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Seasonal and spatial variations in pelagic community respiration on the southeastern U.S. continental shelf

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Abstract—Pelagic microbial community respiratory rates on the southeastern continental shelf show strong seasonal changes, with summer maxima and winter minima. In nearshore waters <20 m, community respiratory rates of 0.1–3 μM O_2 l^{-1} h^{-1} are similar to recent estimates of primary production. In outer shelf water >40 m, strongly influenced by the Gulf Stream, community respiration is 0.1–2.7 μM O_2 l^{-1} h^{-1}, exceeding primary production in summer. The changes in microbial community respiration are partially explained by changes in bacterial numbers. A related potential cause is the inverse relationship between limiting substrate concentration and temperature, affecting rates of growth and respiration, that has been found to exist for aerobic heterotrophic bacterial isolates in the laboratory. These processes result in shifts between net autotrophy in winter and net heterotrophy in summer for the community as a whole, with little excess organic production remaining for export to the ocean's interior.

INTRODUCTION

Although respiratory rates of planktonic communities have been measured less frequently than photosynthesis, the literature suggests that the respiratory rates of bacterioplankton and protozoan plankton on continental shelves often are high, implying that microorganisms utilize much of the organic carbon fixed by photosynthesis on continental shelves and in ocean water generally (Chin-Leo and Benner, 1992; Williams, 1983). The literature further suggests seasonal cycles of bacterial metabolic activity (Pomeroy and Wiebe, 1993). Few studies have attempted to address seasonal changes in microbial respiratory rates, although such seasonal cycles, if present, could have a major influence on planktonic and benthic food web structure and function. For example, work in Newfoundland suggests a seasonal shift from a highly autotrophic spring bloom period to a net heterotrophic summer period, not only in the fjords and coastal waters but on the Grand Banks as well (Pomeroy *et al.*, 1991; Smith *et al.*, 1986; Wiebe and Pomeroy, 1991).

The continental shelf of the southeastern United States is subtropical, with a seasonal temperature range of 10–30°C. The shelf waters have three distinct regions (Atkinson *et al.*, 1985; Menzel, 1993). An inner shelf region is usually separated from the mid-shelf region by a strong density front approximately located at the 20 m isobath. Photosynthesis on the inner shelf is high throughout the year, because the water is strongly mixed by wind

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and tides, and recycling replenishes the nutrient supply (Verity *et al.*, 1993; Yoder, 1985). The outer shelf beyond the 40 m isobath is strongly influenced by the Gulf Stream. Meanders and frontal eddies generate periodic and usually short-lived upwellings of nutrient-rich water with blooms of phytoplankton (Lee *et al.*, 1991; Verity *et al.*, 1993) and microorganisms (Pomeroy *et al.*, 1983). The mid-shelf region is thermally stratified much of the year and relatively isolated from new sources of plant nutrients. In consequence, primary production is somewhat lower than in the inner and outer shelf regions. The seasonal regime of chlorophyll abundance and distribution has been analyzed in some detail over a portion of the time period of our study by means of satellite imagery (McClain *et al.*, 1988).

Few estimates of microbial community respiration have been made on the southeastern continental shelf. Pomeroy and Johannes (1966) measured microbial plankton respiration in the Gulf Stream and at two continental shelf stations south of Cape Hatteras. Turner (1978) estimated respiratory rates in estuarine waters near Skidaway island GA and from a few stations 10 km offshore. The only previous seasonal measurements of respiration were made by Hopkinson (1985) in the nearshore region. Prior to this study, the only measurements of microbial respiratory rates in the waters the middle and outer parts of the southeastern continental shelf were two observations of Pomeroy and Johannes (1966). In this study, we measured community respiratory rates on the inner, middle, and outer regions of the southeastern continental shelf at all seasons. These observations were, however, spread over several years and do not represent a consecutive set of observations through a year, so some of the changes may be owing to interannual variations.

MATERIALS AND METHODS

Respiratory rate measurements were made on six cruises on the southeastern shelf (Fig. 1). R.V. *Cape Florida* made repeated sections across the shelf off Florida, Georgia, and South Carolina and North Carolina during 7–22 April 1985. R.V. *Blue Fin* made one or more sections across the shelf during July 1986, July 1987, September 1987, and January 1991. R.V. *Columbus Iselin* made repeated sections off Cape Canaveral, St. Augustine, Brunswick, and Savannah during 21 October–7 November 1987.

