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MASTER

BIOLOGICAL PROCESSES IN THE WATER COLUMN
OF THE SOUTH ATLANTIC BIGHT

A PROGRESS REPORT SUBMITTED TO
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SECTION 1. OVERVIEW OF PROGRESS

Phytoplankton Dynamics

The following is a summary of what has been learned in the past three years covering phytoplankton dynamics of the southeastern shelf. Details are provided in the manuscripts that comprise sections 4, 5, 9, 11, 12, 18 and 19 of our Progress Report. All data collected prior to GABEX I (spring 1980) are included in these manuscripts as are the productivity measurements made during GABEX I. Other results obtained during GABEX I will be included in manuscripts that are presently in preparation. These include a manuscript that discusses surface chlorophyll distributions as measured by ship, by the Ocean Color Scanner (OCS) flown aboard a NASA U-2 aircraft, and by the Thematic Mapper Simulator (TMS) flown aboard a NASA C-130 aircraft. The latter is a prototype of the radiometer that will be incorporated in the next LANDSAT satellite. A second manuscript in preparation focuses on shelfwide distribution of chlorophyll in relation to hydrography during the GABEX I study.

GABEX II (summer, 1981) samples are still being analyzed and these measurements will primarily be used to develop a water column N budget during the lifetime of a stranded intrusion. A second goal is to construct a time series of primary production during the development and collapse of a phytoplankton bloom within a stranded intrusion. Samples required to accomplish both of the above were collected during GABEX II. We expect that all GABEX II samples will be analyzed by May, 1982. A meeting will be held to discuss the preliminary results of GABEX II at the AGU/ASLO meeting in February, 1982, since most of the southeast-DOE group plans to attend this meeting.

Summary of Phytoplankton Dynamics

1. Unlike the continental shelves north of Cape Hatteras, seasonal patterns in phytoplankton productivity and biomass are not very important on the southeastern shelf, if they exist at all (see section 4).
2. Aseasonal, episodic upwelling caused by disturbances of the Gulf Stream cyclonic front results in frequent, but short-lived, phytoplankton blooms. Upwelling is the major process controlling temporal and spatial changes in phytoplankton productivity and biomass on the middle and outer portions of the shelf (see sections 4, 11, 12, and 19).
3. During winter and spring when the shelf is not stratified, upwelled waters are generally constrained to the outer portion of the shelf. During these months, phytoplankton blooms develop within the upwelled cold core of eddies as they propagate along the Gulf Stream cyclonic front. Strong upwelling can result in surface phytoplankton patches that cover more than 1000 km². However, highest chlorophyll and primary production often occurs within subsurface intrusions of nutrient-rich upwelled waters (see section 12).
4. During summer when the shelf is stratified, subsurface intrusions of upwelled water move onto the shelf. These intrusions remain on the shelf long enough (greater than 1-2 weeks) for virtually all upwelled nitrate to be converted into phytoplankton biomass (see section 19).
5. Recognition and elucidation of the upwelling process and its effect on phytoplankton productivity led to a new estimate of outer shelf primary productivity during winter and spring. This new estimate is 2-3 times higher than earlier estimates that did not take upwelling into account. Our esti-

mate of "new" production is about 10 X higher than those which did not account for the effect of upwelling. More than 90% of primary and "new" production on the outer shelf occurs during upwelling which occurs about 50% of the time (see section 19).

6. Our analysis of data collected during the 1950s shows that fish eggs and larvae are generally higher on the outer shelf (upwelling influenced) than the inner shelf. The abundance of fish eggs and larvae on the outer shelf is independent of season which may in part reflect the aseasonality of primary production (manuscript in preparation, abstract submitted to Ocean Sciences 1982).
7. In conjunction with our NASA colleagues, we showed that multi-spectral scanners flown at high altitudes can quantitatively determine chlorophyll gradients within ocean waters which contain only small amounts of non-biogenic particulate matter (see section 5).
8. In collaboration with others, we showed that benthic organisms are affected by high water column productivity of intrusions (see section 9).
9. We completed preliminary studies showing the effect of copper on phytoplankton of the nearshore region (see section 18).

Zooplankton and Particulate Matter

The results presented in the following 2 chapters are unpublished. Earlier obtained data on zooplankton and particulate matter have either been published or are in manuscript form (see Progress Report).

1. Our goal in 1979 was to determine abundance and distribution of nutrients,

phyto- and zooplankton in upwelled water and describe processes associated with it. Throughout the 7 weekly cruises upwelling was limited and upwelled water masses were restricted to the outer shelf as shown for July 31st in Fig. 1a. Maximum nitrate concentrations in these intrusions ranged from 8.0 to 12.8 μ -moles. Surface waters and thermocline had no detectable amounts of nitrate. The water column was then stratified with a distinct thermocline (Fig. 1b). The concentrations of particulate matter available to zooplankton (2 to 100 μ m particle diameters) ranged from near 0.5 $\text{mm}^3 \cdot \ell^{-1}$ in surface waters to 5 $\text{mm}^3 \cdot \ell^{-1}$ in the bottom intrusion (Fig. 1b).

Several of the zooplankton taxa which were found abundantly were in different stages of assemblage development (Figs. 1c and d): Concentrations of doliolids, the cladoceran Penilia avirostris, the cyclopoid Oncaea sp. and the calanoid Temora turbinata were lowest at St. 370 where water had just upwelled onto the shelf and the zooplankton therefore was in an early state of development. In contrast, zooplankton occurred in largest abundances at St. 374. The intruding water found there had moved onto the shelf earlier and was also of higher temperature. Zooplankton samples had been taken during the night covering with a pump the entire water column from near the surface to within 2 m of the sea floor. Sampling depths (upper mixed layer, thermocline and bottom mixed layer) were determined with temperature and depth sensors. At most times highest abundances were observed in the bottom layer and the thermocline. The relatively high concentrations in the upper mixed layer of the smaller copepods Oithona, Oncaea, Paracalanus and the nauplii is related to the relatively high concentrations of particulate matter ($> 0.5 \text{ mm}^3 \cdot \ell^{-1}$).

Characteristic of summer upwelling are amphioxus larvae (Branchiostoma caribaeum). Fish larvae were observed in concentrations from 2 to $26 \cdot \text{m}^{-3}$ throughout the water column considerably exceeding the concentrations on the west Florida shelf (Houde and Chitty 1976). The densities of nauplii which serve as food for early fish larvae ranged from 8 to 43 specimens $\cdot \ell^{-1}$ and are an underestimate as young nauplii of the small copepods should be able to pass to 30 μm mesh employed in zooplankton pump collections (Beers and Stewart 1967). Nevertheless, the ambient concentrations of nauplii and small copepods should support the survival of 5 to 10% of hatched fish larvae (Houde 1978) which again should lead to the observed high concentrations of fish larvae on the outer shelf.

2. Our goal in 1981 was to determine the frequency and size of upwelled water masses between 29° and $31^{\circ}30'N$ and follow them for several weeks to determine rates and magnitudes of phyto- and zooplankton for development. We achieved this through onshore-offshore transects and standard hydrographic methods, among them the distribution of temperature and particulate matter in the range from 2 to 120 μm diameter.

During mid-July we observed upwelling along the shelf break but no distinct stranding. Particle measurements indicated high concentrations of large particles off Jacksonville (Fig. 2a), and high concentrations ($> \text{mm}^3 \cdot \ell^{-1}$) over most of the shelf. One week later the upwelling had moved onshore as observed by temperature, and by particle measurements (Fig. 2b). The particle size spectra hardly changed from July 13-16 to July 22-23. One week later (Fig. 2c) a new upwelling was observed by temperature; yet we could follow the "old" intru-

sion using particle concentration. These high particle concentrations consisted mostly of large diatoms which cannot be eaten (eaten) by small copepods (Paffenhöfer et al., 1980). The "new" water observed on July 27-29 remained on the shelf for the following 3 weeks (Figs. 2d, e and f). High particle concentrations were observed near the 20°C isotherm and increased from near 3 to 7 mm³·ℓ⁻¹, consisting mostly of the large diatom Guinardia flaccida. Part of this new intrusion had low concentrations of particles (< 0.5 mm³·ℓ⁻¹) which is partly attributed to high concentrations of pelagic tunicates (doliolids) in that particular part of the upwelling. Zooplankton samples taken at all stations through the entire water column are now being analyzed and additional hydrographic data are processed. A synthesis of all data should allow us to construct a nitrogen budget for each observed intrusion.

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FIGURES

Fig. 1a. Horizontal distribution of near bottom temperature off northeastern Florida: July 31, 1979.

Fig. 1b. Onshore-offshore transect of temperature and particle concentration ($\text{mm}^3 \cdot \ell^{-1}$) at $30^{\circ}00'N$ on August 1 to 2, 1979.

Figs. 1c to d. Zooplankton abundance and vertical distribution at 3 stations on August 1 to 2, 1979. Light bars = Upper mixed layer; stippled bars = Thermocline; dashed bars = Bottom layer (intrusion).

Figs. 2a to f. Distribution of near bottom temperature and near bottom particle concentration ($\text{mm}^3 \cdot \ell^{-1}$) on the southeastern continental shelf.

Fig. 1 a. Horizontal distribution of near bottom temperature off northeastern Florida: July 31, 1979.

August 1-2, 1979 (Stations 370, 372 and 374)

Fig. 1c. Zooplankton abundance and vertical distribution at 3 stations on August 1 to 2, 1979. Light bars = Upper mixed layer; stippled bars = Thermocline; dashed bars = Bottom layer (intrusion).

Fig. 1b. Onshore-offshore transect of temperature and particle concentration ($\text{mm}^3 \cdot \text{L}^{-1}$) at $30^{\circ}00'N$ on August 1 to 2, 1979.

August 1-2, 1979 (Stations 370, 372 and 374)

Fig. 1d. See Fig. 1c.

Fig. 2a. Distribution of near bottom temperature and near bottom particle concentration ($\text{mm}^3 \cdot \text{l}^{-1}$) on the southeastern continental shelf.

Fig. 2b. See Fig. 2a.

Fig. 2c. See Fig. 2a.

Fig. 2d. See Fig. 2a.

Fig. 2e. See Fig. 2a.

Fig. 2f. See Fig. 2a.

SECTION 2. TITLES OF PUBLISHED ABSTRACTS

ASLO, June, 1979

Yoder, J.A. and S.S. Bishop. Upwelling events in the South Atlantic Bight: Phytoplankton response to an intrusion of nutrient-rich water onto the continental shelf.

Atkinson, L.P., J.A. Yoder and T.N. Lee. Upwelling events in the South Atlantic Bight: Gulf Stream induced nutrient flux compared to other sources.

Paffenhöfer, G.-A. and D.C. Herring. Upwelling events in the South Atlantic Bight: Concentration and size distribution of particulate matter as related to zooplankton abundance and composition in intruding water masses.

Bishop, S.S. and W.M. Dunstan. Upwelling events in the South Atlantic Bight: The effects of Gulf Stream intrusions on the distribution of phytoplankton in Onslow Bay, North Carolina.

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Bishop, S.S., S.R. Lasley, L.P. Atkinson and J.A. Yoder. Effect of eddy-forced upwelling on nutrient and phytoplankton distribution near the shelf break in the South Atlantic Bight.

O'Malley, P.G., L.P. Atkinson and J.A. Yoder. The nitrogen pool of a mid-shelf intrusion.

Singer, J.J., L.P. Atkinson, J.A. Yoder and T.N. Lee. Hydrographic observations of the Charleston Bump.

Paffenhöfer, G.-A. and S.C. Knowles. Omnivorous feeding of planktonic copepods.

Bishop, S.S. and W.M. Dunstan. Effects of ionic copper on natural populations of phytoplankton grown in continuous culture.

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Kim, H.H., C.R. McClain, W.D. Hart, L.P. Atkinson, and J.A. Yoder. Thermal and visible color expressions of an upwelling off the Gulf Stream.

ASLO, December, 1980

Yoder, J.A., L.P. Atkinson, S.S. Bishop, E.E. Hofmann, T.N. Lee, H.H. Kim and C.R. McClain. Effect of upwelling on primary productivity of the outer southeastern shelf.

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O'Malley, P.G., L.P. Atkinson and S.S. Bishop. Nutrient dynamics of summer Gulf Stream intrusions off Florida and Georgia. (Submitted)

Paffenhöfer, G.-A. Environmentally oriented copepod feeding studies. (Submitted)

Symposium on Biological Productivity of Continental Shelves. Kiel, March, 1982

Atkinson, L.P., J.A. Yoder and T.N. Lee. Gulf Stream associated upwelling off the southeastern United States and its effect on continental shelf nutrient concentrations and primary productivity. (In Press)

Reprint from Journal of Marine Research, Volume 37, 1, 1979.

Ecological implications of fecal pellet size, production and consumption by copepods

by Gustav-Adolf Paffenhöfer¹ and Sally C. Knowles¹

ABSTRACT

The volume of fecal pellets produced by the calanoid copepods *Temora turbinata* and *Eucalanus pileatus* increases with increasing weight of the copepod. Pellets produced by nauplii of *E. pileatus* are eaten by adult females of the same species at about the same rates as phytoplankton which has a volume similar to that of the pellets ($10^6 \mu m^3$). Pellet production rates of juveniles, being generally in the range of 80 to 120 pellets produced $\cdot$ copepod⁻¹ $\cdot$ 24 h⁻¹, change little with increasing body weight. By comparing two copepod populations it is concluded that the size distribution of feeding copepods determines the percentage of fecal matter produced which reaches the sea floor.

1. Introduction

In the marine environment nonliving particulate organic matter (detritus) generally occurs in larger concentrations than living particulate matter (Krey, 1960; Poulet, 1976). Although the availability of detritus to zooplankton has been frequently discussed, its quantitative importance as a food source has been described only twice (Petipa *et al.*, 1970; Poulet, 1976). One constituent of detritus is zooplankton fecal material, the production of which has been measured numerous times, usually under unnatural conditions (Raymont and Gross, 1942; Marshall and Orr, 1955; Corner *et al.*, 1972; Gaudy, 1974; Honjo, 1976; Reeve and Walter, 1977; Reeve *et al.*, 1977; Grice *et al.*, 1977; Honjo and Roman, 1978). Other investigations have concentrated on determining the rate of vertical transport of fecal pellets to the deep-sea with interest focused mainly on fast-sinking ($> 100 \text{ m} \cdot 24 \text{ h}^{-1}$) large pellets (Smayda, 1969, 1971; Schrader, 1971; Small and Fowler, 1972; Honjo, 1976; Wiebe *et al.*, 1976; Turner, 1977; Honjo and Roman, 1978).

Paffenhöfer and Strickland (1970) noted that *Calanus helgolandicus* ingests fecal pellets. Davies *et al.* (1973) concluded that copepods "rework" fecal pellets based on the fact that only 2 to 25% of the primary production was recovered as pellets in experimental bags while one-third recovery was obtained outside the bags. Riley (1970) stated that "they (fecal pellets) may be a source of particulate food that is

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TABLES

Table I. Summary of the conditions of the laboratory experiments. All data are the arithmetic mean $\pm$ standard error. I = I. galbana, P = P. trochoideum, NG = no growth estimates were made.

EXPERIMENT	STAGE	ZOOID CONC ($\mu\text{gC} \times 1^{-1}$) (# $\times 2.5 \times 1^{-1}$)	DURATION (days)	TEMP ($^{\circ}\text{C}$)	DIET	FOOD COL. ($\text{mm}^3 \times 1^{-1}$)
A1	<u>T. democratica</u> aggregates	190 ± 29 (29-9)	5	17.9 ± 0.2	I(NG)	0.24 ± 0.04
A2		30.2 ± 2.1 (4-2)	3	18.6 ± 0.5	I	0.34 ± 0.05
A3		159 ± 16 (61-9)	8	20.6 ± 0.2	I+P	0.38 ± 0.07
		29.7 ± 5.7 (53-8)			I(NG)	0.48 ± 0.04
A4		87.8 ± 13 (64-3)	8	20.2 ± 0.4	I+P	0.44 ± 0.1
		75.8 ± 14 (120-20)			P(NG)	0.16 ± 0.3
P1	<u>D. gegenbauri</u> phorozooids	27.3 ± 8.5 (17-17)	3	18.6 ± 0.4	I	0.37 ± 0.3
P2		23.5 ± 0.7 (10-10)	8	20.1 ± 0.2	I+P	$0.43 \pm 0.$
P3		12.4 ± 0.5 (15-12)	5	20.3 ± 0.1	I+P(NG)	$0.69 \pm 0.$
G1	<u>D. gegenbauri</u> gonozooids	25.5 ± 3.0 (10-3)	20	19.0 ± 0.6	I	0.40 ± 0.04
G2		55.0 ± 0.0 (6-2)	12	20.3 ± 0.2	I+P(NG)	0.43 ± 0.07
		55.0 ± 0.0 (4-2)			I+P(NG)	0.34 ± 0.08
O1	<u>D. gegenbauri</u> oozooids	29.8 ± 5.3 (68-5)	20	19.4 ± 0.9	I(NG)	0.34 ± 0.03
		33.2 ± 4.6 (68-4)			I(NG)	$0.32 \pm$
		39.7 ± 3.3 (65-11)			I(NG)	0.41 ± 0.0

Table II. Arithmetic mean ($\pm$ standard error) mortality rates ($\% \times 24 \text{ h}^{-1}$) of I. democratica aggregates, and D. gegenbauri gonozooids and oozoids. n = the number of mortality rates which were pooled for the calculation of the means. * = a significant difference at the 95% confidence level. NS = no significant difference at the 90% confidence level.

STAGE	MORTALITY RATE ($\bar{X} \pm \text{SE}$)	n	p
<u>I. democratica</u> aggregate	15 $\pm$ 2.5	27	
<u>D. gegenbauri</u> gonozooid	4.9 $\pm$ 3.2	17	*
oozooid	10 $\pm$ 2.7	23	NS

NS

Ta III Fecundity of the solitary stage of I. demc .tica. SE = standard error of the mean.

(---) = data not available. SOL = solitary, and AG = aggregate stages. There is no difference between seasons in the total number of aggregates released x solitary⁻¹ ($p>0.3$).

Date	Field temp. (°C)	SOL length (mm)	# of chains x SOL ⁻¹	# of AG x chain ⁻¹	AG length (mm)	Total # of AG x SOL ⁻¹
12 Jan. 77	15.2	---	1	29	1.4-2.1	29
29 June 77	28.2	8.2	1	62	---	62
		8.4	1	42	---	42
16 Sept. 77	29.3	---	1	64	2.1	64
		---	1	21	1.1	21
		---	1	42	1.4	42
		---	1	33	1.4	33
6 Oct. 77	26.0	---	2	85	---	120
		---		35	---	
		---	1	64	---	64
12 Jan. 78	19.9	---	2	44	---	88
		---		41	---	
28 Jan. 78	18.3	6.2	1	32	---	32
		6.2	1	50	---	50
Range	15.2- 29.3	6.2- 8.4	1-2	21- 85	1.1-2.1	21- 120
$\bar{X} \pm SE$	--	--	--	46±5	--	54±8

Table IV. Fecundity of the gonozooid stage of D. gegenbauri. SE = standard error of the mean. (---) = data not available. GZ = gonozooid stage. There is no effect of diet or season on the number of larvae released x gonozooid⁻¹ ($p > 0.20$). The larvae are significantly shorter during March and April ($p < 0.01$).

Date	Food	# of GZ	GZ length (mm)	# of larvae x GZ ⁻¹	Larval length (mm)
18 Mar. 77	<u>I. galbana</u>	7	3.7-3.9	2	---
		4	4.8-5.2	4	---
		3	4.9-5.6	4	---
		3	4.7-5.7	6	0.6 ± 0
		3	5.8-6.2	4	---
		5	4.9-5.0	5	0.6 ± 0
1 Apr. 77	<u>I. galbana</u>	4	3.9-6.2	3	0.6 ± 0
26 Aug. 77	<u>I. galbana</u> + <u>P. trochoideum</u>	2	---	4	1.2 ± 0.3
1 Sept. 77	<u>I. galbana</u> + <u>P. trochoideum</u>	1	6.2	2	1.0 ± 0
Range	--	--	3.7-6.2	2-6	0.6-1.2
$\bar{X} \pm SE$	--	--	--	3.8 ± 0.1	--

Table V. Daily growth coefficients ($k \times 24 \text{ h}^{-1}$) in contiguous weight classes ($\mu\text{g C}$) for T. democratica aggregates (experiments A3 and A4) and D. gegenbauri gonozooids (experiment G1). (---) = no coefficients available for zooids of that weight class. SE = standard error of the mean. There is no difference between the mean coefficients of the three experiments ($p > 0.25$).

WEIGHT CLASS (μgC)	AGGREGATE		GONOOZOID
	A3	A4	
3.0-5.0	----	0.03 0.06 0.18	0.09 0.08
5.0-7.0	----	0.18 0.12	0.24 0.21
7.0-9.0	0.36 0.15	0.12	0.18
9.0-11	----	----	0.22
11-13	0.34	----	0.21
13-15	0.21	----	0.25
15-17	0.05 0.04 0.04	----	----
17-19	----	----	----
19-21	----	----	0.08
21-23	----	----	0.11
$\bar{X} \pm \text{SE}$	0.19 $\pm$ 0.04 0.12 $\pm$ 0.04		0.17 $\pm$ 0.03

Table VI. Fecundity of the solitary stage of I. democratica. SE = standard error of the mean.

(---) Data not available

Source	Field temp. (°C)	SOL length (mm)	# of chains x SOL-1	# of AG x chain ⁻¹ range (X) ± SE	AG length (mm)	Total # of AG x SOL ⁻¹ range (X) ± SE
This report	15.2-29.3	6.2-8.4	1-2	21-85 45 ± 5	1.1-2.1	21-120 54 ± 8
Braconnot, 1963	14	10-12	2	- 32 ± 4	-	- 71 ± 13
Heron, 1972a	--	10		20-80 -	1.5-2.0	- -

Table VII Estimated generation time of T. democratica. Data are the arithmetic mean $\pm$ standard error.

	Length at birth (mm)	Length at birth of first progeny (mm)	Weight at birth (μ gC)	Weight at birth of first progeny (μ gC)	Time from initial to final weight (days)
SOLITARY	2.8 ± 0.1	7.3 ± 0.3	7.0	52	11-13
AGGREGATE	1.6 ± 0.1	5.0 (estimate)	2.1	23	8-10
GENERATION TIME					19-23

Table VIII Estimated generation time of D. gegenbauri. Data are the arithmetic mean $\pm$ standard error.

