratica</i>	13.9 (25)	6.9 (12)	20.4 (2)	0.761	0.519
1986					
Mesozooplankton (7–9 Apr.)	18.2 (4)	10.8 (2)	26.0 (1)	0.695	0.487
(10–12 Apr.)	16.3 (4)	6.1 (2)	20.5 (1)	0.891	0.708
(13–16 Apr.)	13.9 (4)	9.2 (2)	20.5 (1)	0.613	0.416
$\bar{x}$	16.1	8.4	23.3	0.748	0.517
Mixed copepods	16.1 (12)	8.4	37.6 (1)	0.616	0.264
Microzooplankton	16.1 (12)	12.5 (6)	16.7 (5)	0.889	0.857

**Table 8.** Assimilation efficiencies ( $D$ ) of copepods in terms of C, N, P and their ratios ( $a_4 = D_N:D_P$ ,  $a'_4 = D_C:D_N$ ). Calculations made by method of Conover (1966) using organic carbon, nitrogen and phosphorus percentages of dry weight in faeces and food. nd: no data

Species	Faeces ( $e'$ )			Food ( $f'$ )			$D$ (%)			$a_4$	$a'_4$
	C	N	P	C	N	P	C	N	P		
1985											
<i>Undinula vulgaris</i>	0.395	0.100	0.048	2.36	0.25	0.081	83.6	60.1	38.3	1.57	1.39
1986											
Small copepods	0.59	0.17	0.0254	15.48	1.86	0.258	96.8	91.0	90.2	1.01	1.06
	0.62	0.09	–	5.37	0.85	0.139	89.0	89.5	nd	nd	0.99

## Zooplankton production, assimilation and ingestion

### Production rates

The particulate N:P ratio ( $a_1$ ) shown in Table 7 is the mean of all N:P values recorded along the water column, since net growth-efficiency includes all zooplankters living between the bottom and surface water-layer. Particles were sampled at the same time as zooplankton excretion ( $a_2$ ) and body constituents ( $a_3$ ) were determined, since the method is based on simultaneous measurements of the ratios of Eqs. (3) and (4),  $a_2$  denoting the utilization of assimilated nitrogen and phosphorus by zooplankton. No variation of  $a_1$  with depth

was observed in April 1985, but surface values were lower than values for deeper layers in April 1986.

Assimilation efficiencies,  $D$ , were calculated for mixed copepods in April 1986 (Table 8) and are similar to those reported by Gerber and Gerber (1979) for *Undinula vulgaris* (85.8 for C and 89.2% for N) and mixed small copepods (86.8 and 90.8% for C and N, respectively). They are, however, greater than those found by Gottfried and Roman (1983) for *Acartia* sp. and *Mysidium* sp. feeding on coral mucus detritus: 68 and 57% for C and 36 and 55% for N, for these two species, respectively. Efficiencies were similar for C, N and P (Table 8), so that  $a_4$  ( $D_N:D_P$ ) can be considered as equal to 1. There are but few values reported in the



**Table 9.** Zooplankton. Production rates in terms of C, N, P ( $\mu\text{g mg}^{-1}$  dry wt  $\text{d}^{-1}$ ) and daily P:B ratios at Station 6. Body C, N and P, as percentages of dry weight, allows conversion of rates into P:B

Size class/species	Production rates			Body constituents			P:B (%)
	C	N	P	C	N	P	
April 1985							
Mesozooplankton	164	44.65	3.565	20.7	4.12	0.37	102.0
<i>Undinula vulgaris</i>	108	29.97	2.604	31.4	8.73	0.76	34.3
<i>Thalia democratica</i>	190	42.88	5.859	1.91	0.43	0.0725	816.0
April 1986							
Mesozooplankton	331	73.64	7.061	38.4	8.50	0.81	86.4
Mixed copepods	147	39.80	2.346	27.1	7.31	0.43	54.4

literature for nitrogen and phosphorus efficiencies (Le Borgne 1982), and the validity of  $a_4 = 1.6$  calculated for *U. vulgaris* in April 1985 is questionable.