Respiratory rate measurements

Microbial community respiratory rate was estimated from changes in oxygen concentration over time using a precision respirometer described by Griffith (1988). The method involves short-duration incubations in the dark, which minimize the artifacts of 24 h incubation of confined samples (Pomeroy *et al.*, 1994), and provides a continuous record of oxygen concentration. Acrylic chambers were filled with 45 ml of seawater freshly collected in HCl-cleaned Niskin samplers. Seawater was not allowed to stand in the samplers between stations. Oxygen was measured with Nester electrodes having negligible drift. The electrodes were calibrated daily at saturation. Output from the Nester electrodes was linked by an analog-to-digital converter to a computer that calculated, displayed and stored oxygen partial pressure, chamber temperature, and barometric pressure as a function of time. Dissolved oxygen concentration was calculated after compensation for the effects of temperature and barometric pressure. Incubations began within 20 min of sample collection and lasted <2 h. Incubation temperature was
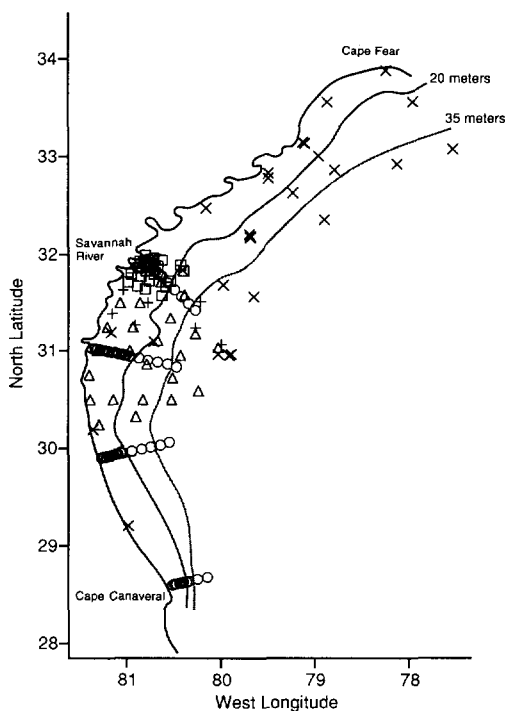
Fig. 1. Geographical distribution of respiratory rate measurements on the southeastern continental shelf. + = January 1991. × = March 1985. □ = July 1987. △ = September 1987. ○ = November 1987.

maintained within ±2°C of *in situ* temperature. During the January cruise, a similar respirometer using an ENDECO/YSI oxygen measurement system was employed. Because this system was less sensitive than the Nester system, incubations lasted 4–5 h. Incubation times were sufficiently short with both methods so that departures of respiratory rate from linearity were not a problem.

Bacteria were counted on four of the six cruises by the acridine orange method of Hobbie *et al.* (1977) as modified by Douglas *et al.* (1987). Chlorophyll fluorescence was measured with a SeaTek fluorometer attached to a Sea Bird profiler. Fluorescence was calibrated against HPLC measurements of chlorophyll *a* in water samples.

RESULTS

During April 1985, river runoff was less then half the long-term mean for that month (Windom *et al.*, 1993), and winds were light and to the south, trapping less saline water on the inner shelf (Hanson *et al.*, 1988; Blanton *et al.*, 1989). Stratification developed in response to solar heating during the cruise. The July and September cruises were in typical summer weather of light, variable winds and a strong thermal stratification of shelf waters. During October–November 1987, northeast gales caused rapid flushing of middle and outer shelf waters during the cruise (Moran, 1991). Strong horizontal gradients of temperature and salinity were present on all sections across the shelf during that time.
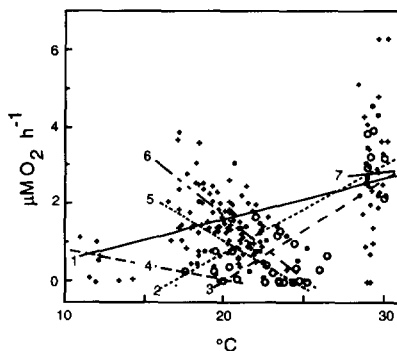
Fig. 2.   Microbial respiratory rates vs water temperature on the southeastern continental shelf at
all seasons of the year and best fit of slopes for inner, mid, and outer shelf. + = inner shelf. ● = mid
shelf. ○ = outer shelf. Data points for the January cruise form the cluster on the left. Data points
for the March and November cruises form the cluster in the center. Data points for the July and
September cruises form the cluster on the right. Regression lines 1–3 are for data from all seasons
for the inner, mid, and outer shelf regions (r^2 = 0.17, 0.51 and 0.51, respectively). Regression lines
4–7 are for seasonal data in all regions in winter, fall, spring and summer (r^2 = 0.28, 0.41, 0.15 and
0.03, respectively).

