Bacterial production in an arctic pond

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Article:

Bacteria of natural waters have an important role in recycling nutrients. As we accumulate information on the biomass of bacteria, however, we realize that these large quantities of bacteria may also be an important source of particulate matter for animals. While these statements have been made before, there have been few attempts to quantify the role of bacteria as producers of particulate matter in freshwater systems. The study reported here deals with biomass and production rates of bacteria in a tundra pond in arctic Alaska.

In recent years, satisfactory techniques have been developed for direct counting of bacterial numbers in freshwaters, but there are still no easy and direct methods for measuring bacterial production. The main problem is that bacteria do not all use a single substrate, so that a method similar to the $^{14}CO_2$ uptake method for algal primary productivity does not work. Bacteria do, however, take up a small amount of CO_2 as they grow so a $^{14}CO_2$ uptake method has been proposed but appears to have many problems such as interference by dark uptake of algae (KUSNETSOV & ROMANENKO 1966). Another recent method, using $^{35}SO_4$ = uptake is promising but also needs work before it is a proven method (MONHEIMER 1974; JASSBY 1973). Thus, as the direct methods have not yet been successful, we have used an indirect method of measuring bacterial production that is similar to methods of estimating secondary production of zooplankton. In this method, the total bacterial production (as carbon) is the sum of changes in biomass over time, plus quantities of carbon given off (as CO_2 and CH_4), plus losses due to feeding of animals (protozoa, zooplankton, chironomids, etc.). The study was carried out as a part of the U.S. Tundra Biome (IBP) Study of an arctic pond (supported by NSF Grant GV 33853 to North Carolina State University).

The study ponds are located on the northern coastal plain of Alaska, several kilo-meters from the Arctic Ocean and 2 km from Barrow, Alaska (71° 18' N, 156° 42' W). In this area, thousands of small ponds have formed on old lake beds as a result of permafrost processes (BRITTON 1967). The ponds are shallow, averaging 20 cm deep (maximum depth 40 cm), with a diameter of 20 to 45 m. The average air temperature is — 12.5 °C and daily minimums drop below 0 °C on 324 days of the year. As a result, the ponds are completely frozen from mid to late September until early June. Water temperatures average about 7 °C (range 0° to 15 °C) during the ice free period, while the temperatures of the highly organic sediments are always a few degrees cooler.

Methods

Direct counts of bacteria in the water and sediments of the pond were made with an epi-illuminated (auflicht) microscope and acridine orange stained bacteria (FRANCISCO et al. 1973; DALEY & HOME in prep.). In this method, the dye (0.01%) is added (1:1) to a sample of natural water, the sample is incubated for 1 minute, filtered (0.1m1) through a black membrane filter (0.45 μ pore size), and then the bacteria are counted immediately under UV light. Sediment samples were diluted 1:100 with filtered water and mixed in a high-speed blendor before counting.

Respiration in the sediments (planktonic respiration was too low to measure) was measured by changes in both the O_2 and CO_2 in the water over cores inoculated for 4 to 24 hours (see MILLER & REED 1975). Calculated respiration of the sediment algae and micro- and macroanimals (4.3 g C/m^2/yr) was subtracted from the total annual respiration (13.7 g C/m^2/yr) to give bacterial respiration. Methane gas, from anaerobic bacterial metabolism, was also produced at an annual rate of 1.1 g C/m^2/yr as determined by gas chromatography of gas bubbles collected in funnels in the water column.

Bacterial losses to protozoan grazing in the sediments, assessed by FENCHEL (in press) from feeding rate measurements, were 2.0 g C/m^2/yr. The feeding of micrometazoa, chironomids, and oligochaetes was assessed from our measurements of their growth rate, from the findings of KAJAK & WARDA (1968) that chironomids are selective feeders in the sediments, and from our assumption that chironornids obtain most of their food from the algae and bacteria in the sediments and not from the abundant Carex detritus. Thus, an annual production rate of 3.7 g C/m^2 for the chironomids and oligochaetes accounts for a maximum consumption of 3.9 g C/m^2 of sediment bacteria. Zooplankton are abundant in the water column (Daphnia, copepods, fairy shrimp) and can potentially filter the entire water column every two days or so (CHISHOLM & STROSS in press). We do not know, however, if these animals retain all of the small bacteria that they filter, so a range of values is given that reflects a 30% to 100% retention.

