16. WATER COLUMN NUTRIENT MINERALIZATION BY ZOOPLANKTON AND MICROBIAL POPULATIONS

16.1 Macro- and Microzooplankton

Particulate organic nitrogen and phosphorus in the water column are continuously mineralized to dissolved inorganic forms by macrozooplankton (e.g. copepods, chaetognaths, ctenophores), microzooplankton (e.g. copepod nauplii, tintinnids, ciliates) and other heterotrophic microbes (bacteria, flagellates). Bacteria also have the capability to mineralize and recycle significant amounts of nitrogen and phosphorus from dissolved organic matter. Estimates of water column mineralization fluxes in both temperate (e.g. Harrison et al., 1983; Furnas et al., 1986) and subtropical systems (e.g. Caperon et al., 1979) clearly show that in all but the shallowest of water bodies, water column mineralization processes provide most of the nitrogen and phosphorus required by phytoplankton and pelagic bacteria (e.g. Furnas, 1991). No direct measurements of either water column nitrogen or phosphorus mineralization rates were made during the course of the present study. However, a relevant body of experimental results from work carried out earlier in the GBR, Hawaii and elsewhere, used in combination with estimates of macrozooplankton community biomass, permit a first order estimate of the magnitude of water column nitrogen and phosphorus recycling fluxes to be made.

Tables 33 and 34 summarize measurements of zooplankton community biomass (as dry weight - mg m^{-3}) and standing crop (as dry weight - mg m^{-2}) derived from net collections for the Cairns and Tully boxes. To the extent possible, the biomass data are separated by season and cross-shelf depth band. The collections were made with a 73 µm mesh net and are therefore subject to contamination by large phytoplankton (e.g. certain diatoms, *Trichodesmium*) and amorphous (gelatinous) detrital organic matter. There are at present few equivalent measurements (published or otherwise) of either microzooplankton and heterotrophic microbial biomass for waters in the Cairns and Tully boxes *per se*. (Ayukai, 1992; Hopkinson et al., 1987). Using material from water bottle samples collected off Townsville, Ikeda et al. (1982b) calculated that microzooplankton biomass ranged between 4 and 15 percent (mean 7.7 percent) of macrozooplankton biomass collected with a 202 µm net with a mean of 7.7 percent. On a dry weight basis, the 73 µm mesh nets used in the present study collect 186 percent of the material collected by a 200 µm mesh net (Mitchell, unpubl. data).

On a volume basis, zooplankton biomass varied only slightly with increasing depth across the shelf in both the Cairns and Tully boxes. The difference was most pronounced in the winter (May-September) when the median biomass levels in outer shelf waters of the Cairns box were 20 percent of those measured inshore (25 percent for median values). During the summer, the onshore-offshore differences, as shown by the median values, were less than 1.5-fold. Overall, seasonal differences in mean biomass within depth bands were not significant (2-way ANOVA, $p = 0.14$), though considering the offshore depth band (> 40 m depth alone), there was a quite significant 4-fold difference from inshore biomass levels (t-test). There were insufficient zooplankton biomass data available for the Tully box to make a similar statistical comparison. Inspection of the summary data suggests that seaward of the 10 m isobath, the cross-shelf gradients in biomass was weak, and likely non-significant statistically.

When the biomass values are integrated over depth, clear and statistically significant ($p= 0.003$) cross-shelf increases in zooplankton standing crop (mg dry weight m^{-2}) are clearly apparent. The increase in depth over which biomass estimates were integrated more than compensates for the slight declines in volume-specific biomass. The median summer standing crop on the outer shelf was approximately 50 percent greater than that measured during the winter months. Cross shelf trends in zooplankton standing crop in the Tully box were similar to those observed in the Cairns box.

Table 33. Summary statistics for depth-averaged zooplankton biomass (mg dry weight m^{-3}) in the Cairns and Tully boxes.