During January 1991, typical winter conditions prevailed with water temperature 10–12°C
and 30–34‰ salinity near shore, with a warming temperature gradient across the shelf to
the edge of the Gulf Stream at the shelf break.

Because we could process a very small number of samples concurrently, and it was
necessary for the ships to keep moving to serve other projects, it was not possible to
measure respiratory rate at multiple depths on a single station. While most of our emphasis
was on rates in the upper mixed layer, we made a limited number of measurements near
bottom and in mid-water as well. We did not detect major, consistent vertical differences
in respiratory rates, although the possibility that they sometimes occur cannot be ruled
out.

With the exception of winter, respiratory rates vary widely, from 0.1 to >4 μM O_2 h^{-1}.
In winter, the highest rates were slightly more than 1 μM O_2 h^{-1}. When plotted against
temperature, the results from different seasons fall into a distinct pattern. Within each
region of the continental shelf, respiration increases with increasing temperature across
the seasons (regression lines 1–3, Fig. 2). Within seasons, respiratory rate is inversely
related to temperature (regression lines 4–7, Fig. 2), except in summer when it is unrelated
to temperature. In summer, we find the full range of respiratory rates, from <0.1 to >6 μM
O_2 h^{-1}, over a very narrow range of temperatures. Respiratory rates from spring and fall
show a similar pattern in response to temperature. There is some overlap of temperatures
between the winter and the spring–fall data, in that winter outer shelf temperatures and
spring–fall inner shelf water temperatures are both in the 18–20°C range. The winter outer
shelf respiratory rates fall below the lowest of the spring–fall rates.

Mean winter respiratory rates on the inner shelf are significantly higher (ANOVA F
test, $P < 0.05$) than those on either the middle or outer shelf (Fig. 3). Rates in middle and
outer shelf waters in winter approach our limit of detection of 0.1 μM O_2 h^{-1}. In both
spring and fall we find a gradient of mean respiratory rates from the inner to the outer
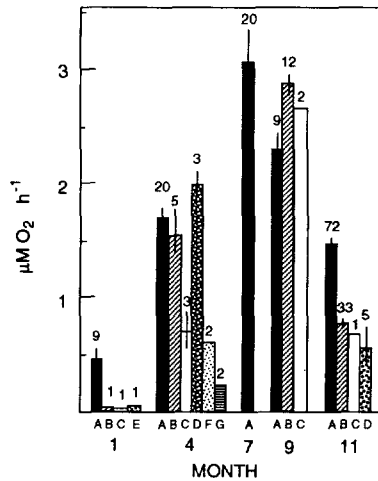
Fig. 3. Mean respiratory rates ± 1 standard error of the mean, in waters of the southeastern continental shelf during different seasons. Filled bars (A) = inner shelf (0–20 m depth) samples near surface. Diagonally hatched bars (B) = mid-shelf (20–40 m depth) upper mixed layer. Unfilled bars (C) = outer shelf and west wall of Gulf Stream (40–150 m depth) upper mixed layer. Heavy stippled bars (D) = inner shelf, near bottom samples. Moderately stippled bars (E) = mid-shelf, near bottom samples. Lightly stippled bars (F) = outer shelf, near bottom samples. Horizontally hatched bars (G) = outer shelf, mid-depth samples. The number of samples is shown above each bar.

shelf, whereas in summer there is no significant difference between means for the different regions, and respiratory rates are high everywhere on the continental shelf.

