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DOE/ER/60451-5

**PRODUCTION AND TURNOVER OF SUSPENDED ORGANIC MATTER IN
THE COASTAL WATER OF THE SOUTHEASTERN CONTINENTAL SHELF**

FINAL REPORT

CONTRACT DE-FC09-86ER60451

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L. R. POMEROY

INSTITUTE OF ECOLOGY, UNIVERSITY OF GEORGIA

ATHENS, GEORGIA 30602

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Report Date: February 15, 1992

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Processing of data and preparation of manuscripts have been the major activities during the last year of the grant.. Several reports have been published, while others are in press or in final stages of preparation at this time. A complete list of publications produced under this grant is included in this report. A book summarizing the work on the southeastern shelf, edited by David Menzel is in press. Our principal role in that has been a chapter on inner shelf processes. That is not included in this report, because the book should be available at about the time this report is submitted. A paper on respiratory rates on the southeastern shelf is under review. A final manuscript on the microbial food web of the southeastern continental shelf, soon to be submitted, is also included in this report.

Laboratory work has focused on completion of analyses of stored frozen samples and data processing. We have completed HPLC analysis of nanomolar concentrations of dissolved free amino acids in seawater with a new and more sensitive instrument recently acquired through a NSF equipment grant. This has also involved extensive tests of procedures used in collecting and storing these samples, since the possibilities for augmentation or loss of such small amounts are many. The results are embodied in the manuscript which is a part of this report.

Principal accomplishments with ERDA-DOE support, 1975-91.

Our project on the southeastern continental shelf began at the time when the concept of a major microbial component of marine food webs was in its formative stages (Pomeroy, 1974). Over the next 15 years, our work evolved with the evolution of the concept of the microbial food web, and several significant contributions to both the concept and to methodology emerged from our work. At the same time, realization of the significance of microbial activities has made it possible to understand processes on the southeastern shelf, as they apply to energy -related concerns, in ways not otherwise possible. We summarize some highlights, not necessarily in their order of development.

- A large fraction of total flux of energy and materials on the continental shelf passes through the microbial food web (Pomeroy, 1979; 1984). On an annual basis, the southeastern continental shelf is a net heterotrophic system. That is, consumer organisms utilize more energy than is produced by primary production (photosynthesis). With a mean residence time of water on the shelf of one month, this suggests that little organic matter, either dissolved or particulate, is exported. Organic pollutants have a high probability of being degraded within the continental shelf ecosystem. On a seasonal basis, the fate of organic matter is more varied. Microbial respiratory

rate decreases sharply in winter, but photosynthesis changes little, and chlorophyll actually increases slightly in winter (Griffith et al., 1990; Griffith and Pomeroy, ms.; Pomeroy et al., ms.). Moreover, winter gales may flush the continental shelf of dissolved organic matter in a matter of days (Moran et al., 1991). So winter is a time when pollutants might be flushed rapidly from the continental shelf into the Gulf Stream and the ocean's interior. It is also a time a maximum secondary productivity of fishes and fish-food invertebrates.

- Bacteria exert a strong influence on the cycle of carbon in several ways. (1) They dominate respiratory processes, except in mid-winter. (2) They play an important role in the formation of organic aggregates which sweep up micro-particulate organic matter into larger units that have a relatively short lifetime before being utilized, principally by the bacteria that are involved in their formation (Biddanda, 1985; 1986; 1988; Biddanda and Pomeroy, 1988). (3) They rapidly utilize fecal pellets of both crustacean zooplankton and thaliacean mucus-net feeders (Pomeroy and Deibel, 1980). Most of the pellets do not reach bottom before they are utilized by the microbial food web (Paffenhöfer and Knowles, 1979; Hofmann et al., 1981)

- Attached bacteria represent about one half of total bacterial biomass in southeastern shelf waters, although they are a small fraction of the numbers. Free and attached bacteria are equally active, as indicated by uptake of labeled ATP. Uptake of dissolved organic compounds is proportional to bacterial biomass or bacterial surface area in all water types examined (Hodson et al., 1981)

- In the nearshore zone, frequent resuspension of bottom sediments carries with it significant infusions of benthic bacteria. These bacteria become a part of the microbial food web of the water column and represent a loss to the food web of the sediments (Wainright, 1987; 1990)