	0-10 m	10-20 m	20-30 m	30+ m
Cairns box				
Summer				
Mean	16.6	14.1	11.0	14.0
Std Dev.	8.6	7.0	8.2	14.5
n	12	25	17	17
Median	15.1	13.0	8.1	10.2
Winter				
Mean	16.0	13.6	12.0	3.4
Std Dev.	0.8	8.9	6.7	1.4
n	6	20	11	8
Median	15.8	12.2	11.5	3.8
Tully box				
Summer				
Mean		7.7	10.2	7.0
Std Dev.		10.5	9.2	6.3
n		4	7	20
Median		2.5	9.5	4.1
Winter				
Mean			6.8	5.0
Std Dev.			1.4	2.0
n			3	8
Median			6.1	4.5

Table 34. Summary statistics for areal zooplankton standing crop (mg dry weight m^{-2}) in the Cairns and Tully boxes.

	0-10 m	10-20 m	20-30 m	30+ m
Cairns box				
Summer				
Mean	138.8	172.8	293.2	517.5
Std Dev.	68.1	99.2	237.9	454.7
n	12	12	17	47
Median	127.5	126.8	225.6	395.0
Winter				
Mean	136.2	220.9	297.3	288.4
Std Dev.	4.8	161.7	193.2	134.6
n	6	20	11	28
Median	137.6	199.7	242.5	254.6
Tully Box				
Summer				
Mean		153.4	229.3	381.9
Std Dev.		210.2	182.7	304.8
n		4	7	23
Median		50.4	205.9	228.3
Winter				
Mean			150.0	214.6
Std Dev.			29.7	128.2
n			3	12
Median			134.1	185.9

Chemical analysis of dried zooplankton (Figure 11) showed that the material collected by a 73 µm mesh net had a mean carbon content of 25.3 ± 6.4 (1 S.D., n=85) percent of dry weight and a mean nitrogen composition of 5.7 ± 1.7 (n=85) percent of dry weight. These estimates of zooplankton carbon and nitrogen content fall at the lower end of the composition range normally found for estuarine and oceanic zooplankton (Parsons et al., 1977). It is unclear at this stage whether the low values represent the true organic composition of net zooplankton in the > 73 µm size fraction, or more likely, are due to the dilution of zooplankton carbon and nitrogen content by inorganic salts or carbonate particles trapped in the zooplankton/macro-aggregate matrix of field collections. The material collected by the 73 µm net frequently, if not usually, contained gelatinous organic material. The carbon and nitrogen content of gelatinous zooplankton are well known to be lower than crustacean zooplankton because much of the mass of gelatinous zooplankton is merely seawater with its constituent salts (Kremer, 1975). Zooplankton samples heavily contaminated by phytoplankton, especially diatoms, are also characterized by low percentages of carbon and nitrogen (Furnas, unpubl. data). The phosphorus content of copepod-dominated oceanic zooplankton assemblages usually falls between 0.5 and 1 percent of dry weight (Parsons et al., 1977). Because the carbon and nitrogen contents of GBR zooplankton fall at the low end of the natural range, it is likely that the phosphorus composition of dried zooplankton (not measured to date) would also fall at the low end. For the purpose of this report, we will assume that the phosphorus composition of the zooplankton collected by the 73 µm netting is 0.5 percent of dry weight.

Results from two experimental studies (Smith et al., 1981; Ikeda et al., 1982 a,b) can be applied to the zooplankton community standing crop measurements to estimate macro- and micro-zooplankton nitrogen and phosphorus mineralization fluxes. Ikeda et.al. (1982a) quantified mass-dependent nitrogen and phosphorus excretion rates for a wide range of zooplankton

species or groups. Macrozooplankton assemblages throughout the GBR are numerically dominated by copepods (Ikeda et al., 1982b; Liston, 1990), which also dominate estimates of community biomass. The relative homogeneity of zooplankton community structure throughout the GBR (Liston, 1990) allows locally measured zooplankton rate processes to be extrapolated to other, oceanographically similar areas with some confidence.

