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Annual Cycle of Bacterial Secondary Production in Five Aquatic Habitats of the Okefenokee Swamp Ecosystem†

ROBERT E. MURRAY* AND ROBERT E. HODSON

Institute of Ecology and Department of Microbiology, University of Georgia, Athens, Georgia 30602

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Rates of bacterial secondary production by free-living bacterioplankton in the Okefenokee Swamp are high and comparable to reported values for a wide variety of marine and freshwater ecosystems. Bacterial production in the water column of five aquatic habitats of the Okefenokee Swamp was substantial despite the acidic (pH 3.7), low-nutrient, peat-accumulating character of the environment. Incorporation of [^{3}H]thymidine into cold-trichloroacetic acid-insoluble material ranged from 0.03 to 2.93 nmol liter^{-1} day^{-1}) and corresponded to rates of bacterial secondary production of 3.4 to 342.2 μg of carbon liter^{-1} day^{-1} (mean, 87.8 μg of carbon liter^{-1} day^{-1}). Bacterial production was strongly seasonal and appeared to be coupled to annual changes in temperature and primary production. Bacterial doubling times ranged from 5 h to 15 days and were fastest during the warm months of the year, when the biomass of aquatic macrophytes was high, and slowest during the winter, when the plant biomass was reduced. The high rates of bacterial turnover in Okefenokee waters suggest that bacterial growth is an important mechanism in the transformation of dissolved organic carbon into the nutrient-rich bacterial biomass which is utilized by microconsumers.

Bacterial biomass represents one of the most readily utilizable and highest-quality (protein-rich) food sources for aquatic microconsumers. Bacteria utilize various compounds in the dissolved organic carbon (DOC) as substrates for growth and repackage this highly dilute organic carbon into a concentrated, nutrient-rich bacterial biomass which can be assimilated by other organisms. Bacteria thus produce high-quality particulate organic carbon (POC) from lower-quality DOC which would otherwise be unavailable to animals at higher trophic levels. It has been estimated for some coastal and offshore marine ecosystems that between 10 and 50% of the carbon fixed by photosynthesis enters the food web via bacterial growth on DOC (1, 8, 15, 20). Similarly, bacteria are likely to play an equally important trophic role in wetland ecosystems which receive large inputs of DOC from decomposition of higher plants. In these systems, little of the net primary production is grazed while living; rather, most of the plant carbon enters the animal food web through microbial processing of nonliving plant material (22, 25).

Some acidic, peat-forming wetlands show reduced microbial biomass relative to that in more neutral pH ecosystems (4, 14), whereas others do not. We concluded from a recent study of the Okefenokee Swamp, an acid, black-water wetland in southeastern Georgia, that the waters and surface sediment support microbial biomass and rates of turnover of simple dissolved organic compounds that are equal to or greater than those of other wetland ecosystems for which comparable data are available (19). Thus, our initial results suggest that bacterial production at the expense of DOC in the Okefenokee Swamp is an important source of highly nutritive POC to aquatic microconsumers.

Most of the POC in the Okefenokee Swamp is composed of peat and detrital material which can be utilized by animals only after microbial modification (22; R. E. Hodson, A. E. Maccubbin, R. Benner, and R. E. Murray, *in* P. J. Godfrey, ed., *Ecological Considerations in Wetland Treatment of Municipal Waste Waters*, in press). Thus, the relatively small percentage of POC that consists of bacterial biomass exerts a disproportionately large influence on production by swamp animals. At steady state, bacterial secondary production is a measure of the rate of supply of this very high-quality food source to the higher trophic levels of the food web.

Production of POC by free-living planktonic bacteria requires a continuous supply of utilizable DOC. Although some DOC may enter the Okefenokee watershed in rainfall, primary production appears to be the major source of DOC for bacterial growth. Primary production by aquatic macrophytes and filamentous algae in Okefenokee marshlands is highly seasonal, and thus the availability of labile substrates for bacterial growth may also vary seasonally. The pattern of uptake of labile DOC by bacterioplankton in Okefenokee waters supports this assumption. Turnover of dissolved D-glucose is fastest during the warm months of the year and reduced during the winter (19). Although the overall concentration of DOC in Okefenokee Swamp water is high (usually between 30 and 60 mg liter^{-1}), most of this material is probably refractory to microbial degradation consisting of tannins, fulvic acids, and humic acids. Concentrations of easily utilizable substrates are probably very low; for example, kinetic analysis of glucose utilization by free-living bacterioplankton in the Okefenokee Swamp places an upper limit on glucose concentration of a few nanomolar (19). It is reasonable to assume that other labile substances also exist at similarly low concentrations.