The  $K_{2,N}$  and  $K_{2,P}$  efficiencies in Table 7 are greater for total zooplankton populations than for *Undinula vulgaris* or mixed copepod species. This is probably a sampling artefact: sorting of larger animals is easier, but their growth rates have slowed down or are zero and the food they assimilate is mainly used for reproduction and catabolism; unsorted samples, selected randomly from amongst moving animals, consist mainly of young developmental stages which devote a higher proportion of assimilated matter to growth. A similar difference between net growth efficiencies of sorted and mixed plankton was evident also in the results of Gerber and Gerber (1979): their  $K_{2,N}$  was 0.500 for small copepods and 0.273 or 0.230 for *U. vulgaris* and *Creseis acicula*, respectively. Incidentally, the growth efficiencies reported by these authors for carbon were very low, but still support the view that mixed plankton has higher growth efficiencies than sorted species (0.089 for small copepods, 0.072 and 0.050 for sorted species). Finally, our net growth-efficiency data were abnormally high for microzooplankton in 1986 and mesozooplankton in 1985, indicating that more than 80% of the food assimilated would be used in production (growth, moults and eggs). N:P ratios for seston ( $a_1$ ) and zooplankton body-constituents ( $a_3$ ) differed only slightly, perhaps because in  $a_3$  the sample included detrital material. The nitrogen and phosphorus production rates in Table 9 were calculated using the total N and P excretion rates from Table 5 and the net growth efficiencies from Table 7. Carbon production rates were calculated using the C:N and N:P constituent ratios derived from the percentages of Table 9. The mesozooplankton  $K_2$  values used in calculations are those of *Undinula vulgaris* in 1985 and values observed on total plankton in 1986, the means of which are  $K_{2,N} = 0.748$  and  $K_{2,P} = 0.517$  (Table 7).

Production:biomass (P:B) ratios are also given in Table 9, since they reflect productivity more truly than rates calculated as a function of dry weight. P:B ratios (in percent) were obtained by dividing growth rates by C, N and P content of the dry weight and are equal for the three elements. All P:B values of Table 9 are  $>34\%$ , which is equivalent to a 3 d turnover time of the biomass. The turnover time is shorter

**Table 10.** Zooplankton. Assimilation and ingestion rates ( $\mu\text{g C, N}$  or  $\text{P mg}^{-1}$  dry wt  $\text{d}^{-1}$ ) at Station 6

Size class/species	Assimilation			Ingestion		
	C	N	P	C	N	P
April 1985						
Mesozooplankton	656	71.7	10.57	785	102	15.1
<i>Undinula vulgaris</i>	515	48.3	7.75	616	80	20.2
<i>Thalia democratica</i>		56.4	11.28	617	81	16.1
April 1986						
Mesozooplankton	724	98.4	13.54	804	109	15.0
mixed copepods	473	64.6	4.67	526	72	5.2

for mixed mesozooplankton populations, and close to 1 d. Turnover times are even shorter for the salp *Thalia democratica*, for reasons discussed by Le Borgne and Moll (1986): asexual reproduction, high water-temperature, abundance of food. The latter two reasons apply also for all P:B values in Table 9, which are higher than the mean of 33% found for mesozooplankton of the tropical Atlantic Ocean by Le Borgne (1982).

#### Assimilation and ingestion rates

The nitrogen and phosphorus assimilation rates in Table 10 are the sum of production and total excretion rates. Carbon assimilation was assessed from ingestion using Eq. (2). Carbon ingestion,  $I$ , was calculated from nitrogen ingestion using particulate C:N ratios (mass:mass) of 8.95 in April 1985 and 7.35 in April 1986. Finally, nitrogen and phosphorus ingestion rates were computed with Eq. (2), using the assimilation efficiencies given in Table 8. The net growth efficiency of carbon ( $K_{2,C}$ ), which is not presented in Table 7, can now be computed from production and assimilation, and equals 0.25 for mesozooplankton and 0.21 for *Undinula vulgaris* in 1985 and 0.46 for mesozooplankton and 0.31 for mixed copepods in 1986. These results are slightly different from the  $K_{2,P}$  data, because carbon and phosphorus have distinct cycles and because the calculation used approximate conversion ratios.