Tables 35 and 36 present mean seasonal and annual estimates of the volumetric and area-weighted shelf-scale nitrogen and phosphorus excretion rates for macro- and microzooplankton populations using the biomass-specific excretion rate (1.35 μmol N mg DW^{-1} day^{-1}) calculated by Ikeda et al. (1982b) for macrozooplankton. Microzooplankton standing crop estimates were calculated from the macrozooplankton standing crop estimates as 7.7 percent of macrozooplankton dry weight. Ikeda et al. considered microzooplankton to consist of larger ciliates (e.g. tintinnids) and larval or juvenile stages of macrozooplankters (e.g. copepod nauplii and copepodite stages). The contribution of heterotrophic microflagellates and bacteria are not considered in Ikeda et al.'s estimates of microzooplankton biomass and excretion rates. Their mineralization rates were experimentally measured at 27.5°C, then converted to mean seasonal rates at temperatures of 28° and 22°C using a Q_{10} value of 2.53 (Q_{10} is the relative difference between two metabolic rates for a 10°C change in temperature in the normal temperature range for growth). Biomass-specific nitrogen and phosphorus excretion rates of microzooplankton during the summer are approximately 1.7-fold greater than during the winter months. In the case of macrozooplankton, Ikeda et al., calculated a 1.9-fold seasonal difference in the biomass specific excretion rate for nitrogen and 3.7-fold difference for phosphorus.

Based on the work of Szyper et al. (1976), Smith et al. (1981) calculated biomass-specific nitrogen and phosphorus excretion rates for Kaneohe Bay macrozooplankton of 1.78 μmol N mg DW^{-1} day^{-1} and 0.11 μmol P mg DW^{-1} day^{-1}. Verity (1985) calculated a biomass weighted population ammonium excretion rate of 1.73 μmol NH_4 mg DW^{-1} day^{-1} for Sargasso Sea crustacean zooplankton. These estimates lie slightly above the seasonal range of excretion rates estimated by Ikeda et al. (1982b) for GBR zooplankton. The measurement or estimation of zooplankton community excretion rates is a difficult process, subject to a number of experimental artefacts and procedural problems (Ikeda, 1977; Takahashi and Ikeda, 1975), so the discrepancy between the estimates is not large or surprising. The general agreement between estimates of dry-weight specific nitrogen and phosphorus rates between studies indicates that the rates taken from Ikeda et al. are reasonable estimators of community excretion rates, particularly as the dry weights used are likely to be affected by some degree of dilution with detrital organic matter and phytoplankton.

Based on the available data for zooplankton standing crop in the Cairns box, annual mineralization fluxes of NH_4-N and PO_4 were estimated to be 870 x 10^3 and 59.9 x 10^3 kmol, respectively (Table 35). The respective estimates for annual zooplankton N and P mineralization fluxes in the Tully box are 647 x 10^3 and 37.6 x 10^3 kmol (Table 36). Microzooplankton were estimated to have contributed approximately 10 percent of the nitrogen mineralized and 17 percent of the phosphorus. For macrozooplankton, 72 percent of the nitrogen mineralization and 83 percent of the estimated phosphorus mineralization occurs during the summer (October-April) season. In the case of microzooplankton, we calculate that 70 percent of both the nitrogen and phosphorus mineralization occurs during the summer.

Table 35. Estimates of water column nitrogen and phosphorus mineralization by macro- and microzooplankton in the Cairns box.