- The microbial food web in outer continental shelf waters response very rapidly to intrusions of cold, subsurface Gulf Stream water and the rapid increase in phytoplankton production in the subsurface water. Although there is no increase in phytoplankton in the upper water layer, bacterial numbers rise, within one day, from 10^5 ml^{-1} to $>10^6 \text{ ml}^{-1}$. Stimulation of bacterial production cannot be the result of direct utilization of phytoplankton or their exudates but must be mediated by zooplankton that migrate through a density interface into the upper water layer (Pomeroy et al., 1983)

- The dissolved organic matter in continental shelf water has a high chelation capacity for metals. This protects phytoplankton from metal toxicity. Even though the absolute concentrations of metals, such as copper, may be higher in coastal waters, phytoplankton are more strongly

affected by copper toxicity in water of the open sea (Wood, .1983; Wood et al. 1983). If offshore nuclear power plants had been sited in the southeast, as was envisioned in 1975 when this project originated, this quantitative information on copper toxicity to phytoplankton would have been very useful.

- Lignins are a class of organic compounds having an exclusively terrestrial origin in higher plants. Dissolved lignins are therefore tracers of the fate of fresh water from rivers as it crosses the continental shelf. We found that in winter lignin concentrations tended to build up over a period of days in the coastal water and to then be flushed off the shelf rapidly by gale winds. In summer, however, lenses of brackish water drift across the shelf slowly for weeks. This further validates our findings that organic matter in shelf waters is largely utilized while on the shelf, except in mid-winter (Moran et al, 1991). It further shows us that while physical modeling provides general, mean rates of flushing of the continental shelf, the real variance around those means is high. The lignin studies would permit more refined predictions of the movement of dissolved materials on the shelf.

- Simulation modeling of the food web of the southeastern continental shelf, and comparative modeling of other kinds of shelf ecosystems, predicted that most primary production would be utilized by the microbial food web, and that circumstances where energy from the microbial food web could pass up into macro-consumers were possible but probably unusual (Pomeroy, 1979; Pace et al., 1984). That prediction has been borne out, both on the southeastern shelf and by other investigators generally. The Pace et al. model has been widely cited and both its methods and conclusions have been applied in other environments by other investigators.

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DRAFT MANUSCRIPT

Abundance and microbial utilization of dissolved free amino acids
in continental shelf waters of the southeastern U. S. A.

Lawrence R. Pomeroy, Joan E. Sheldon,
Wade M. Sheldon, Jr. and Francesc Peters

Department of Zoology and Institute of Ecology,
University of Georgia
Athens, Georgia 30602 USA

Abstract

Of 16 primary amino acids sampled, none had concentrations exceeding 10 nM, and most were in the 1-3 nM range with low variances. Bacterial secondary production, however, was variable and patchy. Bacterial growth yield was also highly variable, but all nearshore values were >50%, while all samples from the shelf break and Gulf Stream were <20%, and some Gulf Stream values were as low as 2%. So, although there may be low bacterial production on the outer shelf, the demand on organic substrates for maintenance respiration is high. A seasonal change of an order of magnitude in bacterial secondary production, with a January minimum, was observed on the inner continental shelf, where temperature variation was greatest, and a lesser variation was seen offshore. During the warm seasons, bacteria appear to be utilizing all available substrates at low efficiency, leading to a net heterotrophic system, while in winter, with greatly reduced bacterial metabolism and little change in the rate of photosynthesis, the system is net autotrophic. This has implications for the life history strategies of fishes and invertebrates on the southeastern continental shelf.

Introduction

One difficulty in understanding marine food webs is our inability to quantify DOC that is available to microorganisms. On the southeastern U. S. continental shelf, humic carbon is usually around 10% of total DOC (Moran et al. 1991), but there is no assurance that the remaining 90% is labile. Dissolved free amino acids (DFAA), typically present in nanomolar concentrations, are a small fraction of total DOC, but they have been shown to turn over rapidly and to represent a significant source of both C and N for bacterial secondary production (Fuhrman 1987; Fuhrman 1990). Because we are able to measure most DFAA's at the nanomolar concentrations at which they commonly occur, and we also can use labeled amino acids of high specific activities in tracer experiments, DFAA's provide a key to trophic transfers of dissolved materials in microbial food

webs. We have measured the concentration of DFAA's, the rates at which they are assimilated, respired, and turned over by bacteria in the waters of the southeastern continental shelf during all seasons of the year. A pronounced seasonal cycle follows water temperature rather than phytoplankton productivity, and it is of sufficient magnitude to influence the net trophic status of the shelf waters.

