Journal of Marine Research, 44, 795–813, 1986

Grazer control of the fine-scale distribution of phytoplankton in warm-core Gulf Stream rings

by M. R. Roman,[1] C. S. Yentsch,[2] A. L. Gauzens[1] and D. A. Phinney[2]

ABSTRACT

We measured *in situ* rates of primary production, zooplankton grazing and the fine-scale distribution of zooplankton abundance, along with continuous observations of salinity, temperature and fluorescence in vertical profiles of two warm-core Gulf Stream rings and a station in the northern Sargasso Sea. A subsurface chlorophyll maximum was located within the pycnocline at all nineteen of the pump stations. In the majority of pump profiles, subsurface chlorophyll maxima coincided with maxima in particulate organic carbon and ATP. However, neither zooplankton biomass or numerical abundance were related to chlorophyll concentrations. Maxima in zooplankton biomass and grazing generally occurred at depths of highest primary production. Zooplankton grazing and biomass were more closely coupled to phytoplankton production per unit chlorophyll (*P*-chl) rather than production per unit volume (absolute production). Our results suggest that after the seasonal thermocline is established, phytoplankton removal by zooplankton is greatest in the upper water column where *P*-chl is higher. This phytoplankton removal by zooplankton limits the amount of absolute primary production in the upper water column and results in a subsurface maximum of absolute production at depths where grazing pressure is reduced. In contrast, the subsurface chlorophyll maximum, likely formed from both production at depth and sinking, does not appear to be a site of enhanced zooplankton grazing activity.

1. Introduction

The vertical distribution of phytoplankton and zooplankton in the sea is usually heterogeneous, being concentrated in discrete layers. Phytoplankton may accumulate at density interfaces both from reduced sinking rates (Steele and Yentsch, 1960; Smayda, 1970) as well as from enhanced growth rates (e.g., Anderson, 1972; Holligan, *et al.,* 1984b). In oceanic waters maxima in phytoplankton production and biomass may coincide (e.g., Cox *et al.,* 1982; Hitchcock *et al.,* 1985). However, it is more typical that, after the seasonal thermocline is established, phytoplankton production is maximal near the surface and phytoplankton biomass (as measured by chlorophyll-*a*) is highest at the base of the mixed layer or within the pycnocline (e.g., Venrick *et al.,* 1973; Ortner *et al.,* 1980; Herman and Platt, 1983).

1. Horn Point Laboratories, University of Maryland, P.O. Box 775, Cambridge, Maryland, 21613, U.S.A.

2. Bigelow Laboratory for Ocean Sciences, McKown Point, West Boothbay Harbor, Maine, 04575, U.S.A.

This observed spatial separation of phytoplankton production and standing crop may be an artifact of using chlorophyll as an index of phytoplankton biomass. Both inter- and intra-species photoadaptation can occur whereby phytoplankton grown under low light often contain more chlorophyll per cell than phytoplankton grown under high light conditions (e.g., Bannister and Laws, 1980; Falkowski, 1980). Thus, it has been found in waters off Southern California that phytoplankton biomass maxima derived from cell counts can be shallower than maxima of chlorophyll (Beers *et al.*, 1975). This phenomenon is not universal however, as subsurface chlorophyll maxima have co-occurred with maxima in phytoplankton cell counts (e.g. Chester, 1978; Holligan *et al.*, 1984a) and biomass measurements such as ATP (Ortner *et al.*, 1980; Cullen and Eppley, 1981; Nelson *et al.*, 1985) and particulate organic carbon (Holligan *et al.*, 1984b; Cullen and Eppley, 1981; Nelson *et al.*, 1985).

The role of zooplankton grazing in determining the vertical distribution of phytoplankton biomass has been inferred from the spatial coherence of zooplankton biomass with chlorophyll and primary production measurements. Often these comparisons have been made from discrete water samples which have been separated in time from zooplankton tows taken over relatively long intervals. With the improved spatial/temporal resolution accessible by high volume pumping systems (e.g. Beers *et al.*, 1967; Holligan and Harbour, 1977; Herman *et al.*, 1984) and electronic zooplankton counters, (e.g. Boyd, 1973; Herman and Dauphinee, 1980) it has been generally observed that zooplankton biomass maxima occur at depths of maximum primary production rather than chlorophyll concentration (e.g. Herman *et al.*, 1981; Fiedler, 1983; Herman, 1984). Often in these studies primary production has been inferred from light distributions and P/I curves (Herman and Platt, 1983; Herman, 1984) and zooplankton grazing has been extrapolated from laboratory grazing measurements. This latter approach may not be appropriate as zooplankton (primarily copepods) exhibit both functional and developmental feeding responses which are affected by the species composition and biochemical constitution of their phytoplankton prey (e.g., Conover, 1981).

In this paper we examine the role of zooplankton grazing in controlling the vertical distribution of phytoplankton biomass. We present data on the fine-scale distribution of zooplankton biomass and the numerical abundance of copepod developmental groups (nauplii, copepodites, adults) collected with continuous measurements of salinity, temperature and fluorescence. We compare these fluorescence and zooplankton profiles to *in situ* measurements of both primary production and zooplankton grazing rates to examine how primary production and zooplankton grazing are related in two warm-core Gulf stream rings and at a station in the northern Sargasso Sea.

2. Methods

Seawater from the surface 110 m was continuously sampled with a large volume pumping system which delivered water to shipboard zooplankton nets and sensors for

conductivity, temperature and fluorescence (Phinney *et al.*, 1984). The intake of a 7.5 cm-diameter flexible hose was secured to a rosette with CTD and lowered to the desired depth. The Flygt Model B205 submersible pump was deployed just below the surface. Shipboard, the pumped seawater (200 liters min^{-1}) was split so that 160 liters min^{-1} flowed into 64 μm-mesh zooplankton nets and the remaining water flowed into a bubble trap which contained an Inter Ocean Model 195R conductivity transducer and Fenwal GC3218 thermistor. The output from these sensors was logged every 10 seconds on a microcomputer. A pump inside the bubble trap pumped seawater (10 liters min^{-1}) to Turner Design Fluorometers (for chlorophyll; excitation filter = CS5-60, emission filter = CS2-64, reference filter = CS3-66, for fucoxanthin; excitation filter = CS4-64, emission filter = CS2-64, reference filter = CS3-66).

The CTD was lowered to 110 m and after the entire system had been allowed to flush (several minutes), sampling began by raising the rosette 1 m every 30 seconds. Depth corrections from the CTD were applied to the sensor readings to compensate for the residence time through the pumping system. Discrete seawater samples for chlorophyll analysis were collected from the fluorometer outflow for calibration of the instrument.

Zooplankton were collected from integrated depth intervals (100-70 m, 70-40 m, 40-20 m, 20-10 m, 10-5 m, 5-0 m June samples; 110-70 m, 70-50 m, 50-30 m, 30-10 m, 10-0 m August samples) by switching the outflow hose to 64 μm-mesh zooplankton nets which were submerged in garbage cans to avoid extrusion of the zooplankton through the mesh. Water filtered per depth interval ranged from 0.4 to 3.5 m^3. Zooplankton were preserved in 5% formalin buffered with sodium borate. Biomass estimates of zooplankton were determined by weighing an aliqout of the preserved sample and assuming that 32% of the dry weight was carbon (Roman *et al.*, 1985).