Although it is not possible to measure bacterial uptake of each individual potential substrate, bacterial secondary production by free-living bacteria is a conservative estimate (uncorrected for respiration and predation losses) of the rate of turnover of the available DOC pool. An understanding of the seasonal dynamics of bacterial production thus provides information concerning both the seasonal availability of high-quality POC (the bacterial biomass itself) and the seasonal fate of DOC released by primary producers. This study reports rates of bacterial secondary production from five aquatic habitats in the Okefenokee Swamp. We conclude that bacterial secondary production is seasonally high,

* Corresponding author.
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varies by up to 98-fold over the year, and parallels the annual cycle of macrophyte growth and decomposition. The high rates of bacterial secondary production suggest that the transformation of DOC into high-quality bacterial biomass is an important process in the flow of energy from primary producers to other trophic levels.

MATERIALS AND METHODS

Sample sites. The Okefenokee Swamp, located in southeastern Georgia and northeastern Florida, is one of the largest freshwater wetlands in the United States. It is an acidic (pH 3.1 to 4.4), black-water, peat-accumulating environment consisting primarily of forested swamp and open-marsh prairies. Five aquatic habitats, including four prairies and one open-water lake, which together represent 28% of the total cover of the Okefenokee Swamp, were sampled as part of this study. These areas were chosen to be representative of aquatic environments in which water column processes are likely to be important. Water depth in the swamp can range from dryness to up to 1.2 m, and the average depth is approximately 0.6 m. The five sample sites are described below.

(i) Rookery. The Rookery is an aquatic macrophyte prairie dominated by the yellow pond lily *Nuphar luteum*. Water milfoil (*Myriophyllum heterophyllumm*), *Cabomba caroliniana*, and filamentous algae also occur. The sample area is adjacent to an abandoned white ibis rookery. The rookery was active from 1970 to 1981 and received substantial nutrient enrichment from bird guano during this period (30). The rookery was abandoned by the birds in 1981, 1 year before the beginning of this study. The extensive duckweed (*Lemna* spp.) bloom, which developed in response to the nutrient enrichment, was not present during the study period. The average depth of water at the rookery site was 68 cm.

(ii) Rookery Control. The Rookery Control is located approximately 2 km from the Rookery and contains vegetation similar to that of the Rookery. The Rookery Control, however, did not receive any nutrient enrichment from the white ibis rookery.

(iii) Little Cooter Prairie. The Little Cooter Prairie is an aquatic macrophyte prairie dominated by lady's hatpin (*Eriocaulon compressum*), sedge (*Rhynchospora inundata*), white water lily (*Nymphaea odorata*), and golden club (*Orontium aquaticum*). The average water depth in Little Cooter Prairie was 43 cm.

(iv) Mizell Prairie. The Mizell Prairie is a sedge prairie dominated by *Carex walteriana*. *Sphagnum* spp., filamentous algae, and arrow arum (*Peltandra sagittaefolia*) occur occasionally. Maiden cane (*Panicum hemitomon*) grows on the edges of the prairie. Mizell Prairie is the driest of the five habitats, and standing water was not present during the first 5 months of the study. Average water depth when flooded was 27 cm.

(v) Buzzards Roost Lake. Buzzards Roost Lake is a small (40,000-m^2) open-water area devoid of aquatic macrophytes. The lake occupies a depression in Grand Prairie. Approximately 7% of the Okefenokee Swamp consists of open-water areas.