The southeastern shelf is a subtropical environment(10-30°C) in which wide variations in primary and secondary productivity occur (Atkinson, Menzel, and Bush 1985; Menzel 1992). Because of the array of physical forcing, which is now well defined, the shelf is an instructive region in which to follow the production and fate of dissolved organic materials. Nearshore, a band of water of reduced salinity, enriched in dissolved organic matter (DOM) of terrestrial or estuarine origin, is held against the shore by geostrophic forces (Blanton and Atkinson 1983). That nearshore region is fully mixed by tides and is replete with inorganic plant nutrients, both regenerated from the sediments and released from estuaries. As a result, nearshore primary production is $>1 \text{ gC m}^{-2} \text{ d}^{-1}$ with little variation throughout the year (Thomas 1966; Verity et al. 1992). The distribution of chlorophyll and primary production is very patchy, however, because of the influence of river plumes and tidal jets from estuaries at several points along the coasts of Georgia and South Carolina (Blanton et al. 1989). Flushing time of the nearshore water is on the order of 30 d, except during fall and winter gales (Atkinson, Blanton, and Haines 1977; Moran et al. 1991). Bacteria in the nearshore water are relatively large in size, and their numbers exceed 10^6 ml^{-1} throughout the year. Bacterial secondary production is high (Pomeroy et al. 1983; Griffith, Douglas, and Wainright 1990). The distance from shore to shelf break in the center of the bight is 100 km. The Gulf Stream impinges on the shelf break, inducing approximately fortnightly upwellings at the break and occasional intrusions of nutrient-rich North Atlantic Central Water onto the shelf, especially during summer (Atkinson et al. 1987b). As a result, the outer shelf exhibits high but pulsed primary productivity, driven by the nitrate-rich intrusions (Menzel 1992). Bacteria in outer shelf water are small and numbers are near 10^5 ml^{-1} , except in the vicinity of the intrusions (Pomeroy et al. 1983). In between the continuously productive nearshore water and the

pulsed-productive outer shelf is a mid-shelf region that is relatively depleted of plant nutrients and lower in primary productivity, with 10^5 bacteria ml^{-1} . The Gulf Stream, beyond the shelf break, is more productive than the Sargasso Sea but less so than most of the continental shelf.

Total dissolved organic carbon (DOC) in shelf water varies from $>4 \text{ mgC l}^{-1}$ very near shore to 1 mg C l^{-1} on the middle and outer shelf (Moran et al. 1991). The presence of dissolved lignin indicates that some of the nearshore excess has a terrestrial origin (Ibid). However, a significant part of the DOC is of local, phytoplankton origin, either directly from release of soluble products of photosynthesis or indirectly via food web processes.

Materials and Methods

Each station was begun with a cast of a SeaBird Sea Cat CTD, equipped with a SeaTech fluorometer. Chlorophyll *a* fluorescence was calibrated by comparison with samples analyzed by HPLC. Water sampling was done with cleaned Niskin samplers, using surgical grade silicone rubber elastic closures. Water was drawn as soon as the samplers were on board, with samples for DFAA's taken first.

Seawater samples for DFAA analysis were taken from Niskin bottles using sterile plastic 60 ml syringes. Samples were filtered through sterile Anotop $0.2 \mu\text{m}$ 25 mm syringe filters (Anotec Separations) into glass vials with polyethylene-lined phenolic caps and frozen at -20°C or below until analysis. Triplicate 15-20 ml samples were taken at each station and depth. For all of the January 1991 samples and half of the September 1991 samples, filters were changed between replicate samples so that only 15-20 ml seawater passed through each filter. For all of the May 1991 samples and half of the September 1991 samples, one filter was used for all three samples for each station and depth. At some stations, extra samples were taken using Nuclepore Syrifil-MF $0.22 \mu\text{m}$ 25 mm and Millipore Millex-GS $0.22 \mu\text{m}$ 25 mm syringe filters for comparison. Storage times were 2-11 months. Samples were held at 4°C for less than 24 hours to thaw before analysis. Because variances of sets of replicate DFAA samples filtered through $0.2 \mu\text{m}$ Anopore filters were lower than those of sets filtered through other types of filters, we routinely used the Anopore

filters. Variance was also lower when a new filter was used for each replicate sample, presumably because buildup and destruction of organisms on the filters was minimized (Fuhrman and Bell 1985). To evaluate possible effects of storage of frozen samples, we prepared large numbers of replicates of some water samples and performed analyses of sets of the replicates periodically over 5 weeks. No significant artifacts of storage were found.