Zooplankton avoidance of the pumping system was assessed by comparing pump collected samples to zooplankton samples collected with a 0.25 m^2 MOCNESS (Wiebe *et al.*, 1985b). We compared the integrated zooplankton biomass (mgC m^{-2}) in the surface 100 m for 6 daytime samples collected by both methods in the same water mass (as indicated by the temperature structure). Using a paired-sample *t*-test, we found no significant ($P > 0.05$) differences in zooplankton biomass (>64 μm) caught with the two systems. Similarly, no significant differences ($P > 0.05$, *t*-test, $N = 8$) between samples collected by the two methods were found for any of the major zooplankton groups (copepod nauplii, calanoid copepods, cyclopoid copepods) or for total zooplankton abundance. Larger zooplankton such as chaetognaths, decapod crustaceans, amphipods and large calanoid copepods (e.g. *Rhincalanus* spp. and *Eucalanus* spp.) were more abundant in the net-collected samples. However, we cannot attribute this difference to avoidance because the small volumes of water sampled by the pump (0.4 to 3.5 m^3) were not sufficient to assess the abundance of these larger and usually less abundant (1–5.100 m^{-3}) zooplankton.

Primary production and zooplankton grazing were estimated from the uptake of ^{14}C in short-term *in situ* incubations (Roman and Rublee, 1981). Plexiglas 5-liter grazing

chambers (General Oceanics) with 64 μm-mesh covering the bottom opening were lowered to the desired sampling depths (100, 60, 36, 22, 8 and 3% surface light levels) and allowed to equilibrate for one minute after which a messenger triggered the close of the bottle and release of radioactive tracers ($NaH^{14}CO_3$, 50 μCi l^{-1}) into the chambers. If zooplankton densities were low (<5 liter^{-1}) the chambers were lowered past the desired sampling depth so that zooplankton could be gently concentrated by raising the chambers several meters prior to closing and release of the isotopes. Niskin bottles, similar in design to the *in situ* grazing chambers used, have been shown to collect a representative sample of the micro- and mesozooplankton community as compared to net-collected samples (Houde and Lovdal, 1985). Large, fast moving macrozooplankton >2 mm were not usually collected in the chambers. The grazing chambers were incubated on the hydrowire for 1 h after which they were retrieved and the zooplankton collected on nested 333 μm and 64 μm sieves. The zooplankton were rinsed onto preweighed filters, dried, detritus and phytoplankton removed with a sable brush, the filters weighed and the weight-specific dpm's of the isotope measured. The labelled particulate matter in the chambers (<64 μm) was measured on 0.2 μm and 3.0 μm Nuclepore Membrafil filters. Time-0 controls indicated that adsorption of ^{14}C to filters, particulate matter and zooplankton was less than 10% of experimental values.

Pump profiles were conducted on a transect across warm core Gulf Stream Ring 82-B in June, in rings 82-B, 82-E and the Sargasso Sea in August (Fig. 1). General hydrographic characteristics of warm-core rings are given by Joyce and Wiebe (1983).

3. Results

a. Subsurface chlorophyll maximum. There was a subsurface chlorophyll maximum present at all nineteen of the pump stations (Table 1). The ratio of chlorophyll in the subsurface maximum to surface chlorophyll values ranged from 2.3 to 10.4. Although the depth of the chlorophyll maximum layer was variable, it was usually located within the pycnocline at 26.16 sigma-*t* (sd = 0.32, Table 1). Based on measurements of downwelling irradiance (Phinney *et al.*, 1984) the percent of surface light reaching the subsurface chlorophyll maximum was 1.7% in WCR 82-B in June, 3.2% in 82B in August, 0.4% in the Sargasso Sea in August and 2.2% in WCR 82-E in August.

Since we are interested in chlorophyll as an indicator of food for zooplankton, it is important that we establish whether the chlorophyll maximum represents a plant biomass maximum. In fifteen of the nineteen pump stations water was collected during profiling from discrete depths using the CTD/rosette (General Oceanics, Go-Flo bottles) to which the pump hose was attached. As alternate estimates of phytoplankton biomass, we use measures of particulate ATP (Karl and Holm-Hansen, 1976) and particulate organic carbon (Perkin-Elmer Elemental analyzer). Neither of these measurements are specific for phytoplankton. ATP (0.8 μm–153 μm) measurements

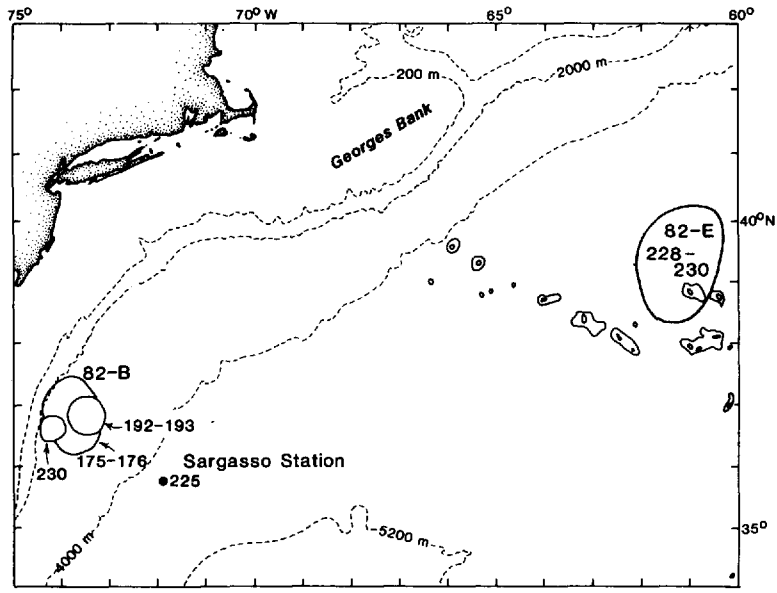

Figure 1. Sampling area showing positions of warm-core Gulf Stream ring 82-B in June and 82-B, 82-E and Sargasso Sea station in August.

include bacteria, phytoplankton and microzooplankton, whereas particulate carbon (0.7 μm) ⟨153 μm) estimates include bacteria, phytoplankton, microzooplankton and detritus. However, following the rationale of Cullen and Eppley (1981), each of the biomass estimates should increase as a monotonic function of actual phytoplankton abundance with noise contributed by the other aforementioned seston components. Because the data are not normally distributed, we have ranked the variables in the profiles and used Spearman's correlation procedure (Zar, 1974). Both ATP ($r_s = 0.539$; $r_{0.05} = 0.234$; $N = 73$) and particulate carbon ($r_s = 0.449$; $r_{0.05} = 0.224$; $N = 79$) were significantly ($p < 0.05$) correlated with pump derived chlorophyll estimates. In the majority of the pump profiles, the discrete depth estimates of maximum chlorophyll concentration coincided with the maximum concentrations of ATP (80%) and particulate organic carbon (60%) (Fig. 2).

b. Vertical distribution of zooplankton abundance and chlorophyll. Zooplankton collections represent integrated measurements over discrete depth intervals whereas chlorophyll measurements are continuous over the pump profiles. In comparing the distributions of chlorophyll and zooplankton we have used a trapezoidal integration to estimate the average chlorophyll concentration over the depth interval sampled for zooplankton (Table 2) and ranked the concentrations of chlorophyll and zooplankton for the Spearman correlation analysis. Neither estimates of zooplankton biomass ($r_s = 0.052$; $r_{0.05} = 0.197$; $N = 102$) or abundance ($r_s = 0.136$; $r_{0.05} = 0.197$; $N = 102$)

Table 1. Station locations and dates for chlorophyll and zooplankton vertical profiles. Surface and chlorophyll maximum values are given with the depth, sigma-*t* at chlorophyll maximum, and ratio of chlorophyll in the subsurface maximum to surface chlorophyll.