Bacterial secondary production. Triplicate water samples from each site were passed through a 110-μm (pore size) mesh screen to remove large particles and collected in separate sterile polyethylene bottles. Each sample was then assayed in triplicate for thymidine incorporation. All samples were incubated at in situ temperatures and processed within a few hours of collection. The incorporation of [^{3}H]thymidine into cold-trichloroacetic acid (TCA)-insoluble material (primarily DNA) was used as an index of bacterial secondary production in the water column (9, 10). Triplicate 10-ml water samples and Formalin-killed controls were incubated with 5 nM [*methyl*-^{3}H]thymidine (40 to 60 Ci/mmol; New England Nuclear Corp. or ICN Pharmaceuticals) for 0.5 to 2 h. Incubations were terminated by the addition of 10 ml of ice-cold 10% TCA and stored at 4°C until filtered. Samples could be stored in TCA at 4°C for at least 1 week with no effect on incorporation rate. Samples were filtered on 0.2-μm (pore size) membrane filters (Millipore Corp.), washed twice with 5% TCA, and then combusted in a biological oxidizer (OX-300; R. J. Harvey Co.) to oxidize the incorporated radiolabel to ^3H_2O. Tritiated water was collected in 14 ml of ScintiVerse (Fisher Scientific Co.) counting medium, and the samples were radioassayed in a Beckman LS 9000 liquid scintillation spectrometer. Quench corrections were made by the sample channels ratio method. Rates of bacterial production (in cells per liter per day) were calculated from thymidine incorporation rates by multiplying by 6.9×10^9 cells produced per nmol of [^{3}H]thymidine incorporated (see below). The rate of bacterial carbon production was calculated by multiplying the cellular production rate by mean cell volume and using a carbon/volume conversion factor of 1.21×10^{-13} g of carbon μm^3 (32).

Conversion factors. The conversion factor, which relates rates of thymidine incorporation to rates of bacterial secondary production (in cells per liter per day), was obtained by the empirical dilution technique of Kirchman et al. (13). For dilution experiments, 50 ml of swamp water was added to 500 ml of filtered (pore size, 0.2 μm) swamp water, mixed well, and sampled every 4 h for thymidine incorporation and direct counts. The average exponential growth rate (μ) of the bacteria in the sample was obtained from semilogarithmic plots of change in thymidine incorporation over an 8-h period of exponential growth, and the conversion factor was calculated by using equation 5 from Kirchman et al. (13).

An alternative method for determining the conversion factor based on enrichments (2) was also used for comparison. Enrichment experiments were conducted with a leachate prepared from the white water lily *Nymphaea odorata*. Senescent leaves were collected at Little Cooter Prairie and dried at 50°C. Two grams of dried leaves was placed in 500 ml of filter-sterilized swamp water and leached for 5 h at 4°C. The leachate was then filter sterilized, lyophilized, and resuspended in distilled water. Low-molecular-weight (<500) and high-molecular-weight (>500) fractions of leachate were separated by Amicon ultrafiltration (Amicon Co.). Leachate fractions were added to 500 ml of screened (pore size, 110 μm) Little Cooter Prairie water at a concentration equivalent to 0.5 g of dried leaf material per 500 ml of swamp water. Incubations were placed in the dark and sampled every 6 h for 48 h. Exponential growth occurred between 12 and 24 h after the addition of leachate (based on epifluorescence microscopy), and this time period was used to compute exponential growth rates and conversion factors as described above.

Bacterial abundance and biomass. Bacterial abundance was determined by epifluorescence microscopy of acridine orange-stained cells (12). Water samples were preserved with 2% Formalin and refrigerated until counted. Bacteria were filtered onto 0.2-μm (pore size) membrane filters (Nuclepore Corp.) which had been previously treated with irgalan black (Ciba-Geigy Corp.) and were stained with 0.01% acridine orange. At least 10 randomly selected fields

with ≥50 cells per field were counted on each filter with an Olympus BHS microscope.

Bacterial biovolume was estimated from acridine orange-stained slides by measuring cell dimensions with an ocular micrometer. Cells were grouped into several size classes (<0.7 and 0.7 to 1.5 μm in diameter), spheres, and cylinders of measured length and diameter. At least 100 cells from randomly selected fields were measured. Mean cell volumes were calculated by dividing total volume by total cell count. The coefficient of variation was 21% for mean cell volume.

