

Major Findings

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INTRODUCTION

Studies in the extreme environments of mountains, tropics, and the Arctic have long been an important part of ecological research. Apart from the stimulation and enjoyment of visiting new places, ecologists have compared these extreme habitats with one another and with temperate habitats in order to test hypotheses about general principles. This approach of comparative natural history requires a large body of data collected from many habitats; both descriptions and a good understanding of processes are required. The data from extreme environments are especially valuable as they extend the range of important variables and may even allow analyses of the effect of certain factors that always vary together in temperate regions.

The IBP study of arctic ponds reported in this book is primarily a description of the habitat, the biota, and the processes by which organisms interact with other organisms and with their physical and chemical environments. In the report, the comparative aspects of the study have been deliberately de-emphasized, as constant reference to temperate and tropical lakes would have quickly doubled the size of the book. The value of the study in this comparative sense will become apparent later, when this study is referred to to find out what controlled photosynthesis, how rapidly a sedge leaf decomposed, or what the community structure was in an arctic pond.

In addition to the comparative importance of the arctic ponds, there are certain advantages to investigating aquatic processes in the Arctic. For example, low diversity of the higher plants and animals allows cohorts and age classes to be identified and followed through time; this simplifies productivity measurements. In some groups, such as most of the zooplankton, there may be only a single generation each year which also greatly simplifies growth measurements. The low diversity also permits a more complete study to be carried out with fewer scientists but does not, of course, make the study of an individual process any easier.

There are other tactical advantages to arctic research. First, the ponds freeze completely in mid-September, so they need to be studied for only 3 months a year (which fits into academic schedules quite well). During the field research months the scientists were working in crowded laboratories in an isolated location where there were few distractions from

beaches, families, or television. The resulting intense interactions and scientific excitement could only be maintained for a month or so, but helped immensely to stimulate creativity and to integrate the various projects.

Description of the Ponds

Small ponds formed on old lake beds are abundant on the flat coastal plain of northern Alaska (Figure 1-1). A number of these ponds, several kilometers from the Naval Arctic Research Laboratory at Barrow, were studied for several years to improve our understanding of the controls of aquatic populations and processes that operate in this extreme environment.

The ponds are small, only about 30 x 40 m, and shallow, up to 0.5 m deep (Figure 1-2, 1-3). Each pond is surrounded by wet tundra, mostly low grasses and sedges, and is cut off from adjoining ponds by a network of