	Length at birth (mm)	Length at birth of first progeny (mm)	Weight at birth (μ gC)	Weight at birth of first progeny (μ gC)	Time from initial to final weight (days)
OOZOOID	0.8 ± 0.1	8.0 (estimate)	0.5	63	13-15
PHOROZOOID	2.5 (est.)	7.5 ± 1.0	5.5	55	8-12
GONOOZOOID	0.8 ± 0.1	5.1 ± 0.1	0.5	24	8-14
GENERATION TIME					29-41

FIGURE LEGENDS

Figure 1. Weight versus length for I. democratica aggregates. Each point is a mean of measurements of 2 to 5 zooids. The power function is $W = 0.8L^{2.1}$ ($n = 49$, $R^2 = 79\%$, $p < 0.001$). The equation was calculated by the natural log transform method of Draper and Smith (1966).

Figure 2. Mean ($\pm$ standard error) daily mortality rate versus time since release for I. democratica aggregates ($\blacksquare$) and all D. gegenbauri zooids (x). Since there was no difference between gonozooid and oozooid mean mortality rates, these data were pooled. 2 to 4 observations were pooled for the calculation of each aggregate mean, and 3 to 5 observations for each doliolid mean. Doliolid mortality is time independent ($p > 0.25$). The aggregate regression equation is:

$$MR = 2.44T + 0.85 \quad (n = 28, R^2 = 20\%, p < 0.05).$$

Figure 3. Zooid weight versus time since release. Weight was plotted only for those populations with less than 15% daily mortality.

($\bullet$) - I. democratica aggregates (experiment A3, I + P - Table 1). $\log_{10} W = 0.07T + 0.72$ ($n = 8$, $R^2 = 90\%$, $p < 0.001$).

(O) - I. democratica aggregates (experiment A4, I + P - Table 1). $\log_{10} W = 0.06T + 0.45$ ($n = 7$, $R^2 = 96\%$, $p < 0.001$).

(x) - D. gegenbauri gonozooids (experiment G1, I - Table 1). $\log_{10} W = 0.06T + 0.35$ ($n = 11$, $R^2 = 96\%$, $p < 0.001$).

LABORATORY MEASURED GRAZING AND INGESTION
RATES OF THE SALP, Thalia democratica FORSKAL,
AND THE DOLIOLID, Dolioletta gegenbauri ULJANIN
(TUNICATA, THALIACEA)

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Running Head: Grazing and ingestion rates of Thalia and Dolioletta

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ABSTRACT

Grazing and ingestion rates of laboratory born Thalia democratica aggregates and Dolioletta gegenbauri gonozooids, phorozoids and oozoids were determined while fed Isochrysis galbana (4-5 μ m diameter) alone or I. galbana and Peridinium trochoideum (16-18 μ m diameter) in combination at concentrations of 0.15 to 0.70 $\text{mm}^3 \times 10^{-1}$. Grazing rates ($\text{ml} \times \text{zoid}^{-1} \times 24 \text{ h}^{-1}$) ranged from 10 to 355 and at zoid weights greater than 5 μ g carbon were in the order oozoid > gonozoid > aggregate. Grazing rates increased exponentially with increasing zoid weight. Weight-specific grazing rates ($\text{ml} \times \mu\text{gC}^{-1} \times 24 \text{ h}^{-1}$) were independent of the fourfold initial food concentration. Mean weight-specific grazing rates increased linearly with increasing zoid weight for the aggregates and oozoids but the gonozoid mean rates were independent of zoid weight. Aggregate and gonozoid ingestion rates ($10 \mu\text{m}^3 \times \text{zoid}^{-1} \times 24 \text{ h}^{-1}$) ranged from 4 to 134 while oozoid rates ranged from 3 to 67. All ingestion rates were independent of the initial food concentration but increased linearly with increasing zoid weight at similar rates for all zooids. All mean weight-specific ingestion rates ($\text{ml} \times \mu\text{gC}^{-1} \times 24 \text{ h}^{-1}$) were independent of zoid weight. The mean aggregate daily ration ($\mu\text{gC ingested} \times \mu\text{g body C}^{-1}$) was 59% and the mean doliolid ration was 132%. Based on field and laboratory studies it is estimated that normal concentrations of D. gegenbauri in the Georgia Bight clear their resident water volume (1 m³) in about 5 months but that highly concentrated, swarm populations which occur along thermohaline fronts clear their resident water volume in less than 1 day.

INTRODUCTION

In coastal waters off the southeastern United States the concentration of thaliaceans ranges from less than $20 \times 10^{-3} \text{ m}^{-3}$ to over $3000 \times 10^{-3} \text{ m}^{-3}$. Highest concentrations are associated with mid-shelf thermohaline fronts (Atkinson, et al., 1978; Deibel, 1980). The two dominant thaliaceans in the Georgia Bight are Thalia democratica and Doliioletta gegenbauri. These species range in length from 1.0 to 15 mm, and in weight from about 2.0 to 300 μg carbon. Salps graze small particles ($< 1 \mu\text{m}$ in diameter) at high rates ($> 1 \text{ l} \times \text{h}^{-1}$), using an efficient and continuously produced internal mucus net (Madin, 1974; Harbison and Gilmer, 1976). Though Thalia and Doliioletta often dominate macrozooplankton biomass and numbers (Thompson, 1948; Braconnot, 1971a, b; Atkinson, et al., 1978) their role in the tropho-dynamics of neritic waters has been given limited attention. Knowledge of the grazing performance of the various life-history stages of T. democratica and D. gegenbauri is essential to understand the transfer of materials in neritic plankton communities.

Small particle retention by oceanic salps has been studied (Silver, 1971; Braconnot, 1971b; Harbison and Gilmer, 1976; Harbison and McAlister, 1979) but there is little information on feeding by coastal species. Oceanic salps retain small particles which adhere to the mucus feeding net (Madin, 1974; Harbison and Gilmer, 1976). The maximum size of ingestible particle is not known but presumably is constrained by mouth diameter (Silver, 1971; Deibel, unpublished). Although net-collected salps often do not feed in culture due to damage during collection or to collisions with vessel walls (Silver, 1971;

Pavlova, et al., 1973) salp filtration rates have been found to range from 2 to 300 $\text{l} \times \text{zooid}^{-1} \times 24 \text{ h}^{-1}$, increasing exponentially with increasing body length (Silver, 1971; Harbison and Gilmer, 1976).

Filtration rates are not affected by changes in food concentration.

Salps have higher weight-specific grazing rates ($\text{ml} \times \mu\text{gC}^{-1} \times 24 \text{ h}^{-1}$) than ascidians, ranging from 2 to 50 (Harbison and Gilmer, 1976).

Salp weight-specific grazing rates increase with increasing body weight in contrast to the rates of ascidians which decrease. Neritic salps and doliolids feed at higher rates during the night than in the daytime and there is no particle selection in the range of 6 to 14 μm diameter (Braconnot, 1971b). There may be fundamental differences in the feeding performances of salps and doliolids due to differences in mechanisms used to pump water. Salps contract circumferential muscle bands and swim continuously to feed and respire. Doliolids utilize stigmatal cilia to pump water and are usually motionless while feeding.

Comprehensive field and laboratory studies of neritic thaliacean feeding are essential to define the role of salps and doliolids in particle consumption in continental shelf ecosystems. The laboratory experiments reported were designed to answer the following questions:

(1) What are the range of grazing ($\text{ml} \times \text{zooid}^{-1} \times 24 \text{ h}^{-1}$) and ingestion ($10 \mu\text{m} \times \text{zooid}^{-1} \times 24 \text{ h}^{-1}$) rates of the various life-history stages?

(2) How do these rates change as the zooids grow?

(3) How do the weight-specific grazing ($\text{ml} \times \mu\text{gC}^{-1} \times 24 \text{ h}^{-1}$) and ingestion ($10 \mu\text{m} \times \mu\text{gC}^{-1} \times 24 \text{ h}^{-1}$) rates change as the zooids grow?

Do changes indicate fundamental differences in salp and doliolid feeding performance due to known differences in feeding mechanisms?

(4) How does weight-specific ingestion (i.e., the daily ration) change as zooids grow?

(5) Given the known concentrations, life-history stages, and sizes of thaliaceans in the Georgia Bight (Deibel, 1980) what is the grazing pressure ($\text{ml} \times \text{population}^{-1} \times 24 \text{ h}^{-1}$) of naturally occurring salp and doliolid populations?

METHODS

Thaliaceans were collected from outer continental shelf waters off the coast of Georgia, U.S.A. and were reared in the laboratory (Deibel, 1980). Grazing rates were determined while thaliaceans were fed Isochrysis galbana Parke (4.0-6.0 μm diameter) at 0.15 to 0.70 $\text{mm}^3 \times \text{l}^{-1}$ concentration. Grazing rates were also determined while thaliaceans were simultaneously fed I. galbana and Peridinium trochoideum Lemmermann (16-18 μm diameter).

Feeding studies were conducted with zooids which were released in the laboratory from net-collected parents (Table 1). Feeding rates were monitored daily beginning 24 to 48 h after release. Measurements were terminated when mortality exceeded 15% $\times 24 \text{ h}^{-1}$, 8 to 15 days later. Grazing rates were estimated by the difference between particle concentrations at the beginning and end of a feeding interval using a Coulter Counter model TA II. Particles in the I. galbana channels were counted with coefficients of variation (precision) of 1 to 10%. Feeding intervals ranged from 18 to 26 h and included day and night periods to integrate over possible diel grazing rate differences (Braconnot, 1971b). At the end of each interval, thaliaceans were transferred to a fresh food suspension and the next feeding interval was initiated.

Increases in cell numbers in the phytoplankton suspensions were estimated from paired control bottles without thaliaceans. The presence of the tunicates was assumed not to alter phytoplankton growth over the short feeding intervals. Feeding over each interval reduced the total particle concentration 5 to 30% in doliolid experiments and 10 to 60% in experiments with salps (see Results).

Phytoplankton growth constants in the control bottles ($\mu \times 24$ h⁻¹), thaliacean grazing (ml x zooid⁻¹ x 24 h⁻¹), and ingestion ($10^6 \mu\text{m}^3 \times 24 \text{ h}^{-1}$) rates were calculated using the equations of Frost (1972) and Harbison and Gilmer (1976). Growth constants were calculated for each Coulter Counter channel covering the size range of particulate food. Background counts were less than 5% of the particle numbers so no subtractions were made. Although algal growth constants were often an order of magnitude lower than thaliacean grazing rates they were routinely subtracted in calculating grazing rates. Zooids which died during a feeding interval were assumed not to have fed over that interval (Mullin and Brooks, 1970). Variability in grazing rates was without an apparent trend between contiguous channels covering the size ranges of I. galbana and P. trochoideum. Therefore a mean grazing rate was calculated using rates from all channels containing at least 10% of the total particle volume. Accuracy of the Coulter Counter was monitored frequently with inverted microscope counts of the food suspension.

RESULTS

Although the Coulter Counter slightly underestimated true particle numbers, regression coefficients between cell concentrations determined with the counter (CC in particles x ml⁻¹) and with the inverted

microscope (IM) were not significantly different from 1.0;

$$CC = 0.95(IM) - 224 \quad (N = 6, r = 0.97, p > 0.50). \quad (1)$$

Assuming that the inverted microscope reflects true particle numbers, this indicates that the Coulter Counter yielded accurate estimates of particle concentration for I. galbana at concentrations up to 16,000 cells x ml⁻¹.

Grazing Rates

There was no significant difference between I. democratica aggregate mean grazing rates when fed I. galbana or P. trochoideum (Table 2); an observation which was supported by several single measurements from two other feeding experiments. Thus, grazing rates of both phytoplankters were pooled for further analyses. Due to the morphological similarity of gonozooids and phorozoids of D. gegenbauri, and to the small number of phorozoids observed, all gonozooid and phorozoid data were combined. In the following discussion this group will be referred to as gonozooids. Aggregate grazing rates ranged from 13 to 305, D. gegenbauri gonozooid rates from 10 to 335, and D. gegenbauri oozoid rates from 14 to 355 ml x zooid⁻¹ x 24 h⁻¹ (Figure 1). The grazing rates of all three life-history stages are logarithmic functions of zooid weight. Since no oozoids of greater than 11 µgC were observed in the feeding experiments, aggregate and gonozooid regression equations were recalculated using data from the same weight range. These equations are not shown. Over the 0-11 µgC weight range there is a significant difference ($p < 0.001$) between the aggregate regression coefficient (0.07, $n = 20$) and the oozoid coefficient (0.14, $n = 18$), but no difference ($p > 0.20$) between the oozoid and gonozooid (0.11, $n = 13$) coefficients. However, gonozooid grazing rates were initially higher

than those of oozoids ($p < 0.001$). Over the entire 0 to 20 μgC weight range the gonozoid intercept is significantly greater ($p < 0.01$) than the aggregate intercept (1.16). This indicates that at weights greater than 5 μgC grazing rates of the three life-history stages are in the order oozoid > gonozoid > aggregate.

Grazing rates were corrected by calculating the weight-specific rates shown in Figure 2. Weight-specific grazing rates ranged from 1 to 13 $\text{ml} \times \mu\text{gC}^{-1} \times 24\text{h}^{-1}$ for aggregates, from 3 to 30 for the gonozoids and from 6 to 33 for the oozoids. Weight-specific rates were independent of the fourfold range in initial food concentration ($p > 0.10$).

I. democratica aggregates are released from the solitary stage in chains of 21 to 85 zooids (Deibel, 1980). Breaking these chains damages individual zooids. Thus, complete chains were used in the feeding experiments often resulting in excessive decreases in food concentration over 24h feeding intervals. Since decreased food concentration may alter grazing rates, the weight-specific grazing rates were screened for dependence on food concentration using regression analysis of variance (Figure 3). No dependence of aggregate and gonozoid weight-specific grazing on food concentration was apparent, but 28% of oozoid weight-specific grazing rate variability was related to decreases in food concentration. However, since the range of oozoid weight-specific grazing rate was only twofold between food concentration decreases of greater than or less than 30%, all oozoid grazing rate data were used in subsequent analyses.

By pooling grazing rate estimates from contiguous 1 μgC weight classes, mean weight-specific grazing rates can be calculated. Size class mean aggregate and oozoid weight-specific rates depended

on zooid weight but gonozooid rates were weight independent (Figure 4). Aggregate and oozooid size class mean rates increased with increasing zooid weight, ranging from 6 to 15 $\text{ml} \times \mu\text{gC}^{-1} \times 24 \text{ h}^{-1}$ for aggregates and from 10 to 33 for oozooids. The grand mean gonozooid weight-specific grazing rate, computed over all size classes, was 17.0 ± 1.6 ($\pm \text{SE}$).

Ingestion Rates

Aggregate ingestion rates ranged from 4 to 112 $10^6 \mu\text{m}^3 \times \text{zooid}^{-1} \times 24 \text{ h}^{-1}$, gonozooid rates from 5 to 134 and oozooid rates from 3 to 67 (Figure 5). Ingestion rates of all three stages were independent of the initial food concentration but were dependent on zooid weight. Over the weight range of 0 to 11 μgC , the aggregate regression coefficient (1.85) was significantly lower ($p < 0.001$) than the oozooid coefficient (6.64), but the oozooid and gonozooid equations were colinear ($p > 0.10$). Over the full 20 μgC weight range (Figure 5), aggregate and gonozooid regression coefficients were not significantly different, but the gonozooid intercept was significantly greater ($p < 0.01$) than the aggregate intercept. At a given weight, aggregate ingestion rates were lower than gonozooid and oozooid rates and the ingestion rates of all life-history stages increased with increasing zooid weight at similar rates.

Doliolid and aggregate mean weight-specific ingestion rates (Figure 6) were independent of zooid weight. Aggregate weight-specific ingestion ranged from 1.7 to 6.0 $10^6 \mu\text{m}^3 \times \mu\text{gC}^{-1} \times 24 \text{ h}^{-1}$, and doliolid rates ranged from 4.0 to 8.0. Since mean weight-specific ingestion rates were independent of zooid weight data from all weight classes were pooled and grand means calculated. The

aggregate grand mean ($\pm$ SE) weight-specific ingestion rate (2.8 ± 0.5 , $n = 25$) is significantly lower ($p < 0.001$) than the grand mean doliolid ingestion rate (6.3 ± 0.4 , $n = 40$).

DISCUSSION

Grazing Rates

Thaliacean grazing rates (Figure 1) are similar to those of large calanoid copepods (Paffenhöfer, 1971; Corner, et al., 1972) but are lower than those of larger, oceanic salps (Harbison and Gilmer, 1976; Harbison and McAlister, 1979). In my experiments, net-collected, adult aggregates decreased their grazing rates with time, indicating deleterious effects of capture or containment, which agrees with other studies of net-collected thaliaceans (Silver, 1971; Heron, 1972a; Harbison and Gilmer, 1976). However, I found that laboratory released zooids had linear increasing grazing rates over 7 to 14 days, indicating that they maintained vitality at a relatively constant level. The use of laboratory released zooids is an alternative method to hand collection for procuring undamaged zooids.

Thaliacean grazing rates depended on zooid weight, as is common among oceanic salps (Harbison and Gilmer, 1976), appendicularia (Paffenhöfer, 1976a) and copepods (Paffenhöfer and Harris, 1976). Aggregate weight-specific grazing rates increased with increasing zooid weight (Figure 4), supporting observations of the oceanic salp, Pegea confederata (Harbison and Gilmer, 1976). This contrasts with ascidians (Harbison and Gilmer, 1976) and calanoid copepods (Mullin and Brooks, 1970; Paffenhöfer, 1971) which decrease weight-specific grazing rate with increasing weight. Harbison and Gilmer (1976) hypothesized that

muscular-driven water pumping and continuous swimming allow salps to filter exponentially increasing volumes of water as they grow. Unlike salps, doliolids and ascidians pump water by ciliary mechanisms. Gono-zooids swim briefly to escape physical assault, e.g., contact with other zooplankton or rigid surfaces. Thus, one expects doliolids to resemble ascidians more than salps, i.e., doliolids should have decreasing weight-specific grazing rates with increasing zooid weight. This was not the case. Rather, oozoids increased weight-specific grazing rates with increasing weight and gonozooid rates were unrelated to increasing weight. These relations support the hypothesis of Harbison and Gilmer (1976) that planktonic tunicates may derive increased grazing efficiency as they grow by being able to move through the water. My notion that doliolids may be similar to the muco-ciliary feeding ascidians may be false since doliolids also move through the water, although aperiodically in comparison to salps.

Increasing grazing rates with a decrease in food concentration is common in appendicularia (Paffenhöfer, 1976a) and several copepods (Mullin, 1963; Anraku, 1964; Paffenhöfer, 1971, 1976b, c; Frost, 1972). Evidently, oceanic salps are unable to adjust grazing rates to changing food concentration (Silver, 1971; Harbison and Gilmer, 1976; Madin, 1974). In my study the grazing rates of all thaliaceans were independent of food concentration changes (Figure 2). This evidence supports the unmodulated feeding behavior of salps which may explain the exclusion of most salps from particle rich coastal and estuarine waters (Harbison and Gilmer, 1976).

Although oceanic salps have greater weight-specific grazing rates than do ascidians (Harbison and Gilmer, 1976), the rates of salps,

doliolids, appendicularians and copepods are similar (Table 3). There is only a 25 fold range in weight-specific grazing rate ($2-52 \text{ ml} \times \mu\text{gC}^{-1} \times \text{individual}^{-1}$) over a 900 fold range of zooplankton weight ($2-1800 \mu\text{gC} \times \text{individual}^{-1}$). Even though this similarity exists, a single, large, oceanic salp can have the grazing impact of ten to a hundred copepods due to its great weight (Harbison and Gilmer, 1976). Also, thaliaceans can have a pronounced impact on small cells due to efficient small particle retention.

Ingestion Rates

Ingestion rates were independent of the 4 fold range in initial food concentration indicating that grazing rates may be inversely related to food concentration. However, variability in grazing rates from separate replicate experiments masks possible inverse relations between grazing rates and food concentration (Figure 2).

Thaliacean ingestion rates depended on zooid weight (Figure 5), as has been observed for other zooplankton (Mullin and Brooks, 1970; Paffenhöfer, 1971; Paffenhöfer and Harris, 1976; Paffenhöfer and Knowles, 1978a, b). Since weight-specific ingestion rates are independent of zooid weight (Figure 6) as weight increases, the daily ration ($\mu\text{gC ingested} \times \mu\text{g body C}^{-1}$) must remain constant. Such observations also have been made of two copepod species (Paffenhöfer and Harris, 1976; Harris and Paffenhöfer, 1976).

Using the mean weight-specific ingestion rates for aggregates and doliolids (Figure 6), and the following equation to convert the food volume of Isochrysis galbana to carbon, one can compute the mean daily ration.

$$C(\mu\text{g}) = 211(V, \text{mm}^3) - 1.31 \quad (n = 13, r = 0.99) \quad (2)$$

The aggregate mean daily ration was 59%, and the doliolid mean daily ration was 132%. There are no comparable ration data for any thaliacean although these values are similar to those of appendicularia (Paffenhöfer, 1976a) and copepods (Paffenhöfer, 1971, 1976b; Paffenhöfer and Knowles, 1978a,b; Paffenhöfer and Harris, 1976) determined at similar food concentrations. Although the difference between the aggregate and doliolid daily rations may represent true biological differences between these species in feeding mechanism, a degree of uncertainty is introduced into the computation of the doliolid ration because of the necessity of estimating doliolid weight from the aggregate length-weight regression (Deibel, 1980).

To estimate the population grazing rate of Dolioletta the following calculations were made. In non-swarm conditions there are approximately $25 \text{ zooids} \times \text{m}^{-3}$ with a known life-history stage and size-class composition (Deibel, 1980). Since grazing rates were not determined for the largest zooid size classes in the field populations, a median weight-specific grazing rate of $20 \text{ ml} \times \mu\text{gC}^{-1} \times 24 \text{ h}^{-1}$ was chosen (Figure 4) as the best estimate for all size classes. Some inaccuracy results but this is sufficient for a first estimate. The median grazing rate was multiplied by the biomass in each size class and then the individual size class grazing rates were summed over all classes to arrive at a population grazing rate estimate. These $25 \text{ zooids} \times \text{m}^{-3}$ sweep clear $8 \text{ l} \times 24 \text{ h}^{-1}$, or their resident water volume (i.e., 1 m^3) each 125 days. In doliolid "swarms" gonozooids often number more than $3000 \times \text{m}^{-3}$. This swarm population sweeps clear $1142 \text{ l} \times 24 \text{ h}^{-1}$, or its resident water volume every 21 h. Since swarms may persist for days and possibly for weeks (Deibel, 1980) phytoplankton

must double their number each day simply to maintain the food supply for the doliolid population. This production can only occur through phytoplankton reproduction or by the advection of phytoplankton and non-living particulate matter into the swarm area from a surrounding zone of higher particle concentration.