Results and discussion

The bacterial numbers over six seasonal cycles (measured in four ponds) ranged from 0.1 to 6.5 million/ml in the plankton (Fig. 1). The surface sediments contained from 0.1 to 55.0 × 10^9 cells/g dry wt (Fig. 2). Based on a 20 cm depth of water and a 5 cm depth of sediments, the sediments contained 3 to 4 orders of magnitude more bacteria per m^2.

Biomass was calculated from a conversion factor of 1.8 × 10^{-8} µg C/cell for the planktonic bacteria and 3.7 X 10^{-8} µg C for the benthic bacteria. Peak biomass in the water column was 0.018 to 0.022 g C/m^2 and in the sediments was 15 to 20 g C/m^2.

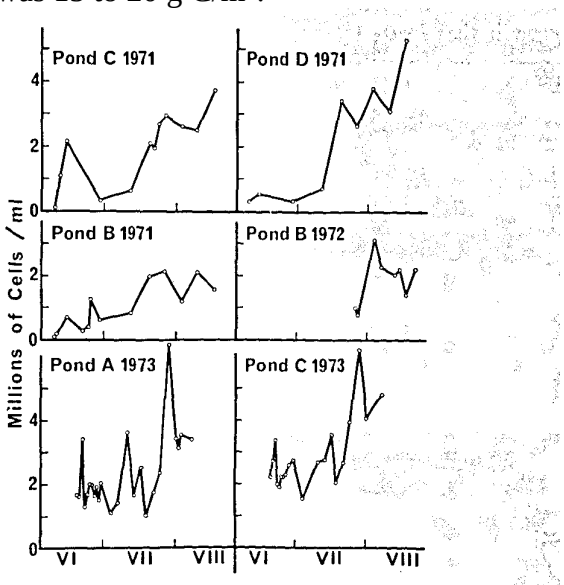

Fig. 1. Bacterial counts in the plankton of tundra ponds, 1971—1973.

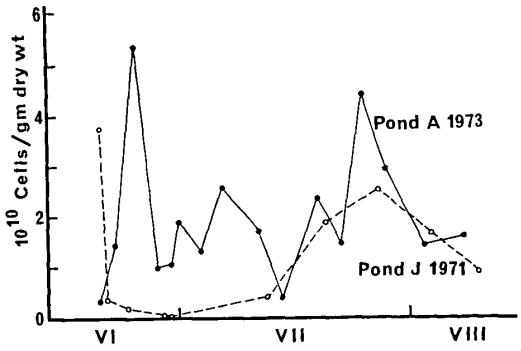

Fig. 2. Bacterial counts in the sediments of tundra ponds, 1971 and 1972.

There was a peak in bacterial numbers and biomass in mid to late June in both the plankton and sediments (Fig. 1 and 2). This peak occurs immediately after the ponds thaw. In the plankton, the high concentrations of bacteria are caused partly by the influx of soil bacteria in melt water and partly by dissolved organic matter brought in during the melt. The peak in the sediments is unexplained but there is a similar peak in tundra soils at the time of thaw (R. BENOIT pers. comm.).

Following this early season peak, the numbers and biomass drop due to less favorable environmental conditions

and predation from the zooplankton P in the water column. Then, beginning in June, both populations begin log-arithmic growth that leads to a second peak in early August. During this period the average net growth constant for both sediment and planktonic bacteria was only 4.8%/day (range 3.4% to 6.0%), a very low growth rate indeed.