RESULTS AND DISCUSSION

Thymidine concentration. An important consideration in using thymidine incorporation into DNA as a measure of bacterial secondary production is correcting for possible dilution of the added radiolabeled thymidine by intracellular and extracellular pools of unlabeled thymidine. If substantial isotope dilution occurs, then the measured rates of bacterial production will be underestimates. Intracellular isotope dilution of incorporated [^{3}H]thymidine may occur as a result of de novo synthesis of deoxythymidine (16). Increasing the total concentration of added [^{3}H]thymidine in the incubation not only overcomes isotope dilution due to the presence of extracellular dissolved thymidine but also eliminates or greatly reduces intracellular isotope dilution by inhibiting de novo synthesis. Riemann et al. (27) have reported that [^{3}H]thymidine concentrations of up to 10 nM may be required to overcome isotope dilution in some freshwater systems. They determined the amount of [^{3}H]thymidine needed to overcome isotope dilution by measuring the amount of [^{3}H]thymidine required to maximally label cold-TCA-insoluble cellular material. We found that, in Okefenokee waters, additions of 5 nM [^{3}H]thymidine were adequate to produce maximal labeling of cold-TCA-insoluble material. Incubation of water samples from Little Cooter Prairie with 16.5 nM [^{3}H]thymidine increased incorporation by only 13% relative to the incorporation rate at 4.1 nM, suggesting that 4.1 nM was sufficient to saturate extracellular and intracellular thymidine pools. Saturation was achieved at even lower thymidine concentrations (1.5 nM) for water samples from the Rookery site.

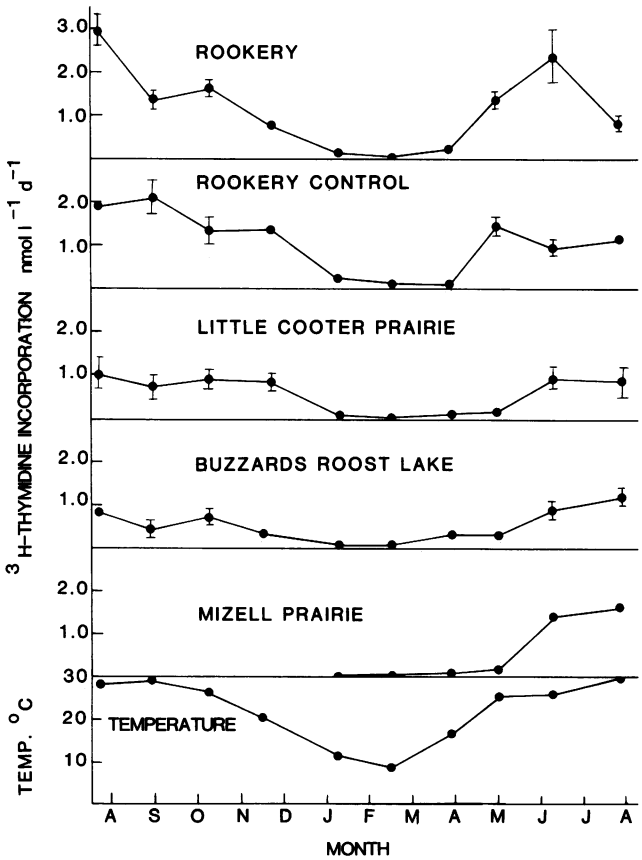

FIG. 1. Annual cycle of thymidine incorporation into cold-TCA-insoluble material in five aquatic habitats of the Okefenokee Swamp, August 1982 to August 1983. Each point represents the mean of triplicate water samples assayed in triplicate. Bars, ±1 standard deviation. Points without visible bars indicate that ±1 standard deviation was less than the size of the point. Temperatures are the averages of surface water temperatures for the five sites at the time of sample collection.

