Micro-grazer biomass, composition and distribution across prey resource and dissolved oxygen gradients in the far eastern tropical north Paci“c Ocean

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a r t i c l e i n f o

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The ecology of micro-grazers (M_g) was investigated across prey and dissolved oxygen (DO) gradients in the eastern tropical north Paci“c Ocean (ETNP) during October…November 2007. Surface (o 200 m) chlorophyll a (Chl a) across a 1700 km north…south transect ranged between the seasonal average of 0.2 mg Chl a L^{-1} to 1.8 mg Chl a L^{-1} in an extensive Chl a-rich patch in the center of the transect.

To determine what environmental and biological variables in”uence M_g community composition, vertical distribution and biomass concentration, discrete sampling depths were chosen based on chemical and biological signatures, rather than arbitrary, yet consistent, depths. Our de“ned biological and chemical sampling regimes across all stations were surface waters, the pigment maximum (determined from CTD ”uorescence), and, because a de“ning feature of this region is the vast extent of the OMZ, both vertically and horizontally, we sampled the upper oxycline (UO; the depth near surface where the decrease in DO concentration is greatest), the middle of the OMZ, and the lower oxycline (LO; depth below OMZ where DO concentrations increase). The depths of the biological and chemical features were determined from vertical pro“les using the Sea-Bird Electronics 911plus CTD pro“ler described above. For each discrete location and depth, duplicate samples of 200 ml were taken for M_g analysis (described in Section 2.4).

2.3. Micro-grazer grazing experiments

Two M_g grazing experiments were conducted to preliminarily explore the degree to which grazing regulates the accumulation of phytoplankton production in two contrasting regions in the ETNP (Sta. 1, core of the eastern Paci“c warm pool, and Sta. 8, mean position of the Costa Rica Dome). Speci“c growth rate (μ, d^{-1}) and speci“c M_g grazing rate (g, d^{-1}) for the aggregate Chl a community were estimated simultaneously using the seawater dilution technique (e.g., Landry et al., 1995b). Seawater was collected in 10 L Niskin bottles from depths in the upper-mixed layer corresponding to 50% surface PAR. Particle-free diluent water was made by gently draining the entire contents of two 10 L Niskin bottles through silicone tubing into a 20 L polycarbonate carboy. This pooled water was then gravity-“ltered through a 0.2 μm Pall Gelman pleated capsule “lter into a second 20 L carboy. Whole seawater for our dilution experiments was collected from the same CTD cast as diluent water. Whole seawater was very gently drained through silicone tubing encased with 200 μm mesh to remove abundant mesozooplankton and dispensed into a 20 L carboy.

Measured volumes of particle-free seawater were transferred into a series of 1.125 L polycarbonate bottles. Whole seawater was gently siphoned from the whole seawater carboy into the bottles containing particle-free water. Although large, rapidly-sinking phytoplankton were seemingly rare, the whole seawater was kept well-mixed by very gentle stirring with a polyethylene plunger. Combinations of particle-free to whole seawater were made to achieve target dilutions in duplicate of 20%, 40%, 60%, 80% and 100% whole seawater. Experimental bottles were amended with nutrients (5 μM NH_4^+ and 0.31 μM PO_4^{3-}) in order to remove potential bias from enhanced phytoplankton growth rate due to variable M_g nutrient excretion across dilution treatments. An additional set of 100% whole seawater bottles were incubated without nutrient-addition to correct for this potential bias (see below). Quadruplicate samples of whole seawater were taken at random intervals from the whole seawater carboy during experimental set-up for analysis of initial Chl a (100 ml to 500 ml), and duplicate samples were drawn for analysis of inorganic nutrient concentration (20 ml) and M_g abundance and biomass (200 ml each).

Experimental dilution bottles were screened with a single layer of neutral density screening to mimic in situ light levels at the depth of collection (50% surface PAR). Bottles were then

In general, M_g biomass increased between the northern (Sta. 1) and

Table 2
Micro-grazer functional group biomass across the ETNP. Biomass is expressed as mg C L $^{-1}$. Depths are expressed as both meters and the biochemical regime (see Section 2.2). S: surface; PM: pigment maximum; UO: upper oxycline; OMZ: oxygen minimum zone; LO: lower oxycline: HNF: heterotrophic nano"agellates; Tint: tintin nid ciliates; Holo: holotrich ciliates; Gymno: Gymnodinium-like; Gyro: Gyrodinium-like; Sarco: Sarcodines; ND: no data.