In summary, (1) net-collected zooids could not be used for feeding studies because of decreasing grazing rates with time. Instead, laboratory released offspring were successfully maintained and studied for weeks; (2) grazing rates increased exponentially with increasing zooid weight, while ingestion rates increased linearly with increasing zooid weight. Rates compared to those reported for large calanoid copepods but were less than those of larger oceanic salps; (3) weight-specific grazing rates were a linear function of increasing zooid weight for oozoids and aggregates, but were constant for gonozooids. Weight-specific rates are similar to those of a wide range of copepods and tunicates; (4) daily rations, in terms of carbon, were independent of increasing zooid weight and were lower for Thalia than for Dolioletta; (5) non-swarm concentrations of doliolids clear their resident water volume in about 5 months, but during swarms they clear their resident water volume in less than 24 h.

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TABLES

Table 1. A summary of the conditions of the laboratory experiments. All data are the arithmetic mean $\pm$ standard errors. I = *I. galbana*, P = *P. trichoides*, NG = no growth estimates were made.

EXPERIMENT	STAGE	ZOOID CONC. ($\times 10^3 \pm 1$) ($\times 2.5 \pm 1$)	DURATION (days)	TEMP (°C)	DIE	FOOD CONC. ($\times 10^3 \pm 1$)
A1	<i>I. democratica</i> aggregates	190 $\pm$ 25 (29-9)	5	17.9 $\pm$ 0.2	I(NG)	0.24 $\pm$ 0.04
A2		30.2 $\pm$ 2.1 (4-2)	3	18.6 $\pm$ 0.5	I	0.34 $\pm$ 0.05
A3		159 $\pm$ 16 (61-9)	5	20.6 $\pm$ 0.2	I+P	0.38 $\pm$ 0.07
		29.7 $\pm$ 5.7 (53-8)			I(NG)	0.48 $\pm$ 0.04
A4	<i>D. gegenbaumi</i> phorozooids	67.8 $\pm$ 13 (14-3)	8	20.2 $\pm$ 0.4	I+P	0.44 $\pm$ 0.04
P1		27.3 $\pm$ 8.5 (17-17)	3	18.6 $\pm$ 0.4	I	0.37 $\pm$ 0.05
P2		23.5 $\pm$ 0.7 (10-10)	8	20.1 $\pm$ 0.2	I+P	0.43 $\pm$ 0.06
P3		12.4 $\pm$ 0.5 (15-12)	5	20.3 $\pm$ 0.1	I+P(NG)	0.69 $\pm$ 0.05
G1	<i>D. gegenbaumi</i> gonozooids	25.5 $\pm$ 3.0 (10-3)	20	19.0 $\pm$ 0.6	I	0.40 $\pm$ 0.04
G2		55.0 $\pm$ 0.0 (6-2)	12	20.3 $\pm$ 0.2	I+P(NG)	0.43 $\pm$ 0.07
		55.0 $\pm$ 0.0 (4-2)			I+P(NG)	0.34 $\pm$ 0.05
O1	<i>P. gegenbaumi</i> oozooids	29.6 $\pm$ 5.3 (66-5)	20	19.4 $\pm$ 0.9	I(NG)	0.34 $\pm$ 0.03
		33.2 $\pm$ 4.6 (66-4)			I(NG)	0.32 $\pm$ 0.04
		36.7 $\pm$ 3.3 (55-11)			I(NG)	0.41 $\pm$ 0.04

Table II. Mean grazing rates ($\text{ml} \times \text{zoid}^{-1} \times 24 \text{ h}^{-1}$) of I. galbana and P. trochoideum by T. democratica aggregates.
 NS = difference not significant at the 95% confidence level.
 The means were compared by one-way ANOVA. SE = standard error of the mean.

FOOD	GRAZING RATE ($\bar{X} \pm \text{SE}$)	n	$F_{1,11}$
<u>I. galbana</u>	38.4 ± 5.3	7	0.36 (NS)
<u>P. trochoideum</u>	33.8 ± 5.7	6	

Table III. Weight-specific grazing rates of assorted marine zooplankton. Food concentrations were between 20 and 200 $\mu\text{gC} \times \text{l}^{-1}$ for all studies except Harbison and Gilmer (1976), which was from 200 to 1400 $\mu\text{gC} \times \text{l}^{-1}$. AG = aggregate stage, SOL = solitary, GZ = gonozoid, and OZ = oozoid.

Organism	Stage	Temp. (°C)	Length (mm)	Weight (μgC)	Weight-Specific Grazing Rate ($\text{ml} \times \mu\text{gC}^{-1} \times 24\text{h}^{-1}$)	Source
<u>C. helgolandicus</u>	-	15	-	10 80	19 10	Paffenhöfer, 1971
<u>P. elongatus</u>	-	12.5	-	4.0	8.0 52	Paffenhöfer and Harris, 1976
<u>T. longicornis</u>	-	12.5	-	4.0	11 32	Harris and Paffenhöfer, 1976
<u>O. dioica</u>	-	13	-	4.0 8.0	27 38 32 44	Paffenhöfer, 1976a
<u>P. confederata</u>	AG	25-29	15 50	106 1416	2.0 38	Harbison and Gilmer, 1976
	SOL		15 50	242 1821	4.0 8.0	
<u>T. democratica</u>	AG	20	2.7 3.3 4.2	6.4 9.8 16	7.0 9.0 12	This study
<u>D. gegenbauri</u>	GZ	20	1.7-4.9	2.4-23	$17 \pm 1.6(\bar{X} \pm \text{SE})$	
	OZ	20	1.4 2.5 3.4	1.5 5.5 10.5	8.0 17 28	

FIGURE LEGENDS

Figure 1. Grazing rate versus weight for T. democratica aggregates and D. gegenbauri gonozooids and oozooids. All points are means $\pm$ standard error. Grazing rates were calculated only for those days with mortality rates of less than 15%. The regression equations are:
 Aggregates ($\bullet$ — $\bullet$), $\log_{10}GR = 0.07W + 1.16$ ($n = 25$, $R^2 = 85\%$, $p < 0.001$).
 Gonozooids ($\blacksquare$ -- $\blacksquare$), $\log_{10}GR = 0.06W + 1.50$ ($n = 23$, $R^2 = 58\%$, $p < 0.001$).
 Oozooids (x --- x), $\log_{10}GR = 0.14W + 1.07$ ($n = 18$, $R^2 = 88\%$, $p < 0.001$).

Figure 2. Weight-specific grazing rate versus the initial food concentration for T. democratica aggregates ($\bullet$), D. gegenbauri gonozooids ($\circ$), and oozooids (x). Rates are independent of the initial food concentration ($p > 0.10$).

Figure 3. Weight-specific grazing rate versus the % food concentration decrease for T. democratica aggregates ($\bullet$), D. gegenbauri gonozooids ($\circ$), and oozooids (x). The % food concentration decrease = $\{(\text{initial food concentration} - \text{final food concentration}) \div (\text{initial food concentration})\} \times 100\%$. The aggregate and gonozooid rates are independent of the food concentration decrease ($p > 0.05$) but R^2 for the oozooids = 28%, and the regression coefficient is significantly different from zero ($p < 0.05$).

Figure 4. Mean ($\pm$ standard error) weight-specific grazing rates versus zooid weight. From 2 to 5 values were pooled for the calculation of each mean. Points without error bars were single observations for that weight class. The regression equations are:

Aggregates ($\bullet$ — $\bullet$) $WSGR = 0.42W + 5.16$ ($n = 12$, $R^2 = 59\%$, $p < 0.01$).

Oozooids (x -- x) $WSGR = 2.22W + 5.07$ ($n = 8$, $R^2 = 81\%$, $p < 0.01$).

The gonozooid ($\blacksquare$) mean rates are independent of zooid weight ($p > 0.10$).

The grand mean for this group is $17.0 \pm 1.6 \text{ ml} \times \mu\text{gC}^{-1} \times 24 \text{ h}^{-1}$ ($n = 23$).

Figure 5. Ingestion rate versus zooid weight for T. democratica aggregates (●—●), and D. gegenbauri gonozooids (■--■), and oozooids (x---x).

The regression equations are:

Aggregates IR = $4.43W - 10.4$ ($n = 25$, $R^2 = 76\%$, $p < 0.001$).

Gonozooids IR = $4.51W + 14.5$ ($n = 22$, $R^2 = 41\%$, $p < 0.01$).

Oozooids IR = $6.64W - 3.18$ ($n = 18$, $R^2 = 85\%$, $p < 0.001$).

Figure 6. Mean ($\pm$ standard error) weight-specific ingestion rate versus zooid weight. (●) = T. democratica aggregates, and (x) = all D. gegenbauri zooids. All rates are independent of zooid weight ($p > 0.05$).

The grand mean ($\pm$ standard error) for the aggregates is 2.8 ± 0.5

($n = 25$), and for the doliolids it is $6.3 \pm 0.4 \cdot 10^6 \mu\text{m}^3 \times \mu\text{gC}^{-1} \times 24 \text{ h}^{-1}$ ($n = 40$).

NITROGEN REGENERATION BY THE SUBTROPICAL
MARINE COPEPOD EUCALANUS PILEATUS¹

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Marine Copepod Eucalanus pileatus

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ABSTRACT

Ammonium release rates by individual marine copepods (Eucalanus pileatus) were examined kinetically over successive 10-min intervals after exposing the animals to three concentrations of the diatom Thalassiosira fluviatilis as food. Food concentrations spanned those expected in the natural environment. "Well-fed" ($3 \text{ mm}^3 \text{ T. fluviatilis liter}^{-1}$) copepods released ammonium significantly ($p < 0.05$) faster than those fed zero or low concentrations of food, but differences were not dramatic. Mean excretion rates ($\pm \text{SE}$) for animals removed from food for 18-22 h [$30 \pm 6 \text{ nmoles NH}_4 \text{ (mg ash free dry weight)}^{-1} \text{ h}^{-1}$] were about 60% of those for "well-fed" animals [$49 \pm 8 \text{ nmoles NH}_4 \text{ (mg ash free dry weight)}^{-1} \text{ h}^{-1}$]. Depending on food concentration, animals released ammonium at rates ranging from 40 to greater than 100% of their N ingestion rates over the previous 18-22 h. Long-term (4 to 6h) kinetic excretion experiments with "well-fed" animals indicated that, on the average, release rates decreased with time after food removal, but patterns varied among individual copepods. In addition to ammonium release, o-phthalaldehyde reactive amino acid nitrogen was occasionally released by E. pileatus in large "spurt events" lasting from 20 to 60 min.

INTRODUCTION

Nitrogen in food ingested by copepods is incorporated for growth and reproduction, released in soluble form, egested in fecal pellets, or lost as molted exoskeletal or other materials. The percentage of ingested nitrogen incorporated into body tissue of copepods can range from a negative value (loss) to 49.2 depending on the ration (Corner et al. 1976). Thus, considerable amounts (often more than 50%) of ingested nitrogen are released by the feeders. Several studies have indicated that increases in food levels are accompanied by increases in dissolved nitrogen release rates (Corner et al. 1972; Takahashi and Ikeda 1975; Corner et al. 1976; Nelson et al. 1979). Although organic compounds such as urea (Corner and Newell 1967; Eppley et al. 1973; Corner et al. 1976; Smith 1978) and amino acids (Johannes and Webb 1965; Webb and Johannes 1967; Kremer 1977) account for a portion of nitrogen released by marine invertebrates, ammonium is thought to be the primary form of dissolved nitrogen released by zooplankters (Corner et al. 1972; Corner et al. 1976; Gardner and Miller 1981). Release of ammonium by copepods is relevant to marine ecosystem dynamics both because it is the preferred form of nitrogen for phytoplankton uptake and because regenerated nitrogen is essential to maintaining phytoplankton production in regions of nitrogen limitation (McCarthy and Goldman 1979). Except for studies involving special precautions (Peters and Rigler 1973; Takahashi and Ikeda 1975; Lehman 1980; Gardner and Scavia 1981), previous zooplankton excretion experiments have tended to underestimate natural rates of nutrient release, either because nutrients were taken up by phytoplankton during incubation or because partially starved animals were used (Takahashi and Ikeda 1975).

✓ In this study, we hypothesized that ammonium excretion by feeding copepods may account for a large portion of ingested nitrogen and that excretion rates may be directly related to food supply. To consider the effects of food on the magnitude and kinetics of nitrogen regeneration, we measured ammonium release rates for the subtropical marine copepod Eucalanus pileatus as a function of food concentration, ingestion rate, and time after food removal. Individuals were used to provide information on time-related patterns as well as magnitude of ammonium release. Amino acid release patterns were observed, but not quantified, for several hours after food removal on animals fed relatively high levels of food. ✓

METHODS

The Eucalanus pileatus (1 copepodid Stage V and 28 adult females) used for this study were either collected from the Atlantic Ocean in coastal waters offshore from Savannah, Ga., or reared from eggs in the laboratory (Paffenhöfer and Knowles 1978). They were maintained at 20°C on a diet of 1.0 to 1.5 mm³ Thalassiosira fluviatilis liter⁻¹ for 1 to 2 weeks before experiments. The animals were contained in sea water in a closed bottle attached to a rotating wheel (1 rpm). Animals were of uniform size [$\bar{x} + SD = 75 \pm 14$ µg ash free dry weight (AFDW), N = 29] and all appeared healthy during experiments. Before nitrogen release experiments, the copepods (4 animals for each food level bottle) were maintained for 18 to 22 h in 960 ml volumes of aged sea water supplemented with various concentrations of food (0, 0.3, 1.0, and 3.0 mm³ T. fluviatilis liter⁻¹) to simulate the range of phytoplankton concentrations in upwellings on the southeastern shelf of

the U.S.A. (Paffenhöfer et. al. 1980). Except for the unfed animals, all individuals had green guts at the beginning of ammonium release experiments. Ammonium release rates for individual copepods were measured kinetically (Gardner and Scavia 1981) over five successive 10-min intervals after food removal. Ammonium (and amino acid) release rate patterns of six animals exposed to high food concentrations (3 mm^3 T. fluviatilis liter⁻¹) before incubation were monitored at 10-min intervals for more than 4 h after food removal to provide detailed information on nutrient release over extended periods.

Ammonium release rates were estimated by measuring the quantity of ammonium accumulated over discrete periods (10 min) by individual animals in incubation flow cells (0.05 ml). The cell was initially purged with fresh sea water (1.1 ml min^{-1} for 1.5 min) to clear original culture water from the system. At 10-min intervals thereafter, the water in the cell was automatically displaced with fresh sea water and injected into an analyzer for ammonium and amino acid release measurements (Gardner and Scavia 1981). The ammonium analyzer separated ammonium from amino acids by cation exchange chromatography and reacted the isolated compounds with o-phthalaldehyde to form fluorescent derivatives (Gardner 1978). For this study, two incubation cells with corresponding analytical systems were operated in parallel (a Beckman 420 microprocessor controlled both units simultaneously). Animals from each feeding treatment were examined with both systems.

The effects of food concentrations, time after food removal, and analytical system on excretion rates were statistically evaluated for the 50-min experiments using a two-factor ANOVA with repeated measure (Winer 1971; Dixon and Brown 1979).

Mean zooplankton food ingestion rates for the different food concentrations were calculated from mean phytoplankton biomass removed from the feeding bottles (mm^3 T. fluviatilis liter^{-1} ; Coulter Counter method of Paffenhöfer 1971), a nitrogen conversion factor of $1.14 \mu\text{g-atm N per mm}^3$ T. fluviatilis, and the mean mg AFDW of experimental animals at each food level.

RESULTS AND DISCUSSION

Experimental considerations. In agreement with previous observations on Daphnia magna (Gardner and Scavia 1981), confinement in the incubation flow cells did not appear to adversely affect Eucalanus pileatus. All animals survived the experiments and appeared to be in good physiological condition after removal, even after spending more than 6 h in the cells.

Although food level experiments were designed to examine the effects of food concentration and time (for 50 min after food removal) on ammonium release rates of E. pileatus, the zero food concentrations also provided a way to differentiate "handling effects" from "food effects". Significantly ($p < 0.01$) elevated ammonium release rates were observed for all food concentrations during the first 10 min interval after removal from food (e.g., Table 1). Rates for this interval were about double the rates for the other intervals during the 50 min experiments. Because this was observed for unfed, as well as fed animals, we concluded that this initial elevated rate was likely due to experimental effects other than food; data from the first intervals were therefore not included in our excretion rate estimates. Exact reasons for these early elevated rates are unclear, but transferring animals into the flow cells may cause metabolic rates and ammonium release rates to

be increased. Alternatively the increased rates may reflect the animals' adjustments to the incubation flow cells or their reaction to the initial purging of the cells with low-nutrient sea water.

Examination of data from both analytical systems indicated that one system yielded about 30% lower excretion rates on average than the other for animals subjected to the same treatments. A posteriori considerations suggested that this apparent discrepancy was an analytical error caused by inadequate time programed for sample injection into one of the ammonium analyzers. (Appropriate injection interval is determined by ammonium analyzer buffer flow and injection loop size.) Since numbers obtained from this system therefore likely did not represent complete excretion rates, they were not included on Tables 1 and 2. However, because the injection error did not affect the relative patterns of nitrogen release for given animals, data from both analytical systems were included in our statistical treatment of food and time effect on release rates; analytical system effects were considered as the second factor in a two-factor ANOVA with one repeated measure (Winer 1971). Although rates were significantly lower for one system than the other, the ANOVA showed no evidence of interactions between system effects and either food level or time.

Ammonium release patterns. Except for the first 10-min intervals mentioned above, mean nitrogen release rates did not change significantly with time for any food concentration during the first 50 min after food removal. These results contrast with the pronounced progressively decreasing nitrogen (Gardner and Scavia 1981) and phosphorus (Peters and Rigler 1973) release rates observed for freshwater cladocerans during the first hour after food

removal. These different excretion patterns may reflect physiological differences between taxa or differences in food composition or gut passage time.

Because mean ammonium release rates (excluding data from the first interval) did not change significantly with time ($p > 0.1$) during the first 50 min for animals exposed to any of the food concentrations, we assumed these mean rates to be reasonable estimates of ammonium release rates for feeding animals. In agreement with data on other species (Corner et al. 1972; Takahashi and Ikeda 1975; Corner et al. 1976; Nelson et al. 1979), animals exposed to high concentrations of food released ammonium significantly ($p < 0.05$) faster than similar animals exposed to low or zero concentrations of food. However, the mean rate over 50 min (excluding the first interval) for E. pileatus exposed to the high food level of 3 mm^3 Thalassiosira fluviatilis liter^{-1} ($49 \text{ nmole NH}_4 (\text{mg AFDW})^{-1} \text{ h}^{-1}$) was less than double the mean rate for animals starved for 18-22 h ($30 \text{ nmole NH}_4 (\text{mg AFDW})^{-1} \text{ h}^{-1}$; Table 1). Copepods exposed to intermediate levels of food (0.3 and 1.0 mm^3 algae liter^{-1}) yielded mean excretion rates of $33 \text{ nmoles NH}_4 (\text{mg AFDW})^{-1} \text{ h}^{-1}$. If dry weight to AFDW conversions are considered, our data for starved animals compare favorably with preliminary data we obtained previously (by the method described by Gardner and Miller 1981) for individual E. pileatus fed on Rhizosolenia alata and then incubated without food for 6 to 8 h ($\bar{x} \pm \text{SE} = 23 \pm 4 \text{ nmole NH}_4 (\text{mg dry weight})^{-1} \text{ h}^{-1}$, $N = 16$); unpublished data). Other data on E. pileatus were not available for comparison. Our release rates for E. pileatus were typical of those reported for other marine zooplankters (Harris 1959; Beers 1964; Butler et al. 1969; Eppley et al. 1973; Jawed 1973; Conover and Mayzaud 1976; Szyper et al. 1976; Ikeda 1977; Smith and Whitledge 1977; Kremer 1977; and Biggs 1977), but exact comparisons are not meaningful

because of differences in species, animal sizes, and experimental methodology.

To compare nitrogen ingestion rates with measured ammonium excretion rates, we calculated the mean ingestion rates for zooplankters at each feeding level and compared them to the mean release rates of the animals over the second through fifth 10-min incubations after food removal (Table 2). In agreement with previous data on Calanus helgolandicus during 4 h incubations (Corner et al. 1976), the ratio of ammonium-N release rates to nitrogen ingestion rates progressively increased with decreasing food levels (Table 2). These data indicate that a relatively large fraction (40 to >100%) of nitrogen ingested by E. pileatus is released as ammonium over comparable time intervals. After periods of low ingestion rates (0 or 24 ng-atm N (mg AFDW)⁻¹ h⁻¹ in our experiments), the animals released nitrogen faster than they had been ingesting it during the pre-incubation periods. Although significant, ammonium release rates were only weakly related to ingestion rates (Table 2). As would be expected for "endogenous" (as contrasted to "food dependent") release, E. pileatus continued to release substantial quantities of ammonium after extensive periods without food. In support of this observation, we have observed relatively continuous ammonium release by E. pileatus in 6-ml vials over a period of 5 days after food removal (data not shown).

Our 4 to 6 h experiments allowed a detailed examination of the rate of change of nitrogen release rates with time after food removal. During these experiments, ammonium release rates by E. pileatus decreased with time, on average, for animals fed high levels of food. If results from both analytical systems are included, the mean ammonium release rate ($\pm$ SE) of six

animals for the 24th 10-min interval (4 h after food removal) was 26 ± 5 as compared to a mean rate of 40 ± 5 nmoles NH_4 (mg AFDW) $^{-1}$ h $^{-1}$ for the second through fifth intervals after food removal. Although ammonium release rates tended to decrease with time, release rate patterns varied among animals and were not entirely predictable (Figure 1). The slowly decreasing trends in release rates with time after food removal for some animals suggests that ammonium release by E. pileatus could be characterized into "endogenous" and "food related" mechanisms as was done for D. magna (Gardner and Scavia 1981), but that apparent food effects sometimes continue for several hours after food removal. The mean rate for a 10-min interval after 4-h incubations was similar to that obtained for animals starved for 18 to 22 h before the 50-min experiments (23 ± 5 nmoles NH_4 (mg AFDW) $^{-1}$ h $^{-1}$; N = 8; mean rate for both analytical systems) and indicates that direct food effects on excretion occur within about 4 h of ingestion. The average rate of change of nutrient release with time was slower for E. pileatus than was previously observed for cladocerans (Peters and Rigler 1973; Gardner and Scavia 1981).