Bacterial numbers show a significant seasonal difference, with a winter minimum in all regions of the continental shelf. In contrast to the seasonal pattern of microbial respiratory rates and bacterial numbers, chlorophyll *a* concentrations on the shelf show little seasonal trend (Fig. 4), a conclusion largely borne out by McClain *et al.* (1988) who find seasonal variations to be generally small in magnitude. Although there is a pronounced onshore–offshore gradient in chlorophyll concentrations, the variances around the means are high, reflecting a patchy distribution in time and space. Place-to-place differences and inter-annual variation probably exceed the seasonal differences in chlorophyll *a*, at least within each of the three onshore–offshore regions.

DISCUSSION

Seasonal changes

Mean microbial community respiratory rates show a seasonal pattern, with a winter minimum and summer maximum in all regions of the continental shelf (Fig. 3), and so do bacterial numbers (Table 1). The seasonal change in bacterial numbers may be in response to observed changes in bacterial biomass production that results from substrate limitation at minimum annual temperature (Pomeroy and Wiebe, 1993). Changes in bacterial numbers potentially explain 85% of seasonal changes in microbial community respiratory rate in waters inside the 20 m isobath and 50% of changes in deeper water. However, not
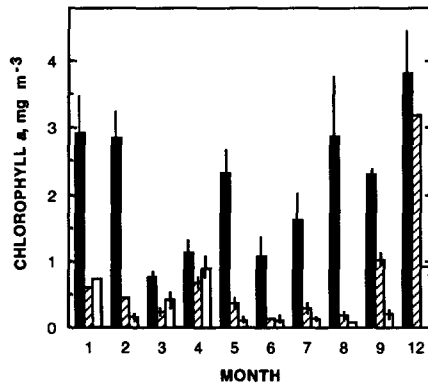
Fig. 4.   Monthly mean chlorophyll *a* concentrations collected over several years on the southeastern continental shelf ±1 standard error of the mean. Filled bars = inner shelf (0–20 m depth). Hatched bars = mid-shelf (20–40 m depth) upper mixed layer. Unfilled bars = outer shelf and west wall of Gulf Stream (40–150 m depth) upper mixed layer.

Table 1.   *Numbers of bacteria in the upper mixed layer of the southeastern continental shelf. Nearshore* = <20 m *depth*; *mid-shelf* = 20–40 m; *outer shelf* = >40 m

Date	10^5 cells ml^{-1} ± standard error (number of samples)		
	Nearshore	Mid-shelf	Outer shelf
January 1991	0.58 ± 0.15 (8)	0.12 (2)	0.15 (1)
April 1985	1.74 ± 0.36 (24)	0.37 ± 0.10 (5)	0.58 ± 0.18 (5)
September 1987	3.68 ± 0.37 (9)	1.86 ± 0.17 (15)	
November 1987	1.60 ± 0.07 (52)	1.28 ± 0.07 (24)	

all of the measured respiration is bacterial. Protozoans and phytoplankton, including autotrophic bacteria, make up an unknown and potentially variable fraction. Mechanical separations of bacteria from other autotrophic and heterotrophic microorganisms are crude at best, and we did not attempt them during these cruises. Those who have, estimate that 50–94% of microbial respiration is bacterial (Griffith *et al.*, 1990; Laanbroek and Verplanke, 1986; Schwaerter *et al.*, 1988; Williams, 1981).

In spite of the apparent seasonal trend in respiratory rates, mean rates are not highly correlated with water temperature, and the range of rates becomes large in the warmer seasons, suggesting that temperature alone is not controlling respiratory rate. Wiebe *et al.* (1993), working experimentally with bacterial isolates from southeastern continental shelf waters, found that the limiting substrate concentration for growth of aerobic heterotrophic bacteria is a nonlinear, inverse function of temperature. When bacteria are grown on minimal media at concentrations similar to those expected to be present in natural ocean waters, growth rates are strongly inhibited at temperatures near the annual minimum. At summer temperatures, the isolates are less sensitive to substrate concentration, growing on four orders of magnitude less substrate. Obviously, there is always a lower limit to substrate concentrations, below which bacterial growth will be limited, and our respiratory