TABLE 1. Annual mean and range of thymidine incorporation rates and bacterial secondary production in the water column of five Okefenokee Swamp habitats, August 1982 to August 1983

Habitat	Mean (range) thymidine incorporation (nmol liter^{-1} day^{-1})	Mean (range) bacterial secondary production	
		Cells liter^{-1} day^{-1} (10^9)	μg of carbon liter^{-1} day^{-1}
Rookery	1.12 (0.03–2.93)	7.7 (0.2–20.2)	130.4 (3.4–342.2)
Rookery Control	1.04 (0.05–1.87)	7.2 (0.4–12.7)	122.0 (6.8–215.1)
Little Cooter Prairie	0.54 (0.03–1.01)	3.7 (0.2–7.0)	62.7 (3.4–118.6)
Buzzards Roost Lake	0.50 (0.06–1.22)	3.5 (0.4–8.4)	59.3 (6.8–142.3)
Mizell Prairie	0.55 (0.03–1.56)	3.8 (0.2–10.7)	64.4 (3.4–181.3)

Thymidine incorporation. Incorporation of [^{3}H]thymidine by water column bacterioplankton exhibited distinct seasonal trends (Fig. 1). Rates of thymidine incorporation from July 1982 to July 1983 (Fig. 1 and Table 1) ranged over 2 orders of magnitude, from 0.03 to 2.93 nmol liter^{-1} day^{-1} (mean, 0.75 nmol liter^{-1} day^{-1}). The Rookery and Rookery Control sites were the most variable, as thymidine incorporation ranged from 1 to 3 nmol liter^{-1} day^{-1} during the warmer months and 0.03 to 0.2 nmol liter^{-1} day^{-1} in winter. Little Cooter Prairie and Buzzards Roost Lake exhibited generally lower rates of thymidine incorporation than did the other sites (less than 1 nmol liter^{-1} day^{-1}) during the warmer months and similarly low rates (0.03 to 0.07 nmol liter^{-1} day^{-1}) in winter. Water was absent from Mizell Prairie from July 1982 to January 1983. Rates of thymidine incorporation by bacteria in the Mizell Prairie water column were low (0.03 to 0.07 nmol liter^{-1} day^{-1}) during the winter and increased from 0.2 to 1.6 nmol liter^{-1} day^{-1} between May and August of 1983. All sites exhibited substantial rates of thymidine incorporation from May to November, when water temperatures were above 20°C, and reduced rates between December and April. This trend generally follows the pattern of glucose utilization by Okefenokee water column bacteria (19) and is similar to the seasonality of water column respiration (18) and cellulose decomposition (3) reported for other swamp ecosystems in the southeastern United States.

Averaged over the entire year, the rates of [^{3}H]thymidine incorporation at the five sites were not statistically different from each other, as indicated by one-way analysis of variance. This result was particularly interesting with regard to the Rookery and Rookery Control sites, which had been

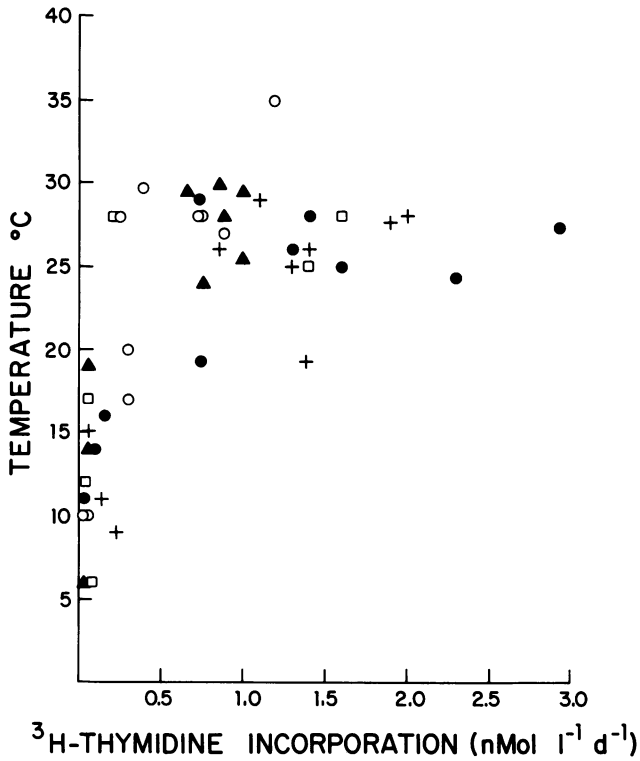

FIG. 2. Scatter plot of thymidine incorporation into cold-TCA-insoluble material versus temperature. Symbols: ●, rookery; +, Rookery Control; ▲, Little Cooter Prairie; ○, Buzzards Roost Lake; □, Mizell Prairie.

shown previously to differ in inorganic nutrient concentration and plant biomass (30). Sampling for this study began in July 1982, 1 year after the rookery was abandoned by the birds; thus, the similar rates of thymidine incorporation at these two sites suggest that either the effects of nutrient enrichment did not enhance bacterial production in the water column or that any enhancement which may have occurred was relatively transitory.