The continued relatively high ammonium release rates for long periods (at least 5 days) after food was removed suggests that E. pileatus may require frequent ingestions of food to maintain an adequate nitrogen balance. Assuming an "endogenous" release rate of 30 ng-atm N (mg AFDW) $^{-1}$ h $^{-1}$ (Table 1) and a body content of 10 $\mu\text{g-atm N}$ (mg AFDW) $^{-1}$ (based on a C to AFDW mass ratio of 0.5:1 and a C to N mass ratio of 3.6:1), E. pileatus without food would lose half of its body nitrogen through ammonium release in about 7 days at 20°C. We have observed that E. pileatus cannot survive more than about 8 days in the laboratory without food. In agreement with this hypothesized need for frequent food ingestion, E. pileatus is rarely found in waters having low particle (phytoplankton) concentrations, but is frequently observed in particle-rich Gulf Stream intrusions. When occasionally encoun-

tered in particle-poor environments, E. pileatus is physiologically weak and in a nonreproductive state (unpublished observations of E. pileatus in waters off the southeastern U.S.A.). Thus E. pileatus apparently cannot adequately adjust to long periods of low food conditions in nature. In contrast, some other species of copepods are more adaptable to periods of food shortage. For example, the temperate copepod Calanus helgolandicus/pacificus (adult females) can survive in good condition for 3 weeks without food at 15°C (unpublished observation).

Amino acid release patterns. Patterns of o-phthalaldehyde-reactive amino acid release were followed, but not quantified, for E. pileatus during the long-term experiments. Amino acid release rate patterns for these "well-fed" animals were pronounced and showed dramatic and unexpected variations during the course of the experiments (Figure 1). Amino acids were generally released at very low rates (only slightly above analytical detection), but occasionally the release rates increased suddenly to high, offscale levels for periods lasting from 20 to 60 min (Figure 1). Except for a few relatively small amino acid peaks after the high release events, amino acid levels in incubation waters returned to almost undetectable levels soon after the events. The high-concentration amino acid spurts followed no recognizable time patterns relative to food removal, but were isolated and appeared to occur randomly. Four out of the six animals yielded high-concentration amino acid spurts during these long-term experiments. Since we did not examine fecal pellet release events, we could not determine whether they and the amino acid spurts were related.

Because levels of amino acids in these spurts were too high to quantify, we could not accurately estimate the relative levels of amino acids released during these events. However, similar phenomena observed in our preliminary

experiments with larger incubation volumes (6 ml) allowed us to make relative comparisons of amino acid levels before and after the spurts. When ammonium and amino acid levels were monitored (by the method described in Gardner and Miller 1981) in 6 ml volumes of filtered sea water surrounding individual E. pileatus (previously fed Rhizosolenia alata) over 6 to 8 h incubations, elevated peak heights from high-concentration amino acid spurts were observed on two occasions. During these events, respective levels of amino acids (based on relative heights of primary amine peaks) increased more than an order of magnitude over the "pre-spurt" levels that had accumulated over periods of 2 to 4 h.

Amino acid release by marine invertebrates may account for a substantial portion (up to 25% of ammonium release) of dissolved nitrogen released by marine zooplankters (Webb and Johannes 1967; Kremer 1977), but the mechanism or kinetics of release have not been adequately examined. Based on the similar relative composition of released amino acids to those in intracellular pools, Webb and Johannes (1967) postulated that release by marine invertebrates could result from simple diffusion across cell membranes. Our data indicate that continuous diffusion is not the major mechanism of release for E. pileatus, but that most amino acid release occurs as occasional discrete events. The quantity, relative composition, and actual mechanism of release is not provided by our data, but the kinetic patterns of release are clearly demonstrated. The occurrence and frequency of these amino acid spurts among other species, their possible dependence on food level and quality, and the amounts of amino acids released in these spurts should be determined to assess their importance to nitrogen regeneration by marine zooplankters.

Although difficult to demonstrate statistically, our results on these animals suggest that ammonium release patterns may also be modified during

the amino acid release events. Ammonium release appeared temporarily elevated and possibly more variable during the spurts than during periods of low amino acid release (Figure 1). These increased ammonium release rates appeared to continue for a period after amino acid release had decreased to near background levels. More studies are needed to verify this tentative observation, but, if true, it could suggest changes in metabolic activity during and after the events.

CONCLUSIONS

Depending on levels of food exposure prior to measurements, ammonium release rates after feeding were from 40 to more than 100% of the nitrogen ingestion rates over the previous several hours. Except for "experimentally induced" elevations of ammonium release rates shortly after the animals were placed in the incubation flow cells, release did not change significantly with time during the first 50 min after food removal. In the course of several hours, however, the mean release rates for previously "well-fed" animals decreased in the absence of food down to about 60% of the mean rates observed soon after food removal. Continued high release rates after extended periods without food suggest that E. pileatus must feed frequently in nature to maintain an adequate nitrogen balance. In addition to ammonium, free amino acids were released by E. pileatus in occasional large spurts extending over periods of 20 to 60 min. The mechanism of release and the quantity of nitrogen in these spurts should be evaluated to assess their importance to copepod nitrogen regeneration processes in marine ecosystems.

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TABLE 1

Mean ammonium release rates $\pm$ SE [nmoles NH_4 (mg AFDW) $^{-1}$ h $^{-1}$]
of Eucalanus pileatus at 20°C for five successive 10 min intervals
after exposure to four levels of food for 18 to 22 h.

Food concentration (mm ³ <u>T. fluviatilis</u> liter ⁻¹)	0	0.3	1.0	3.0
Time interval after food removal (min)	$\bar{x}$ SE(N)	$\bar{x}$ SE(N)	$\bar{x}$ SE(N)	$\bar{x}$ SE(N)
0-10	43 1(4)	64 13(3)	50 9(4)	86 1(2)
10-20	27 6(4)	29 4(3)	34 7(4)	47 9(3)
20-30	30 6(4)	31 5(3)	31 7(4)	52 6(3)
30-40	32 7(4)	36 8(3)	33 9(4)	46 7(3)
40-50	32 5(4)	38 11(3)	36 10(4)	49 11(3)
$\bar{x}$ (0-50)	34	40	37	56
$\bar{x}$ (10-50)	30	33	33	49

TABLE 2

Comparison of mean nitrogen ingestion rates
and mean ammonium release rates for Eucalanus pileatus
exposed to four levels of Thalassiosira fluviatilis at 20°C.

Food concentration added to feeding bottles (mm^3 T. <u>fluviatilis</u> liter^{-1})	Mean nitrogen ingestion rate $[\text{ng-atm N (mg AFDW)}^{-1} \text{h}^{-1}]$	Mean nitrogen release rate $[\text{ng-atm N (mg AFDW)}^{-1} \text{h}^{-1}]$	Release rate Ingestion rate
0	0	30	undefined
0.3	24	33	1.37
1.0	72	33	0.46
3.0	125	49	0.39

LIST OF FIGURES

Figure 1. Patterns of ammonium and o-phthalaldehyde-reactive amino acid nitrogen release with time after feeding for six individual Eucalanus pileatus fed on 3 mm^3 Thalassiosira fluviatilis liter⁻¹ for 18 to 22 hr. Ammonium was not determined for the first interval of the 100.4 g animal because of recorder malfunction. The magnitude of release rates reported for the 79.2, 80.0, and 84.0 μg AFDW animals may be low because of incomplete sample injections (see text).

Figure 1

CALANOID COPEPOD FEEDING: GRAZING ON
SMALL AND LARGE PARTICLES

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ABSTRACT

Removal of phytoplankton cells by adult females of the calanoid copepods Eucalanus pileatus and Paracalanus sp., when simultaneously offered cells of 3 different sizes, were determined over 48h. Concentrations of the 2 larger algae were reduced below $0.05 \text{ mm}^3 \cdot \ell^{-1}$ without large changes in grazing rates. Only Paracalanus removed significant amounts of the smallest alga. While copepods from temperate waters reduce their grazing rates when metabolic costs cannot be met, the 2 subtropical copepods studied here feed at near maximum rates even when their metabolic costs cannot be met. Thus, it appears that not only algal concentration, but also algal size determines the feeding thresholds of copepods which reduce removal rates as smaller particles ($\leq 6 \mu\text{m}$) are eaten. These findings are based on visual counts of cells. Electronic counts overestimate the amount of phytoplankton present as the experiments advance in time.

INTRODUCTION

The basic goal of most quantitative zooplankton feeding studies is to understand events which occur in the ocean but cannot be accurately determined in situ. Experiments are designed to answer important environmental questions, one of them being: At what rates are particles of different sizes ingested by copepods? All feeding studies covering the entire particle spectrum have been conducted so far with naturally occurring particulate matter.

Poulet (1978) showed that 5 species of neritic copepods removed large quantities of particles in a size range from 2.5 to 60 μ m diameter at equal rates. However, Koeller *et al.* (1979) found that female Pseudocalanus minutus, a species used by Poulet (1978) removed only particles larger than 6 μ m diameter. In both studies the concentrations of copepods used ranged from 50 to 100 $\cdot L^{-1}$, at least one order of magnitude higher than found in nature. Also, because their conclusions were based on one measurement at the beginning and one at the end of the 24h experiments information was not obtained on possible changes in feeding sequences on different particle sizes or on changes in feeding rates with time. Richman *et al.* (1980) and Roman and Rublee (1980) obtained intermediate measurements. Richman *et al.* (1980) showed that grazing rates on particles larger than 8 μ m remained even throughout the experiments for Diaptomus oregonensis and decreased moderately for Diaptomus siciloides. Both copepods started feeding on particles smaller than 8 μ m as the experiments progressed. In contrast, in 48h experiments

Acartia tonsa drastically reduced its grazing rate after 12h and rates continued to decrease moderately for the next 36h (Roman and Rublee, 1980). The results of Richman *et al.* (1977) using A. tonsa and Eurytemora herdmani tend to support those of Roman and Rublee (1980) who found that at low copepod densities (5/180ml) highest grazing rates were obtained (for particles $>10\mu\text{m}$), that rates dropped sharply at the next higher density (10/180ml) and remained low at all higher concentrations.

Discrepancies between the findings of Poulet (1978) and Koeller *et al.* (1979) and between Richman *et al.* (1980) and Roman and Rublee (1980) prompted the experiments described here. These experiments were designed to determine how copepods feed over extended time in phytoplankton patches when the concentration of phytoplankton and temperature of water masses upwelled during summer on the southeastern continental shelf (SE-shelf) of the U.S.A. were simulated.

The specific objectives/questions of this study were:

1. to determine if particles of $6\mu\text{m}$ and $>10\mu\text{m}$ diameter are eaten simultaneously or consecutively. The former should be assumed from Poulet's (1978) result. However, cinematography techniques (Paffenhöfer; Strickler and Alcaraz, unpubl.) show that Eucalanus pileatus females use different feeding modes for small ($<6\mu\text{m}$) and large ($>10\mu\text{m}$) particles.
2. to determine if grazing rates ($\text{volume swept clear} \cdot \text{copepod}^{-1} \cdot \text{day}^{-1}$) on various food sizes change when food concentrations decrease.

3. to determine if thresholds occur at low food concentration.

Several authors found feeding thresholds under different conditions (Corner *et al.* 1972, Frost 1975, Gamble 1978) and stressed the importance (Steele 1974) or limited importance (Landry 1976) of these thresholds. In my experiments copepods were allowed to reduce the phytoplankton to near or below the concentration at which assimilation approximately equals basic metabolic expenditures.

4. to compare determinations of cell concentration obtained by electronic and visual counting techniques. This type of comparison tells whether, and to what extent, particle production occurs in the size range of the phytoplankton cells offered and should help to determine the extent of particle production while copepods feed (Frost 1977, Richman *et al.* 1980). As earlier cited, most feeding studies have been based on electronic particle counts (for a critical evaluation see Harbison and McAlister, 1980) and comparisons of electronic and visual counts are needed.

MATERIAL AND METHODS

Experiments were conducted with late copepodid stages and adult females of laboratory-reared Paracalanus sp. and field-collected Eucalanus pileatus. The food initially offered consisted of equal volume concentrations of Thalassiosira pseudonana (6 to 6.5 μ m equivalent spherical diameter=ESD), Thalassiosira fluviatilis (13 μ m ESD) and Prorocentrum micans (25 μ m ESD). All experiments were started with a nominal concentration of approximately 0.5 mm³l⁻¹ of each algal species. The experimental vessels were jars of 1900 ml capacity and controls held 960 ml. The concentrations of animals used were 32 to 45 Paracalanus or 12 to 17 E. pileatus per liter. The total mass of each species was approximately equal. Paracalanus is usually the most abundant zooplanktonic genus on the SE-shelf; E. pileatus is abundant in upwelled water masses which intrude onto the SE-shelf during summer (Paffenhöfer 1980).

Food concentrations in control and experimental vessels were determined with a Coulter Counter TALL (100 μ m diameter orifice) at 0, 6, 12, 24, 36 and 48h and by inverted microscope at 0, 12, 24, 36 and 48h after the start of each experiment. The temperature was constant at 20°C and animals and food were exposed to 14h light and 10h darkness. Algae were added to the containers 16h before the start of the experiments. The water had previously contained copepods for preconditioning, was filtered through 0.8 μ m membrane filters and enriched with $\frac{f}{10}$ medium (2 μ g-at $\cdot$ l⁻¹ of ammonia) to allow the algae to grow. Copepods were adapted to the 3 algal species by keeping them for 48h at food concentrations with appropriate cell mixtures close to those used in the experiments. Each time food concentrations were measured

55 to 70 ml were removed by pipette and this volume was replaced with 0.8 μ m membrane-filtered seawater. From the volume of water added the new concentration of each food species was calculated. Dilution was between 3 to 6.5%. From each sample withdrawn 2 subsamples of 5.0 ml or 22.0 ml were preserved with Lugol's solution, placed in settling chambers and counted by inverted microscope 14 to 20h later. The remainder of each subsample was used to make at least 2 replicate Coulter counts within 30 min of withdrawing the sample. The algal species used could be clearly distinguished from each other in separate channels. At the end of each 48h experiment the surviving copepods were collected, counted, staged and dried to determine ash-free dry weights. Copepod mortality was always below 12% over 48h. Dead or weak animals were removed as soon as detected.

To compare Coulter Counter and microscope counts, the cells visually counted were multiplied by average cell volumes which were 125 μ m³ (T. pseudo-nana), 1620 μ m³ (T. fluviatilis) and 7200 μ m³ (P. micans). Particle concentrations in the environment were determined with a Coulter Counter Model TALL with 100 and 400 μ m diameter orifices.

RESULTS

I conducted 3 experiments with each species of copepod. As somewhat different stages and algal concentrations were used for each experiment, feeding rates and decreases in food concentrations differed over time. Thus, the experiments are discussed separately.

In each 48h experiment concentrations of I. fluviatilis and P. micans decreased to below $0.05 \text{ mm}^3 \cdot \ell^{-1}$, here shown (Figs. 1 and 2) for one experiment each with the two species of copepods. E. pileatus removed few T. pseudonana ($6 \mu\text{m}$) whereas Paracalanus ingested considerable amounts of this species when the combined concentrations of the 2 larger algae were reduced to below $0.2 \text{ mm}^3 \cdot \ell^{-1}$.

Electronic and visual counts of I. pseudonana compared quite well in both experiments. The Counter Counter, however, overestimated the concentration of I. fluviatilis and P. micans when their concentrations reached levels near or below 40% of that initially present (Figs. 1 and 2). The electronic counter data for the 2 larger algae were 145 to 900% higher than those of visual counts at concentrations below $0.1 \text{ mm}^3 \cdot \ell^{-1}$. Differences were less for P. micans than for I. fluviatilis. At the beginning of the experiments the number of cells $\cdot \text{mL}^{-1}$ measured with the Coulter Counter and the inverted microscope differed by 3 to 7%.

Grazing rates (volume swept $\cdot \text{copepod}^{-1} \cdot \text{day}^{-1}$) corrected for algal growth (Frost 1972), served to indicate how feeding effort changed during the 48h experimental period. Visual counts showed a slight decrease of the

feeding rate of E. pileatus females (39 μ g ash free dry weight) on T. fluviatilis, increased consumption of P. micans and little change for T. pseudonana (Fig. 3). To compare rates derived from electronic and visual counts, the electronic counts for hours 0 to 6 and 6 to 12 were averaged. Rates based on electronic and visual counts compared well for P. micans only during the first 24h. All grazing rates based upon electronic data for T. fluviatilis and for the second 24h for P. micans are considerably below the visually obtained data.

Grazing rates of Paracalanus sp. females (8.6 μ g ash-free dry weight) based on electronic counts were close to visual data for T. pseudonana throughout the experiment and for T. fluviatilis and P. micans for the first 12h (Fig. 4). After 12h visually obtained rates considerably exceeded those from the Coulter Counter. Grazing rates based on visual counting of P. micans and T. pseudonana increased with time whereas those on T. fluviatilis were higher during the night than during the day.

To obtain a more complete understanding of the above observations, grazing rates derived from visual counts in 2 other experiments are presented in Fig. 5. The feeding rates of E. pileatus (Copepodid stages IV and V weighing on the average 25 μ g ash-free) on T. fluviatilis and P. micans increased similarly during the first 12h followed by a decrease of 10% (T. fluviatilis) and 16% (P. micans) during the 36-48h period. Feeding rates on T. pseudonana increased as concentrations of the 2 larger algae decreased.

Grazing rates of Paracalanus sp. females ($7.7\mu\text{g}$ ash-free dry weight) on I. fluviatilis and P. micans again changed with the time of day (Figs. 4 and 5). In this experiment (Fig. 5) Paracalanus reduced the 2 large algae to the limits of detection in large settling chambers (22ml). The average concentrations of the 2 larger algae were, $0.2\mu\text{g C}\cdot\ell^{-1}$ (I. fluviatilis) and $1.7\mu\text{g C}\cdot\ell^{-1}$ (P. micans) during the final 12 hours. As in the 2 other experiments with Paracalanus there was a marked increase of grazing rate on I. pseudonana when the combined volumetric concentration of the larger cells dropped to about 20% of the total algal volume (Fig. 6). Grazing rates of E. pileatus females on I. pseudonana changed little during the experiments; copepodid stages IV/V of the same species increased their consumption of this small algae as concentrations of the larger phytoplankton decreased.

DISCUSSION

Feeding on Small and Large Particles:

Female E. pileatus and Paracalanus sp. reduced T. fluviatilis (11-14 μ m equivalent spherical diameter=ESD) and P. micans (25 μ m ESD) to as low as 0.3 cells $\cdot$ ml $^{-1}$. E. pileatus females ingested only small amounts of T. pseudonana (6 μ m ESD) even when the combined concentrations of the 2 larger algae dropped to 0.05mm 3 $\cdot$ l $^{-1}$. Paracalanus, however, considerably reduced the concentration of T. pseudonana when the larger algae were reduced to 0.2mm 3 $\cdot$ l $^{-1}$ or less (Fig. 5). This means that large algae must be quite low in volumetric concentration before Paracalanus females start eating significant amounts of algae of 6 μ m or less in diameter. This agrees with observations of Richman *et al.* (1977, 1980) on Acartia tonsa, Eurytemora affinis, Diaptomus siciloides and Diaptomus oregonensis.

My studies show that copepods always remove algae larger than 10 μ m ESD at much higher rates than cells <6 μ m when both sizes of cells are equally abundant by volume. In contrast, Poulet (1978) showed that small and large particles were removed at similar rates. Poulet's experimental concentrations of 50 to 100 adult copepods $\cdot$ l $^{-1}$ exceed natural densities by about one order of magnitude. Thus, large particles were removed at least 10 times faster than in the sea. This resulted in unnaturally low concentrations of large particles after a relatively short feeding period leading to the ingestion of small particles by the copepods. Such rapid depletion of large particles should not occur in the sea at natural concentrations of adult copepods although

they preferentially remove large particles (Koeller *et al.* [1979] using female Pseudocalanus minutus; Richman *et al.* [1980] using Diaptomus siciloides, their Figs. 3 and 3a). It would also be ecologically unfavorable if reproducing females intensively competed with juveniles of the same species for the same food size. In my opinion, adults only resort to feeding on small particles when larger particles have been depleted. Reduced feeding rates on small particles prevents exhaustion of food which is so important to nauplii (Paffenhöfer and Knowles 1978). Here particle size dictates feeding threshold of adult copepods.

However, there may be exceptions when smaller particles are removed at higher rates than large ones. For example, Small and Donaghay (1979) demonstrated that Acartia clausii removed small and large algae and ignored intermediate sized plastic spheres. Acartia, and probably many other calanoids possess non-mechanical means to select particles. From Friedman and Strickler (1975) and recent unpublished observations by Dr. Rudolf Strickler one concludes that calanoids may select cells by chemosensory perception. Organs located on mouthparts sense chemicals which constitute phycospheres surrounding the cells (Bell and Mitchell 1971). If large particles in Poulet's (1978) experiments consisted of mostly detritus and relatively few algae the copepods, after detecting and removing the algae by chemosensory perception, would have turned their attention to small particles (perhaps flagellates): Larger algal cells would have been rapidly depleted resulting in a relatively high ingestion rate of small over large particles.

Grazing Rates and Feeding Thresholds:

The concept of threshold concentrations below which feeding does not occur has been addressed in various experimental studies. Corner *et al.* (1972) showed a marked decrease in volume swept clear by Cananus helgolandicus when concentrations of Biddulphia sinensis ($>60\mu\text{m}$ diameter) were at or below $500\text{ cells}\cdot\text{L}^{-1}$. Frost (1975) demonstrated a reduction of about 50% in clearance rates by adult female Calanus pacificus when concentrations of Thalassiosira fluviatilis ($13\mu\text{m}$ diameter) were about $150\text{ cells}\cdot\text{mL}^{-1}$. The filtration rates of Acartia tonsa decrease from maximum to near zero as phytoplankton concentrations decrease from 10 to near 0.2 to $0.5\mu\text{g chlorophyll-a}\cdot\text{L}^{-1}$ (Reeve and Walter 1977). Using particulate matter (PM) from the sea Adams and Steele (1966) showed marked reductions of grazing rates of Calanus finmarchicus at PM concentrations below $150\mu\text{g C}\cdot\text{L}^{-1}$. Calanus plumchrus, Calanus pacificus and Pseudocalanus minutus did not feed when PM concentrations were reduced to 50 and $190\mu\text{g C}\cdot\text{L}^{-1}$ (Parsons *et al.* 1969). Roman and Rublee (1980) observed that grazing rates of Acartia tonsa copepodid stage V and adults feeding on particulate matter from nearshore decreased over a period from 3 to 8h. My experiments showed the Paracalanus and Eucalanus pileatus reduced phytoplankton cells of 13 and $25\mu\text{m}$ ESD from more than $300\text{ cells}\cdot\text{mL}^{-1}$ to below $1\text{ cell}\cdot\text{mL}^{-1}$ without a marked reduction in grazing rate.