Station	Date	Time	Latitude	Longitude	Surf. chl	Max. chl	Depth (m)	Sigma-*t*	Chl max surf. chl
82-B transect 13	6/23	0810	37° 20.7′	72° 57.1′	0.539	1.227	29	25.983	2.276
14	6/23	1235	37° 08.2′	73° 0.92′	0.549	3.008	39	25.378	5.479
15	6/23	1825	37° 00.0′	73° 24.0′	0.383	1.798	34	26.578	4.694
16	6/24	0634	36° 36.0′	74° 36.5′	0.277	1.347	35	26.762	4.863
17	6/24	1040	36° 4.24′	74° 24.2′	0.282	1.823	34	26.180	6.464
18	6/24	1616	36° 50.1′	74° 05.2′	0.660	2.164	21	—	3.279
20	6/25	0622	36° 56.9′	73° 35.4′	0.431	1.401	25	26.585	3.251
22	6/26	0843	36° 45.4′	73° 00.0′	0.637	2.776	27	26.131	4.358
82-B	8/9	1220	36° 37.4′	73° 49.1′	0.248	1.385	41	26.430	5.585
82-B	8/12	1200	36° 55.0′	73° 42.2′	0.152	1.070	42	25.586	7.040
Sargasso Sea	8/13	0643	35° 44.3′	71° 51.5′	0.113	0.670	114	26.090	5.929
82-E	8/16	1028	40° 17.2′	61° 04.3′	0.320	1.932	47	26.229	6.038
82-E transect 1	8/18	0600	40° 50.2′	61° 49.6′	0.211	0.764	42	25.927	3.621
2	8/18	1104	40° 34.2′	61° 34.3′	0.300	1.816	39	25.799	6.053
3	8/18	1604	40° 25.0′	61° 27.1′	0.268	2.782	51	26.447	10.381
4	8/19	0713	39° 42.5′	60° 53.9′	0.209	0.987	59	26.266	4.722
5	8/19	1349	39° 46.9′	61° 08.9′	0.268	1.842	40	25.966	6.873
6	8/19	1756	39° 51.7′	61° 15.2′	0.322	1.013	41	26.029	3.146
7	8/20	0838	40° 17.7′	61° 20.2′	0.304	1.218	50	26.499	4.007

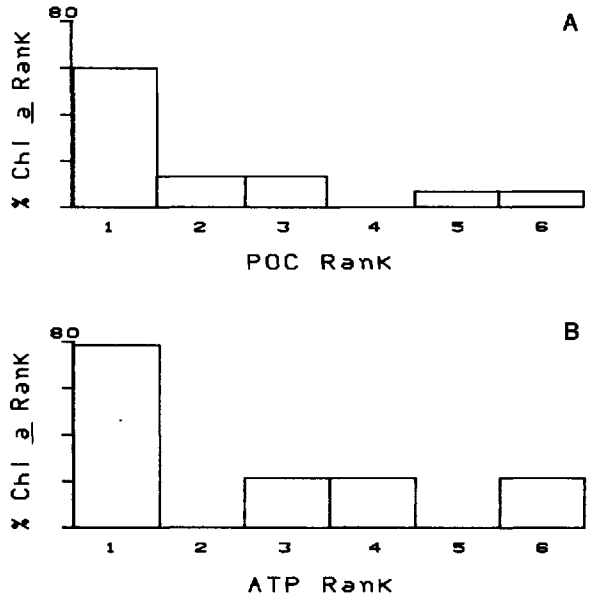

Figure 2. The relationship between chlorophyll and particulate organic carbon (A) and particulate ATP (B) expressed as the frequency of occurrence of number 1 ranked chlorophyll value with rank of POC or ATP in vertical profiles taken across WCR's 82-B and 82-E ($N = 15$).

were significantly related to measurements of chlorophyll in the nineteen pump profiles. In most of the profiles, the depth interval of highest chlorophyll concentration contained the lowest zooplankton abundance and biomass (Fig. 3).

Typical vertical distributions of chlorophyll and zooplankton biomass and abundance in relation to hydrographic structure of the water column are presented for WCR 82-B (Fig. 4a) and WCR 82-E (Fig. 4b). In general, while the chlorophyll maximum occurred within the thermocline, maximum concentrations of zooplankton were present in the upper mixed layer. A similar pattern was found for the distribution of copepod nauplii, copepodite and adult stages (Table 2).

c. Primary production and zooplankton grazing. In WCR 82-B in June and August, the Sargasso Sea and WCR 82-E we conducted *in situ* primary production and zooplankton grazing measurements in conjunction with the pump profiles (Fig. 5). Zooplankton grazing rate, expressed as liters filtered m^{-3} h^{-1}, was calculated as the product of the weight-specific grazing rate determined with the *in situ* chambers and the fine-scale biomass distribution determined from the pump samples. Comparing the distribution of the biomass and rates of phytoplankton production and zooplankton grazing, we found that maxima in both zooplankton biomass and grazing activity occurred at depths shallower than the chlorophyll maximum. Generally the depths of

Table 2. Depth intervals (100–70 m, 70–40 m, 40–20 m, 20–10 m, 10–5 m, 5–0 m June; 110–70 m, 70–50 m, 50–30 m, 30–10 m, 10–0 m August) of maximum concentrations of chlorophyll, zooplankton biomass, nauplii abundance, copepodite and adult abundance and total >64 μm zooplankton abundance.

Station		Date	Chl.	Zoopl. Bio.	Naup. #	Cop. + Ad. #	Total Zoopl. #
82-B Transect	13	6/23	40-20	40-20	40-20	40-20	40-20
	14	6/23	40-20	10-5	10-5	10-5	10-5
	15	6/23	40-20	10-5	10-5	40-20	10-5
	16	6/24	40-20	5-0	10-5	5-0	5-0
	17	6/24	40-20	5-0	40-20	5-0	5-0
	18	6/24	40-20	10-5	10-5	10-5	10-5
	20	6/25	40-20	20-10	20-10	5-0	20-10
	22	6/25	20-10	20-10	10-5	10-5	10-5
82-B		8/9	50-30	10-0	50-30	30-10	50-30
82-B		8/12	70-50	10-0	10-0	10-0	10-0
Sargasso Sea		8/13	110-70	10-0	10-0	50-30	10-0
82-E		8/16	70-50	10-0	10-0	110-70	10-0
82-E Transect	1	8/18	70-50	10-0	50-30	50-30	50-30
	2	8/18	50-30	10-0	30-10	10-0	30-10
	3	8/18	70-50	30-10	50-30	30-10	50-30
	4	8/19	110-70	10-0	50-30	70-50	70-50
	5	8/19	50-30	30-10	30-10	30-10	30-10
	6	8/19	50-30	10-0	30-10	10-0	10-0
	7	8/20	70-50	30-10	50-30	50-30	50-30

maximum grazing activity occurred within or above the primary productivity maximum (Fig. 5). The rank correlations between either zooplankton biomass ($r_s = 0.068$; $r_{0.05} = 0.350$; $N = 34$) or grazing activity ($r_s = 0.020$; $r_{0.05} = 0.350$; $N = 34$), and primary production were not significant. The depth intervals at maximum primary production and maximum zooplankton biomass or grazing usually did not coincide (Fig. 6a,b). In contrast, using primary production per unit chlorophyll (*P*-chl) we found that maxima in zooplankton biomass and grazing activity usually occurred at the depth of maximum *P*-chl (Fig. 6c,d). Using a larger data set ($n = 19$) based on *in situ* grazing estimates, *P*-chl determined from discrete bottle casts (Hitchcock *et al.*, 1985; Hitchcock, unpublished) and zooplankton biomass determined from 25 m interval MOCNESS tows (Roman *et al.*, 1985; Roman, unpublished) from several warm-core Gulf Stream rings, the Slope water and Sargasso Sea, we see that in general the highest zooplankton grazing activity occurs at depths with the highest *P*-chl (Fig. 7a). Highest *P*-chl occurred in the upper water column where light is >36% surface intensity (Hitchcock *et al.*, 1985). There is also good evidence that weight-specific grazing rates (liters filtered · mg zooplankton $C^{-1}h^{-1}$) are related to *P*-chl. Using the same 19 *in situ* grazing and primary production profiles, we found that the depth