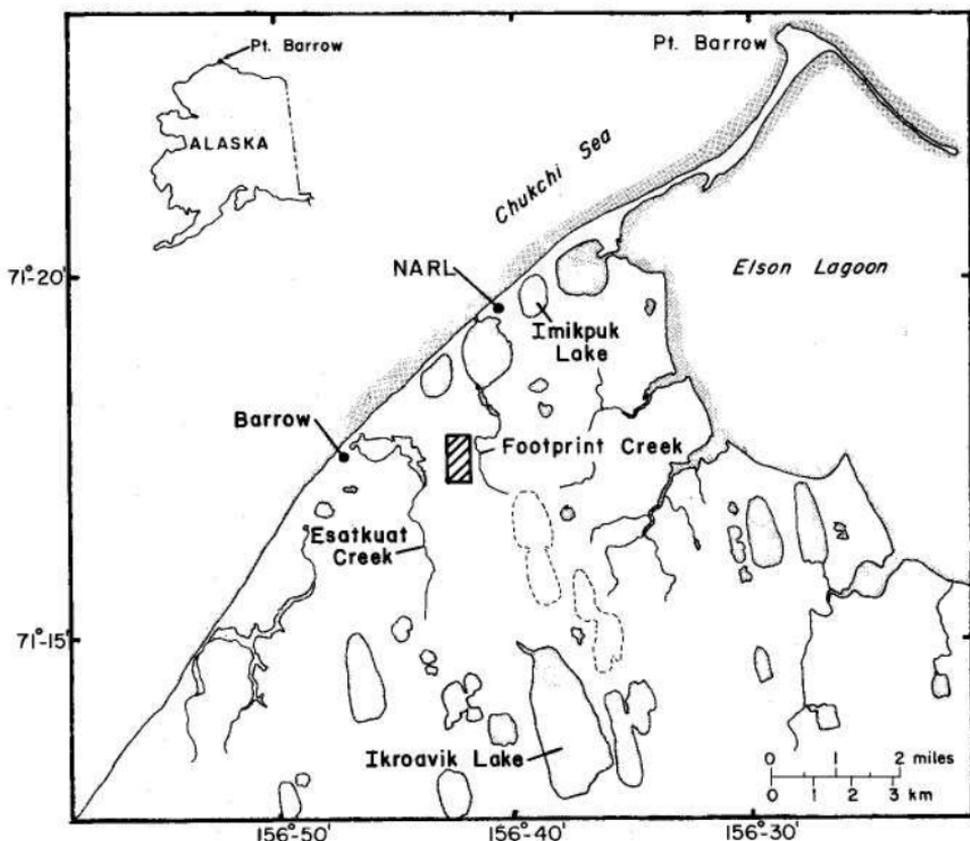


FIGURE 1-1. Location of IBP Tundra Biome Project, showing the Naval Arctic Research Laboratory, the village of Barrow, and the research sites (cross-hatched area).

small ridges pushed up by the growth of underlying ice wedges. The total area enclosed by the ridges is about double the pond area. Despite the minuscule drainage basins and the desert-like levels of precipitation (12 cm annual, 50% falls as rain in June through September), the surrounding tundra is often saturated and the ponds do not dry up. Water flows from one basin to another for only a few days during the spring runoff. There is no belowground water movement from basin to basin or into the sediments because of the underlying permafrost.

From late September until mid-June, the ponds and their underlying sediments are solidly frozen. Melting of the ice in the ponds occurs over a few days in the spring and water temperatures can reach as high as 16°C any time thereafter. Thawing of the sediments continues throughout the summer until 30 cm are thawed. The ponds are so shallow that the water temperature can change as much as 10°C per day in response to sunlight, air temperature, and wind. June, July, and August are cool (mean air temperature is 2.8°C), cloudy (83% cloud cover), and windy (an average of 6.1 m sec⁻¹) so the mean water temperature is low, around 6°C.



FIGURE 1-2. *The intensively studied ponds near Barrow, Alaska. A small field lab is at the upper left of the picture and experimental subponds in Pond B are at right. An aerial cable car is suspended above the subponds.*