Because of these different findings the following questions may be addressed: 1. Why are grazing rates reduced over time (Roman and Rublee, 1980), 2. What could cause the copepods to almost cease feeding at low food concentrations, and 3. Why can grazing rates be maintained as particle concentrations decrease, or: must there be threshold concentrations of food?

1. Using high-speed cinematography I have observed that phytoplankton cells of 10 to 13 μ m diameter (I. fluviatilis) and larger are "individually" removed from the surrounding water by E. pileatus. The second maxillae are used to transport the cells in a parcel of water to the mouth. When cells of 6 μ m diameter and smaller are present at concentrations of 10,000 cells mL^{-1} or less E. pileatus does not employ "individual" feeding mode but rather appears to use a not yet fully understood and less efficient "filtration" mode. Grazing rates on small, compared to large cells under this condition are very low. I assume that when large (>10 μ m) particles become less abundant in the spectrum of particulate matter available to copepods (i.e., 2 to 32 μ m) that grazing rates on the total particulate matter decreases as small particles become more abundant = when the number of large cells is reduced relatively fewer particles are removed by the "individual" (high rate) and more by the "filtration" (low rate) mode.

When visual counts showed that large cells were depleted the electric particle counter still showed a considerable number of such particles. These were either artifacts or represented particles which do not trigger a feeding response by the copepod. Figures 3 and 4 show that feeding rates on I. fluviatilis and P. micans between hours 24 to 48 are far higher than estimated by Coulter Counter measurements of particles in the size range of these algae. Figures 1 and 2 show that many particles were produced in the experimental jars. Thus, time dependant reductions in overall grazing rate observed by Roman and Rublee (1980) could have been due to: (1) small particles becoming relatively more abundant as large particles were removed; (2) the production

of particles lead to underestimates of grazing rates based on electronic counts; and (3) particles of terrestrial origin found in nearshore waters may not trigger a feeding response by calanoid copepods. Terrestrial detritus has low nutritive value (Tenore 1981).

2. For a copepod to ingest particles feeding responses must be triggered. Cinematographic observations and experimental studies show that particles are efficiently removed when E. pileatus and Paracalanus use their second maxillae (Paffenhöfer, Strickler and Alcaraz, unpubl. observations). There may be considerable amounts of particulate matter in the water and no measurable feeding response. The lowest concentration of particulate matter we have measured on the SE-shelf was $0.28\text{mm}^3 \cdot \text{L}^{-1}$ (Fig. 7), with chlorophyll- α concentrations below $0.1\mu\text{g} \cdot \text{L}^{-1}$. From my findings (Figs. 1 and 2), where electronically measured volumes were 145-900% higher than observed visually, one could assume that most of the particles measured (Fig. 7), were not phytoplankton and were not removed by copepods which were abundant (Paffenhöfer, unpubl. observations). Otherwise particle concentrations in the sea - at least for $>10\mu\text{m}$ ESD should be lower, approaching values found visually in my experiments.

3. Feeding thresholds are food levels below which feeders reduce or cease feeding. The ecological significance of thresholds is to prevent complete depletion of a food source, i.e., maintain survival (Steele 1974). In experiments with Paracalanus sp. and E. pileatus I observed no concentration thresholds, in contrast to the studies by Corner *et al.* (1972) and the other authors referenced earlier. To attempt to explain this discrepancy I com-

pared metabolic expenditures with the food assimilated (Table 1) and then compare copepods behaviour in their natural environment. The approach has limitations as there are no respiration data available on actively feeding specimens of the species I used. However, applying respiration rates for wild C. helgolandicus (pacificus) (Mullin and Brooks 1970) I calculated metabolic expenditures for C. helgolandicus and E. pileatus females (transforming CIV data to 20° C). Expenditures were also calculated from Ivleva (1980). The assimilated food was then calculated using a 35% assimilation efficiency for C. helgolandicus (Vidal, 1980, his Table 1) and 90% for E. pileatus and Paracalanus at 20°C (extrapolating roughly from Vidal 1980).

The calculations (Table 1) indicate that when C. helgolandicus reduces its grazing rates at cell concentrations below $32\mu\text{g C}\cdot\text{l}^{-1}$ its metabolic expenditures are no longer met. Paracalanus can meet its metabolic needs when food concentrations of $66\mu\text{g C}\cdot\text{l}^{-1}$ were reached during the second 24 hours of my experiments, whereas E. pileatus cannot (Table 1).

E. pileatus is abundant on the S.E. continental shelf only when relatively high concentrations ($>1\text{mm}^3\cdot\text{l}^{-1}$) of large algae (Rhizosolenia sp., e.g., 15 to $120\mu\text{m}$ cell width) are found. Without large particles it (E. pileatus) seemingly cannot exist as unlike some temperate species it stores few wax esters. Thus, to minimize metabolic losses it continues to graze intensively at low levels (Lam and Frost 1976). Paracalanus is abundant when cell concentrations are as low as $0.5\text{mm}^3\cdot\text{l}^{-1}$ (2 to $100\mu\text{m}$ diameter) as it can obtain sufficient energy from small particles (Figs. 4 and 5). For these animals there is no refuge in shallow subtropical waters of 20° to 29°C other than to migrate vertically to find food or to minimize metabolic losses by continued grazing at high rates.

In contrast, temperate copepods like Calanus helgolandicus, store energy (Lee *et al.* 1971) and can, in times of food shortage, migrate to deeper, colder waters where metabolic expenditures are sharply reduced; or, if low food concentrations are found in shallow areas metabolic losses can be temporarily compensated by using stored energy reserves.

My study attempted to determine, by simulation, how adult females of Paracalanus and E. pileatus feed in upwelled water mass initially rich in phytoplankton and low in detritus. This situation is common during summer on the SE-shelf. In such water masses females of the 2 species studied can remove almost all phytoplankton cells larger than 10µm diameter. My data reveals that particle size is more important than absolute phytoplankton concentration in determining the rate at which copepods graze cells. Therefore not only the absolute food concentration but the size of the cells available serves to determine feeding thresholds. By reducing the removal rate of small cells sharply late juveniles and adults do not deplete the main food of early juveniles.

In waters in which copepods have fed for up to 48h measurements of phytoplankton abundance by electric particle counter differ from that determined by inverted microscope counts. This difference is not due to the presence of fecal pellets alone. To obtain reliable electronic data experiments should be run with few animals over short periods. Otherwise visual counts are necessary. Feeding data from electronic counts usually underestimate feeding performance.

Various questions arose from this study:

1. Why are small algae ($\leq 6\mu\text{m}$ ESD) grazed at much lower rates than larger ones ($\geq 10\mu\text{m}$ ESD)?
2. Are phytoplankton cells grazed at different rates than detritus particles of the same size and shape? Do chemosensors allow the copepod to discriminate particles? Donaghay and Small (1979) showed that diatoms, irrespective of their size, were eaten while plastic spheres were not. This strongly suggests a chemosensory behaviour, especially after Friedman and Strickler (1975) observed chemosensors on the mouthparts of calanoids.
3. At what level of food concentrations/compositions do different calanoids, especially subtropical species, start searching for food by migrating vertically? Is it at levels at which they can no longer fully meet their metabolic costs? How does searching differ for different copepodid stages? How do low phytoplankton levels affect the ingestion of detritus?

To understand the feeding behaviour and performance of entire copepod populations it is essential to offer the entire spectrum of sizes of food to developing cohorts of early juveniles and allow them to develop to adulthood. This type of study is presently being conducted in our laboratory.

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FIGURE LEGENDS

Figure 1. Eucalanus pileatus. Food concentrations over time as measured electronically (Coulter Counter TAPI) and visually (inverted microscope). The diluted concentration after sample removal is shown by the lower of two symbols at the same time. When food concentrations reached very low levels one symbol was chosen as the difference between final and the following initial (diluted) food concentrations was very small.

Figure 2. Paracalanus sp. For legend see Figure 1.

Figure 3. Eucalanus pileatus. Volume swept clear per adult female per day over 48 hours measured electronically and visually. Symbols as in Figure 1.

Figure 4. Paracalanus sp. Volume swept clear per adult female per day over 48 hours measured electronically and visually.

Figure 5. Eucalanus pileatus CIV (large symbols) and Paracalanus sp. females (small symbols). Volume swept clear is presented for each 12 hour feeding period. The cell concentrations presented are from hours 0, 12, 24, 36 and 48 of each experiment, made with an inverted microscope.

Figure 6. Paracalanus sp. Changes in grazing rates on T. pseudonana compared to changes in the relative amount of large algae (% of total algal volume).

Figure 7. Particle size spectra from near surface and near bottom of Onslow Bay, North Carolina. The total concentration amounts to $0.28\text{mm}^3 \cdot \ell^{-1}$. Modified after Paffenhöfer *et al.* (1980).

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TABLE 1. INGESTION, ASSIMILATION AND METABOLIC EXPENDITURES OF CALANOID COPEPODS.

SPECIES	TEMPERATURE (°C)	AMOUNT INGESTED ($\mu\text{g C}\cdot\text{day}^{-1}$) at $\mu\text{g C}\cdot\text{L}^{-1}$	AMOUNT ASSIMILATED ($\mu\text{g C}\cdot\text{day}^{-1}$)	AMOUNT RESPIRED ($\mu\text{g C}\cdot\text{day}^{-1}$)
<u>Calanus helgolandicus</u> female (Corner <i>et al.</i> 1971)	12.5	24.4 at 37 3.88 at 11	8.54 1.36	4.2 (Mullin and Brooks 1970)
<u>Eucalanus pileatus</u> female June 2-4, 80 h24-36 h36-48	20°C	2.26 at 109 1.01 at 103	2.03 0.91	4.0 (Ivleva 1980) and 2.3 (Mullin and Brooks 1970)
<u>Paracalanus</u> sp. female May 15-18, 80 h24-36 h36-48	20°C	1.68 at 91 1.07 at 66	1.51 0.96	1.03 (Ivleva 1980)

Figure 1

Figure 2

Figure 3

Figure 4

Paracalanus sp.

June 2-4, 1980

TA II

Inverted scope

□	T. pseudonana	■
△	T. fluviatilis	▲
○	P. micans	●

Figure 5

16-29

Figure 6

Figure 7

LETTER TO THE EDITOR

Grazing by Copepods in the Peru Upwelling

Dear Editor:

In the article "Grazing and excretion by zooplankton in the Peru upwelling system during April 1977" Dagg et al. (1980) calculated, from experimental data, the grazing impact of adult females of the 3 calanoid copepods Centropages brachiatus, Eucalanus inermis and Calanus chilensis on phytoplankton populations. Impact was considered small, which implied ingestion rates only 0.5 and 4.7% of the daily primary production. From data on the abundance of small copepods the authors suggest a much greater impact by the total zooplankton population but do not estimate what this might be.

Dagg et al. calculated the grazing impact of adult (I assume females) Paracalanus denudatus assuming a body weight of $1.4 \mu\text{g}$ carbon and an ingestion rate of $1.20 \mu\text{g C}\cdot\text{day}^{-1}$ at 1.0 PPM ($1.0 \text{ mm}^3\cdot\text{l}^{-1}$) at 15°S . However, concentrations as high as 1.0 PPM were not found on their transect. P. denudatus adults were assumed to have removed on the average 8.0% of the daily primary production and the 3 large calanoids 2.9% resulting in a total of 10.9%. This calculation takes into account only a small fraction of the abundant small copepods and bases grazing calculations on experiments conducted at particle concentrations of 1.0 PPM, about three times higher than the average found (Fig. 2 of Dagg et al. [1980]).

Here I calculate the daily ingestion rate of Paracalanus copepodids and adults (females) using the animal concentrations from Table 3 of Dagg et al.

(1980). Ingestion data were derived from feeding experiments conducted at 20°C with all copepodid stages and adult females of Paracalanus sp. (Paffenhöfer, unpublished). Shushkina et al. (1978) found that the surface temperature off Peru at 8°S increased from 16.5°C nearshore to 24.0° offshore, making 20°C a reasonable comparison.

As Dagg et al. (1980) sampled with 102 µm mesh net all Paracalanus copepods except CI were probably sampled quantitatively (Paffenhöfer, unpublished results). One can expect that most Paracalanus collected were younger copepodid stages. Here I assume that the average copepodid stage collected was CIII which weighs 0.72 µg C at 20°C (Paffenhöfer, unpublished). The average weight of adult females is 3.75 µg C.

Ingestion data are taken from experiments which simulated early upwelling conditions, were conducted at an average particle concentration of $0.1 \text{ mm}^3 \cdot \text{l}^{-1}$ each of mixed cultures of Isochrysis galbana (4.5 µm diameter), Thalassiosira fluviatilis (11 µm width) and Rhizosolenia sp. (16 µm width, 350 µm length). These algae, in order, contain 251, 82 and 20 µg C·mm⁻³ of cell and cover the size range from 4 to 70 µm equivalent spherical diameter. Three times $0.1 \text{ mm}^3 \cdot \text{l}^{-1}$ results in a total cell concentration of $0.3 \text{ mm}^3 \cdot \text{l}^{-1}$ which is close to the average particle concentration found in the upper 100 m at 15°S (Fig. 2 of Dagg et al. 1980). It should be noted that the copepods in my experiments encountered relatively small amounts of detritus (their own fecal pellets) whereas in the experiments of Dagg et al. (1980) particulate matter from the ocean was used which probably had higher amounts of detritus.

Table 1 shows ingestion rates for adults (females) and copepodids (CIII) per m^3 . In my experiments one adult female Paracalanus sp. ingested $2.58 \mu\text{g C}$ and one CIII $0.64 \mu\text{g C}$ daily. The total daily ingestion of Paracalanus is expressed as a percentage of the daily primary production at 15°S , which was $1.15 \text{ g C} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ or $11.5 \text{ mg C} \cdot \text{m}^{-3} \cdot \text{day}^{-1}$ (Barber et al., 1978). Calculated total ingestion rates range from 4.6% (Station 192) to 68.1% (Station 196) with an average of 32.7%, almost three times the 10.9% calculated by Dagg et al. for the 3 larger calanoid adults and P. denudatus adults. On the average the females then graze 18.2% and the copepodids 14.5% of the daily primary production.

If one also takes into account the abundance of the copepodids of the cyclopoids Oncaea and Oithona, and the nauplii of the small copepods which all pass $102 \mu\text{m}$ mesh, one could easily obtain total ingestion rates close to 100% of the average daily productivity. Accurate calculations for cyclopoid copepodids have to wait as information on their ingestion performance is scarce. However, it is obvious that small copepods, which have been largely ignored in most studies, can have a grazing impact on the available particulate matter well in excess of that of larger copepods.

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TABLE 1. Ingestion rates of *Paracalanus* sp. ($\text{mg C}\cdot\text{day}^{-1}\cdot\text{m}^{-3}$) at stations of a transect 15°S off Peru. Abundance values are given in Table 3 of Dagg *et al.* (1980).

STATION	ADULTS		COPEPODIDS	TOTAL	% OF DAILY PRIMARY PRODUCTION
192	0.315	+	0.210	= 0.525	4.6
193	1.422	+	3.045	= 4.467	38.8
194	0.464	+	0.139	= 0.603	5.2
195	4.125	+	2.648	= 6.773	58.9
196	4.381	+	3.454	= 7.835	68.1
197	3.096	+	2.113	= 5.209	45.3
198	1.638	+	1.281	= 2.919	25.4
236	1.274	+	0.451	= 1.725	15.0
$\bar{X} =$	18.2%	+	14.5%		= 32.7%

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EFFECTS OF IONIC COPPER ON NATURAL POPULATIONS OF
PHYTOPLANKTON GROWN IN CONTINUOUS CULTURE.

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Running Head: Effects of Copper on Phytoplankton

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TABLE II

Summary of Continuous Culture experiments; values are means with standard deviations in parentheses.
Copper column represents particulate copper extracted at the conclusion of the experiment.

EXPERIMENT	DURATION (Days)	DILUTION RATE (Day ⁻¹)	COPPER ADDED ($\mu\text{g L}^{-1}$)	YIELDS				RATIOS		PRODUCTION ($\mu\text{gC L}^{-1} \text{ hr}^{-1}$)
				COPPER ($\mu\text{g L}^{-1}$)	POC ($\mu\text{g L}^{-1}$)	CHLOROPHYLL ($\mu\text{g L}^{-1}$)	CELL CONC. ($\times 10^7 \text{ L}^{-1}$)	CU/POC ($\times 10^{-5}$)	CU/Chl ($\times 10^{-3}$)	
1	9	0.25	0	0.264 (0.06) n=3	2330 (202) n=4	11.23 (0.70) n=5	2.66 (0.35) n=3	11	24	-
			1.0	0.349 (0.10) n=3	2090 (316) n=4	10.22 (0.68) n=5	1.68 (0.37) n=3	17	34	-
2	18	0.25	0	0.080 (0.01) n=6	1150 (174) n=9	10.00 (1.15) n=12	0.822 (0.23) n=6	7	8	19.70 (5.1) n=2
			2.0	0.229 (0.02) n=5	1240 (222) n=5	8.84 (0.50) n=6	0.956 (0.12) n=3	18	26	19.80 (4.6) n=2
3	15	0.25	0	0.057 (0.02) n=6	1430 (49) n=6	1.93 (0.33) n=6	1.98 (0.62) n=6	4	30	3.80 (0.01) n=2
			1.0	0.232 (0.04) n=6	1360 (173) n=6	2.16 (0.35) n=3	2.11 (0.66) n=6	17	107	4.00 (0.01) n=2

EFFECT OF UPWELLING ON PHYTOPLANKTON PRODUCTIVITY ON THE OUTER
SOUTHEASTERN U.S. CONTINENTAL SHELF

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ABSTRACT

Gulf Stream frontal disturbances cause nutrient-rich waters to frequently upwell and intrude onto the southeastern U.S. continental shelf between Cape Canaveral, Florida and Cape Hatteras, North Carolina. Phytoplankton response in upwelled waters was determined with three interdisciplinary studies conducted during April, 1979 and 1980 and in summer, 1978. The results show that when shelf waters are not stratified, upwelling causes productive phytoplankton (diatom) blooms on the outer shelf. Phytoplankton production averages about $2 \text{ g C m}^{-2} \text{ d}^{-1}$ during upwelling events, and "new" production is 50%, or more, of the total. When shelf waters are stratified, upwelled waters penetrate well onto the shelf as a subsurface intrusion in which phytoplankton production averages about 5 X higher than the nutrient-depleted overlying mixed layer. Phytoplankton within the intrusion deplete upwelled NO_3 in about 7-10 days at which point no further net increase in phytoplankton biomass occurs.

Current meter records show that upwelling occurs roughly 50% of the time on the outer shelf during November-April (shelf not stratified), and we estimate that seasonal primary production in upwelled waters is $175 \text{ g C m}^{-2} \text{ 6 mos}^{-1}$ of which at least 50% is "new" production. More than 90% of outer shelf primary and "new" production occurs during upwelling, and thus upwelling is the dominant process affecting primary productivity of the outer shelf. Our seasonal estimates of outer shelf primary and "new" production are, respectively, 2 X and 10 X higher than previous estimates that did not account for upwelling.

INTRODUCTION

Circulation on the outer southeast U.S. continental shelf is directly and frequently affected by Gulf Stream frontal processes. The cyclonic front generally follows the shelf break from Miami, Florida to Cape Hatteras, North Carolina, a distance of more than 1000 km. The front is disturbed by wave-like meanders and eddies which occur every several days to two weeks, have along- and cross-shelf dimensions greater than 100 km and 20 km, respectively, and propagate along the front from south to north at average speeds of approximately 35 km d^{-1} (Webster, 1961; Lee, 1975; Lee and Mayer, 1977; Pietrafesa and Janowitz, 1979; Lee and Brooks, 1979; Vukovich, Crissman, Bushnell and King, 1979; Blanton, Atkinson, Pietrafesa and Lee, 1981; Lee, Atkinson and Legeckis, 1981). Physical and hydrographic characteristics of eddies along the cyclonic Gulf Stream front off the southeast U.S. coast were described with satellite IR images (Vukovich et al., 1979), current meters (Lee and Brooks, 1979; Pietrafesa and Janowitz, 1979), shipboard hydrographic observations (Atkinson, 1978), and by integrating all three types of measurements (Lee et al., 1981). All investigators agree (so far) that frontal eddies are common features; the "disturbance" propagates northward along the front; eddies cause upwelling and intrusion of upwelled waters onto the shelf; and they are a primary cause of subtidal frequency current fluctuations on the outer shelf. The investigators disagree on the appropriate name for the features (shingles, filaments, spin-off eddies are, or were, used), the circulation within the "warm tongue" (compare Chew, 1981 with Lee et al., 1981), and whether upwelled waters are removed from a fixed position on the outer shelf primarily by downwelling off the shelf (Pietrafesa, personal communication) or by northward advection (Lee et al., 1981). Of the issues in dispute the latter has the most important biological implication because it affects the calculation of shelf residence time for upwelled waters, and

because it will determine where some of the biological production within upwelled waters eventually will go. However, all investigators agree that eddies induce upwelling and from a phytoplankters perspective, this is the "first order" effect and the one we consider in this manuscript.

Upwelling source water is a mixture of water masses dominated by Western North Atlantic Water (also referred to as North Atlantic Central Water) but can also include continental edge water, Gulf Stream surface water, Subtropical Underwater and Antarctic Intermediate Water. Hereafter, we will refer to upwelled water as Gulf Stream Water (GSW) to distinguish it from shelf water. An important and useful characteristic of GSW is that NO_3 is linearly related to temperature below about 21°C . In general, the temperature of freshly upwelled GSW found on the southeastern continental shelf ranges from about 15 to 22°C which corresponds to about 15 and $0\ \mu\text{M}\ \text{NO}_3$, respectively. Upwelled NO_3 is virtually the only important source of "new" nitrogen for the outer shelf (Lee *et al.*, 1981); since resident shelf waters contain negligible amounts of inorganic nitrogen, and river inputs are important only to the inner shelf (Dunstan and Atkinson, 1976; Bishop, Yoder and Paffenhöfer, 1980; Yoder, Atkinson, Blanton, Deibel, Menzel and Paffenhöfer, 1981).

Before the effects of upwelling were known, outer shelf primary production was believed to be relatively low - ca. $130\ \text{g C m}^{-2}\ \text{y}^{-1}$ (Haines and Dunstan, 1975). Because the importance of offshore nutrient sources was not recognized at the time, Haines (1974) concluded that recycling within the water column provided more than 95% of the nitrogen required to support primary production on the outer shelf. Others (Turner, Woo and Jitts, 1979; Turner, 1981) concluded that outer and inner shelf plankton dynamics were closely coupled and implied that outwelling of nutrients from estuaries and marshes controlled plankton productivity across the shelf.