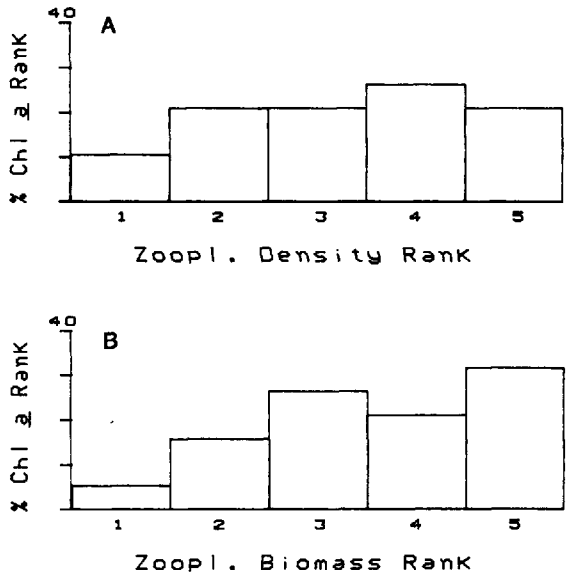

Figure 3. The relationship between chlorophyll and >64 μm zooplankton density (A) and zooplankton biomass (B) expressed as the frequency of occurrence of number 1 ranked chlorophyll value with rank of zooplankton density or biomass in vertical profiles from WCR's 82-B, 82-E and the Sargasso Sea (N = 19).

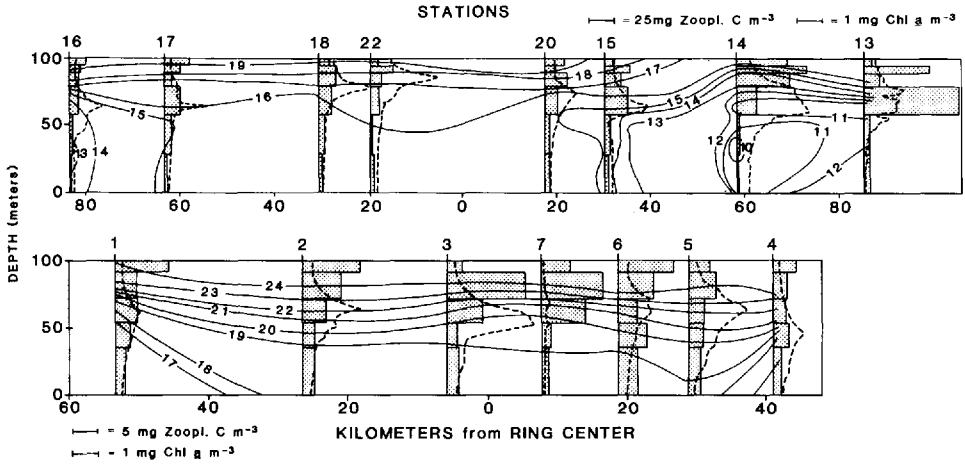

Figure 4. Zooplankton (>64 μm) biomass (mgC m^{-3}; histograms) and chlorophyll (mg m^{-3}; dashed lines) distribution with temperature contours in WCR 82-B in June (A) and 82-E in August (B). Stations are plotted (upper abscissa) as well as distance from ring center (lower abscissa).

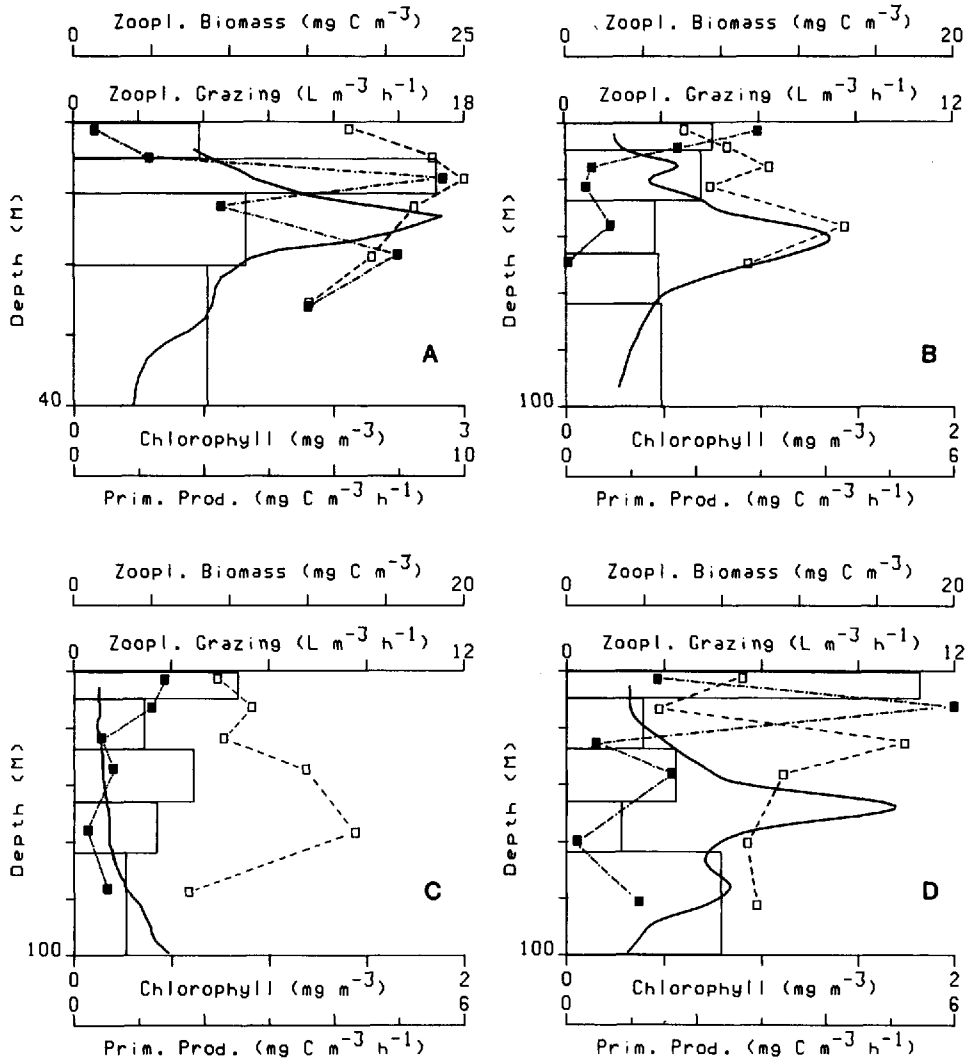

Figure 5. Zooplankton (mgC m^{-3}) biomass (upper abscissa), zooplankton (L m^{-3}h^{-1}) grazing (upper abscissa), chlorophyll (mg m^{-3}) distribution (lower abcissa) and primary (mgC m^{-3}h^{-1}) production (lower abscissa) in WCR 82-B in June (A), 82-B in August (B), Sargasso Sea in August (C) and 82-E in August (D). Solid line = chlorophyll, open squares = primary production, closed squares = zooplankton grazing, bars = zooplankton biomass.

interval of maximum *P*-chl usually also contained maximum weight-specific zooplankton grazing rates (Fig. 7b). The Spearman rank correlations for both volume-specific zooplankton grazing ($r_s = 0.299$; $r_{0.05} = 0.202$; $N = 97$) and weight-specific zooplankton grazing ($r_s = 0.207$; $r_{0.05} = 0.202$; $N = 97$) and production per unit chlorophyll were significant ($p < 0.05$).