DFAA were analyzed via high-performance liquid chromatography using a modification of the (Lindroth and Mopper 1979) technique for pre-column derivatization with *o*-phthaldialdehyde (OPT). All glassware was fired at 450°C for at least 4 hours. Plastics which were not supplied sterile and clean were rinsed with methanol (HPLC grade, J.T. Baker Inc.) prior to use. We primarily followed the method of (Henrichs and Williams 1985). OPT reagent was made by combining 50 mg *o*-phthaldialdehyde and 60 µl 2-mercaptoethanol (Sigma Chemical Co.) in 5 ml methanol. The OPT reagent was aged for 24 hours at 4°C in the dark before first use, and 10 µl 2-mercaptoethanol was added every 2 days (Jones, Pääbo, and Stein 1981). Each batch of reagent was used for 5 days or less. An internal standard (10 nM alpha-aminoadipic acid, final concentration) was added to 2 ml subsamples of thawed seawater. The pH was adjusted to 9.5 by addition of 20 µl borate buffer (0.8 M boric acid adjusted to pH 12.5 with 10 N sodium hydroxide) (Mopper and Lindroth 1982), 20 µl OPT reagent was added, and the sample was mixed twice before injecting 300 µl into a 250 mm x 4.6 mm column (with 10 mm guard column) packed with Spherisorb ODS-1, 5µm particles (Alltech Associates, Inc). Borate and OPT addition, mixing, and injection was carried out by a Shimadzu SIL-9A autosampler and controller.

The remainder of the HPLC system consisted of a Shimadzu LC-610 pump with LPM-600 mixing proportioning valve, a Kratos FS 970 L. C. Fluorometer (excitation 330 nm, emission >418 nm), and a Shimadzu CR501 Chromatopac integrator. Mobile phases were made with HPLC grade solvents (J.T. Baker Inc) and reagent grade salts (Sigma Chemical Co.) and were filtered through 0.2 µm nylon filters (Micron Separations, Inc.) and degassed via helium sparging (Kontes Ultra-Ware Gradient HPLC Degassing System) prior to use. Phosphate buffer (0.025 M, pH 6.9) was composed of equimolar mono- and di-basic sodium phosphate. Mobile phases were

(A) a mixture of 15% methanol and 85% phosphate buffer, and (B) 100% methanol. A convex gradient from 15% to 75% methanol over 26 min was used, and the flowrate was 1 ml min⁻¹. Histidine, threonine, and glycine coeluted under these conditions. Amino acid standards (Sigma Chemical Co.) diluted in aged seawater were used to determine characteristic retention times and integrator responses for the individual amino acid derivatives. Peak areas were used in calculations, and responses were linear over the range tested (0-20 nM)

Tracer experiments were performed in disposable borosilicate tubes that had been acid-washed, capped with foil, and baked at 450° for >4h. Bacterial secondary production was estimated by incorporation of ³H-leucine (Du Pont-NEN, 150 Ci/mM) into protein (Kirchman, K'nees, and Hodson 1985; Simon and Azam 1989). Isotope dilution by the internal amino acid pool was assumed to be a factor of 2 (Simon and Azam 1989). Turnover time of leucine in seawater was estimated in 1990 by isotope dilution and in 1991 from HPLC analyses, together with rate measurements of ³H-leucine uptake.

Short-term effects of temperature on bacterial secondary production, estimated from uptake of ³H-Leucine were measured at sea using an aluminum temperature-gradient block. Temperature in the block was controlled by circulating water from a NesLab refrigerated water bath through one end and water from a Braun Thermomix temperature controller through the other. Temperature, monitored with thermistors inserted at intervals in the block, varied <0.5° during an experiment. Aliquots of seawater samples were placed in acid-washed, fired borosilicate tubes and arranged in holes in the block, where they acclimated for 1-2h before tracer was added.

The efficiency of assimilation of uniformly labeled ¹⁴C-leucine (Du Pont-NEN, 318 mCi mM⁻¹) and ¹⁴C-glutamic acid (DuPont-NEN, 250 mCi mM⁻¹) were estimated by adding 1 µCi to 10 ml aliquots and incubating for 2 h. Added carrier of 0.3 µM was added to a mean ambient leucine concentration of 3 nM, and 0.4 µM to a mean ambient glutamic acid concentration of 3.5 nM, significantly increasing the concentration of both amino acids relative to their ambient concentrations and to that of other amino acids. Thus, these are not truly tracer experiments, and this has been the case with most similar investigations using radiocarbon labeled amino acids in

seawater because of the limitations imposed by the specific activities of labeled amino acids that are available.