rate measurements suggest that on the southeastern continental shelf, substrate concentrations vary around that limiting range. During spring and fall, and to a lesser extent in winter, respiratory rate decreases with increasing temperature (regression lines 4–6, Fig. 2). We suggest that, since the warmer water temperatures occur in the outer shelf and Gulf Stream, the negative relation to temperature reflects the differences in available substrates between the cooler inner shelf and warmer outer shelf, which show a strong onshore–offshore gradient of chlorophyll a concentrations (McClain et al., 1988). At winter temperatures, at which Wiebe et al. (1993) found the limiting substrate concentration to be orders of magnitude higher, the bacterial populations may be limited by the combined low temperatures and generally low substrates. We see a release from that limit in inner shelf waters, which are the coldest part of the continental shelf in winter but also probably have the highest concentrations of substrates. This is because photosynthesis remains relatively high there at all times and is augmented by a substantial input of dissolved materials from rivers and estuaries to the coastal waters during seasonally high river runoff in winter and spring.

Comparison with previous estimates

The respiratory rates reported by Pomeroy and Johannes (1966) from the Gulf Stream and continental shelf south of Cape Hatteras probably represent a lower limit for respiratory rates on the southeastern continental shelf for several reasons. First, they were sampling water comparable to our spring or fall stations on the mid- or outer shelf. Secondly, their technique (reverse-flow concentration) underestimated respiratory rate, because many bacteria were retained in the membrane filters that were in use at that time (Sheldon, 1972). Nevertheless, the range of values reported by Pomeroy and Johannes (0.004–$0.055\,\mu\text{M O}_2\,\text{h}^{-1}$) overlapped our lower estimates of community respiration on the outer continental shelf (0.01–$0.5\,\mu\text{M O}_2\,\text{h}^{-1}$).

The community respiration data of Turner (1978) from the inner shelf and estuaries near Skidaway Island, Georgia, are more difficult to reconcile with our data. He, too, used the reverse-flow concentration technique, modified with a correction factor of 3 to approximate bacteria retained in the filter after resuspension of the concentrates. The peak seasonal estimates that he reported from a station in the estuarine plume were in the range of rates that we reported on the inner shelf. However, his mean community respiratory rate, $0.12\,\mu\text{M O}_2\,\text{h}^{-1}$, is lower than ours by an order of magnitude. Moreover, Turner reported a decrease in community respiration, to $<0.08\,\mu\text{M O}_2\,\text{h}^{-1}$, in samples taken about 10 km from shore, well within the inner shelf waters and probably inside the coastal front. Our more extensive data are not consistent with Turner's suggestion that respiration declines precipitously within the first 10 km from shore, at depths <5 m. Nor does our present knowledge of processes on the southeastern continental shelf support Turner's hypothesis that microbial activity in shelf waters is supported principally by organic matter derived from estuarine macrophytes. Although more than 30% of the standing stock of nearshore dissolved organic carbon sometimes may be of terrestrial or estuarine macrophyte origin, that is probably not the most labile material available to bacteria (Moran, 1991). Phytoplankton-derived organic carbon has a shorter turnover time. So the actual proportion of support of bacterial growth and respiration attributable to organic carbon of macrophyte origin probably is lower than its proportion of the standing stock would suggest. On the other hand, the highest rates of respiration we observed probably exceed

concurrent photosynthetic rates, and the excess demand for organic substrates must be made up from resuspension or from allochthonous sources.

Hopkinson (1985) and Hopkinson *et al.* (1989) reported community respiration from a station in the estuarine plume off Sapelo Island, Georgia. Hopkinson used samples of coastal water pumped into 20 l carboys and returned to the laboratory. Incubations were begun 3 h after sampling and lasted 48 h. Oxygen was measured with a Clark electrode. He reported mean pelagic community respiratory rates of 0.8 μM O_2 h^{-1} for April and November and 1.8 μM O_2 h^{-1} for August, a factor of 1.5–2 lower than our means, but within the range of our measurements. He also pointed out that the inner shelf waters are net heterotrophic much of the year, and that a strong seasonal variation in respiratory rate correlates significantly with temperature.