Recent studies of upwelling and its effect on biological processes of the southeastern shelf led to a different view of outer shelf plankton productivity and the processes responsible for it (Dunstan and Atkinson, 1976; Atkinson, Paffenhöfer and Dunstan, 1978; Bishop *et al.*, 1980; Hofmann, Pietrafesa, Klinck and Atkinson, 1980; Paffenhöfer, 1980; Paffenhöfer, Deibel, Atkinson and Dunstan, 1980; Yoder *et al.*, 1981A; Yoder, Atkinson, Lee, Kim and McClain, 1981B). Briefly, these studies show that chlorophyll *a* within upwelled waters is roughly 10 X higher than observed when there is no upwelling (ca. 5 versus 0.5 mg m⁻³), primary production may be several times higher during upwelling than under non-upwelling conditions, large phytoplankton (diatom) patches (ca. 1000 km²) form on the outer shelf within upwelled waters, chlorophyll *a* concentrations are often higher within subsurface intrusions of GSW than in the overlying mixed layer, higher numbers of zooplankton are found within upwelled waters than in resident shelf waters and finally, the biological response to upwelling is more pronounced at the outer shelf than at the middle or inner shelf. Based primarily on the cross-shelf distribution of chlorophyll *a* and nutrients, Bishop *et al.* (1980) proposed that the southeastern continental shelf could be roughly divided into three zones of approximately equal width (40 km) off the Georgia coast: the outer, middle, and inner shelf. Phytoplankton dynamics of the outer shelf (ca. 40-200 m isobaths) are controlled by periodic inputs of offshore nutrients, whereas inner shelf (0-20 m isobaths) production is primarily affected by river and estuarine outwelling. Production on the middle shelf ultimately depends on nutrients that cross either of the other two zones.

Results presented to date (references above) were primarily descriptions of biological distributions (e.g., chlorophyll *a*, phytoplankton and zooplankton numbers), and the conclusions were limited to what these distributions imply to productivity. Among the conclusions (generally presented as hypotheses) were

that: (1) upwelling is the most important process controlling phytoplankton productivity of the outer shelf, (2) outer shelf productivity is higher than originally believed, (3) a relatively high percentage of primary production is "new" production (in sensu Dugdale and Goering, 1967), (4) a significant percentage of primary production in the water column occurs below the mixed layer, and (5) episodic upwelling causes frequent highly productive short-lived phytoplankton blooms that occur throughout the year. The purpose of this paper is to address the above hypotheses primarily using phytoplankton "rate measurements" (e.g., C and NO_3 uptake), or when appropriate, to infer rates from temporal changes in phytoplankton biomass. We describe the response of phytoplankton to individual upwelling events and estimate the importance of upwelling to seasonal outer shelf primary and "new" production.

METHODS

Figure 1 shows the continental shelf off the South Carolina, Georgia, and north Florida coasts (hereafter referred to as the Southeastern Shelf) and locations where our studies were conducted. Cruises were during April (spring) and July/August (summer) of 1978, 1979, and 1980 using the R.V. Bluefin, Eastward, Gilliss, or Iselin. A different sampling strategy was used in the spring and summer. During spring, shelf waters are 5-10°C colder than Gulf Stream surface waters making it possible to use satellite thermal imagery to locate frontal eddies prior to, and during the cruises (see Lee et al., 1981; Yoder et al., 1981B). In addition, upwelled waters are generally restricted to the shelf break and do not penetrate more than 20-40 km onto the shelf (see Atkinson, 1977; Lee et al., 1981; Yoder et al., 1981B). To determine the spatial scales of upwelling features, surface and subsurface hydrography of upwelled waters were mapped using a thermosalinograph and XBTs, and surface chlorophyll was determined by underway measurements of in vivo fluorescence (see Lee et al., 1981; Yoder et al., 1981B).

During summer, shelf waters are stratified and upwelled GSW moves onto the shelf as subsurface intrusions, and differences in surface temperature between shelf and Gulf Stream waters are slight. Under these conditions satellite imagery is not useful for detecting upwelled waters. However, the temperature of resident shelf surface water in summer is about 28°C, and subsurface intrusions of upwelled waters (ca. 15-22 C) can be located with XBTs or by towing a temperature probe at a depth of 20-40 m.

Water samples were generally collected with a General Oceanics rosette sampler attached to a Plessey CTD. When the rosette was not available water was collected with Niskin bottles after first determining the vertical temperature structure with an XBT. In the latter case salinity of discrete samples was determined with a Plessey Model 6230 N salinometer. During spring, both temperature and salinity characteristics were required to identify upwelled waters, since the temperature of upwelled GSW and shelf water is often the same. However, the T-S characteristics of GSW distinguish it from shelf waters (e.g., Lee et al., 1981).

The CTD was calibrated using procedures described by Chandler et al. (1978). Current meter data were processed according to Lee et al. (1981). Nutrients were determined with a Technicon AutoAnalyzer (Glibert and Loder, 1977). In general, NO_2 was not determined separately from NO_3 but has never been found to be a significant component of $\text{NO}_3 + \text{NO}_2$ in upwelled GSW. Hereafter, we refer to $\text{NO}_2 + \text{NO}_3$ as NO_3 . Samples not immediately analyzed were frozen. Vertical profiles of subsurface irradiance were obtained with a LI-COR spherical quantum sensor. Incident irradiance was continuously monitored during simulated in situ productivity experiments with LI-COR quantum sensor, model LI-190S, equipped with a LI-COR integrator, model LI-550. Lugols solution was used to preserve phytoplankton for later identification and enumeration. An inverted microscope was

used to identify and count the samples.

For the analyses and experiments described below, water samples were first filtered through 183 μm Nitex netting to remove the larger zooplankton. Nets with a smaller mean pore size were not used to avoid excluding larger phytoplankton cells and colonies. Chlorophyll a and phaeopigment a were determined using the fluorometric method of Yentsch and Menzel (1963) as described by Strickland and Parsons (1972). For particulate C and N measurements, a known volume of water (0.5 - 1 liter) was filtered onto 25 mm pre-combusted Gelman type A/E glass fiber filters, the filters were frozen; then freeze-dried, and analyzed for C and N content with a Perkin-Elmer Elemental Analyzer. Particulate Si was determined using the filter method of Paasche (1980).

Primary production (C uptake) was determined using the ^{14}C -labelled sodium bicarbonate method (Steemann Nielsen, 1952). Five μcuries of $^{14}\text{CO}_2$ were added to 125 ml flasks (2 light and 1 dark) containing prescreened water samples as described above. After incubation the contents were filtered through 0.45 μm , 25 mm Millipore HA filter disks. Filters were dried in a dessicator, fumed with HCl to remove labelled "inorganic" carbon, and ^{14}C activity was determined with a Beckman liquid scintillation counter using New England Nuclear's "Omnifluor" cocktail (98% PPO, 2% Bis-MSB).

NO_3 uptake was determined using the stable isotope method ($^{15}\text{NO}_3$) of Dugdale and Goering (1967). The added label usually did not increase the total NO_3 concentration by more than 10-20%. However, because at least 0.2 $\mu\text{moles NO}_3 \text{ liter}^{-1}$ was added, the total NO_3 concentration was occasionally increased by as much as a factor of 2. During summer 1978, 4 liter glass bottles were used for NO_3 uptake experiments. After incubation, the contents were filtered onto 47 mm pre-combusted type A/E Gelman glass fiber filters. The filters were then frozen and eventually freeze-dried. In 1979 and 1980, 1 liter glass bottles were used and after

incubation, the contents were filtered onto 25 mm pre-combusted type A/E Gelman glass fiber filters. The isotope ratios of 1979 and 1980 samples were determined by Dr. Hans Paerl, University of North Carolina Marine Institute, using model NTA-1 Jasco emission spectrometer. The rate of $\text{NO}_3\text{-N}$ uptake was calculated using equation 1.

$$\text{NO}_3\text{-N uptake (mg N m}^{-3} \text{ h}^{-1}) = [\text{PN} (\text{N}_p - \text{N}_b) / (\text{N}_s - \text{N}_p)]/t \quad (1)$$

where, PN = particulate N (mg N m^{-3})

N_p = % ^{15}N on the filter

N_b = natural ^{15}N abundance (%)

N_s = % $^{15}\text{NO}_3\text{-N}$ in seawater after enrichment

t = incubation time (h)

Several different procedures were used to incubate samples for carbon and NO_3 uptake experiments. Because intruded waters were often up to 10°C colder than the surface mixed layer in summer, surface water could not be used to maintain temperature control during incubations of samples from these waters. Instead, water collected from intruded waters was incubated at 1 or more irradiance levels in temperature controlled "laboratory" incubators using Sylvania "Plant Light" as the light source. For spring cruises, bottles were incubated under simulated in situ conditions. The bottles were placed in bags constructed of different numbers of layers of plastic screen to simulate incident irradiance at the depth which water was collected. The bottles were incubated "on deck" within tanks through which surface water was continuously pumped. In 1980, better temperature control was obtained using 2 plexiglass tanks which were kept at 2 different temperatures with Forma Scientific "Masterline" cooling and heating units.

In 1978, the incubation time for both primary production and NO_3 uptake experiments was 4 hours. In spring 1979, 4 and 24 hour incubations were used. The 4 hour results agreed within about 20% with those from the 24 h after the 4 hour rates were converted to daily rates using a factor based on the ratio of

light received during 24 hours to that received during the shorter incubation. In 1980, all incubations were for 24 hours.

In summer, 1978, a drogue designed by Dr. G. -A. Paffenhöfer was followed and used as a reference station. The drogue sail was a plastic sheet wrapped around aluminum hoops to form a cylinder (diameter = 1 m, height = 2 m) open at each end.

RESULTS

APRIL, 1979

Physical Description

The only current record for the April, 1979 study was from shelf break (75 m isobath) and mid-shelf (30 m isobath) moorings located about 90 km north of the area sampled by the ship (see Fig. 1). Assuming the average propagation velocity of 35 km d^{-1} , the shelf break mooring detected Gulf Stream disturbances about 3 days after they affected the area where biological and hydrographic observations were made. The current and temperature record at the shelf break mooring showed that two large frontal eddies moved past the mooring in rapid succession between 15-27 April, and a smaller one reached the mooring on 30 April. All three eddies were also observed with satellite IR imagery (Lee, unpublished; C. R. McClain, personal communication) and the last two by shipboard measurements. Shipboard sampling on 20-22 April determined temperature, salinity, nutrient, and chlorophyll structures of the southerly part of the second of the two large eddies. These results showed that a large phytoplankton patch was present within upwelled waters that formed the cold core of the frontal eddy (Yoder *et al.*, 1981B). The patch was more or less elliptically shaped having an along-shelf dimension of approximately 100 km and maximum width of 40 km.

Figure 2 shows that winds were very strong (ca. 20 m s^{-1}) from 24 to 27 April and were upwelling-favorable on 26-27 April. However, the current and

temperature record at the shelf break mooring 90 km to the north of the study area did not indicate any significant wind driven upwelling. On 26 and 27 April, shelf break currents rotated counter-clockwise from southward to northward flow which was coherent with increasing temperatures throughout the water column. This signature indicates northward passage of the southern extremity of the second of the large frontal eddies (see Lee et al., 1981 for description of eddy current signatures). However, the strong winds probably had a biologically important effect by mixing nutrients upwelled by the frontal eddies farther up into the euphotic zone.

Hydrographic time series at the 45 m and 75 m isobath are shown in Figure 3. These two locations were 5 km apart and all primary production stations were between, or at, these two locations. Salinity was always greater than 36×10^{-3} and is not shown. Note the position of the 20°C isotherm. At both stations this isotherm is always above 40 m and is occasionally above 15 m. In the absence of upwelling, the 20°C isotherm is close to 100 m at the shelf break during April (e.g., Atkinson, 1978). At the 75 m isobath, changes in the depth of isotherms colder than about 18°C reflect the northward passage of the second of the two large frontal eddies (22-24 April) and the presence and passage of the third (and smaller) eddy (24-30 April). Changes in the depth of isotherms warmer than about 20°C were influenced by the strong winds between 24-27 April. Surface waters at both stations were about 1°C cooler during this 3 day period than at other times in the record which suggests strong vertical mixing in the upper portion of the water column.

Biological Effects

Figure 4 shows the vertical distributions of density, NO_3 , chlorophyll a, and the rates of C and $\text{NO}_3\text{-N}$ uptake at shelf break stations occupied in April, 1979. All production stations were at, or between, the two locations (5 km

apart) where we showed the hydrographic time series (see Figure 3). At all stations, the upper 50 meters was strongly stratified with a density gradient of at least one sigma-t unit through the pycnocline. The base of the euphotic zone (1% isolume) extended to a depth of 30-45 m, whereas the pycnocline started no deeper than 25 m. Thus, the euphotic zone always extended into the pycnocline. The pycnocline separated a NO_3 -depleted surface mixed layer from NO_3 -rich GSW below it. The average chlorophyll a concentration in the mixed layer was 1.5 mg m^{-3} , and primary production exceeded $5 \text{ mg C m}^{-3} \text{ h}^{-1}$ in the mixed layer at 4 of 6 stations. Maximum C assimilation numbers in the mixed layer at each station ranged from 15-19 $\text{mg C} \cdot \text{mg Chl a}^{-1} \text{ h}^{-1}$. NO_3 uptake measurements were not obtained in the surface mixed layer, but the vertical distribution of C and NO_3 -N uptake were similar below the mixed layer at 3 of 4 stations.

A time series of euphotic zone integrals of NO_3 , chlorophyll a, primary production, and other measurements are presented in Figure 5. Because all primary production stations were within 5 km of each other, the results are merged into one time series. Euphotic zone NO_3 and chlorophyll a showed 2 peaks (Fig. 5). The chlorophyll a peak lagged NO_3 by about 1 day. Temporal changes in primary production tracked chlorophyll a. The first peak in euphotic NO_3 (resulting from upwelling associated with the second large frontal eddy) was observed on 22 April. The decrease in euphotic zone NO_3 from 22-24 April was probably caused by a combination of phytoplankton uptake and either downwelling or advection of nutrient-rich water as the frontal eddy passed through this area. Because C assimilation numbers increased slightly from 23 to 24 April, the decrease in primary production was solely a result of lower euphotic zone chlorophyll a rather than a decline in the physiological activity of the phytoplankton. The storm interrupted sampling on 25 and 26 April. When sampling was resumed on 27 April, the third eddy was in the study area. A second peak

in euphotic zone NO_3 was observed on 27 April which was caused by upwelling associated with the third eddy as well as vertical mixing resulting from the strong winds. Chlorophyll a peaked on 28 April, and primary production reached the highest value (ca. $6 \text{ g C m}^{-2} \text{ d}^{-1}$) observed by us; a rate that may have been characteristic of much of the shelf break. A multispectral scanner flown by a NASA U-2 aircraft on 28 April showed that a 10-20 km wide surface chlorophyll patch (ca. 5 mg m^{-3}) extended for at least 90 km along the shelf break through our study area (Kim, McClain, Blaine, Hart, Atkinson and Yoder, 1980; Yoder et al., 1981b). A similar instrument in the Nimbus 7 satellite showed that the patch extended along the inshore edge of the Gulf Stream front for several hundred km (C. R. McClain, personal communication). C assimilation number (euphotic zone integral) also reached its highest value ($90 \text{ mg C mg Chl a}^{-1} \text{ d}^{-1}$) on 28 April, apparently in response to the relatively high levels of euphotic zone NO_3 and to a 50% increase in solar irradiance from 27 to 28 April (Fig. 6). By 30 April, primary production decreased to $1 \text{ g C m}^{-2} \text{ d}^{-1}$, < 20% of the rate two days earlier. The decrease was a result of both lower euphotic zone chlorophyll a and lower C assimilation numbers. The decrease in C assimilation number was probably related to the sharp drop in euphotic zone NO_3 from 27-30 April as the third eddy moved out of the study area. In addition, incident irradiance was lower on 30 April than on the two previous days (Fig. 6).

Chain-forming centric diatoms and a pennate, Nitzschia sp., dominated the phytoplankton on 28 April (Table 1) when we observed highest rates of primary production (Fig. 5). At the 3 depths where phytoplankton were counted, diatom concentration was highest ($10^6 \text{ cells liter}^{-1}$) at 12 m (Table 1). Dinoflagellates and coccolithophorids were present at very low concentrations. Skeletonema costatum was the single most dominant species with a maximum concentration of $3.5 \times 10^5 \text{ cells liter}^{-1}$ at 12 m. The species composition was similar within

upwelled waters at other shelf break stations that we sampled. In addition to the species shown in Table 1, large mats (ca. 1 mm² or larger) of thousands of individual cells of the diatom, Thalassiosira subtilis (or similar species) were also observed, particularly below the mixed layer (see Summer Results). These mats were concentrated during oblique tows for zooplankton, and at times were so abundant that they discolored the nets and made the zooplankton samples difficult to process (G. -A. Paffenhöfer, personal communication).

APRIL, 1980

Physical Description

During the April, 1980 study, hydrographic, current meter, and production stations were all on the same transect at 30°N (Fig. 1). River runoff along the Georgia and South Carolina coasts was unusually high during the winter and spring of this year (approximately 2 X the 20 year mean) and peaked in early April (J. O. Blanton, unpublished) causing anomalously low surface salinities ($< 35 \times 10^{-3}$) along the middle and outer shelf (Fig. 7). The low surface salinities were a factor in stratifying the shelf earlier than was found in 1979 and other years. Stratification generally occurs later in the spring and is primarily a result of temperature difference. Early stratification of the shelf may explain why intruded GSW moved farther onto the shelf in April 1980 than in April 1979 (see Atkinson, 1977). Figure 8 shows that the 5 μM NO₃ isopleth extended as far shoreward as the 20 m isobath within a subsurface intrusion of upwelled GSW (confirmed by T-S analysis). In comparison, spring studies of upwelling in 1979 (Yoder et al., 1981b) and 1977 (Lee et al., 1981) found that NO₃-rich waters only penetrated to about the 40 m isobath.

Current meter moorings were located near the production stations at the 40 m and 75 m isobaths. The shelf break moorings (75 m isobath) was equipped with 6 meters between 7 and 72 m. At the 40 m isobath, 4 current meters were located

between 7 and 37 m. Data from these instruments indicated strong Gulf Stream influence throughout the study period (10-26 April). Current speeds at the shelf break were frequently in excess of 150 cm s^{-1} near the surface (17 m) and 50 cm s^{-1} near the bottom (72 m) (Fig. 9). Vertical shears between the top and bottom meter ranged from about 8×10^{-3} to $2 \times 10^{-2} \text{ s}^{-1}$. Upper layer mean flows were toward the north at about 60 cm s^{-1} at the shelf break and 5 cm s^{-1} at the 40 m isobath. Subtidal fluctuations of the along-shelf (v) and cross-shelf (u) velocity components and temperature (T) indicate four Gulf Stream frontal disturbances propagated northward past the current meter arrays between 9 to 28 April (Fig. 9). Northward propagation speeds were higher than observed in other years and ranged from $40\text{--}60 \text{ km d}^{-1}$ as determined from current meters located north and south of the 30°N transect. The first event passed through the 30°N transect on 9-10 April, the second from 12-15 April, the third from 20-22 April, and the fourth from 23-27 April. Each event produced a cyclonic perturbation in the mean northward flow that occurred simultaneously with a large oscillation of temperature. These fluctuations were highly coherent and close in phase throughout the water column at both the 40 and 75 m isobaths. The onset of each disturbance produced onshore flow with decreasing temperature and decreasing northward speed throughout the water column at each location, however the effect was more pronounced near the shelf break.

Hydrographic time series from 12-26 April at the 30 m, 40 m, and 50 m isobaths at 30°N are presented in Figure 7. The series started after the first event and in the middle of the fourth, but the second and third events are apparent in the change in isotherm depth at the 40 m and 50 m isobaths. Wind speeds are shown in Figure 2B and were never as strong as during the storm in April, 1979. However, winds were frequently in excess of 10 m s^{-1} and may have been an important contributor to vertical mixing. Salinity changes at the 30 m

and 40 m isobaths suggest a gradual mixing of relatively low salinity surface waters (initially 34×10^{-3}) with higher salinity water (initially 36×10^{-3}) lower in the water column during the course of the study (Fig. 7).

Biological Effects

Figure 10 shows the vertical distributions of density, NO_3 , chlorophyll a, and the rates of C and NO_3 -N uptake at the 50 m isobath (shelf break) at 30°N . As for the 1979 study, the water column was strongly stratified. The euphotic zone (1% isolume) at the shelf break was not as deep as in 1979 and was never deeper than 30 m. The average chlorophyll a concentration of the mixed layer was 0.6 mg m^{-3} (compared to 1.5 in 1979), and primary production exceeded $5 \text{ mg C m}^{-3} \text{ h}^{-1}$ in the mixed layer at only 1 of 7 stations (compared to 4 of 6 in 1979). Maximum primary production occurred below the mixed layer at 5 of 7 stations in 1980. The vertical distribution in primary production generally closely followed the vertical distribution in the rate of NO_3 -N uptake being grossly different at only 1 station (April 20).

Figure 5 includes a time series (euphotic zone integrals) of primary production and NO_3 uptake, chlorophyll a specific uptake rates of C and NO_3 (assimilation numbers), and chlorophyll a and NO_3 at the 50 m isobath (shelf break) at 30°N during April, 1980. In general, euphotic zone integrals of chlorophyll a and NO_3 were similar in 1979 and 1980, but at the shelf break, primary production was generally much lower in 1980. Figure 5 shows that lower C assimilation numbers, rather than the amount of chlorophyll a, accounted for lower primary production. Temporal changes in primary production at the shelf break in 1980 showed a strong, visual correlation with NO_3 uptake (Fig. 5). Temporal changes in primary production and NO_3 uptake closely followed the trend in chlorophyll a specific uptake (i.e., C and NO_3 assimilation numbers) and did not correlate with chlorophyll a or NO_3 . The peak in C and NO_3 uptake (and in C and NO_3 assimilation numbers) on 20 April may

have been caused by a higher incident solar irradiance than on the two previous days (Fig. 6). The good correlation of C and NO_3 uptake with C and NO_3 assimilation numbers contrasts with 1979 results. In 1979, primary production correlated better with chlorophyll a than with C assimilation number.