Station/depths	HNF	Micro-grazer biomass (mg C L $^{-1}$)										
		Ciliates					Heterotrophic dino"agellates					
		Spirotrichs										
		o 20 mm	20…40mm	4 40 mm	Tint.	Holo.	Gymno.	Gyro.	Other	Sarco.	Nauplii	Total
1												
S	1.3	0.5	1.1	1.9	0.1	0.1	2.1	5.1	0.1	…	0.2	12.4
PM-30 m	1.6	0.3	0.5	1.1	…	0.2	0.8	1.3	o 0.1	1.5	1.1	8.6
UO-60 m	0.6	0.2	0.7	0.2	…	0.3	1.0	2.5	o 0.1	0.2	…	5.6
OMZ-200 m	0.5	o 0.1	…	…	…	…	0.1	0.2	o 0.1	…	…	0.8
LO-1100 m	0.2	…	…	…	…	…	0.1	…	…	…	…	0.3
2												
S	9.2	0.4	1.0	0.7	…	…	3.1	1.1	0.6	…	…	16.1
PM-30 m	2.8	0.3	1.3	2.7	…	…	3.0	2.5	0.7	…	0.9	14.0
UO-40 m	0.7	0.6	0.9	0.5	0.1	…	2.5	2.2	o 0.1	0.4	0.4	8.1
OMZ-500 m	0.1	…	o 0.1	…	…	0.1	0.1	o 0.1	…	…	…	0.4
LO-1000 m	o 0.1	…	…	…	…	…	0.1	…	…	…	…	0.2
3												
ND												
4												
S	1.7	0.4	0.5	1.2	o 0.1	…	4.2	1.4	…	0.6	3.9	13.8
PM-18 m	1.2	0.5	0.6	0.8	o 0.1	0.1	3.7	1.0	o 0.1	1.5	…	9.4
UO-24 m	0.7	0.7	0.4	0.8	…	o 0.1	2.5	0.8	0.1	o 0.1	0.5	6.5
OMZ-80 m	0.2	o 0.1	0.1	…	…	o 0.1	0.4	0.1	…	…	…	0.8
LO-200 m	0.2	o 0.1	0.1	0.2	…	o 0.1	0.6	o 0.1	o 0.1	…	…	1.3
5												
S	10.2	1.4	2.6	5.0	o 0.1	…	3.6	3.5	1.9	1.3	…	29.6
PM-20 m	10.8	1.7	1.7	9.8	0.4	…	5.1	2.9	0.1	0.7	3.4	36.6
UO-50 m	0.5	0.4	0.4	1.1	o 0.1	…	2.2	1.2	o 0.1	0.1	…	5.8
OMZ-200 m	0.2	o 0.1	…	…	o 0.1	0.1	0.4	0.7	o 0.1	…	0.2	1.5
LO-1000 m	0.1	…	o 0.1	…	…	…	0.1	o 0.1	…	…	…	0.3
6												
S	2.4	0.3	16.4	2.1	…	…	4.9	3.9	0.1	…	1.5	31.4
UO-24 m	2.0	1.9	2.4	4.0	…	0.1	6.8	2.1	0.1	…	2.3	21.7
PM-30 m	0.8	0.8	1.7	0.6	0.1	0.1	1.7	1.2	…	0.1	0.7	7.9
OMZ-200 m	0.3	o 0.1	o 0.1	…	…	o 0.1	0.4	o 0.1	…	o 0.1	…	0.7
LO-ND												
7												
S	2.1	0.7	0.8	0.5	o 0.1	…	7.1	0.6	0.2	…	3.9	15.8
PM-30 m	2.7	0.8	1.8	0.3	…	…	4.2	1.6	o 0.1	o 0.1	…	11.3
UO-40 m	1.4	0.9	1.5	0.4	…	…	2.3	0.6	…	…	1.0	8.0
OMZ-200 m	0.3	0.1	0.1	…	…	…	0.6	o 0.1	…	…	…	1.2
LO-ND												
8												
S	2.6	0.6	1.0	1.3	o 0.1	0.1	7.9	1.4	o 0.1	0.1	3.1	18.0
PM-30 m	6.8	2.1	3.6	0.5	0.2	…	14.3	3.1	0.1	0.5	1.8	32.9
UO-35 m	3.0	1.0	2.2	0.1	0.1	0.1	12.4	1.4	…	0.1	…	20.4
OMZ-355 m	0.2	0.1	o 0.1	0.6	…	0.3	0.7	0.9	…	0.2	…	2.9
LO-1200 m	0.1	o 0.1	0.1	…	…	…	0.1	0.2	…	…	…	0.5

and salinity against M_g biomass from all depths at all locations, Chl a concentration alone accounted for 68% of the M_g biomass variability. Chl a concentration combined with temperature was the best predictor of M_g biomass, accounting for 83% of M_g variability.