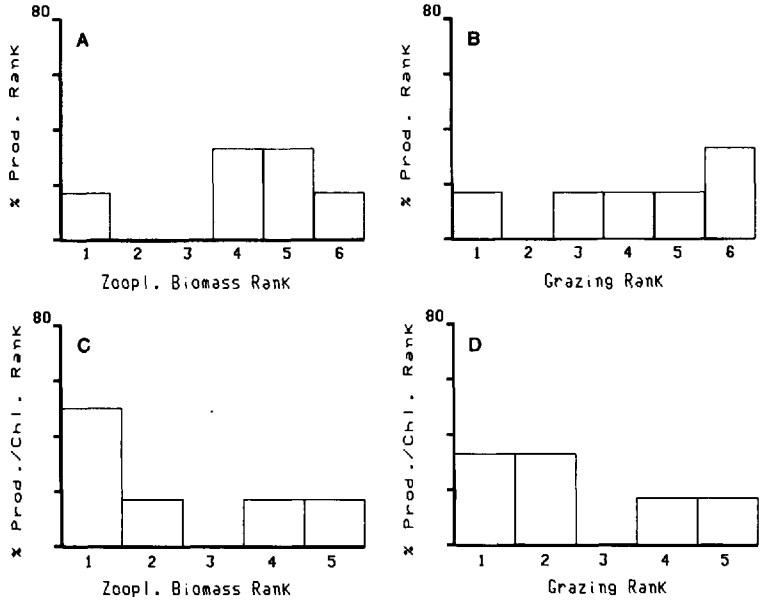

Figure 6. The relationship between primary production (mgC $m^{-3}h^{-1}$) and zooplankton biomass (A), primary production and zooplankton grazing (B), *P*-chl (mgC mg $chl^{-1}h^{-1}$) and zooplankton biomass (C) and *P*-chl and zooplankton grazing (D) expressed as the frequency of occurrence of number 1 ranked primary production (A,B) or *P*-chl (C,D) with rank of zooplankton grazing and biomass in vertical profiles from WCR's 82-B, 82-E and the Sargasso Sea ($N = 7$).

4. Discussion

In the majority (17 of 19) of our fine-scale vertical profiles there was no evidence that the distribution of chlorophyll and zooplankton were related. Several investigators (e.g., Anderson *et al.*, 1972; Mullin and Brooks, 1972; Haury, 1976; Fairbanks and Wiebe, 1980; Ortner *et al.*, 1980) found that in stratified waters the vertical distributions of zooplankton and chlorophyll coincided. In contrast, other studies (e.g.) Longhurst, 1976; Fiedler, 1983; Herman and Platt, 1983; Herman, 1984) have shown that zooplankton aggregations are highest at depths shallower than the subsurface chlorophyll maximum layer, usually occurring at depths where primary production is maximum. It is difficult to discern whether these two different types of observations are real or an artifact of sampling strategies, phytoplankton fluorescence/biomass variations, or vertical migration patterns of zooplankton. Additionally as Cullen (1982) has pointed out, there are a variety of mechanisms that can generate subsurface chlorophyll maxima. The differences in both physiological adaptations and species assemblages of phytoplankton that result may vary in their ability to attract and support zooplankton.

Pump sampling has the advantage of catching both zooplankton and water for

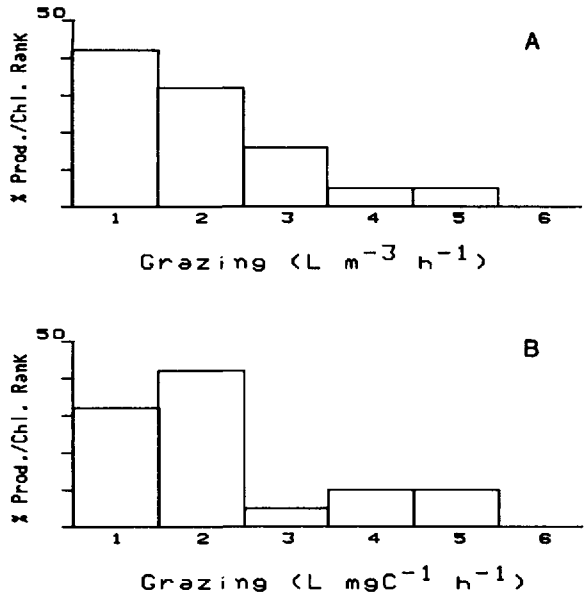

Figure 7. The relationship between *P*-chl and volume-specific zooplankton grazing (A), and weight-specific zooplankton grazing (B) expressed as the frequency of occurrence of number 1 ranked *P*-chl with rank of zooplankton grazing in vertical profiles from WCR's 82-B, 82-E, 82-H, the Slope Water and Sargasso Sea ($N = 19$).

fluorescence, temperature and salinity measurements simultaneously. However, ship-roll and turbulence within the hose both reduce vertical resolution. We applied depth corrections from the CTD attached to the intake of the hose to the shipboard sensor readings to compensate for the residence time through the hose. The hose was raised 2 m min^{-1} to reduce smoothing of the vertical profiles due to smearing in the pump system (Anderson and Okubo, 1982). In order to convert fluorescence readings to chlorophyll, we collected discrete samples from the fluorometer outflow every few meters for extracted chlorophyll analysis. The depths of maximum chlorophyll concentrations generally coincided with depths of maximum concentrations of particulate organic carbon and ATP (Fig. 2). Thus we assume that the subsurface chlorophyll maximum layer in the vertical profiles presented represents a phytoplankton biomass maximum.

Pumping systems may not be as effective as towed nets in catching large, fast moving zooplankton. We did not find statistically significant differences between either zooplankton biomass or abundance estimated with the pumping system and a 0.25 m^2 mouth area, 64 μm-mesh MOCNESS. However, in June when there was an abundance of euphausids, decapod crustaceans and large copepods (Davis and Wiebe, 1985), a larger, 1.0 m^2 mouth area, 333 μm-mesh MOCNESS gave higher zooplankton biomass estimates than the smaller (only >333 μm fractions compared) net system

(see Roman *et al.*, 1985; Wiebe *et al.*, 1985a). Although we may be missing some of the larger zooplankton with the pumping system, many of these larger animals are carnivores (Davis and Wiebe, 1985) and thus are not relevant to our discussion of the utilization of phytoplankton standing stocks.