A subsurface intrusion of nutrient-rich GSW penetrated much farther onto the shelf in 1980 than in 1979 (Fig. 8). Time series of primary production and euphotic zone NO_3 at the 30 m and 40 m isobaths at 30°N are presented in Figure 11. Primary production there averaged 1.8 and $2.2 \text{ g C m}^{-2} \text{ d}^{-1}$ compared to $0.7 \text{ g C m}^{-2} \text{ d}^{-1}$ at the shelf break. Average euphotic zone NO_3 at the 40 m isobath ($2.1 \text{ g NO}_3\text{-N m}^{-2}$) was about twice the average at the shelf break ($1.2 \text{ g NO}_3\text{-N m}^{-2}$) and 30 m isobath ($1.1 \text{ g NO}_3\text{-N m}^{-2}$). Chlorophyll a measurements, available from only 3 samplings at the 30 m and 40 m isobaths, showed that chlorophyll a and C assimilation numbers were higher at the 30 m and 40 m isobaths than at the shelf break. C assimilation numbers were 33, 48, and $25 \text{ mg C} \cdot \text{mg Chl a}^{-1} \text{ h}^{-1}$ and average chlorophyll a was 40, 44, and $30 \text{ mg chlorophyll a m}^{-2}$ at 30 m, 40 m, and shelf break, respectively. Thus, primary production was higher at the 30 m and 40 m isobaths than at the shelf break due to both higher chlorophyll a and C assimilation numbers. The trends in Figure 11 suggest that primary production at the 30 m and 40 m isobaths was related to the amount of NO_3 in the euphotic zone.

PRIMARY PRODUCTION IN RELATION TO BIOMASS

To obtain average values for the 1979 and 1980 studies, C uptake was linearly integrated with time and 1980 NO_3 uptake data were similarly integrated. Primary production was $21.5 \text{ g C m}^{-2} \text{ 8 d}^{-1}$ ($\bar{x} = 2.7 \text{ g C m}^{-2} \text{ d}^{-1}$) and $10.3 \text{ g C m}^{-2} \text{ 15 d}^{-1}$ ($\bar{x} = 0.7 \text{ g C m}^{-2} \text{ d}^{-1}$) in 1979 and 1980, respectively. Euphotic zone $\text{NO}_3\text{-N}$ uptake during the 1980 study was $1.4 \text{ g N m}^{-2} \text{ 15 d}^{-1}$ ($\bar{x} = 0.09 \text{ g NO}_3\text{-N m}^{-2} \text{ d}^{-1}$). Thus, the 15 day average C: $\text{NO}_3\text{-N}$ uptake ratio in 1980 was 7.6 (by weight). A possible explanation for

higher shelf break primary production in 1979 than in 1980 is that there was more chlorophyll a in the mixed layer in 1979 than in 1980. The base of the mixed layer was generally close to the 10% isolume. When nutrients reach the mixed layer, one expects higher specific growth rates than deeper in the water column because of higher mean levels of irradiance. Thus, a given amount of mixed layer chlorophyll a makes a larger contribution to primary production than the same amount deeper in the water column. We regressed ^{euphotic zone} primary production against chlorophyll a in the mixed layer to ascertain if the two were related (Fig. 12). Excluding the point with the highest residual, the regression had a linear correlation coefficient (r) of 0.82 ($n=14$). Thus, mixed layer chlorophyll a explains about 67% (r^2) of the variability in our primary production measurements within upwelled waters at the shelf break. A similar regression using the mean chlorophyll a concentration of the mixed layer rather than the integral yielded a similar result. Thus, mean chlorophyll a concentration of the mixed layer was more important to primary production than the depth of the mixed layer in our studies.

Particulate C and N were integrated over depth in the euphotic zone and compared with integrated uptake rates (Table 2). Both studies in spring showed similar euphotic zone integrals for POC, PON, and chlorophyll a. POC:PON ratios generally ranged from 5 to 10 (by weight), which is within the range often cited for marine waters containing significant amounts of phytoplankton (e.g., Collos and Lewin, 1976; Eppley, Renger and Harrison, 1979). The commonly used C:N ratio of marine plankton (Redfield ratio), 5.7 (by weight), is lower than all but one of our measurements. During both spring studies, euphotic zone POC:Chl a ratios generally exceeded 100 with 4 of 13 stations having values higher than 200. Most ratios reported for marine waters that contain significant amounts of phytoplankton range from 50 to 150 (e.g., Durbin, Krawiec and Smayda, 1975;

Huntsman and Barber, 1977; Malone, 1977; Eppley, Harrison, Chisholm and Stewart, 1977).

At the two depths at stations where NO_3 uptake measurements were made in 1979, the $\text{C}/\text{NO}_3\text{-N}$ uptake ratio varied between 3.6 and 23 (Table 2). Some of this variability may be attributed to the limited number of NO_3 uptake measurements in the 1979 study, since the 1980 results (euphotic zone integrals) fell within a relatively narrow range (6.3-13) (Table 2). High $\text{C}:\text{NO}_3$ uptake ratios indicate that another form of N provided a significant fraction of phytoplankton N demand. To calculate the importance of NO_3 as a source of N ("new production" in sensu Dugdale and Goering, 1967), the uptake rates of other forms of N (e.g., NH_4) should be known but were not measured. To obtain an estimate of new production, we assumed that phytoplankton assimilated C and all forms of N (total-N) according to the Redfield ratio. By comparing observed $\text{C}:\text{NO}_3$ uptake ratios with this ratio (5.7), we calculated the percentage of total N demand that could be accounted for solely by NO_3 uptake and refer to this percentage as "new production". New production at the 2 depths sampled at each station in 1979 ranged from 25-100% of total primary production (Table 2). In 1980, euphotic zone new production ranged from 44 to 90% of the total. The 15 day average $\text{C}:\text{NO}_3$ uptake ratio (7.6) in 1980 yields an average new production of about 75%.

The last columns of Table 2 are estimates of C and "new N" euphotic zone doubling times. By doubling time, we mean the time it takes to synthesize an amount of C and N equivalent to the observed POC and PON at each station using observed rates of C and $\text{NO}_3\text{-N}$ uptake. Carbon doubling time was much faster in 1979 ranging from 1.7 to 9.5 days versus 3.5 to 68 days in 1980. Using average values for both POC and C uptake, C doubling time averaged 4 days in 1979 and 13 days in 1980. Our definition of "new N" doubling time (i.e., based only on NO_3 uptake, not total-N uptake) is not the same as our definition of C doubling

time. With high grazing rates and efficient nutrient recycling, one could observe rapid C doubling times without significant net increases in POC nor a significant net C flux into other pools (e.g., zooplankton, sinking losses). However, since upwelled NO_3 is an addition of new N to the euphotic zone, NO_3 uptake should cause an increase in PON or net N flux into another pool. New N doubling time ranged from 2.7 to 100 days in 1980. The average euphotic zone PON and average NO_3 uptake rate yielded an average new N doubling time of 10.5 days. Though average new N doubling time is significantly less than the duration of our study (15 days) PON did not increase in the euphotic zone at the shelf break (Table 2). Thus euphotic zone PON was either transferred to another pool or was advected away from the shelf break.

Relatively high POC:Chl a and POC:PON ratios imply that phytoplankton were not the only important contributor to POC and PON. We calculated the percentage of POC not accounted for by phytoplankton C by three different methods (Table 3): (1) a constant phytoplankton C:Chl a ratio of 50, (2) a constant phytoplankton C:Chl a ratio of 100, and (3) the equation of Eppley et al. (1977), where phytoplankton $C = 0.158 (\text{POC}) + 0.0007 (\text{POC})^2$. Non-phytoplankton C was obtained by subtracting the result of each of the estimates from measured POC. For each of the three methods, we used phytoplankton C:N ratios of 5 and 10 and calculated by difference the C:N ratios of the non-phytoplankton particulates (Table 3). The equation of Eppley et al. (1977) yielded results similar to those of either one or the other of the other two estimates, so the results of estimate (3) are not shown. Since phytoplankton C:Chl a ratios generally fall between 50 and 100, and phytoplankton C:N ratios are generally between 5 and 10, the matrix shown (Table 3) should cover the range of probable values for non-phytoplankton C. Regardless of which method was applied to estimate phytoplankton C, the results show that if the phytoplankton C:N ratio was closer to 5 than to 10, then the

C:N ratio of non-phytoplankton particulates was much greater than 10 (Table 3). C:N ratios greater than 10 imply that non-phytoplankton particulates are primarily detritus rather than small zooplankton or bacteria which have C:N ratios less than 5. Results from 1979 and 1980 showed that non-phytoplankton C ranged from about 30% to 70% depending on whether we assumed a phytoplankton C:Chl a ratio of 100 or 50, respectively.

AUGUST, 1978

Physical Description

XBTs taken along the outer shelf on 4 August, 1978, showed a subsurface intrusion of GSW between 30° and 30°30' N. Bottom temperatures were as low as 17°C at the 40 m isobath compared to surface mixed layer temperatures of 28°C (see Blanton et al., 1981). The cold water intrusion had been on the shelf for only a few days because a cross-shelf section at 30°N on 27 July, 1981, showed bottom temperatures of 21.1°C, 24.2°C, and 24.7°C at the 50, 40 and 30 m isobaths, respectively. XBT and CTD surveys on 4 and 5 August showed that the intrusion was about 40 km in diameter, and that isotherms less than 22°C were cut off from source waters farther offshore ("stranded") in the cross-shelf axis and possibly also in the along-shore axis (Blanton et al., 1981). A drogue was deployed on 5 August near the center of the intrusion. The top of the drogue sail was at 24 m which corresponded to the 22°C isotherm. The drogue which was used as a reference station from 5 August (T=0) until 14 August (T=9) was located at the 37 m isobath on 5 August and near the 30 m isobath by 7 August. It remained close to the 30 m isobath for the remaining days of the study. During the 9 day study the drogue moved 61 km on a bearing of 345 degrees with a mean velocity of about 8 cm s⁻¹ (Fig. 1). Prevailing winds were light from the south and southeast, and seas were calm. Four temperature sections, each centered by the position of the drogue, show that the drogue stayed near the center of the intrusion

as defined by stranded isotherms less than 22°C (Fig. 13).

Biological Effects

Chlorophyll a and NO_3 time series at the drogue are shown in Figure 14. NO_3 was initially as high as 10 μM within the intrusion and less than 1.0 μM 7 days later. Dissolved inorganic Si and P also decreased with time with dissolved Si as high as 12 $\mu\text{g-atoms liter}^{-1}$ initially, decreasing to less than 3 $\mu\text{g-atoms liter}^{-1}$ by the final two days. Chlorophyll a was less than 2 mg m^{-3} in the subsurface intrusion for the first 3 days and exceeded 7 mg m^{-3} by the sixth day. Temporal increases in chlorophyll a within the intrusion were accompanied by decreased NO_3 (Fig. 14).

From 7 August (T=2) until the end of the study (T=9), the surface mixed layer and the intrusion (temperatures less than 25°C) were each about 15 m thick. Mean chlorophyll a concentration in the mixed layer ranged from 0.2 to 0.35 mg m^{-3} and NO_3 was always below detection limits. Mean chlorophyll a concentration in the intrusion was initially 0.4 mg m^{-3} and peaked at 4 mg m^{-3} on 12 August (T=7), i.e., a 10 fold increase. During the final 3 days of the study, mean chlorophyll a in the intrusion was 10-15 times greater than in the surface mixed layer. Mean NO_3 and chlorophyll a concentrations of the intrusion are shown as a function of time in Figure 15. From T=1 until T=7, the doubling time of intrusion chlorophyll a was 1.5-2.0 days assuming exponential increase (Fig. 15). During the same period, the half-life of NO_3 was 1.5-2.0 days assuming exponential decrease (Fig. 15). After T=7, average chlorophyll a in the intrusion decreased. Further decay of the phytoplankton bloom was not followed.

Light-limited cultures of the marine diatom, Skeletonema costatum grown at 16 and 22°C with NO_3 as the source of N, had PON:Chl a ratios close to 6 (Yoder, 1979). Mean NO_3 concentrations of intrusion waters decreased to 6 μM (91 mg m^{-3}) from T=1 to T=7 (peak of the phytoplankton bloom). If the

PON:Chl a ratio of intrusion phytoplankton was similar to light-limited S. costatum cultures, the average chlorophyll a concentration should have been 15 mg m^{-3} on $T=7$, rather than the observed 4 mg m^{-3} . This implies that a high proportion of phytoplankton production was lost from the phytoplankton pool during the bloom. If the loss occurred at a constant exponential rate (e.g., due to zooplankton grazing), the average specific rate of "new production" of intrusion phytoplankton was 0.6 d^{-1} between $T=1$ and $T=7$ compared to the specific rate of chlorophyll a increase of 0.4 d^{-1} (i.e., a measure of net growth).

During the first 5 days C and NO_3 uptake rates were determined at a single depth within the intrusion. C uptake was measured in a laboratory incubator at 10 levels of irradiance ranging from 5 to $60 \text{ } \mu\text{Einst. m}^{-2} \text{ s}^{-1}$. In comparison, the average daily irradiance (light period only) of the intrusion (15-30 m) ranged from 46 to $82 \text{ } \mu\text{Einst. m}^{-2} \text{ s}^{-1}$ (calculated from equation 4). NO_3 uptake was measured at $35 \text{ } \mu\text{Einst. m}^{-2} \text{ s}^{-1}$, the average daily light period irradiance at 24-29 m. The relation between assimilation number ($\text{mg C} \cdot \text{mg Chl } \underline{a}^{-1} \text{ h}^{-1}$) and irradiance was linear at these low irradiance levels, and straight lines were fit to the results of each experiment ($n=6$). Examples of the regressions having highest and lowest correlation coefficients are shown in Figure 16. The x-axis intercept of the regression lines (compensation irradiance) ranged from -1.2 to $8.3 \text{ } \mu\text{Einst. m}^{-2} \text{ s}^{-1}$ (400-700 nm). Excluding the single negative result for I_c (compensation irradiance), average I_c was $4.3 \text{ } \mu\text{Einst. m}^{-2} \text{ s}^{-1}$ ($n=5$). This corresponds to about 0.4% of average incident solar irradiance on a cloudless summer day. The attenuation coefficient at the drogue station was 0.11 m^{-1} , and thus I_c occurred at 50 m. The slope (a) of the regressions ranged from 19-36 $\text{mg C mg Chl } \underline{a}^{-1} \text{ Einst.}^{-1} \text{ m}^{-2}$ and averaged 25.2 excluding the slope associated with the negative I_c . C: NO_3 -N uptake ratio at $35 \text{ } \mu\text{Einst. m}^{-2} \text{ s}^{-1}$ ranged from 3.4 to

58 and showed no trend with time, temperature, or NO_3 concentration.

We used equations 2-5 to estimate daily primary production in the intrusion during the period of rapid increase in mean chlorophyll a and decrease in mean NO_3 concentration (T=1 to T=7).

$$I_{0m} = I_{\max} (A)(B)(C)(D) \quad (2)$$

where, $I_{\max} = 600 \text{ ly d}^{-1}$ (from pyranometer located at Skidaway Institute of Oceanography, Savannah, Georgia)

A = photosynthetically active irradiance ($0.5 I_{\max}$)

B = % sunshine (Fig. 6).

C = 0.85 (i.e., 15% reflectance off the sea surface; Strickland, 1958)

D = 1 ly of sunshine = $0.2 \text{ Einst. m}^{-2}$ (Strickland, 1958)

$$I_{15m} = I_{0m} e^{-kz} \quad (3)$$

where, $z = 15 \text{ m}$

$k = 0.11 \text{ m}^{-1}$ (measured)

$$\bar{I}_{15-30m} = [I_{15m} (1 - e^{(15 k)})] 15 k \quad (4)$$

where, $\bar{I}_{15m-30m}$ is the mean irradiance between 15-30 m

$$\text{Daily primary production} = (\bar{I} - \bar{I}_c) (\bar{a}) (\Sigma_{15m}^{30m} \text{Chl } \underline{a}) \quad (5)$$

where, $\bar{a}$ = mean initial slope (see text)

$\bar{I}_c$ = mean compensation irradiance (see text)

$\Sigma \text{Chl } \underline{a}$ = average daily chlorophyll a (from Fig. 13)

Equations 2-5 yielded daily primary production estimates ranging from 0.4 (T=1) to 4.1 (T=7) $\text{g C m}^{-2} \text{ d}^{-1}$. The total primary production for the 7 day period at depths between 15 and 30 m was 13.5 g C m^{-2} or an average of $1.9 \text{ g C m}^{-2} \text{ d}^{-1}$. Primary production of the surface mixed layer (15 m thick) measured on two separate days (T=4 and T=7) averaged $0.4 \text{ g C m}^{-2} \text{ d}^{-1}$. Thus, primary production in the upper 15 m (mixed layer) was approximately equivalent to that of the intrusion (15-30 m) during the early stages of the bloom within the intrusion,

but was only about 10% of intrusion primary production at the peak of the bloom. Average C assimilation number was higher in the surface mixed layer than in the intrusion, but the intrusion had substantially higher chlorophyll a concentrations. The change in NO_3 concentration in the intrusion during the same period was $-1.3 \text{ g NO}_3\text{-N m}^{-2} \text{ 7 d}^{-1}$. Thus, the 7 day primary production and $\text{NO}_3\text{-N}$ uptake estimates yield a calculated C: $\text{NO}_3\text{-N}$ uptake ratio of 10.4 or 55% new production using earlier assumptions.

Cell counts and particulate Si analyses showed that the intrusion at the drogue station was dominated by diatoms. Of the phytoplankton taxa commonly found in marine waters, diatoms are the only important group that contain significant amounts of Si. A linear regression (minus the point having highest residual sums of squares from an initial regression) of chlorophyll a against particulate Si below 15 m at different times yielded a correlation coefficient of 0.93 ($n=26$) with a Y-axis intercept close to zero ($-.06$) (Fig. 15). Diatom species listed in Table 4 are ordered by their approximate cell volume. The dominate diatoms in the intrusion initially had a wide range in mean cell volume (10^2 to $4 \times 10^6 \mu\text{m}^3$). By the end of the study, however, larger diatoms dominated. As in spring, 1979, mats of the diatom, Thalassiosira subtilis (or similar species), occurred in large numbers. The mats, particularly noticeable in zooplankton nets after tows within the intrusion (G. -A. Paffenhöfer, personal communication), were composed of a gelatinous matrix consisting of thousands of individual cells approximately $10 \mu\text{m}$ in diameter, and thus accurate enumeration of this species was not attempted. The relative abundance of T. subtilis, however, was determined by microscopically examining the area covered by the mats on the bottom of settling chambers. This method showed that T. subtilis became a major component of the phytoplankton by the end of the intrusion study (Table 4).

DISCUSSION

Comparison of the Three Studies

Our results show that shelf break upwelling and intrusion of NACW onto the outer shelf leads to moderately high rates of primary production (ca. $1 \text{ g C m}^{-2} \text{ d}^{-1}$ or more) of which a significant percentage ($> 50\%$) is "new production". Despite differences in average primary production and the seasons during which our studies were conducted (spring and summer), all three showed important similarities. During all three studies, a high proportion of primary production was "new production" - i.e., upwelled NO_3 was a principal source of N. Best supporting evidence was obtained during spring, 1980, when the vertical changes in primary production closely followed NO_3 uptake rates. Secondly, temporal changes in primary production closely followed trends in NO_3 uptake (both integrated over the euphotic zone). Because of the small number of NO_3 uptake experiments conducted in 1979, evidence supporting a high percentage of new production is not as convincing. However, temporal changes in primary production in 1979 followed trends in euphotic zone NO_3 (with a 1 day lag) suggesting a relation between the two. Finally, during summer 1978, the decline in intrusion NO_3 coincided with increase in plant biomass (chlorophyll a), providing strong indirect evidence that NO_3 was a primary source of N.

Phytoplankton species were not enumerated in April, 1980 but during the other two studies upwelled waters were dominated by diatoms. Detailed floristic surveys (Marshall, 1971; Hulburt, 1967) earlier showed that, in general, southeastern shelf waters are dominated by diatoms. Marshall (1971), who analyzed samples from all seasons of the year, concluded that S. costatum and Rhizosolenia spp. were the most abundant diatoms. Other investigators later reported that diatoms generally dominate intruded GSW, but the dominate species were not always the same. Bishop et al. (1980) showed that an April intrusion

of GSW was principally dominated by S. costatum, whereas Paffenhöfer (1980) found that large Rhizosolenia spp. were abundant in a summer intrusion into Onslow Bay, North Carolina. Summer intrusions off the Georgia/Florida coasts were also characterized by significant numbers of Rhizosolenia spp. (Paffenhöfer and Dunstan, unpublished). The Chrysophyte, Phaeocystis pouchetii, was so abundant in a summer intrusion off the north Florida coast that quantitative zooplankton tows could not be made (Atkinson et al., 1978).

Phytoplankton productivity differed significantly during our three studies, and these differences are at least partially explained by differences in the physical dynamics of water motion. Primary production was highest ($\bar{x} = 2.7 \text{ g C m}^{-2} \text{ d}^{-1}$) in spring, 1979. Prior to, and during the early phase of this study, two large Gulf Stream frontal eddies passed through our study area, and measurements were initially near the center of an upwelled cold core (Yoder et al., 1981B). A third eddy came through only days later, and strong winds may have enhanced nutrient flux into the euphotic zone. To examine the relative "strength" of upwelling in spring, 1979, we calculated the net nitrate flux to the outer shelf over 12 days using the method described by Lee et al. (1981). In brief, Lee et al. used continuous temperature and current records and the constant NO_3 /temperature relation of GSW to calculate the net onshore flux of NO_3 at the shelf break. During the 7 day duration of a frontal eddy studied in April, 1977, Lee et al. (1981) showed that net onshore NO_3 flux averaged $18.6 \mu\text{moles m}^{-2} \text{ s}^{-1}$ compared to the average onshore flux between December, 1976 and April, 1977, of $8.5 \mu\text{moles m}^{-2} \text{ s}^{-1}$. The latter estimate reflects the averaged contribution of many separate upwelling events. In comparison, the net onshore NO_3 flux during our 1979 study averaged $34.4 \mu\text{moles m}^{-2} \text{ s}^{-1}$, or about twice the rate of the 1977 eddy and about 4 times the seasonal average. This suggests that upwelling was unusually strong during the 1979 study.

No large frontal eddy passed through the study area during the April, 1980 study. However, four smaller upwelling-favorable events were detected by shelf break current meter arrays, and NO_3 -rich GSW penetrated well onto the shelf at 30°N . Early stratification of the shelf was the probable cause of seasonally-atypical cross-shelf penetration. At the 30 and 40 m isobaths, temporal changes in vertical salinity distributions suggested vertical mixing between NO_3 -rich bottom waters and the mixed layer during the 15 day time series. Primary production was higher at the 30 and 40 m isobaths than at the shelf break which may have been in part due to more NO_3 within the euphotic zone.