On the inner shelf in depths <20 m, the water is fully mixed, and resuspension of benthic sediments may contribute periodically not only to particulate and dissolved organic standing stocks in the water column, but also to the number of bacteria in the water (Wainright, 1990). Dissolved and particulate carbon from the salt-marsh estuaries also flow into the nearshore coastal waters and vary with seasonal productivity in the marshes, the occurrence of storms, fortnightly variations in tidal height, and seasonal variations in river flow which flushes material from the estuaries. These inputs of organic matter to the southeastern U.S. continental shelf appear sufficient to support the intensity of respiration that both we and Hopkinson have found. Of course, not all of the respiration is bacterial, as discussed above.

Trophic status of the southeastern continental shelf

Our data for total microbial community respiration can be compared with published rates of photosynthesis to predict the trophic status of the southeastern shelf waters during the year. Verity *et al.* (1993) have provided a new estimate of primary production on the inner continental shelf off Georgia. Their mean summer rate of 1.3 μM C h^{-1} and mean winter rate of 0.1 μM C h^{-1} are essentially in agreement with those of Thomas (1966). They note, however, that there appears to be substantial interannual variation, which they and others attribute to differences in the supply of new nitrogen in river flow onto the inner shelf. Although variation in both photosynthesis and microbial respiration is large, both spatially and temporally, the mean microbial respiratory rates on the inner shelf suggest that this region is a net heterotrophic system some of the time, especially at summer temperatures. These measurements do not include benthic respiration, which adds additional oxygen demand.

If the continental shelf ecosystem is sometimes net heterotrophic, one might expect to find confirmation by looking for depletion of dissolved oxygen in the water column. Oxygen data from the extensive sampling of the R.V. *Gill* cruises (Anderson *et al.*, 1957) reveal no evidence for nearshore oxygen depletion, and it may be that ventilation of this shallow water by tides and winds is sufficient to keep it very near saturation, as the R.V. *Gill* data indicate. Verity *et al.* (1993) estimate that vertical eddy viscosity owing to tidal currents alone will typically move water from bottom to surface every hour. Middle shelf water, between the 20 and 40 m isobaths, with its relatively high respiratory rates and usually low photosynthesis rates, may also be net heterotrophic for substantial periods of time. R.V. *Gill* data show no evidence of oxygen depletion in the upper mixed layer and provide little information on conditions below the thermocline.

Because primary production on the outer continental shelf is driven largely by episodic upwellings at the shelf break associated with meandering of the Gulf Stream (Lee *et al.*, 1991), both photosynthesis and microbial respiration in outer shelf water probably vary widely, with rates that are not randomly distributed about a mean. Therefore, it is difficult to estimate rates accurately from occasional observations. Yoder (1985) estimated annual primary productivity on the outer southeastern shelf to be 360 g C m^{-2}. At a mean productivity of 0.01–0.04 μM C h^{-1}, the upper mixed layer of the outer shelf appears to be potentially net heterotrophic, especially in summer. Further respiratory rate data are needed to verify this. Dissolved oxygen in the upper mixed layer remains near saturation (Anderson *et al.*, 1957). However, *Gill* Sta. 3-42, which is clearly in an upwelling of the west wall of the Gulf Stream, shows oxygen at 70% of saturation at 50 m and at 57% of saturation near bottom at 100 m. Bacterial communities of the upper mixed layer of the outer shelf, in their between-upwellings mode, have been shown to have assimilation efficiencies on the order of 1% (Griffith *et al.*, 1990). This suggests that those communities are subsisting on dilute, refractory, or nutritionally unbalanced substrates in between interludes of more abundant and labile organic carbon sources during upwelling events.

The emerging view of trophic relations on the southeastern continental shelf is one of high nearshore primary production that is essentially all utilized on the inner or middle shelf, with the possible exception of rapid flushing events during winter gales. The outer shelf is a pulsed system driven by brief upwellings every 5–10 days. Primary production not flushed off the shelf immediately after the passage of an eddy along the shelf break is respired by the residual resident community of microorganisms. There is little evidence here for loss to the ocean's interior of excess organic carbon in amounts that could be significant in the global cycle of carbon. A similar conclusion was reached regarding export of organic matter from the northeast U.S. continental shelf (Rowe *et al.*, 1986). This appears to conform to the view of continental shelf waters as net heterotrophic systems (Smith and Hollibaugh, 1993), except in winter when bacterial respiratory rates become low while primary production changes little.

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