3.3. Micro-grazer grazing

The environmental conditions found at the M_g grazing experiment stations varied in some aspects, yet were similar in others (Table 3; Fig. 6). Surface seawater temperature was 1 1C warmer at Sta. 1 than at Sta. 8, while surface Chl a concentrations at both Stas. were 0.2 mg Chl a L $^{-1}$ (Table 3), despite observed seasonal differences in productivity (Pennington et al., 2006). Inorganic macronutrient concentrations were higher at Sta. 8 compared to those found at Sta. 1 (Table 3). The pigment maximum occurred near the base of the UO at both stations (Fig. 6). At Sta. 1, there was a second deeper pigment maximum (ca. 60…70 m) associated with a sub-surface accumulation of Rhizosolenia spp. diatoms. In addition, the depth of the UO was shallower (20 m) at Sta. 8.

Although the phytoplankton community growth rate was on average higher at Sta. 1 (0.72 d $^{-1}$) than at Sta. 8 (0.47 d $^{-1}$), these rate measurements were not statistically different (P4 0.05, paired t-test). The phytoplankton community at Sta. 1 did, however, show evidence of nutrient limitation. The results from the Sta. 1 experiment showed that the aggregate phytoplankton

Table 3
Micro-grazer grazing experiment dates, locations, depth of water collection, surface temperatures, and initial biological and environmental parameters determined from whole seawater during experimental setup. The depths correspond to 50% surface irradiance. Sta: station.

Sta	Date	Latitude (N)	Longitude (W)	Depth (m)	Temp (°C)	Chl a (mg L^{-1})	Nutrients (mM)			
							Nitrate	Ammonium	Phosphate	Silicic acid
1	11/01/07	13°10.94′	105°11.13′	9	28.0	0.21 ± 0.02	0.0	0.53	0.26	1.1
8	11/08/07	8°159.85′	90°10.06′	9	27.0	0.27 ± 0.03	5.4	1.08	0.70	3.1

Fig. 6. Hydrographic and biological vertical profiles from M_g grazing experiment stations. Dissolved oxygen concentrations below 20 mmol kg^{-1} are denoted as grey circles.

environments (Sherr and Sherr, 1988; Calbet and Landry, 2004). This linkage is especially strong in oligotrophic regions where microbial processes dominate, and where perturbations to the equilibrium status of the physical and chemical environment are, compared to coastal environments, infrequent, thus preventing large variation in the concentration and size structure of the phytoplankton community (e.g., open subarctic Pacific Ocean). Others have reported that M_g are the dominant herbivores in the central equatorial Pacific (Landry et al., 1995a; Verity et al., 1996) and in the western edge of the ETNP (Yang et al., 2004). Less is known, however, about M_g community structure and the role of M_g in regulating surface carbon dynamics in the far eastern ETNP, where hydrographic and biological variability is comparatively more substantial than other equatorial regions (Fiedler and Talley,

waters, are higher than have been reported in the tropical Paci“c (reviewed in Yang et al., 2004). For example, Yang et al. (2004) observed micro-grazer biomass as high as 11.3 $\mu g\ C\ L^{-1}$ at the western edge of the ETNP, whereas we observed M_g biomass as high as 36 $\mu g\ C\ L^{-1}$ in the eastern ETNP. In an early study in the eastern tropical Paci“c, high biomass (estimated as biovolume) of M_g was observed at stations near our own (Beers and Stewart, 1971

other equally, if not more plausible, explanations for low M_g growth rates include low prey concentrations (0.2 mg Chl a at both stations), poor prey nutritional quality (phytoplankton at Sta. 1 were nutrient limited), or intra-bottle predation. The latter may explain the negative growth rate of HNF in both experiments, as they are likely prey for both ciliates and heterotrophic dino"agellates.

5. Conclusions

A primary "nding from this research was that M_g biomass was quite high relative to estimates from other regions of the equatorial Paci"c, even at locations that were oligotrophic in nature at the time of sampling. The bulk of the M_g biomass was comprised of HNF, small gymnodinoid dino"agellates, and non-loricate oligotrich ciliates. These M_g functional groups graze primarily on bacteria, pico- and nanoeukaryotic phytoplankton. Large, diatom-consuming dino"agellates in the genera Gyrodinium and Protoperidinium were also present in surface waters