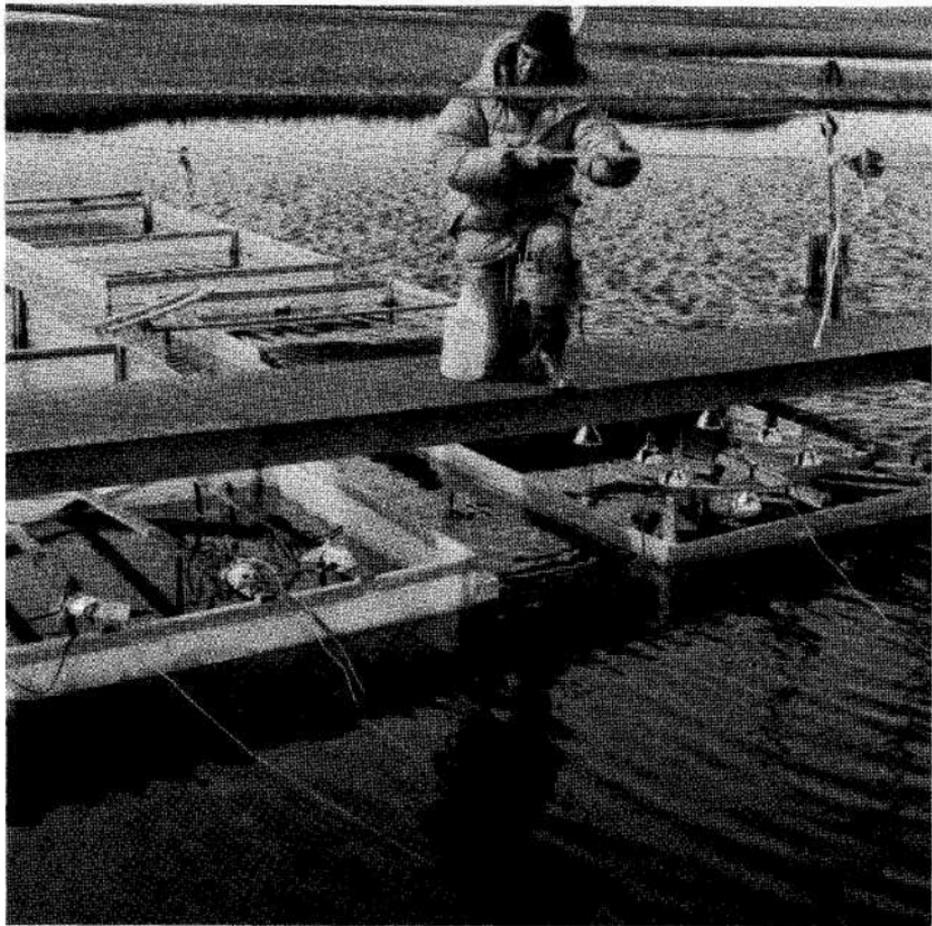


FIGURE 1-3. To avoid disturbing the water and sediments of Pond B, an investigator takes samples from a cable car.

The pond waters contain small amounts of salts and have a pH around 7.3. The light, flocculant sediments are made up of 80% organic matter.

The dominant primary producers of the ponds (Table 1-1) are a sedge (*Carex aquatilis*) and a grass (*Arctophila fulva*) which live in the shallow margins of the pond and cover 30% of the surface (Figure 1-4). Benthic microalgae, mostly diatoms and blue-greens, are also important producers but their numbers are kept low by the continual mixing of the upper few centimeters by animals, which keeps most of the algae away from light. Algae in the water above are all small flagellated nannoplankton, especially greens and chrysophytes. Their total productivity is low and they are heavily grazed by zooplankton such as *Daphnia* and fairyshrimp. In turn, these herbivores are preyed upon by predaceous zooplankton (*Cyclops*, *Heterocope*) but there are no important vertebrate predators (although shorebirds do feed on zooplankton). The leaves, rhizomes, and

TABLE 1-1 Annual Production of Tundra Pond Communities

Type of community	Production $\text{g C m}^{-2} \text{ yr}^{-1}$	Method of measurement
Phytoplankton	1.1	carbon-14
Benthic algae	8.4	carbon-14
Macrophytes	16.4	biomass changes
Zooplankton	0.20	biomass changes
Macrobenthos	1.65	biomass changes
Planktonic bacteria	0.01	biomass changes
Benthic bacteria	8.6	biomass changes
Benthic bacteria	4-16	CO ₂ evolution in cores
Benthic bacteria	20	CO ₂ exchange with atmosphere
Protozoa	0.3	biomass changes, lab growth rates
Microbenthos	0.2	biomass changes, lab growth rates

roots of the grasses and sedges enter the detritus food chain as there are no grazers on the live plants. Most of the detritus is mineralized by bacteria and fungi but some is consumed by chironomid larvae, the dominant animals of the sediment. These larvae eat a few percent of the bacteria and algae per day as do the microfauna of nematodes, harpacticoid copepods, and protozoans.

Flux of Carbon

The measurement of the flux of carbon is a useful way to begin an ecosystem study, as all the important elements can be identified. The techniques we used for the carbon flux and standing stock are standard ecological measurements such as ¹⁴C for the primary productivity of the algae, biomass changes for rooted plants, CO₂ partial pressures by gas analysis to obtain water-air exchange, laboratory respiration studies of larger organisms, and acridine orange direct counts for the bacteria. The only component of the biota not measured was the fungi. A single measurement indicates that in sediments the mass of fungal hyphae is about equal to the mass of bacteria.

The rooted plants in the pond provide most of the input of organic carbon (Figure 1-5, Table 1-1). They release dissolved organic carbon into the water, release a large quantity of CO₂ via root respiration, and add dead leaves, stems, and roots to the detrital pool. Once it reaches the sediments, a leaf of *Carex* takes 4 years to decompose. One reason for this rather long life-after-death is the lack of shredders in the pond ecosystem. Another reason is the 9 months of cold storage each year (however, freezing and thawing does mechanically damage the leaves). When