Annual water temperatures ranged between 6 and 35°C, and temperature clearly influenced the rate of bacterial production (Fig. 1 and 2). Thymidine incorporation was moderately correlated with temperature (r = 0.57, Spearman's rank correlation; Fig. 2). Temperature differences alone, however, did not account for the average increase in thymidine incorporation of 48-fold (range, 20- to 98-fold) from winter to summer. When Okefenokee water temperature was varied between 10 and 30°C in laboratory incubations, increases in thymidine incorporation resulting from the 20°C temperature change averaged only 4- to 19-fold (Fig. 3). Bacterial abundance at the five sites averaged 2.5 × 10^6 cells ml^{-1} over the course of the study and increased by twofold between January and July 1983 (data not shown). The combined effect of temperature and bacterial abundance could account for an increase in thymidine incorporation rate of between 8- and 38-fold. This may be sufficient to explain the annual variation in thymidine incorporation rates for some sites. However, at the Rookery site, for example, the combined effects of temperature and bacterial abundance could not account for the 98-fold increase in thymidine incorporation rate from winter to summer. Other factors, such as substrate and nutrient availability, as well as differences in grazing of bacteria by invertebrates, probably play roles in regulating bacterial production.

The seasonal cycle of bacterial thymidine incorporation parallels that of aquatic macrophyte and filamentous algal growth. Spring growth of these plants begins in March and April, and substantial populations are maintained until November. Plant biomass peaks in June, July, and August and is reduced during the winter months (personal observations). The parallel annual changes in rates of bacterial secondary production and annual cycle of plant growth suggest that bacterial populations in the Okefenokee Swamp may be dependent on primary production as a continuous source of easily utilizable dissolved organic substrates or inorganic nutrients or both.

Several studies of marine and freshwater environments have demonstrated the release of significant amounts of DOC from living vascular plants (24, 31, 33) and macroalgae (26). Moriarty and Pollard (17) reported diel variations in bacterial production in marine waters and sediments associated with growing sea grasses and estimated that 10% of net primary production was utilized by the bacteria. Leaching of DOC from senescent plant material is an additional source of DOC in freshwater swamp and stream ecosystems (3, 5–7, 11, 18, 23).