## Simplified model of pelagic trophic web of the lagoon

The combined data on biomasses ( $\text{mg dry wt m}^{-3}$ ) and metabolic rates (amounts of C, N or P respired, excreted, produced, assimilated or ingested) as a function of dry weight and time (day) enabled us to calculate the fluxes of C, N and P circulating between particulate matter and zooplankton, and to discern a pattern of the interactions comprising the pelagic trophic web in the lagoon. A model enables swift visual comprehension of the biomasses and fluxes of an ecosystem, and the various proportions constituted by the different components of the trophic foodweb and the transfer efficiencies between the components can be more readily followed than from data in tabulated form. In setting up the model, C, N, and P have been considered separately since their respective contributions to dissolved and particulate matter vary.

Fig. 7 illustrates biomass and fluxes of matter of four size-classes, the smallest class (0 to  $35 \mu\text{m}$ ) being assumed to be ingested by the other three – a realistic hypothesis according to the data in Table 2, which show that  $\sim 90\%$  of the microzooplankton dry weight was comprised of copepods and bivalve larvae, which are small-particle feeders; that  $>80\%$  of the mesozooplankton dry weight consisted of copepods, salps, larvaceans and minor groups of other particle feeders, and that  $>86\%$  of the macrozooplankton was made up of copepods and salps in April 1985.

**Table 11.** Contributions (%) of carbon, nitrogen and phosphorus to dry weight of detritus alone and zooplankton alone, of planktonic sample of 3 April 1985

Element	Zooplankton	Detritus
Carbon	22.6	13.7
Nitrogen	4.24	1.90
Phosphorus	1.68	0.20

**Table 12.** Zooplankton. Oxygen respired ( $\mu\text{l O}_2 \text{d}^{-1} \text{m}^{-3}$ ) and soluble nitrogen and phosphorus excreted ( $\mu\text{g N}$  or  $\text{P d}^{-1} \text{m}^{-3}$ ) at Station 6. dry wt: detritus-free dry wt ( $\text{mg m}^{-3}$ ); organic N, organic P: total minus inorganic excretions

Size class	dry wt	$\text{O}_2$ respir.	Excretion of:			
			$\text{NH}_4\text{-N}$	organic N	$\text{PO}_4\text{-P}$	organic P
April 1985						
35–200 $\mu\text{m}$	1.6	249	43.3	28.8	5.9	1.9
200–2 000 $\mu\text{m}$	23.1	5 660	628.6	0.0	126.4	38.8
> 2 000 $\mu\text{m}$	14.5	1 595	143.3	61.4	42.8	18.3
Total	39.2	7 504	815.1	90.2	175.1	59.0
April 1986						
35–200 $\mu\text{m}$	4.5	1 269	119.2	20.4 <sup>a</sup>	28.2	8.4
200–2 000 $\mu\text{m}$	12.4	3 212	338.2 <sup>a</sup>	0.0 <sup>a</sup>	62.0	19.2
> 2 000 $\mu\text{m}$	0	0	0	0	0	0
Total	16.9	4 481	457.4	20.4	90.2	27.6

<sup>a</sup> Calculations made using excretion rates from 1985

Detritus and living organisms are illustrated separately in Fig. 7. The biomass of living particles was assessed from ATP data of Blanchot et al. (1989), using a factor of 250 to convert ATP into living carbon. In zooplankton samples, the detritus was weighed, a not entirely satisfactory method since it assumes that detritus and living animals are of similar elemental composition, which is not the case, carbon and nitrogen contents of detritus being only half those of living organisms, and phosphorus content being even lower (Table 11). This lends support to the classical idea that phosphorus is released more quickly than carbon or nitrogen after living cells have died. Therefore, the carbon contribution of the living organisms to zooplankton weight is in fact higher than shown by Fig. 7, but the flux values are realistic, since their calculation was not based on the elemental composition (dry weights of Table 12 were corrected for detritus content by subtracting percentages of 70 for microzooplankton in 1985 and 1986, 14 for mesozooplankton in 1985, and 21 in 1986, and 0 for macrozooplankton; Table 2). The rates used in the calculations of fluxes of Table 12 and Fig. 7 are those of Tables 5, 9 and 10; missing values for microzooplankton assimilation and production were computed using an assimilation efficiency,  $D$ , of 90% and a P:B ratio of 1.