All of our pump profiles were conducted during the day. However, there were comparative 25 m interval, day/night 0.25 m^2 MOCNESS (Roman *et al.*, 1985) and 1.0 m^2 MOCNESS tows (Wiebe *et al.*, 1985a) taken in WCR 82-B in June and 82-B and 82-E August. In June there were no significant changes in the vertical distribution of zooplankton in the upper water column of WCR 82-B. However in 82-B in August there were more >333 μm zooplankton at night, with the highest biomass in the surface 25 m (chlorophyll maximum was at 42 m). Unpublished results (Roman and Gauzens) from WCR 82-E in August indicate that there were no significant diel differences in the vertical distribution of either 64–333 μm or >333 μm zooplankton biomass fractions. In summary, in the areas studied there were no detectable vertical shifts in 64–333 μm zooplankton biomass (30–40% of total >64 μm zooplankton) and if there were nighttime increases in >333 μm zooplankton, they were greatest in the surface 25 m, well above the subsurface chlorophyll maximum layer (Table 1).

Zooplankton number generally tracked zooplankton biomass (Table 2) with higher densities usually occurring above the subsurface chlorophyll maximum. Nauplii densities exceeded those of copepodites and adults with the highest aggregations found in the surface samples (Table 2). Similar patterns of nauplii distributions have been found off the coast of Washington (Chester, 1978) and in the North Sea (Marshall and Orr, 1955). In contrast, in the Gulf of Maine copepod nauplii often reached maximum densities at the subsurface chlorophyll maximum (Townsend *et al.*, 1984). In coastal waters, the subsurface chlorophyll maximum is usually shallower than in oceanic water columns, and can coincide with the productivity maximum (Holligan *et al.*, 1984a).

Unique to this study are the *in situ* measurements of primary production and zooplankton grazing in conjunction with continuous profiles of fluorescence, temperature and salinity and fine-scale measurements of zooplankton abundance. Most zooplankton feeding estimates in pelagic systems have either been inferred from field biomass measurements and laboratory feeding estimates or have been derived from shipboard feeding experiments. However, because of removal from the natural environment, these shipboard and laboratory experiments often do not reflect ambient conditions of food quality and quantity, light, temperature or pressure. In addition, over long incubations (>4 h), "bottle effects" and improper controls which do not correct for nutrient regeneration by zooplankton may result in an underestimation of grazing rate (Roman and Rublee, 1980). Zooplankton grazing estimated by the short-term *in situ* uptake of labelled food measures zooplankton grazing at ambient food, light, temperature and pressure and avoids the handling of zooplankton that is associated with most other zooplankton grazing methods (Roman and Rublee, 1981). Because primary production and zooplankton grazing are measured in the same bottle,

we can compare their rates in relation to ambient concentrations of phytoplankton and zooplankton. At the seven stations where we estimated zooplankton grazing and primary production, zooplankton biomass and grazing were more closely coupled to primary production per unit chlorophyll (*P*-chl) than to primary production per unit volume (absolute production). In general, vertical profiles show that the highest grazing pressure (liters filtered m^{-3} h^{-1}) occurred at depths shallower than the depth of maximum absolute phytoplankton production. These depths of both maximum zooplankton biomass and grazing activity were in the part of the water column where *P*-chl was higher. Using a larger data set consisting of *in situ* incubations from various warm-core Gulf Stream rings, the Sargasso Sea and Slope Water in April, June, August and October, we found a significant correspondence between the depths of maximum zooplankton grazing and *P*-chl (Fig. 7).

Weight-specific zooplankton grazing is also generally maximum in the upper water column where *P*-chl is higher (Fig. 7). In contrast, there is little evidence from any of the 19 vertical profiles that zooplankton have enhanced weight-specific feeding rates in the subsurface chlorophyll maximum. In the majority of the vertical fluorescence profiles, the subsurface chlorophyll maximum layer contained the highest fucoxanthin/chlorophyll ratios. These pigment ratios imply that relative to the upper mixed layer, the subsurface chlorophyll maximum is rich in diatoms and dinoflagellates (Yentsch and Yentsch, 1979). The floristic composition is corroborated for warm-core ring 82-B in June by measurements of phycoerythrin and chlorophyll accessory pigments (Yentsch and Phinney, 1985) as well direct microscope counts (G.A. Fryxell, personal communication). We have little insight why the observed zooplankton grazing pressure was reduced in the subsurface chlorophyll maximum. Zooplankton have been shown to exhibit enhanced ingestion rates on phytoplankton with higher nitrogen content and growth rate (Mullin, 1963; Cowles *et al.*, 1986) and lower grazing rates on detritus (Roman, 1984), dead phytoplankton (Paffenhöfer and Van Sant, 1985) and senescent phytoplankton (Ryther, 1954). We can only speculate that the greater weight-specific grazing rate (ml · $mgC^{-1}h^{-1}$), water column grazing rate (L m^{-3} h^{-1}) and aggregation of zooplankton biomass in the upper water column as compared to the subsurface chlorophyll maximum was the result of higher food "quality" of phytoplankton where *P*-chl was maximum.

After formation of the seasonal thermocline the vertical distribution of phytoplankton biomass is a consequence of depth differences in the balance between phytoplankton growth, sinking and zooplankton grazing. This phenomenon was first suggested for phytoplankton populations on Georges Bank (Riley, 1946). Longhurst (1976) reached a similar conclusion after reviewing plankton profiles from the eastern tropical Pacific Ocean, and Herman and Platt (1983) used both field data and a numerical model to describe the same phenomena for plankton production off the Scotian shelf. Based on photosynthesis-irradiance curves, chlorophyll and light profiles, Herman and Platt (1983) modelled the depth profile of both *P*-chl and absolute phytoplankton production

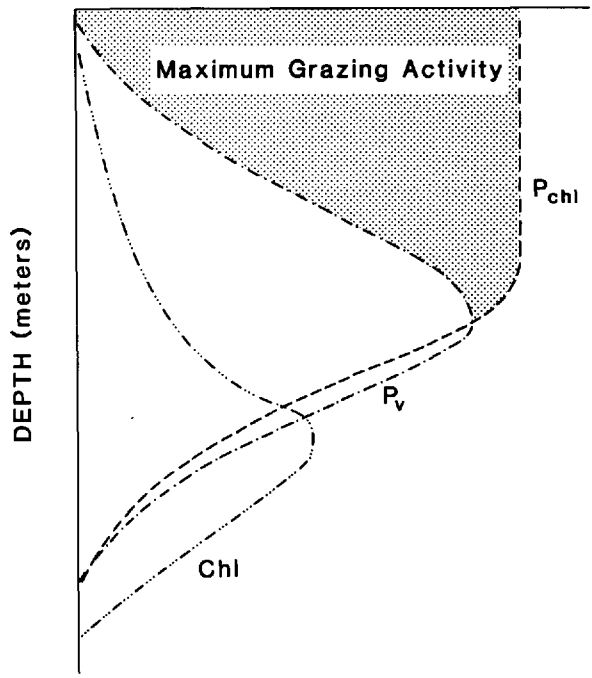

Figure 8. Idealized vertical profiles of *P*-chl (mgC mg $chl^{-1}h^{-1}$ = dashes), absolute primary production (mgC $m^{-3}h^{-1}$ = dashes-dot) and chlorophyll (mg m^{-3} = dashes-dots). Area of maximum zooplankton grazing is shaded. Graph is adapted from Herman and Platt (1983).

(Fig. 8). Our direct measurements of chlorophyll and photosynthesis (Fig. 5) fit this same general pattern. A low standing crop of phytoplankton limits absolute production in the surface waters where *P*-chl is highest whereas light limits phytoplankton production below the subsurface absolute production maximum.