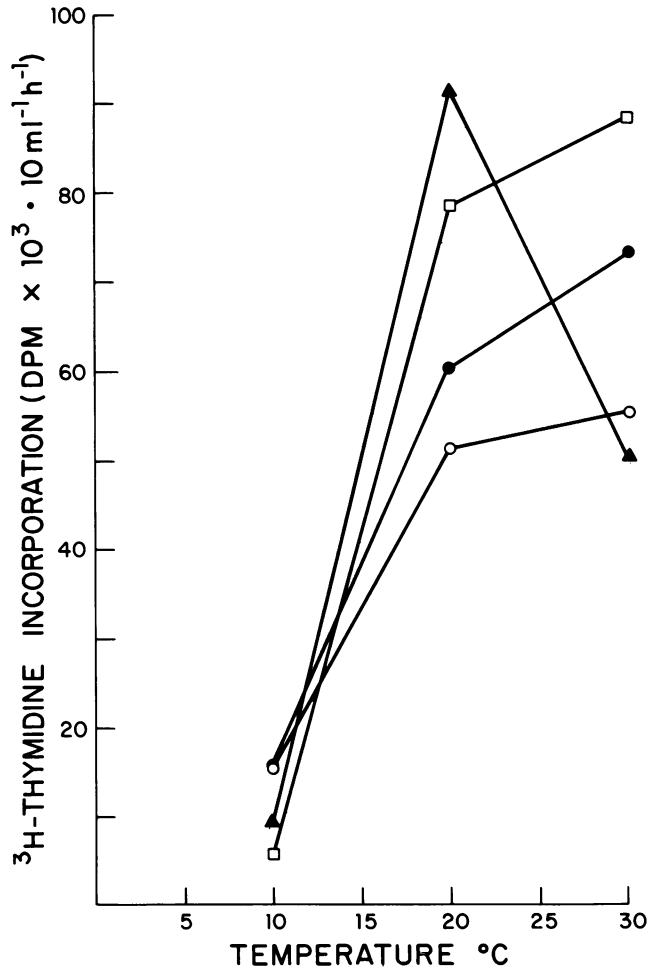

FIG. 3. Effect of increasing temperature on thymidine incorporation into cold-TCA-insoluble material by Okefenokee Swamp bacterioplankton. Each point is the mean of triplicate determinations. Symbols: ▲, March sample incubated at designated temperatures for 46 h before analysis; □, March sample incubated for 26 h; ●, January sample incubated for 12 h; ○, January sample incubated for 24 h.

Aquatic macrophytes represent a significant potential source of DOC to Okefenokee marshes. Auble (G. T. Auble, Ph.D. Thesis, University of Georgia, Athens, 1982) observed substantial losses of DOC from *Nymphaea odorata* leaves in the Okefenokee Swamp; only 15.3% of the initial dry weight remained in litter bags after 1 year. In water lilies, which dominate three of our sites, leaf biomass turns over several times during the growing season as old leaves die and new leaves grow from the rhizome, probably providing a semicontinuous source of DOC and nutrients during the growing season. Periphytic algae and phytoplankton are likely to augment the supply of utilizable DOC, although their contributions relative to macrophytes have not been quantified.

Mulholland (18) suggested that heterotrophic activity in a North Carolina swamp-stream was limited by the availability of high-quality carbon substrates. In that system, a major portion of the total annual microbial respiration occurred in an intensive 1-week burst, when labile substrates were available from leaf litterfall. In contrast, bacterial production in the Okefenokee water column is high throughout the growing season, suggesting that labile substrates are available throughout the growing season. Bacterial growth, however, may be limited by the quality or quantity (or both) of substrates during the winter.

Bacterial secondary production. A conversion factor is required to convert rates of thymidine incorporation (in moles per liter per day) to rates of bacterial secondary production (in cells per liter per day). Fuhrman and Azam (10) proposed conversion factors of 1.7×10^9 and 2.4×10^9 cells produced per nmol of thymidine incorporated by bacterioplankton in nearshore and offshore marine systems, respectively. These conversion factors were developed from a consideration of several biochemical parameters, including isotope dilution of radiolabeled thymidine by de novo synthesis, thymidine content of bacterial DNA, and amount of DNA per bacterial cell. These conversion factors were derived for marine systems, and it is not known whether they are applicable to freshwater environments.

Kirchman et al. (13) proposed an alternate experimental approach for determining conversion factors. This empirical technique involves diluting a bacterial inoculum with filter-sterilized water from which the inoculum originated and simultaneously monitoring changes in bacterial numbers and [^{3}H]thymidine incorporation. The exponential growth rate (μ) is derived from the slope of a semilogarithmic plot of thymidine incorporation versus time, and the conversion factor is calculated from μ, bacterial abundance, and measurements of thymidine incorporation (13). Bell et al. (2) noted that this technique was also applicable to situations in which bacterial growth was stimulated by organic enrichment such as the addition of dissolved glucose. We used both the dilution method and a modified enrichment procedure to obtain empirical conversion factors for Okefenokee bacterioplankton. Organic enrichments were carried out by using additions of low-molecular-weight (<500) and high-molecular-weight (>500) fractions of a *Nymphaea odorata* leachate. Growth rates, conversion factors, and coefficients of determination for the conversion factor experiments are shown in Table 2. The arithmetic mean of results of the conversion factor determinations was 6.9×10^9 cells produced per nmol of [^{3}H]thymidine incorporated. This conversion factor is very similar to those reported by Kirchman et al. (13) for salt marshes, estuaries, and a eutrophic pond. The applicability of conversion factors to measurements of [^{3}H]thymidine incorporation is still an active area of research, and the values of these factors may change slightly as better resolution becomes possible. We have used our conversion factor to convert rates of [^{3}H]thymidine incorporation to rates of bacterial secondary production. If the lower conversion factors reported for some marine ecosystems (10) and European lakes (2) had been applied to the Okefenokee Swamp, our estimates of bacterial secondary production would be lower by approximately threefold. This would not, however, alter any of the basic conclusions of this study.