The seasonal pattern is very similar to that of arctic lakes (BODY & BOYD) 1963; MORGAN & KALFF 1972) and to that of alpine and temperate lakes (TILZER 1972; FRANCISCO 1970; ROMANENKO 1971) studied with similar techniques.

The production of bacteria in a typical pond (Tab. 1) was about 25 g C/m^2/yr. Better than 98 °/o of this production was of benthic bacteria as planktonic bacteria were insignificant both in biomass and productivity even with the most generous estimate of zooplankton feeding rates. The net annual primary production in this pond totaled 52.4 g C/m^2 most of which (42.4 g C/m^2) was produced by a bed of Carex aquatilis, which rings the pond in shallow water, and part (9.0 g C/m^2) by benthic algae (STANLEY 1974) which photosynthesize in the top 2 or 3 mm of sediment. Phytoplankton production (V. ALEXANDER pers. comm.; KALFF 1967) was slightly less than 1 g C/e/yr. It is important to realize that the bacterial production (Tab. 1) is for the center of the pond and not the littoral macrophyte zone. Much of the initial decomposition of the macrophytes occurs in the littoral zone so bacterial production is likely higher there than in the pond center.

Tab. 1. Bacterial production in an Alaskan tundra pond, 1971.

	g Cm²/yr	°/o of total
Sediments		
Biomass change	9.0	35
Respiration	9.3	37
Methane production	1.1	4
Macrobenthic feeding (est.)	3.9	15
Protozoan feeding	2.0	8
Total	25.3	
Plankton		
Biomass change	0.007	
Respiration (est.)	0.07—0.15	
Zooplankton feeding (est.)	0.13—0.26	
Total	0.21—0.41	

The bacterial production is controlled in part by temperature. This acts most strongly during the winter when death of bacteria reduces the numbers of both planktonic and sediment bacteria to low levels. During the open water period, the temperature is also important as an increased temperature would increase the growth rate of the bacteria as well as the decomposition rate of macrophytes and other detritus. In vitro tests of bacterial growth and uptake of glucose gave a Q_{10} of 1.7 to 2.0 but it is doubtful that this rate of increase would hold in nature where the rate of supply of nutrients may be limiting.

Based on our present information, we conclude that a combination of low rates of supply of nutrients and predation by zooplankton and benthic animals is limiting the bacterial production during the summer months. Un-fortunately we know little about most of the rates of supply of organic nutrients as these come from a variety of sources such as excretion from living organisms, leaching of recently dead macrophytes, and hydrolysis of older detritus.

Finally, it is important to note that the pond bacterial production has been calculated from biomass changes and losses in a manner analogous to calculations of zooplankton production. In the case of bacteria, this type of calculation may result in production estimates that are actually higher than the carbon inputs (MACLEAN & HEAL in press). However, these are real production values that include rapidly recycled material. For example, when bacterial cells are eaten by a zooplankter, some of their carbon may be excreted as organic molecules, some goes to growth of zooplankton, some is excreted in feces, and some given off as carbon dioxide. All of these forms, except for CO_2, may be used for new bacterial growth which would be added to the original estimate of loss due to grazing in the production calculations.

Certainly our data show that there is a high bacterial production of particulate matter in arctic ponds. We have not shown, however, that this particulate matter is actually used by zooplankton and macrobenthic animals. This is an important area for further research, but it is important that experiments use the small bacteria actually present in nature rather than large bacteria that invariably grow in laboratory cultures.

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Discussion

Houoll: Is the annual growth of the Carex balanced by the microbial decomposition or is there a general increase in organic sediments through the years?

HOBBIE: Any annual increase is less than 10% of the Carex production and would be impossible to measure. An added complication is that the production rates given here reflect events in the pond center and the Carex de-tritus may take a number of years to move to the center.

REICHARDT: What is the advantage of counting such small forms of bacteria by a fluorescent technique since it is rather difficult to recognize bacterial structures even by usual microscopic techniques.

HOBBIE: The advantage is that with this technique it is much easier to distinguish these small bacteria from small non-living particles.