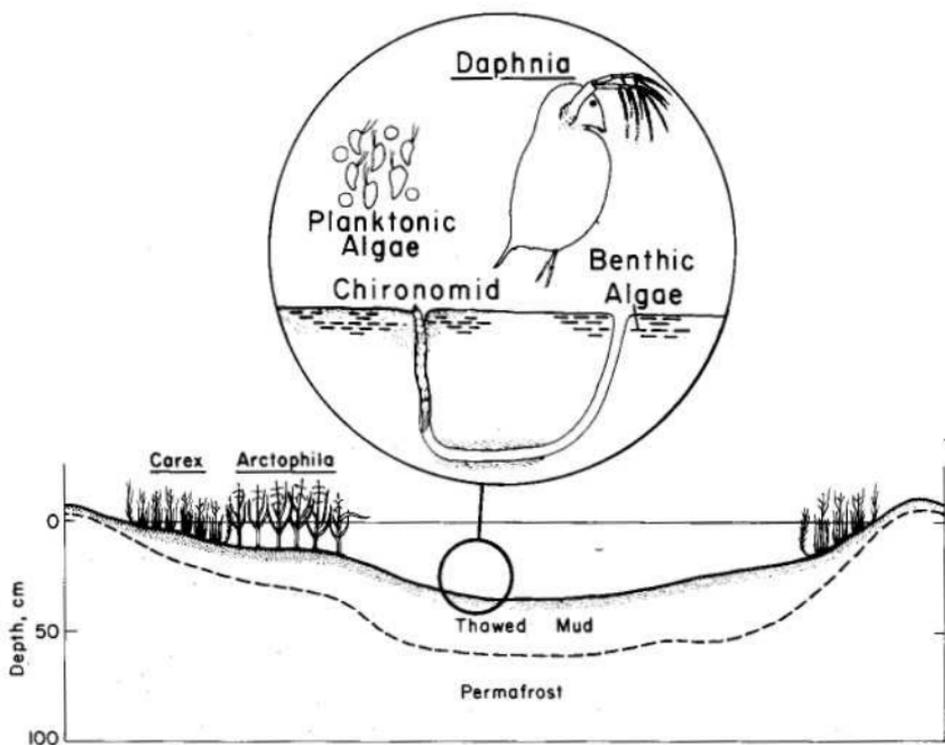


FIGURE 1-4. A cross section of a typical pond.

decomposition is calculated as percent per month of open water, then it appears that the rate is very similar to temperate rates.

Algal photosynthesis in the sediment surface is also an important input of organic carbon. Although photosynthesis occurs only in the top 2 mm, the algal cells were found throughout the upper 5 cm and deeper. The buildup of these benthic algae is prevented by the downward mixing of sediment and algal cells by the animals; in the absence of this mixing, an algal mat would develop, which would have a very high productivity.

Algal photosynthesis in the water column is extremely low, as low as any in the world. This is not caused by low numbers of cells, as millions per liter are always present. These are all very small cells, however, and their mass is also small. Thus, in temperate lakes the algal mass is 100 times greater than the bacterial mass; in the arctic ponds the algal mass was about equal to the bacterial mass (Note: The bacterial mass is the same in both systems). These planktonic algae also show a paradox found in other extremely oligotrophic systems, such as the Sargasso Sea. This is the rapid turnover of cells (the amount of carbon produced per day equals the carbon of the cells) in oligotrophic waters. Grazing by zooplankton, especially *Daphnia*, is likely responsible for much of the rapid turnover in the ponds.

The result of the distribution of primary production, low in the plankton but high in the macrophytes and benthic algae, is a shift of