TABLE 2. Exponential growth rates and conversion factors determined from changes in [^{3}H]thymidine incorporation rates and bacterial abundance

Habitat and expt conditions	Growth rate (h^{-1})	Conversion factor (10^9 cells $nmol^{-1}$)	r^{2a}
Rookery			
1/10 Dilution	0.06	5.8	0.99
Little Cooter Prairie			
Low-mol-wt leachate enrichment	0.14	8.7	0.94
High-mol-wt leachate enrichment	0.13	6.3	0.99

[a] r^2, Coefficient of determination.

Bacterial biovolumes were measured at the sampling sites on two occasions, in early March 1984 and mid-April 1984. Mean (±1 standard deviation) bacterial biovolume was 0.14 ± 0.03 μm^3. Cocci between 0.7 and 1.5 μm in diameter were the predominant organisms in terms of numbers and volume at all sites. Biovolume was not significantly different at the sampling sites on the two sampling occasions. Our calculated bacterial biovolumes in the Okefenokee Swamp waters are very similar to values reported for Georgia coastal water (21), salt marshes (29), and lakes (2).

Rates of bacterial secondary production (in cells per liter per day) were calculated by multiplying the thymidine incorporation rates from Fig. 1 by the empirically determined conversion factor. Cellular production rates were converted to carbon equivalents by multiplying by the average volume per cell (0.14 μm^3) and by 1.21×10^{-13} g of carbon μm^3 (32).

Rates of bacterial secondary production by bacterioplankton in the Okefenokee Swamp are high and comparable to reported values for a wide variety of marine and freshwater ecosystems (2, 8, 9, 28). Bacterial production (Table 1) was substantial in all five aquatic habitats and ranged from 3.4 to 342.2 μg of carbon $liter^{-1}$ day^{-1} in winter and summer, respectively (mean, 87.8 μg of carbon $liter^{-1}$ day^{-1}). The high rates of bacterial secondary production in the summer and fall are similar to rates reported for eutrophic lakes, whereas the lower winter rates are more similar to rates reported for oligotrophic lakes (2).

Overall rates of bacterial production in the aerobic water column are high in the Okefenokee Swamp, despite the acidic, low-nutrient conditions. This finding is consistent with our earlier results that microbial biomass and rates of aerobic glucose turnover are high in the Okefenokee Swamp (19) and suggest that the production of bacterial biomass at the expense of DOC is an important link in the swamp food web.

The mean concentration of DOC in Okefenokee marsh areas is 45.5 mg $liter^{-1}$ (P. A. Flebbe, Ph.D. thesis, University of Georgia, Athens, 1982). Based on our estimates, we conclude that daily bacterial production consumes only between 0.02% (winter) and 1.5% (summer) of the total DOC, assuming that 50% of the DOC taken up by bacteria is respired. This result is consistent with our assumption that most of the DOC in the humic-rich waters of the Okefenokee is refractory and cannot be easily metabolized by bacteria.

Daily bacterial production also accounts for only a small percentage of the total POC (0.7%, based on mean annual POC concentration of 17.7 mg of carbon liter^{-1}; Flebbe, Ph.D. thesis). This very small amount of POC, however, constitutes the highest quality food source available to many small swamp invertebrates.

The high rates of bacterial production coupled with the relative constancy of bacterial abundance suggest that the bacterial biomass in the water turns over rapidly, probably due to grazing by protozoa and zooplankton. Bacterial turnover rates averaged 0.15 day^{-1} in winter and 4.93 day^{-1} in summer and correspond to doubling times of 15 days to 5 h. Free-living bacterioplankton in the Okefenokee Swamp transform DOC into high-quality bacterial biomass which is used as a food source by other organisms. The high rates of production by and rapid turnover of bacterioplankton in Okefenokee waters suggest that carbon flow from DOC to bacterioplankton to bacteriovores is an important pathway in the flow of energy and nutrients from primary producers to other trophic levels of the food wed.

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