The carbon uptake shown for phytoplankton in Fig. 7 is the annual mean ( $0.44 \text{ g C m}^{-2} \text{ d}^{-1}$ ) reported by Charpy-Roubaud et al. (1989) for the whole lagoon divided by average depth (25.2 m). This value is higher than that reported by Charpy et al. (1986) in April 1985: 13.7 vs 17.5  $\text{mg C m}^{-3} \text{ d}^{-1}$  (no uptake measurements were made in April 1986). Nitrogen and phosphorus uptake rates were assessed from carbon rates using the following C:N and N:P conversion factors: C:N = 7.0 (mass ratio), which is the mean value of data given in Table 9 of Gerber and Marshall (1982) for phytoplankton of Enewetak atoll; and C:P =  $33 \pm 8$  (mass ratio), observed by Charpy (unpublished). This C:P ratio is comparable to other phytoplankton uptake ratios in the literature: 38, for the Ebrie lagoon (Ivory Coast), where

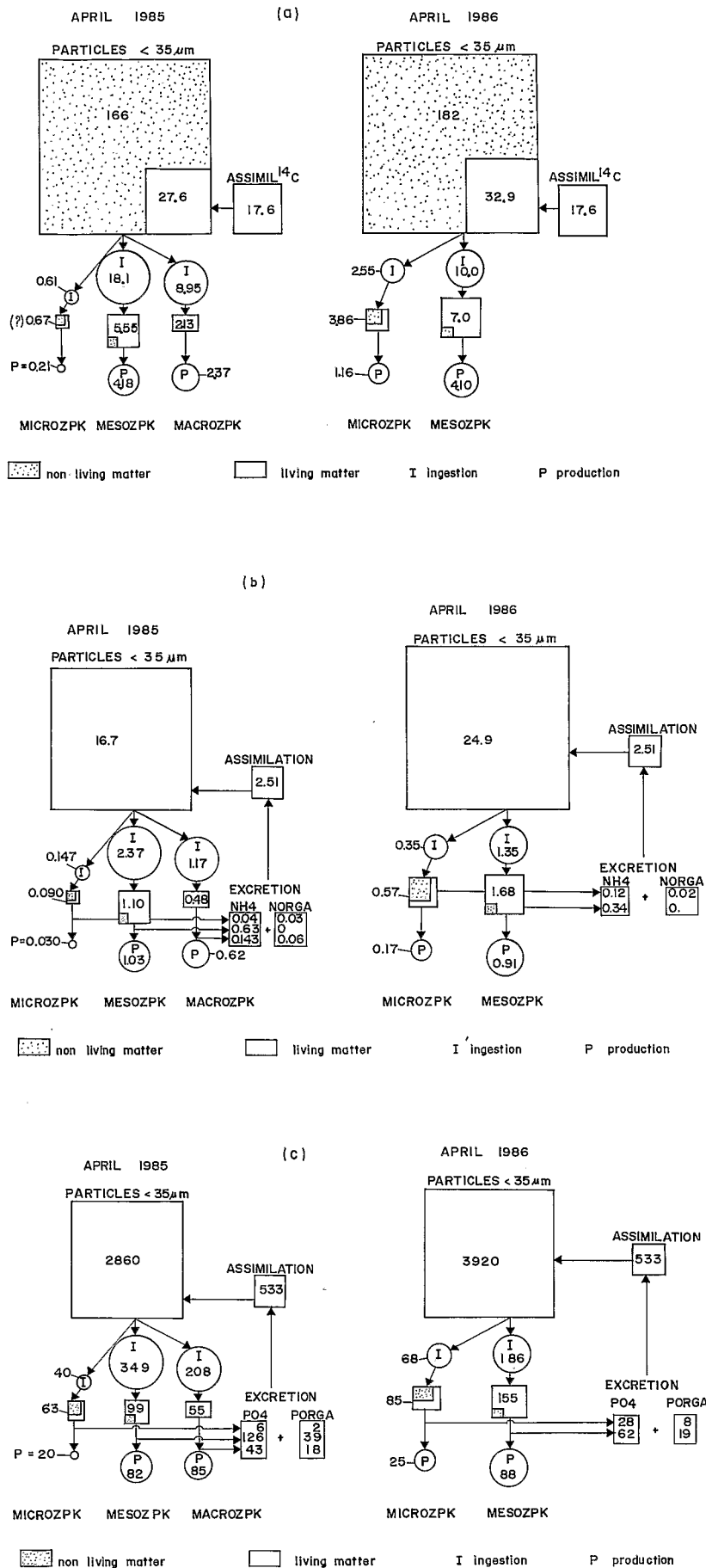


Fig. 7. Schematic drawing of pelagic biomass and fluxes at Tikehau atoll in April 1985 and 1986. Units are  $\text{mg m}^{-3}$  for standing stocks and  $\text{mg m}^{-3} \text{d}^{-1}$  for fluxes of carbon (a), nitrogen (b) and phosphorus (c)

phosphorus was not a limiting element (Lemasson et al. 1980) and between 39 and 78 (mass ratio) in the tropical Atlantic Ocean (Herbland 1984). The data per cubic metre given in Fig. 7 can be converted into data for the whole lagoon, the volume of which is  $10^{10} \text{ m}^3$  (Lenhardt 1987).

### Discussion

Fig. 7 illustrates the structure and functioning of part of the pelagic ecosystem in the lagoon. However, it is an incomplete model, since heterotrophic production by bacteria and nanoplankton, nekton production and exchanges with the edges and the bottom of the lagoon are missing. Comparison of the various fluxes, however, allows the importance of pelagic animals in the total production and their overall consumption to be assessed.