Results

Concentrations of DFAA's

Concentrations of DFAA's were low everywhere on the shelf at all seasons sample (Table 1). In January, 1991, total identified DFAA's were 36.58 ± 4.60 nM ($n = 17$; ± 2 SE) and total derivatized amines, exclusive of α amino adipic acids, were 42.85 ± 4.78 nM. In May, 1991, total identified DFAA's were 41.2 ± 11.6 nM ($n = 19$; ± 2 SE), and total derivatized amines, exclusive of ammonium and α amino adipic acids, were 46.5 ± 12.8 nM. In September, 1991, total identified DFAA's were $31.3 \text{ nM} \pm 4.7$ ($n = 33$; 2 SE) and total derivatized amines, exclusive of ammonium and α amino adipic acids, were 45.2 ± 6.9 nM. At all seasons, most individual amino acids were in the 1-3 nM range. Glutamic acid, arginine, aspartic acid, alanine, and tyrosine showed a tendency to higher concentrations in the first 25 km from shore, but other amino acids showed no trend in concentration with respect to position on the shelf and had low variances.

Leucine utilization and bacterial secondary production

Leucine concentrations in May and September, 1991 varied little in shelf waters (Jan mean ± 2 SE = 2.2 ± 0.77 ; $n = 17$; May = 2.0 ± 0.53 ; $n = 16$; Sept. = 3.3 ± 0.73 nM; $n = 33$), but bacterial production rates in September varied from <3 to $197 \text{ ngC l}^{-1} \text{ h}^{-1}$ (Table 3). Leucine turnover time ranged from 2 to 197 h. All instances of extremely low bacterial production, $<20 \text{ ngC l}^{-1} \text{ h}^{-1}$, were in Gulf Stream water at or just beyond the shelf break. Elsewhere on the shelf, there was not a clear pattern of distribution of bacterial secondary production rates. Both inshore and mid-shelf production rates varied from 15 to $197 \text{ ngC l}^{-1} \text{ h}^{-1}$ and turnover time varied from 2 to 32 h. Variance of bacterial secondary production was high everywhere on the shelf because of patchiness of the physico-chemical environment. This was especially true in summer when boluses of low-salinity water were breaking away from the coastal zone and drifting across the shelf at the surface,

(Moran et al. 1991) and intrusions of cool North Atlantic Central water were breaking away from the Gulf Stream and drifting across the shelf along the bottom (Atkinson et al. 1987a).

Assimilation efficiency

Assimilation efficiency (growth yield) of bacteria utilizing ^{14}C -labeled leucine and glutamic acid was highly variable (Table 2) but showed some pattern. Most nearshore (0-50 km) values were >40%, and most middle and outer shelf (51-150 km) values were <20%. Values on the inner and mid shelf ranged from 1 to 96%, while values in the Gulf Stream or near its influence at the shelf break varied from 5 to 65%. Efficiency was not correlated with temperature on individual cruises nor seasonally. The range of efficiencies was as wide in winter as in summer.

Short-term effects of temperature

Short-term gradient-block experiments in July, 1990 and September, 1991 revealed a consistent difference in response between near-shore bacterial communities and those farther offshore. Mid-shelf and Gulf Stream samples had a Q_{10} of 1.8-2.2, while those within 20 km of shore had a Q_{10} of 3-10. Temperature was varied 5° above and below the ambient temperature of $28-29^\circ$ in July and from 5 to 35° in September. All but one July sample showed a linear response to temperature change, but the wider temperature range used in September produced less regular responses. Samples amended with glucose did not respond differently from those unamended, whether taken nearshore or offshore.

Discussion

DFAA's

Marine bacteria are able to remove DFAA's from seawater down to <1 nM, and some marine bacteria are able to shift up in the presence of high concentrations of DFAA's, thus increasing the rate of utilization when DFAA's are abundant (Fuhrman and Ferguson 1986). So it is a frequent observation that DFAA's are present in very low concentrations, from <1 to 3 nM