Depth band	Zooplankton standing crop mg m^{-3}	Volume m^3	Summer N excretion rate µmol mg^{-1} day^{-1}	Days	Total excretion kmol	Winter N excretion rate µmol mg^{-1} day^{-1}	Days d	Total excretion kmol
Nitrogen								
0-10 m	14.9	1.9E+09	1.35	212	8078	0.7	153	3023
10-20 m	12.7	1.09E+10	1.35	212	39720	0.7	153	14864
20-30 m	8.0	2E+10	1.35	212	45550	0.7	153	17046
30 + m	10.1	1.64E+11	1.35	212	473117	0.7	153	177047
			Seasonal Totals		566465			211979
						Annual N Mineralized		**778445**
	Microzooplankton							
0-10 m	1.14	1.9E+09	2.00	212	921	1.15	153	382
10-20 m	0.98	1.09E+10	2.00	212	4531	1.15	153	1880
20-30 m	0.61	2E+10	2.00	212	5196	1.15	153	2156
30 + m	0.78	1.64E+11	2.00	212	53970	1.15	153	22396
			Seasonal Totals		64619			26815
Phosphorus						**Annual N Mineralized**		**91434**
0-10 m	14.9	1.9E+09	0.08	212	503	0.023	153	99
10-20 m	12.7	1.09E+10	0.08	212	2471	0.023	153	488
20-30 m	8.0	2E+10	0.08	212	2834	0.023	153	560
30 + m	10.1	1.64E+11	0.08	212	29438	0.023	153	5817
			Seasonal Totals		35247			6965
						Annual P Mineralized		**42212**
	Microzooplankton							
0-10 m	1.14	1.9E+09	0.19	212	85	0.108	153	36
10-20 m	0.98	1.09E+10	0.19	212	419	0.108	153	177
20-30 m	0.61	2E+10	0.19	212	481	0.108	153	203
30 + m	0.78	1.64E+11	0.19	212	4992	0.108	153	2103
			Seasonal Totals		5977			2518
						Annual P Mineralized		**8496**

Table 36. Estimates of water column nitrogen and phosphorus mineralization by macro- and microzooplankton in the Tully box.

Depth band	Zooplankton standing crop mg m^{-3}	Volume m^{3}	Summer N excretion rate µmol mg^{-1} day^{-1}	Days	Total excretion kmol	Winter N excretion rate µmol mg^{-1} day^{-1}	Days d	Total excretion kmol
Nitrogen								
0-10 m	2.7	1.5E+09	1.35	212	1139	0.7	153	426
10-20 m	2.7	8.5E+09	1.35	212	6453	0.7	153	2415
20-30 m	9.5	3.1E+10	1.35	212	84724	0.7	153	31705
30 + m	4.2	2.71E+11	1.35	212	329178	0.7	153	123183
			Seasonal Totals		421493			157729
						Annual N Mineralized		**579222**
	Microzooplankton							
0-10 m	0.20	1.5E+09	2.00	212	130	1.15	153	54
10-20 m	0.20	8.5E+09	2.00	212	736	1.15	153	305
20-30 m	0.74	3.1E+10	2.00	212	9665	1.15	153	4011
30 + m	0.33	2.71E+11	2.00	212	37551	1.15	153	15583
			Seasonal Totals		48081			19953
						Annual N Mineralized		**68034**
Phosphorus								
0-10 m	2.7	1.5E+09	0.08	212	71	0.023	153	14
10-20 m	2.7	8.5E+09	0.08	212	402	0.023	153	79
20-30 m	9.5	3.1E+10	0.08	212	5272	0.023	153	1042
30 + m	4.2	2.71E+11	0.08	212	20482	0.023	153	4047
			Seasonal Totals		26226			5183
						Annual P Mineralized		**31409**
	Microzooplankton							
0-10 m	0.20	1.5E+09	0.19	212	12	0.108	153	5
10-20 m	0.20	8.5E+09	0.19	212	68	0.108	153	29
20-30 m	0.74	3.1E+10	0.19	212	894	0.108	153	377
30 + m	0.33	2.71E+11	0.19	212	3473	0.108	153	1463
			Seasonal Totals		4448			1874
						Annual P Mineralized		**6321**