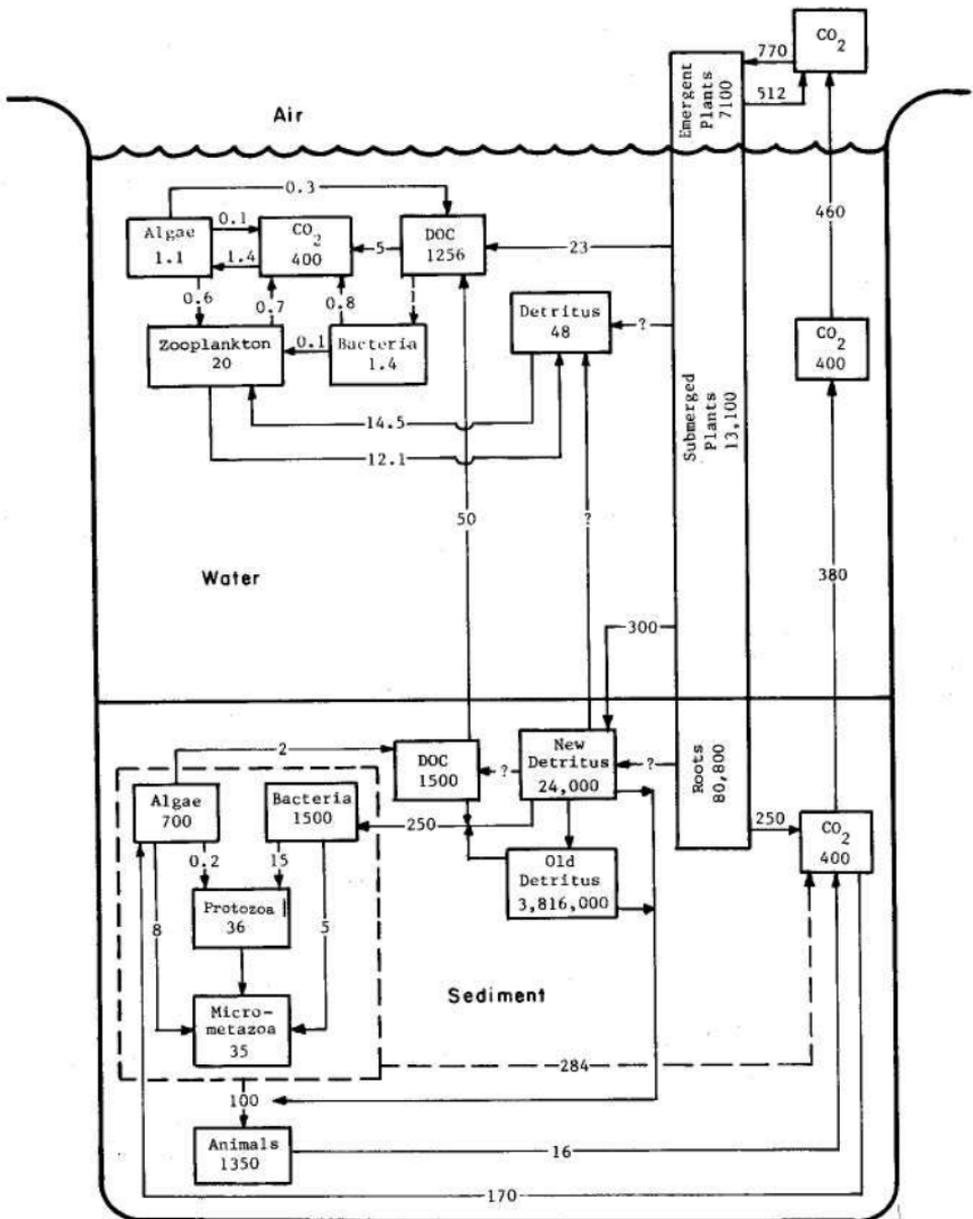


FIGURE 1-5. Carbon flux through a typical tundra pond. Measurements were made on 12 July 1971. On this date, the average depth of the water was 10 cm and the depth of the sediment was taken as 5 cm. Units of the standing crop (in boxes) are mg C m^{-2} and transfer rates (arrows) are $\text{mg C m}^{-2} \text{ day}^{-1}$.

organic carbon to the sediments where it enters the detritus food web (Figure 1-5). Here, the abundant detritus is a large reservoir of food for animals while the decomposition of the organic matter provides a steady supply of nutrients for algae. The contrast between the sediment and water

systems is dramatic; the living mass of organisms is more than 150 times greater per square meter of sediment than of water, and the activity rates (e.g., respiration) reflect the same ratio. In spite of the relatively high sediment activity, most of the detritus pool, nearly 4 kg C m^{-2} , is not being broken down. Instead, the food for the biota comes from recently formed detritus (about 0.02 kg C m^{-2} in Figure 1-5).

In the water column, there is a similar large quantity of carbon, the dissolved organic carbon (DOC), that consists of a large pool of inactive carbon and a much smaller pool of rapidly-cycling carbon. Some of this rapidly-cycling pool of DOC comes from the sediment, as the mass and activity of bacteria is quite high considering the low primary production of the planktonic algae.

The detritus, algae, and bacteria support a large standing crop of zooplankton grazers, a crop that is much larger than algae alone could support. Actually, the relationship between the zooplankton and detritus may be more complicated than this. We observed that from year to year the amount of planktonic algae and bacteria remained about the same (5 to $10 \mu\text{g C liter}^{-1}$) but the amount of detritus fluctuated from 300 to $1400 \mu\text{g C liter}^{-1}$. Zooplankton production was highest in years when the average amount of detritus was lowest and vice versa. This could be cause-and-effect but it is impossible to tell if the high detritus loads prevented the zooplankton from harvesting very much of the nutritious algae and bacteria (blocking) or if the high numbers of zooplankton removed the detritus. It is also possible that the zooplankton excreted enough phosphorus back to the water to increase the phytoplankton production.