(Williams, Berman, and Holm-Hansen 1976; Fuhrman 1987). Nevertheless, several investigators have reported finding very high DFAA concentrations in the sea, usually associated with dense phytoplankton blooms (Haberstroh et al. 1987; Poulet et al. 1991). But not all spring blooms are associated with high DFAA concentrations (Schell 1974). So, in some circumstances, production may outrun utilization, because the ability of bacteria to utilize DFAA's rapidly and reduce them to very low concentrations is variable. A lag in bacterial utilization of DFAA's can result from either of two situations. The latent period involved in a shift up of bacterial uptake rate can be as long as several days (Hollibaugh 1979; Kirchman 1990; Pomeroy et al. 1990), and average bacterial doubling times are sometimes on the order of days or even weeks (Pomeroy et al. 1991). When a delayed bacterial response occurs, it could permit a substantial accumulation of DFAA's to occur and to persist for as much as several weeks before the bacteria remove the excess. Also, bacteria require higher substrate concentrations at some limiting temperature (Wiebe, Sheldon, and Pomeroy 1992; Wiebe 1992b). So, in winter and early spring, bacteria might not always reduce DFAA's to such low concentrations as they do after the water begins to warm.

We found very low concentrations of DFAA's in the waters of the southeastern continental shelf at all times of year, although we know that there are substantial variations in both primary and secondary productivity over the >100 km distance from shore to the Gulf Stream, and alongshore as well. This suggests that production and utilization of DFAA's was tightly coupled on the SE shelf, as was found to be the case in Long Island Sound (Fuhrman 1987). In other words, lag times in response to local changes in DFAA concentrations were usually relatively short, even at the minimum annual temperature. Moreover, the distribution of DFAA's did not follow that of total DOM or humic DOM, which varies by a factor of 3 from coastal water to the Gulf Stream (Moran et al. 1991).

Bacterial assimilation efficiency

Growth yield of bacteria on ^{14}C -leucine and glutamic acid varied widely but showed a trend to lower efficiency in outer shelf waters. In September, growth yield was >20% on the

outer shelf and was as low as 2% in the Gulf Stream. In the latter case, the bacterial community appears to be just surviving at the expense of all available substrates. Griffith, Douglas, and Wainright (1990) also reported extremely low bacterial assimilation efficiency on outer southeastern shelf, based on respiratory rates. In the coastal water, however, efficiency of assimilation of leucine and glutamic acid was 50-88% in September. The inner shelf is a region of consistently high primary production, and although total amino acids are not much higher in the nearshore water, total DOM is. So other substrates are available to support respiratory requirements and amino acids can be conserved for synthesis of biomass. Their consistently low concentrations everywhere and at all times of year suggest that they are being utilized preferentially.

Seasonal changes in rates

We found a reduction of an order of magnitude in the rate of uptake of ^3H -leucine in the nearshore and mid-shelf waters at the minimum annual temperature in January. Rates were also reduced, but not by such a large amount, on the outer shelf and in the Gulf Stream, where seasonal temperature changes are less. Griffith found a similar reduction in microbial respiratory rate on the southeastern shelf in winter (Griffith 1992). Reductions in bacterial activity and secondary production are not a reflection of seasonal changes in primary production on the shelf. Our CTD-fluorometer sampling shows higher chlorophyll in winter than at other seasons. Measurements of primary production by other investigators, however, suggest a slight decrease in photosynthetic rate in winter (Thomas 1966; Yoder 1985; Verity et al. 1992), but not a decrease comparable to that in bacterial activity. Our data support the conclusion from Griffith's (1992) respiratory rate observations that the waters of the southeastern continental shelf are net heterotrophic during the late spring, summer, and fall but become net autotrophic in winter. The rate changes of the largest magnitude are near shore, where the seasonal change in water temperature is greatest. Wiebe et al. (1992) found that at very low temperature, bacteria require significantly higher substrate concentrations in order to assimilate them and grow. More recently, Weibe et al. found that the

substrate affinity problem affects bacterial communities even on the subtropical southeastern continental shelf at the annual minimum temperature of 10-12° Wiebe (1992). In fact, while bacterial growth is low but still measureable in isolates from the Arctic Ocean grown at -1.5°, growth cannot be measured in isolates from the southeastern continental shelf grown at 10°. Our analyses of DFAA's indicate that concentrations are low enough to cause substrate limitation of bacterial growth in winter. While other labile dissolved organic compounds undoubtedly are present in seawater, the empirical evidence suggests that they too are present in limiting concentrations. The result appears to be a switch from a net heterotrophic system to a net autotrophic one. If so, this has obvious implications for life histories and reproductive success of zooplankton and fishes on the southeastern continental shelf.