Zooplankton ingestion, including that of the three size-classes  $> 35 \mu\text{m}$ , which were made up mainly of filter-feeders, accounted for 17% of total particulate organic carbon in April 1985 and 7% in April 1986. If ingestion by other pelagic filter-feeders is regarded as negligible in comparison to that of zooplankton, this result shows that exportation occurs, either down to the bottom, where particles can accumulate or be ingested by benthic animals, or out of the lagoon. If we compare carbon ingestion by zooplankton with living particulate carbon biomass, instead of with total organic carbon, the entire living standing stock would have been consumed in 1985 and 38% in 1986. Part of this living carbon biomass consists of phytoplankton, the production of which accounted for 64% of zooplankton carbon requirements in April 1985 and 140% in April 1986. The large temporal difference may be attributable to the salp bloom in April 1985, the ingestion of which resulted in a decrease in the particulate biomass. Therefore, the data recorded in April 1986 probably represent a more valid reflection of the lagoon ecosystem in a steady state than those in 1985. It would have been difficult to construct a single diagram covering both years because of the successive blooms (Fig. 4); the data are therefore presented separately in Fig. 7. Successive blooms are also evidence of an unstable ecosystem, with primary production occasionally exceeding zooplankton ingestion (April 1986), and occasionally proving inadequate (April 1985). Similar zooplankton swarms have been reported from the neighbouring atoll of Rangiroa by Michel et al. (1971). These authors contend that blooms of *Thalia democratica*, *Creseis virgula*, *Oikopleura rufescens* may result from intense releases of reef organic aggregates during periods of strong swell, a conclusion supported by our observation on the correlation between detritus and wind. Such reef aggregates are readily utilized by their consumers, and are of high energetic value as a result of their content of fatty acids, triglycerides and esters (Gottfried and Roman 1983), in contrast to other marine detritus that can only be ingested in association with bacteria (Gottfried and Roman 1983). These authors consider that zooplankton ingestion could constitute a major conversion process in reef primary production.