At the shelf break, average primary production was much lower during 1980 than 1979 (0.7 versus $2.7 \text{ g C m}^{-2} \text{ d}^{-1}$). Because euphotic zone chlorophyll a was generally similar during both studies, the difference in primary production principally resulted from lower C assimilation numbers in 1980. We hypothesize that assimilation numbers were lower in 1980 than in 1979 because a much higher percentage of chlorophyll a was below the mixed layer (ca. 10% isolume) in 1980, and thus light-limitation was more severe than in 1979.

Physical conditions during the summer, 1978, drogue study were different from both of the spring studies. A subsurface intrusion of upwelled GSW penetrated well onto the shelf and separated from source waters - i.e., isotherms less than 22°C did not extend into deeper offshore waters. Winds were light and displacement of the drogue showed that the intrusion center moved north at a relatively slow speed (ca. 8 cm s^{-1}). The linear relation between primary production and light up to an irradiance level that was close to the mean for the subsurface intrusion showed that phytoplankton were light-limited, at least during the first 5 days of the study. Although all detectable NO_3 (and eventually more than 90% of the chlorophyll a) was below the 10%-20% isolume, the residence time of the intrusion on the shelf (greater than 10 days) was long enough for

light-limited phytoplankton to convert virtually all of the NO_3 into plant biomass. In spite of light-limitation the average production within the subsurface intrusion was about 5 times greater than that of the overlying mixed layer, because chlorophyll a concentrations were much greater.

Seasonal Estimates of Primary Production

Haines and Dunstan (1975) measured primary production across the southeastern shelf during 4 seasonal cruises of about 7 days duration during 1973-74. As their study was completed before the potential importance of upwelling along the Gulf Stream front was recognized, they did not distinguish between rates obtained in upwelled waters and those that were not. For comparative purposes, we assume that their very low average rate of primary production ($0.05 \text{ g C m}^{-2} \text{ d}^{-1}$) reported at the 20-200 m isobaths during April is representative of the outer shelf in the absence of upwelled GSW. Average primary production within upwelled waters during April, 1979 and 1980 reported here was respectively, about 50 and 14 times greater than the average April rate reported by Haines and Dunstan (1975), and the highest rate ($6 \text{ g C m}^{-2} \text{ d}^{-1}$) measured by us was more than 100 times greater than their average. This comparison illustrates why it is important to consider the effects of specific events such as upwelling when estimating seasonal primary production on the outer shelf. Obviously, the extent to which upwelling influences annual or seasonal estimates of areal production depends on the frequency of the upwelling events, their duration, and the area influenced.

The frequency of upwellings was estimated from the records of a long-term current meter mooring located at the shelf break (75 m isobath) off the Georgia coast ($31^\circ 30' \text{N}$). Four records were available between November-April. Upwelling events were identified by onshore flow near the bottom coupled with a drop in near-bottom temperature, and we ignored all interruptions of onshore flow that lasted for less than 24 h. Results from the four records showed that upwelling

occurred from 40%-65%, averaging 53%, of the time. The number of events during the same period averaged 4-5 per month.

Hydrographic data collected during the November-April period shows that nutrient-rich upwelled GSW is usually constrained to the outer shelf between about the 40 m to 200 m isobaths - a distance of about 30-40 km (Atkinson, 1977, unpublished; Lee et al., 1981; Yoder et al., 1981B; Yoder, unpublished manuscript). Except in waters shoreward of the 20 m isobath, relatively high chlorophyll a concentrations occur only within upwelled GSW (Bishop et al., 1980; Yoder et al., 1981A; Yoder et al., 1981B; Yoder, unpublished manuscript). During months when the shelf is not stratified (ca. November-April), wave-like disturbances propagate along the cyclonic Gulf Stream front with characteristic periods and propagation speeds and cause upwelling which generally affects only the outer part of the continental shelf. For these reasons, we will assume that seasonal primary productivity does not change significantly along the length of the outer southeastern shelf when shelf waters are not stratified. Possible exceptions may be the outer shelf just north of Cape Canaveral, Florida and off the coast of North Carolina, where Blanton et al. (1981) showed that upwelling and intrusion of GSW may occur more frequently than off the north Florida, Georgia, and South Carolina coasts. Whether alongshore differences in upwelling frequency cause alongshore differences in primary production is not known.

Average primary production in upwelled waters on the outer shelf during November-April (most measurements were made in April) was $1.8 \text{ g C m}^{-2} \text{ d}^{-1}$ ($n=23$). This average and the average number of days that upwelling occurred (i.e., 53% of the time) implies a 6 month primary production during upwelling of about 175 g C m^{-2} . We assume the average daily primary production during April ($0.05 \text{ g C m}^{-2} \text{ d}^{-1}$) reported by Haines and Dunstan (1975) represents conditions on the outer shelf when upwelled waters are absent. Combining rates for non-upwelling

and upwelling conditions yields a primary productivity estimate of about $180 \text{ g C m}^{-2} \text{ 6 mo}^{-1}$ on the outer shelf during November-April. Based on hydrographic data, the outer 40 km of the shelf (about the outer third of the shelf off the Georgia coast) is the approximate spatial scale to which this productivity estimate applies.

One major limitation of our estimate is that by using an average value for primary production, we ignore the time dependence of primary production during the development of phytoplankton blooms. Secondly, we assume that upwelling events are similar throughout the November-April period even though most of our measurements were made in April. Hydrographic, satellite, and current meter data show that relevant shelf break physical processes (i.e., meanders and eddies) occur throughout the November-April period, supporting the latter assumption. In addition, chlorophyll a measurements show consistent relations with hydrography, i.e., high concentrations on the outer shelf are only found within intruded GSW regardless of season. In spite of the above uncertainties, our productivity estimate is a first attempt to recognize and account for the effects of dominant processes that introduce nutrients into the euphotic zone on the outer southeastern shelf. Obviously a better estimate could be obtained with a long time series (weeks-months), but frequent measurements (ca. 1 per day) would be required to resolve the effects of upwelling events.

Haines and Dunstan (1975) also estimated an annual primary production of $285 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the inner shelf of the Georgia Bight (0-20 m isobaths or roughly the inner third of the shelf). Thomas (1966) showed that primary production near the mouth of the Altamaha River was about $600 \text{ g C m}^{-2} \text{ yr}^{-1}$. Our 6 month estimate for the outer shelf suggests that production there may exceed average inner shelf production and may be as much as 60% the rate of primary production near the mouth of a major southeastern river. This contradicts earlier

conclusions concerning productivity across the southeastern shelf (Haines, 1974; Haines and Dunstan, 1975; Turner et al., 1979) but is consistent with the hypotheses advanced by Dunstan and Atkinson (1976), Bishop et al. (1980) and Yoder et al., (1981A, 1981B).

Our results show that new production during upwelling is 50% (about $85 \text{ g C m}^{-2} \text{ 6 mo}^{-1}$) or more of total primary production. This is more than 10 times higher than the new production estimate of Haines (1974) and Dunstan and Atkinson (1976) for the November-April period. The latter study concluded that intrusions of GSW were an important source of nitrogen only during summer. Lee et al. (1981) estimated that the net flux of nitrate onto the outer shelf from eddies could support a rate of new production of about $60 \text{ g C m}^{-2} \text{ yr}^{-1}$ (ca. $30 \text{ g C m}^{-2} \text{ 6 mo}^{-1}$), which is less than 50% of the new production estimate given here. Lee et al. (1981) estimated nitrate flux using only near-surface and near-bottom current meters to describe onshore-offshore currents during upwelling. More recent studies (Lee, unpublished) that employed up to 6 current meters spaced throughout the water column at the 75 m isobath showed that the results from just 2 current meters grossly underestimated onshore flow (and thus onshore nitrate flux). An improved estimate of eddy-induced NO_3 -flux was made using data from the shelf break mooring located at 30°N during April, 1980. Using this data and assuming 1 eddy every 14 days yields a NO_3 flux to the shelf that could result in maximum "new" production of $160 \text{ g C m}^{-2} \text{ 6 mo}^{-1}$ (assuming the Redfield ratio of 5.7 to convert phytoplankton N to C). Our estimate of "new" production (based on uptake measurements) of $85 \text{ g C m}^{-2} \text{ 6 mo}^{-1}$ is less by half than potential new production from eddy-induced upwelling alone. This suggests that most upwelled NO_3 is not assimilated by phytoplankton during the November-April period.

Shelf break current meter records during May-October (stratified shelf) show that upwelling frequency is comparable to that of November-April (Lee, unpublished).

However, no one has yet reported low temperatures ($< 22^{\circ}\text{C}$), high NO_3 , or high chlorophyll a concentrations in the mixed layer on the outer shelf (ca. 40-200 m isobaths) during summer such as we found during spring (e.g., April, 1979) or observed by others during winter (Bishop et al., 1980; Yoder, unpublished). Thus, our average value for outer shelf primary production during November-April may not apply during the remaining months of the year, since our average includes results obtained during strong upwelling in April, 1979 when mixed layer production was very high. Our summer, 1978 study illustrates another reason why outer shelf primary production may be lower during May-October than in November-April. When the shelf is stratified, upwelled GSW penetrates well onto the shelf and at times, becomes isolated from source waters farther offshore (Atkinson, 1977). This situation arises when an upwelling favorable Gulf Stream disturbance is coupled with southerly winds that increase onshore flow in the bottom layer (Hofmann, Pietrafesa and Atkinson, 1981; O'Malley, 1981). Prevailing winds during summer have a strong southerly component (Weber and Blanton, 1980). When a subsurface intrusion is stranded, water column nutrients are highest at the center of the intrusion, which can be shoreward of the 40 m isobath (e.g., summer, 1978), than on the outer shelf. Under these circumstances, we expect event-averaged primary production to be higher toward the center of the intrusion than on the outer shelf. A major study is planned to address upwelling dynamics and biological effects during summer conditions.

Comparison with Wind-driven Upwelling Systems

The major wind-driven upwelling systems off the west coast of the U.S., Peru, and northwest Africa have been studied for years, and a far larger data base is available for these areas than for the outer southeastern shelf. Despite the relatively few data for the southeast shelf, some preliminary comparisons illustrate important differences between the wind-driven systems and Gulf Stream-

induced upwelling. The most obvious difference is the amount of NO_3 in the mixed layer. We have never observed more than $5 \mu\text{M NO}_3$ in the mixed layer on the outer southeastern shelf and concentrations that high are rare. In comparison, mixed layer NO_3 often exceeds $10 \mu\text{M}$ during upwelling off Baja California (e.g., Walsh, Whitledge, Kelley, Huntsman and Pillsbury, 1977), Oregon (Small and Menzies, 1981), northwest Africa (Codispoti and Friederich, 1978), and Peru (Kelley, Whitledge and Dugdale, 1975). Secondly, upwelling is aseasonal on the southeast U.S. shelf and upwelled nutrient-rich waters are rapidly (days-weeks) removed from the outer shelf inbetween events, especially when the shelf is not stratified. This causes rapid (days-weeks), and extreme, "relaxations" in the biological response, since the outer shelf changes from relatively high primary production during upwelling to essentially oceanic conditions as upwelled waters downwell or advect from a fixed location on the shelf. During the upwelling season in the aforementioned wind-driven systems, relaxations occur inbetween wind events, but the biological response does not drop to oceanic levels. For example, primary production averaged $2 \text{ g C m}^{-2} \text{ d}^{-1}$ during a 2 month (seasonal) study off northwest Africa (Huntsman and Barber, 1977) which slightly exceeds average primary production during upwelling events on the outer southeastern shelf. Finally, strong wind-driven upwelling destratifies the water column to the extent that the mixed layer depth considerably exceeds the depth of the euphotic zone. Under these circumstances, primary production is suppressed until the winds abate (e.g., Huntsman and Barber, 1977; Jones and Halpern, 1981). In contrast, Gulf Stream-induced upwelling increases stratification of the shelf and decreases the depth of the mixed layer as colder water intrudes onto the shelf beneath residence shelf waters. All of these differences will presumably influence the comparative efficiency and nature of the food chains that use phytoplankton production generated during wind-driven and Gulf Stream-induced upwelling.

Speculation

During the 1979 and 1980 studies, some of the cross-shelf transects were extended seaward of the shelf break into the Gulf Stream. Chlorophyll isopleths contoured along these sections suggested continuity between subsurface chlorophyll maxima within the Gulf Stream and phytoplankton blooms within upwelled waters on the shelf. In general, chlorophyll isopleths followed isopycnals (isotherms) which, in turn, reflected the depth of the nitricline. Figure 18 illustrates an example where 4 diatoms that dominated upwelled waters on the shelf were the same 4 species that dominated the subsurface chlorophyll maximum within the cyclonic side of the Gulf Stream. In contrast, these 4 species were relatively unimportant within the shelf water shoreward of the phytoplankton bloom in upwelled waters (Fig. 18). From the results of single transects, one cannot conclude whether upwelling brings phytoplankton to the shelf or whether downwelling introduces shelf species to the subsurface chlorophyll maximum of the Gulf Stream. Results such as those presented in Figure 16 suggest that upwelling/downwelling causes an exchange of phytoplankton between blooms on the shelf and the subsurface chlorophyll maximum of the Gulf Stream. Marshall (1971) found that many phytoplankton species are common to the Gulf Stream and southeastern continental shelf and also suggested that upwelling along the front was a possible cause of the similarities. Dominant currents in the Gulf Stream are alongshelf implying that phytoplankton blooms within upwelled waters along the cyclonic side of the Gulf Stream may be "seeded" by phytoplankton transported long distances. For example, a current of 100 cm s^{-1} could transport a particle about 1000 km in 10 days. Studies in the Gulf of Mexico and Florida Straits identified upwelling zones that coincided with the location of the cyclonic front of the Gulf Stream (Loop Current) (Belousov *et al.*, 1966). The dominant species within upwelled waters was the diatom, Thalassiosira subtilis, just as we observed in summer,

1978, and in other studies of upwelled GSW. Thus, we speculate that phytoplankton bloom dynamics within upwelled waters along the Gulf Stream front in the Gulf of Mexico may be similar to the dynamics on the outer southeastern shelf, and that the strong currents associated with the Stream may have transported the population that "seeds" phytoplankton blooms within upwelled waters on the outer southeastern shelf a considerable distance.

Yentsch (1974, 1980) discussed the relatively high primary production observed along the cyclonic Gulf Stream front and attributed this to "ageostrophic effects" based on Rossby's (1936) model of cross-stream flow. Our studies suggest that frontal meanders and eddies may be the principal cause of the relatively high productivity of the cyclonic front, at least in those regions where the front is adjacent to continental shelves. We speculate that productivity of the cyclonic side of other western boundary currents, such as the Kuroshio, may also be influenced by similar processes.

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Table 1. Most abundant diatom species ($\times 10^{-3}$ cells·liter $^{-1}$) at productivity station occupied on 28 April, 1979.

SPECIES	2	DEPTH (m).	45
		12	
DIATOMS			
<u>Chaetoceros spp.</u>	23	18	n.d.
<u>Leptocylindrus danicus</u>	7	16	0.04
<u>Nitzschia sp.</u>	27	72	0.18
<u>Rhizosolenia fragilissima</u>	20	45	0.14
<u>Rhizosolenia stolterfothii</u>	7	20	0.18
<u>Skeletonema costatum</u>	96	350	0.20
TOTAL	195	570	1.3
DINOFLAGELLATES			
TOTAL	n.d.	9	0.04

Table 2. Euphotic zone integrals of particulate and uptake measurements for shelfbreak productivity stations during April, 1979 and 1980. See text.

Date	PARTICULATE					UPTAKE			
	C	N (g/m ²)	Chl <u>a</u> + Phaeo <u>a</u>	C/N	C/Chl <u>a</u> (g/g)	C/NO ₃ -N (g/g)	New Prod. (%)	Doubling Time C N (days)	
<u>1979</u>									
4-23	13	1.4	0.10	9.3	130	----	-----	3.4	---
4-24	15	1.7	0.06	8.8	250	13*	44*	4.8	---
4-27	8.3	0.72	0.05	11	170	23*	25*	6.9	---
4-28	11	1.3	0.09	8.5	120	6.1*	93*	1.7	---
4-29	8.4	0.83	0.05	10	170	17*	34*	4.9	---
4-30	9.5	0.77	0.06	12	160	3.6*	>100*	9.5	---
<u>1980</u>									
4-12	6.6	1.2	0.14	5.5	47	11	52	18	19
4-13	9.9	1.1	0.03	9.0	330	13	44	68	100
4-17	12	1.0	0.09	12	130	8.0	71	16	11
4-18	9.8	1.1	0.10	8.9	98	9.0	63	11	11
4-20	6.7	0.8	0.06	8.4	110	6.3	90	3.5	2.7
4-22	7.6	0.8	0.03	9.5	250	11	52	18	22
4-26	8.0	0.9	0.02	8.9	400	6.3	90	22	14

*Based on measurements from only 2 depths.

Table 3. Estimates of percent POC not associated with phytoplankton (PP) and of the C/N ratio (g/g) of non-phytoplankton particulates assuming that C/Chl a ratio of phytoplankton is either 50 or 100 and that phytoplankton C/N ratio is either 5 or 10. See text.

	IF PP C/CHL <u>a</u> = 50			IF PP C/CHL <u>a</u> = 100		
	Non-PP POC(%)	Non-PP C/N (g/g) if PP C/N is:		Non-PP POC(%)	Non-PP C/N (g/g) if PP C/N is:	
		5	10		5	10
<u>April, 1979</u>						
RANGE	59-80	11-38	7.6-14	18-60	*	5-21
MEAN (- high and low)	68	20	10	35	*	10
<u>April, 1980</u>						
RANGE	0-87	10-*	7.4-*	0-75	*	3.5-*
MEAN (- high and low)	66	32	10	32	*	13

*Denotes that no N is associated with non-phytoplankton particulates.

Table 4. Daily change in the abundance ($\times 10^{-3}$ cells·liter $^{-1}$ except for I. subtilis) of the dominant diatoms at the drogue reference station during August, 1978. Species are ordered by their approximate cell volume.

SPECIES	SIZE ($\times 10^{-3}$ μm^3)	DAY OF SAMPLE									
		0	1	2	3	4	5	6	7	8	9
<u>Cylindrotheca closterium</u>	0.1	0.1	---	---	----	8.8	No	----	No	----	---
<u>Skeletonema costatum</u>	0.2	----	---	9.2	----	140	Data	----	Data	----	---
<u>Thalassionema nitzschiodes</u>	0.4	0.06	---	2.0	----	1.4		----		----	---
<u>Chaetoceros spp.</u>	0.4	0.3	4.1	7.8	0.2	7.4		0.2		0.3	0.9
<u>Leptocylindrus danicus</u>	3	----	1.0	2.2	----	6.2		----		0.6	0.4
<u>Rhizosolenia fragilissima</u>	7	----	1.3	---	----	6.4		----		0.04	0.2
<u>Cerataulina sp.</u>	40	0.9	1.8	3.4	0.08	18		0.06		0.2	0.2
<u>Rhizosolenia stolterfothii</u>	40	1.0	25	5.6	0.06	8.8		0.2		0.2	2.6
<u>Rhizosolenia styliformis</u>	4000	0.4	1.2	---	0.3	---		0.3		0.8	0.9
<u>Thalassiosira subtilis</u> (relative change)		0.2	---	---	0.3	0.1		3.2		2.1	1.9

FIGURE LEGENDS

- Figure 1. Continental shelf off the north Florida, Georgia, and South Carolina coasts. Current meter moorings and primary production stations during the April, 1979 and 1980 studies and the net displacement of the drogue followed in August, 1978 are shown.
- Figure 2. Wind vectors from shipboard measurements in April 1979 and 1980. During the gap in the 1979 record, winds were from the East shifting to the South at about 20 m s^{-1} .
- Figure 3. Time and depth changes in temperature at the 2 shelf break locations (5 km apart) where primary production measurements were made in April, 1979. See Figure 1.
- Figure 4. Vertical distributions in the euphotic zone at shelf break production stations occupied in April, 1979. See Figure 1.
- Figure 5. Temporal change in euphotic zone (A) C and $\text{NO}_3\text{-N}$ assimilation numbers, (B) C and $\text{NO}_3\text{-N}$ uptake, and (C) chlorophyll a and $\text{NO}_3\text{-N}$ for shelf break production stations occupied in April 1979 and 1980. See Figure 1.
- Figure 6. Relative amount of daily sunshine during the three studies discussed in the text. Data from Jacksonville, Florida, meteorological station.
- Figure 7. Time and depth changes in temperature and salinity at the locations of the production stations (along 30°N) occupied in April, 1980 (A) 30 m isobath (B) 40 m isobath (C) shelf break. See Figure 1.
- Figure 8. Vertical temperature ($^\circ\text{C}$) and NO_3 (μM) sections across the shelf at 30°N during April, 1980.

Figure 9.

Figure 10. Vertical distributions in the euphotic zone at shelf break production stations occupied in April, 1980. See Figure 1.

Figure 11. Temporal change in euphotic zone C uptake and $\text{NO}_3\text{-N}$ at (A) 30 m and (B) 40 m isobaths in April, 1980. See Figure 1.

Figure 12. Euphotic zone C uptake versus mixed layer chlorophyll a. Data from shelf break stations during upwelling in April 1978, 1979, and 1980.

Figure 13. Temperature sections centered at the position of the drogue followed in August, 1978. See Figure 1.

Figure 14. Time and depth changes in chlorophyll a and NO_3 at the drogue reference station during August, 1978.

Figure 15. Temporal change in mean intrusion NO_3 and chlorophyll a at the drogue reference station. Lines illustrate 2 different rates (base 2) of exponential decrease for NO_3 and 2 different rates of exponential increase for chlorophyll a.

Figure 16. Representative (best and worst linear correlation coefficients) photosynthesis versus irradiance measurements from water samples collected from within the subsurface intrusion at the drogue reference station during August, 1978.

Figure 17. Chlorophyll a versus particulate Si concentration from samples collected within the subsurface intrusion during the drogue study in August, 1978.

Figure 18. Outer shelf temperature section, vertical chlorophyll a distribution and dominate diatom species at selected stations on the outer shelf during April, 1979. Inshore edge of the Gulf Stream is delineated by the 23°C isotherm. Arrows indicate depth at which species composition was determined.

Fig 1

Fig 2

Fig 3

Fig 4

Fig. 5

Fig 6

Fig 7

APRIL, 1980

Fig 8

Fig 10

Fig 11

Fig 12

Fig 13

Fig 14

Fig 15

Fig 16

Fig 17.

Fig 18

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