Acknowledgements

This research was supported by U. S. Department of Energy grant DE-FG09-86ER60451

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Table 1. Concentrations of dissolved free amino acids on the southeastern continental shelf during 1991: mean μ moles $\cdot$ liter $^{-1}$ $\pm$ standard deviation (number of samples). Total derivatized amines exclude ammonium and α amino adipic acids. Histidine, threonine, and glycine were eluted as a single peak.

Distance Offshore, km	Month	ARG	GLU	SER	H-T-G	ALA	TYR	ARG	MET	VAL	PHE	ILEU	LEU	LYS	Total AA	Total Amines
0-25	January	1.9 $\pm$ 0.4 (3)	3.1 $\pm$ 0.8 (3)	7.1 $\pm$ 3.2 (3)	11.4 $\pm$ 2.1 (3)	3.2 $\pm$ 0.5 (3)	0.7 (2)	—	—	0.9 (2)	0.6 (2)	2.6 $\pm$ 0.2 (3)	2.5 $\pm$ 0.6 (3)	8.3 $\pm$ 1.1 (3)	28.7 $\pm$ 2.5 (3)	51.1 $\pm$ 5.6 (3)
	May	3.5 (1)	5.8 (1)	10.8 (1)	21.8 (1)	5.1 (1)	0.6 (1)	1.2 (1)	—	0.9 (1)	0.5 (1)	1.3 (1)	1.3 (1)	24.5 (1)	77.2 (1)	90.5 (1)
	Sept.	2.9 $\pm$ 0.7 (9)	8.1 $\pm$ 3.2 (9)	3.1 $\pm$ 1.0 (9)	13.9 $\pm$ 4.5 (9)	3.3 $\pm$ 1.0 (9)	1.3 $\pm$ 2.6 (9)	1.1 $\pm$ 0.3 (9)	0.5 $\pm$ 0.1 (8)	0.5 $\pm$ 0.2 (8)	0.5 $\pm$ 0.1 (6)	2.1 $\pm$ 0.4 (8)	3.9 $\pm$ 2.4 (9)	7.1 $\pm$ 2.1 (8)	47.3 $\pm$ 8.9 (9)	58.4 $\pm$ 31.3 (9)
26-50	January	1.8 $\pm$ 1.1 (7)	2.2 $\pm$ 0.5 (7)	6.1 $\pm$ 4.3 (7)	12.1 $\pm$ 8.9 (7)	3.3 $\pm$ 2.5 (7)	0.7 $\pm$ 0.3 (3)	1.0 (2)	0.76 (2)	1.2 $\pm$ 0.6 (7)	0.5 $\pm$ 0.1 (4)	2.3 $\pm$ 0.3 (7)	2.6 $\pm$ 2.4 (7)	7.8 $\pm$ 1.0 (7)	43.5 $\pm$ 22 (7)	51.4 $\pm$ 23.5 (7)
	May	4.3 (2)	4.3 (2)	16.9 (2)	19.2 (2)	6.2 (2)	0.88 (2)	0.96 (2)	—	1.86 (2)	0.9 (1)	2.3 (2)	3.1 (2)	12.9 (2)	79.8 (2)	87.8 (2)
	Sept.	1.9 $\pm$ 0.5 (4)	5.2 $\pm$ 1.7 (4)	2.7 $\pm$ 0.9 (4)	7.4 $\pm$ 0.8 (4)	1.8 $\pm$ 0.2 (4)	0.66 (2)	0.7 $\pm$ 0.3 (3)	0.5 (2)	0.4 $\pm$ 0.04 (4)	0.38 (2)	1.7 $\pm$ 0.2 (4)	1.9 $\pm$ 0.9 (4)	8.1 $\pm$ 1.9 (3)	30.8 $\pm$ 5.2 (4)	40.6 $\pm$ 5.2 (4)
51-150	Jan.	1.1 $\pm$ 0.1 (3)	1.8 $\pm$ 0.7 (3)	3.0 $\pm$ 0.6 (3)	6.1 $\pm$ 0.6 (3)	1.6 $\pm$ 0.4 (3)	0.6 (1)	0.08 (1)	—	0.4 $\pm$ 0.6 (3)	—	2.0 $\pm$ 0.02 (3)	1.6 $\pm$ 0.3 (3)	9.1 $\pm$ 1.9 (3)	26.9 $\pm$ 2.0 (3)	31.1 $\pm$ 0.3 (3)
	May	1.5 $\pm$ 0.7 (6)	2.3 $\pm$ 0.6 (6)	8.1 $\pm$ 3.5 (6)	7.0 $\pm$ 3.7 (6)	2.1 $\pm$ 0.2 (6)	0.6 $\pm$ 0.07 (4)	0.7 $\pm$ 0.2 (3)	—	0.7 $\pm$ 0.2 (5)	0.3 $\pm$ 0.3 (3)	1.1 $\pm$ 0.3 (6)	2.1 $\pm$ 0.8 (6)	19.5 $\pm$ 6 (5)	38.6 $\pm$ 18 (6)	42.3 $\pm$ 19 (6)
	Sept.	1.6 $\pm$ 0.4 (12)	2.8 $\pm$ 1.6 (12)	2.7 $\pm$ 1.0 (12)	9.1 $\pm$ 9.8 (12)	1.5 $\pm$ 0.4 (12)	1.1 $\pm$ 0.6 (6)	0.8 $\pm$ 0.3 (4)	0.4 $\pm$ 0.1 (5)	0.5 $\pm$ 0.2 (7)	0.7 (2)	1.8 $\pm$ 0.4 (12)	2.7 $\pm$ 1.4 (12)	7.8 $\pm$ 2.0 (7)	23.9 $\pm$ 8.4 (12)	31.9 $\pm$ 13 (12)