Inorganic excretion by zooplankton contributed 32 and 18% to phytoplankton nitrogen requirements and 33 and

17% to phosphorus requirements in 1985 and 1986, respectively. Although the data on nitrogen and phosphorus uptake by phytoplankton are estimated mean annual values, these percentages indicate that other sources of nutrients must be found to enable successful primary productivity, e.g. mineralisation of dissolved organic matter or particulate organic matter by bacteria within the sediment, input from rain, input from the surrounding oceanic waters, or from the base of the atoll through an endo-upwelling process such as that described by Rougerie and Wauthy (1986). Finally, the results of the present study did not reveal any significant organic excretion by zooplankton, most compounds being inorganic (ammonia and phosphate).

The zooplankton production constituted 38% of the  $^{14}\text{C}$  uptake by the phytoplankton in 1985 and 30% in 1986. Provided that  $^{14}\text{C}$  assimilation data correspond only to phytoplankton production before any grazing of its biomass by zooplankton takes place, such percentages would represent the transfer coefficient between primary production and zooplankton production. Both these percentages exceed 10%, a value often used as typical for marine plankton; however, they are not unusual for grazers. Razouls (1975) reported transfer coefficients of 27 to 30%, Parsons et al. (1977) 16 to 42%, Von Martens (1976) 21.4%, Pace et al. (1984) 19 to 42%. Our transfer coefficients for nitrogen were higher: 67 and 43% in April 1985 and 1986, respectively; for phosphorus, we calculated 35 and 21%, respectively. The significance of these coefficients is not clear, since a supposedly direct relationship between productions of phytoplankton and zooplankton is assumed. But, when there is an intermediate trophic link between phyto- and zooplankton, composed of small heterotrophs such as flagellates and ciliates or organic detritus originating from the reef, the gross growth efficiency,  $K_1$ , would provide a better index of ecological efficiency (Pomeroy 1979).  $K_1$  is equal to the product of assimilation efficiency,  $D$ , times net growth efficiency  $K_2$  (Le Borgne 1978), and was calculated using  $D = 0.9$  and the values of  $K_2$  in Table 7, providing values of  $K_1$  of 30% for *Undinula vulgaris* in 1985, and 47% for mesozooplankton and 24% for mixed copepods in 1986, in terms of phosphorus; these values are very similar to the transfer coefficients calculated (in terms of nitrogen,  $K_1$  would equal 56, 67 and 55% in the three cases, respectively).

One of the main features of the plankton of Tikehau atoll is its short turnover times. Charpy-Roubaud et al. (1989) recorded a doubling rate of  $0.24 \text{ h}^{-1}$  for phytoplankton in this lagoon, using a measured carbon:chlorophyll ratio of 50, which they interpret as the result of the combined effects of temperature and kind of primary producers present (Cyanobacteria). Phytoplankton turnover is 5.7 times faster than the turnover time of zooplankton (ca. 1 d: calculated from P:B values in Table 9). This ratio of 5.7 between the two turnovers is consistent with the transfer coefficients for carbon.

The zooplankton turnover in Tikehau is much faster than that of another tropical area, the Gulf of Guinea: 1 d vs 1.6 to 6.7 d (Le Borgne 1982). The short turnover time in Tikehau atoll results from the large amounts of organic

particles present, which form part of the zooplankton diet, as well as from the high temperature (29.5°C) and the specific and larval composition of the zooplankton, all factors known to accelerate growth rates. Compared with Enewetak atoll, Tikehau has a greater pelagic biomass and production. Particulate organic carbon concentrations are 3.4 to 4.8 times greater in Tikehau than in Enewetak and mesozooplankton carbon standing stocks are 1 to 2.5 times greater. Since both atoll lagoons work mainly by regeneration of pelagic or reef organic matter, the difference must arise in the inputs of oxidized nutrients which are used by new primary production. However, the latter does not seem to be sustainable by the surrounding oceanic waters, in which inorganic dissolved nitrogen and phosphorus concentrations in the photic zone are undetectable (Charpy 1985). The recent endo-upwelling concept of Rougerie and Wauthy (1986) could explain the source of new primary production in atolls. This concept involves the upward convection of nutrient-rich deep-ocean water through the coral basement of the atoll, by the geothermal flux originating from the volcanic structure which bears the atoll. The intensity of the convective transport of nutrients is probably linked to the thermal history of the volcano, determining the level of new primary production in the photic layer and, therefore, the success or failure of the entire atoll ecosystem.

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