Our data suggest that zooplankton grazing removes phytoplankton biomass in the upper water column and shifts absolute production to depth (Fig. 8). Comparing our zooplankton grazing estimates in the upper water column (where *P*-chl is highest) to phytoplankton growth rates (Hitchcock *et al.*, 1985) we estimate that 50 to 100% of the daily phytoplankton growth is removed by zooplankton. Considering that our grazing estimates do not take into account zooplankton grazers <64 μm, it is likely that in the upper water column phytoplankton production and grazing are in balance.

An important consequence of zooplankton aggregation in the upper water column is that it becomes the site for intense ammonium regeneration. Hence production per unit chlorophyll will be highest at this site. For example, using an allometric equation to estimate ammonium regeneration (Ikeda, 1974), we find that in the surface waters of WCR 82-E in August (Fig. 5) at the depth where zooplankton grazing and *P*-chl are maximum, there was 56 μg N excreted $m^{-3}h^{-1}$. In contrast, in the remaining portion of

the water column the >64 μm zooplankton above the thermocline excreted 9 μg N $m^{-3}h^{-1}$. Using measurements of the enzyme glutamate dehydrogenase (GDH) to estimate ammonium regeneration, Bidigare *et al.*(1982) found that >80% of the total zooplankton GDH activity as well as GDH activity/zooplankton biomass was greatest above the chlorophyll maximum. If ammonium excretion increases with zooplankton grazing rate (e.g., Corner *et al.*, 1965; Takahashi and Ikeda, 1975) one would expect to find greater biomass-specific excretion in the upper water column where *P*-chl and zooplankton grazing are maximum. In stratified water columns this enhanced excretion may supply much of the N required to support primary production (Harrison, 1980).

In summary, after the seasonal thermocline is established phytoplankton removal by zooplankton is greatest in that part of the water column where primary production per unit chlorophyll is maximum. Grazing by zooplankton limits the amount of absolute primary production (per unit volume) in the upper water column and results in a subsurface maximum of absolute production at depths where grazing pressure is reduced. The subsurface chlorophyll maximum does not appear to be a site of enhanced accumulation of zooplankton biomass or grazing activity. The causes and consequences of this apparent reduced grazing pressure at the subsurface chlorophyll maximum merit further investigation.

Acknowledgments. We thank the captain and crew of the R.V. *Knorr* for their help during the cruises. This research was supported by a NSF grant (OCE-8117562) to M. R. Roman and NASA grant (NAG6-17) to C. S. Yentsch as part of the Warm Core Gulf Stream Ring program. We thank W. M. Kemp, T. C. Malone and J. M. Napp for reviewing an early draft of the manuscript, J. C. Garside and S. L. Houde for assistance in sample collection and data analysis, J. J. McCarthy for providing particulate carbon data and G. L. Hitchcock, C. Langdon and T. J. Smayda for providing particulate ATP data. This is University of Maryland Center for Environmental and Estuarine Studies contribution number 1723 and Bigelow Laboratory contribution number 86022.

REFERENCES

Anderson, G. C. 1972. Aspects of marine phytoplankton studies near the Columbia River, with special reference to a subsurface chlorophyll maximum, *in* The Columbia River Estuary and Adjacent Ocean Waters, A. T. Pruter and D. L. Alverson, eds., Univ. Wash. Press, Seattle, WA, 219–240.

Anderson, G. C., B. W. Frost and W. K. Peterson. 1972. On the vertical distribution of zooplankton in relation to chlorophyll concentrations, *in* Biological Oceanography of the Northern North Atlantic Ocean, A. Y. Takenouti *et al.* eds., Idemitsu Shoten, Tokyo, Japan, 339–345.

Anderson, J. J. and A. Okubo. 1982. Resolution of chemical properties with a vertical profiling system. Deep-Sea Res., *29,* 1013–1019.

Bannister, T. T. and E. A. Laws. 1980. Modelling phytoplankton carbon metabolism, *in* Primary Productivity in the Sea, P. G. Falkowski, ed., Plenum Press, NY, 243–256.

Beers, J. R., G. L. Steward and J. D. H. Strickland. 1967. A pumping system for sampling small zooplankton. J. Fish. Res. Bd. Can., *24,* 1811–1818.

Beers, J. R., F. M. H. Reid and G. L. Stewart. 1975. Microplankton of the North Pacific central gyre. Population structure and abundance, June 1973. Int. Revue ges. Hydrobiol., *60,* 607–636.

Bidigare, R. R., F. D. King and D. C. Biggs. 1982. Glutamate dehydrogenase (GDH) and respiratory electron-transport-system (ETS) activities in Gulf of Mexico zooplankton. J. Plank. Res., *4,* 895–911.

Boyd, C. M. 1973. Small scale spatial patterns of marine zooplankton examined by an electronic *in situ* zooplankton detecting device. Netherlands J. Sea Res., *7,* 103–111.

Chester, A. J. 1978. Micro-zooplankton relative to a subsurface chlorophyll maximum layer. Mar. Sci. Comm., *4,* 275–292.

Conover, R. J. 1981. Shelf-sea ecosystems, *in* Analysis of Marine Ecosystems, A. R. Longhurst ed., Academic Press, NY, 159–196, 741 pp.

Corner, E. D. S., C. B. Cowey and S. M. Marshall. 1965. On the nutrition and metabolism of zooplankton. 3. Nitrogen excretion by Calanus. J. Mar. Biol. Assoc. U.K., *47,* 113–120.

Cowles, T. J., R. J. Olson and S. W. Chisholm. 1986. Food selection by copepods: Discrimination between cells on the basis of food qualtiy. Mar. Biol. (in press.)

Cox, J. L., P. H. Wiebe, P. Ortner and S. Boyd. 1982. Seasonal development of subsurface chlorophyll maxima in Slope Water and the Northern Sargasso Sea of the Northwestern Atlantic Ocean. Biol. Oceanogr., *1,* 271–285.

Cullen, J. J. 1982. The deep chlorophyll maximum: comparing vertical profiles of chlorophyll *a.* Can. J. Fish. Aquat. Sci., *39,* 791–803.

Cullen, J. J. and R. W. Eppley. 1981. Chlorophyll maximum layers of the Southern California Bight and possible mechanisms of their formation and maintenance. Oceanol. Acta., *4,* 23–32.

Davis, C. S. and P. H. Wiebe. 1985. Evolution of zooplankton size structure and taxonomic composition in a warm-core Gulf Stream ring. J. Geophys. Res., *90,* 8871–8884.

Fairbanks, R. G. and P. H. Wiebe. 1980. Foraminifera and chlorophyll maximum: vertical distribution, seasonal succession, and paleo-oceanographic significance. Science *209,* 1524–1526.

Falkowski, P. G. 1980. Light-shade adaption in marine phytoplankton, *in* Primary Productivity in the Sea, P. G. Falkowski, ed., Plenum Press, NY, 99-119.

Fiedler, P. C. 1983. Fine-scale spatial patterns in the coastal epiplankton off southern California. J. Plank. Res., *5,* 865–879.

Harrison, W. G. 1980. Nutrient regeneration and primary production in the sea, *in* Primary Productivity in the Sea, P. Falkowski, ed., Plenum Press, NY, 433–460.

Haury, L. R. 1976. Small-scale spatial pattern of a California Current zooplankton assemblage. Mar. Biol., *37,* 137–157.