Table 2. Assimilation efficiency of ^{14}C -labeled leucine and glutamic acid by natural assemblages of bacteria on the southeastern continental shelf, September, 1991. All samples were taken from 3-10 m. Total water depth at each site is shown in the table.

Region	Latitude, Longitude	Depth, m	km from shore	% efficiency $\pm$ 1 SE	
				Glutamic acid	Leucine
Inner shelf	32° 45.0'N, 79° 35.0'W	14	11.1	82.5 $\pm$ 0.5	88.0 $\pm$ 7.1
	31° 49.0'N, 80° 57.0'W	6	11.1	64.4 $\pm$ 29.4	50.8 $\pm$ 25.5
Mid-shelf	31° 39.5'N, 80° 46.5'W	19	33.4	6.8 $\pm$ 2.4	27.9 $\pm$ 9.1
	32° 21.5'N, 79° 55.5'W	17	29.7	5.4 $\pm$ 7.9	51.2 $\pm$ 21.7
Outer shelf	32° 00.0'N, 79° 28.5'W	40	87.1	1.4 $\pm$ 0.8	6.0 $\pm$ 5.2
	31° 18.5'N, 80° 20.5'W	52	87.1	5.6 $\pm$ 1.2	17.4 $\pm$ 2.6
Gulf Stream	31° 57.0'N, 79° 53.5'W	218	144.5	1.2 $\pm$ 0.5	1.4 $\pm$ 0.8

Table 3. Bacterial Production from ^3H -leucine assimilation (Simon & Azam 1989), $\text{ngC l}^{-1} \text{h}^{-1} \pm 1\text{SE}$ on the U. S. southeastern continental shelf. Arbitrary limits are: inner shelf, <15 km, mid shelf, 16-40 km. Chlorophyll *a* at 5 m depth was estimated from an in-situ Sea Tech fluorometer deployed with a Sea Bird CTD. The fluorescence signal was calibrated against HPLC analyses of chlorophyll *a*.

	90-7	90-9	91-1	91-5	91-9
Bacterial Production					
coastal water	181 $\pm$ 34	180 $\pm$ 33	35.3 $\pm$ 11.6	162.5 $\pm$ 36.4	120.4 $\pm$ 23.2
mid shelf	67 $\pm$ 9.5	78 $\pm$ 19	15.5 $\pm$ 3.2	102.1 $\pm$ 29.0	65.0 $\pm$ 22.1
outer shelf	36 $\pm$ 14	26 $\pm$ 8	19.5 $\pm$ 0.7	55.3 $\pm$ 14.9	35.3 $\pm$ 8.6
	90-7	90-9	91-1	91-5	91-9
Chlorophyll a					
coastal water	1.87 $\pm$ 0.4	2.40 $\pm$ 0.75	3.29 $\pm$ 0.7	3.1 $\pm$ 0.8	3.3 $\pm$ 0.4
mid shelf	0.12 $\pm$ 0.1	0.14 $\pm$ 0.01	1.18 $\pm$ 0.45	0.6 $\pm$ 0.2	0.6 $\pm$ 0.14
outer shelf	0.49 $\pm$ 0.11	0.56 $\pm$ 0.14	1.03 $\pm$ 0.87	0.13 $\pm$ 0.04	0.2 $\pm$ 0.02

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