Herman, A. W. 1984. Vertical copepod aggregations and interactions with chlorophyll and production on the Peru Shelf. Cont. Shelf. Res., *3,* 131–146.

Herman, A. W. and T. M. Dauphinee. 1980. Continuous and rapid profiling of zooplankton with an electronic counter mounted on a Batfish vehicle. Deep-Sea Res., *27,* 79–96.

Herman, A. W., M. R. Mitchell and S. W. Young. 1984. A continuous pump sampler for profiling copepods and chlorophyll in the upper oceanic layers. Deep-Sea Res., *31,* 439–450.

Herman, A. W. and T. Platt. 1983. Numerical modelling of diel carbon production and zooplankton grazing on the Scotian shelf based on observational data. Ecol. Model., *18,* 55–72.

Herman, A. W., D. D. Sameoto and A. R. Longhurst. 1981. Vertical and horizontal distribution patterns of copepods near the shelf break south of Nova Scotia. Can. J. Fish. Aquat. Sci., *38,* 1065–1076.

Hitchcock, G. L., C. Langdon and T. J. Smayda. 1985. Seasonal variations in the phytoplankton biomass and productivity of a warm-core Gulf Stream ring. Deep-Sea Res., *32*,1287–1300.

Holligan, P. M., W. M. Balch and C. M. Yentsch. 1984a. The significance of subsurface chlorophyll, nitrate and ammonium maxima in relation to nitrogen for photoplankton growth in stratified waters of the Gulf of Maine. J. Mar. Res., *42*, 1051–1073.

Holligan, P. M. and D. S. Harbour. 1977. The vertical distribution and succession of phytoplankton in the western English Channel in 1975 and 1976. J. Mar. Biol. Assoc. U.K., *57*, 1075–1093.

Holligan, P. M., R. P. Harris, R. C. Newell, D. S. Harbour, R. N. Head, E. A. S. Linley, M. I. Lucas, P. R. G. Tranter and C. M. Weekley. 1984b. Vertical distribution and partitioning of organic carbon in mixed, frontal and stratified waters of the English Channel. Mar. Ecol. Prog. Ser. *14*, 111–127.

Houde, E. D. and J. A. Lovdal. 1985. Patterns of variability in ichthyoplankton occurrence and abundance in Biscayne Bay, Florida. Est. Cstl. Shelf. Sci., *20*, 79–104.

Ikeda, T. 1974. Nutritional ecology of marine zooplankton. Memoirs of the Faculty of Fisheries, Hokkaido University, *22*, 1–97.

Joyce, T. and P. Wiebe. 1983. Warm-core rings of the Gulf Stream. Oceanus, *26*, 34–44.

Karl, D. M. and O. Holm-Hansen. 1976. Methodology and measurement of adenylate energy charge ratios in environmental samples. Mar. Biol., *48*, 185–197.

Longhurst, A. R. 1976. Interactions between zooplankton and phytoplankton profiles in the eastern tropical Pacific Ocean. Deep-Sea Res., *23*, 729–754.

Marshall, S. M. and A. P. Orr. 1955. The biology of a marine copepod. Oliver and Boyd, London, 195 pp.

Mullin, M. M. 1963. Some factors affecting the feeding of marine copepods of the genus *Calanus*. Limnol. Oceanogr., *8*, 239–250.

Mullin, M. M. and E. R. Brooks. 1972. The vertical distribution of juvenile *Calanus* (Copepods) and phytoplankton within the upper 50 m of water off La Jolla, California, *in* Biological Oceanography of the Northern North Pacific Ocean, A. Y. Takenouti *et al.*, eds., Idemitsu Shoten, Tokyo, Japan, 347–354.

Nelson, D. M., H. W. Ducklow, G. L. Hitchcock, M. A. Brzezinski, T. J. Cowles, C. R. Garside, R. W. Gould, T. M. Joyce, C. Langdon, J. J. McCarthy, C. S. Yentsch. 1985. Distribution and composition of biogenic particulate matter in a Gulf Stream warm-core ring. Deep-Sea Res., *32*, 1347–1371.

Ortner, P. B., P. H. Wiebe and J. L. Cox. 1980. Relationships between oceanic epizooplankton distributions and the seasonal deep chlorophyll maximum in the Northwestern Atlantic Ocean. J. Mar. Res., *38*, 507–531.

Paffenhöfer, G. -A., and K. B. Van-Sant. 1985. The feeding response of a marine planktonic copepod to quantity and quality of particles. Mar. Ecol. Prog. Ser., *27*, 55–65.

Phinney, D. A., E. W. Langton and J. C. Garside. 1984. R/*V Knorr*, warm-core rings No. 2. Tech. Rep. #40 Bigelow Lab for Ocean Sciences.

Riley, G. A. 1946. Factors controlling phytoplankton populations on Georges Bank. J. Mar. Res., *6*, 54–73.

Roman, M. R. 1984. Utilization of detritus by the copepod, *Acartia tonsa*. Limnol. Oceanogr., *29*, 949–959.

Roman, M. R., A. L. Gauzens and T. J. Cowles. 1985. Temporal and spatial changes in epipelagic microzooplankton and mesozooplankton biomass in warm-core Gulf Stream ring 82-B. Deep-Sea Res., *32*, 1007–1022.

Roman, M. R. and P. A. Rublee. 1980. Containment effects in copepod grazing experiments: A plea to end the black box approach. Limnol. Oceanogr., *25*, 982–990.

—— 1981. A method to determine *in situ* zooplankton grazing rates on natural particle assemblages. Mar. Biol., *65,* 303–309.

Smayda, T. J. 1970. The suspension and sinking of phytoplankton in the sea. Oceanogr. Mar. Biol. Ann. Rev., *8,* 353–414.

Steele, J. H. and C. S. Yentsch. 1960. The vertical distribution of chlorophyll. J. Mar. Biol. Assoc. U.K., *39,* 217–226.

Takahashi, M. and T. Ikeda. 1975. Excretion of ammonia and inorganic phosphorus by *Euphausia pacifica* and *Metridia pacifica* at different concentrations of phytoplankton. J. Fish. Res. Bd. Can., *32,* 2189–2195.

Townsend, D. W., T. L. Cucci and T. Berman. 1984. Subsurface chlorophyll maxima and vertical distribution of zooplankton in the Gulf of Maine. J. Plank. Res., *6,*793–802.

Venrick, E. L., J. A. McGowan and A. W. Mantyla. 1973. Deep maxima of photosynthesis chlorophyll in the Pacific Ocean. Fish. Bull., 71, 41–52.

Wiebe, P. H., V. Barber, S. H. Boyd, C. S. Davis and G. R. Flierl. 1985a. Evolution of zooplankton biomass structuré in warm-core rings. J. Geophys. Res., *90,* 8885–8902.

Wiebe, P. H., A. W. Morton, A. M. Bradley, R. H. Backus, J. M. Craddock, V. Barber and T. Cowles. 1985b. New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton. Mar. Biol., *87,* 313–323.

Yentsch, C. S. and D. A. Phinney. 1985. Spectral fluorescence: an atoxonomic tool for studying the structure of phytoplankton populations. J. Plank. Res. *7,* 617–632.

Yentsch, C. S. and C. M. Yentsch. 1979. Fluorescence spectral signatures: the characterization of phytoplankton populations by the use of excitation and emission spectra. J. Mar. Res., *37,* 471–483.

Zar, J. H. 1974. Biostatistical Analysis. Prentice-Hall, N.J. 620 pp.

Received: *3 March, 1986;* revised: *7 July, 1986.*