Carbon dioxide moves rapidly from the water into the air. In fact, an amount of dissolved CO_2 equal to that in the water is replaced each day. The flux of CO_2 , appears to balance the primary production but in spite of the intensive study, we could not say whether or not annual respiration equaled photosynthesis. At best, our measurements were only within 20% of the true value and an accumulation of only 10% of the total primary production each year would easily account for the organic sediments of the pond. (Ten percent each year is 5 cm of sediment in 400 years.)

In the pond ecosystem it was obvious that grazing food chains are unimportant relative to the detritus food chain (Table 1-1). In the sediments, the detritus is either eaten directly by animals or is attacked first by microbes. Our evidence for direct utilization comes mostly from studies of the energy requirements of the chironomid larvae (the "animals" in Figure 1-5). At the rate of particle ingestion that we measured, the larvae had to be digesting mostly detritus. Previous workers postulated that the animals were obtaining enough energy by stripping the microbes from the detrital particles. We actually measured the quantity of bacterial and algal biomass that is included in the detritus and found it to be only 0.06% of the total carbon (Figure 1-5). This amount of carbon is 0.3% of the organic carbon requirement of the larvae. Although these animals may select microbe-rich particles or locations for feeding, they

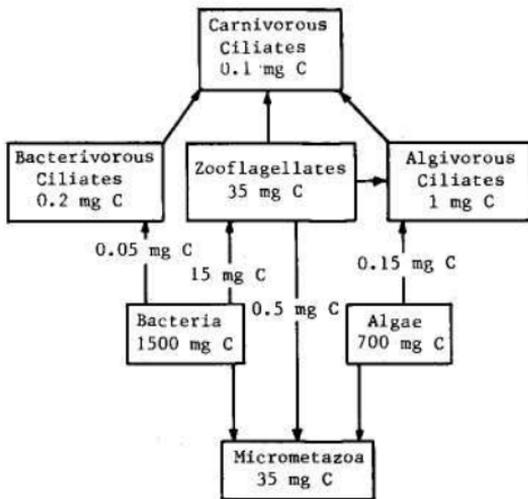


FIGURE 1-6. Carbon flow through the protozoans and micrometazoans of the sediment of a tundra pond. Units are $\text{mg C m}^{-2} \text{ day}^{-1}$ for the fluxes and mg C m^{-2} for the standing crop.

would have to be extraordinarily selective to meet their energy requirements from bacteria and algae alone.

The bacteria which break down detritus are (along with the benthic algae) the base of another food chain of protozoans and micrometazoans such as nematodes. The feeding rates and production of these animals have not previously been studied in the field. Here, these animals grazed only 1 to 2% of the bacteria and algae per day (Figure 1-6). This seems small yet represents 20% of the bacterial production and 5% of the algal production each day; thus, the small animals may control the bacteria to some degree.

The protozoans and bacteria interact in other ways as well. It has long been known that decomposition proceeds faster, and bacteria are more active, when grazing animals are present. One hypothesis has been that nutrients were rapidly released by the grazers and that this release allowed higher microbial activity. This hypothesis was tested in an experiment which investigated the rate of cycling of phosphorus-32 in small flasks containing *Carex*, bacteria, and one species of protozoa (Barsdate et al. 1974). When the protozoan was present, the bacterial biomass was lower, the bacteria were more active, and phosphorus was taken up faster by the bacteria (1.67 vs. $0.25 \text{ pg P cell}^{-1} \text{ hr}^{-1}$), than when the protozoan was not present. Yet, only a few percent of the phosphorus actually cycled through the protozoans. Thus, direct release of phosphorus by the protozoans did not affect the bacteria and the hypothesis was disproved. It is possible that the bacteria are kept in a phase of rapid growth by the grazing and that it is this rapid growth that is responsible for the faster decomposition.

Flux of Phosphorus

Phosphorus enters the ponds in rainfall ($8 \mu\text{g P liter}^{-1}$) and in overland flow. The quantities entering a pond are small and are equaled by the losses. We did measure an annual loss of 0.7 mg P m^{-2} but this amount is minuscule relative to the $25,000 \text{ mg P m}^{-2}$ found in the top 10 cm of sediments. In spite of the large amounts of phosphorus present, the concentrations of inorganic phosphorus in the waters of the pond and in the interstitial water of the sediments is always extremely low, between

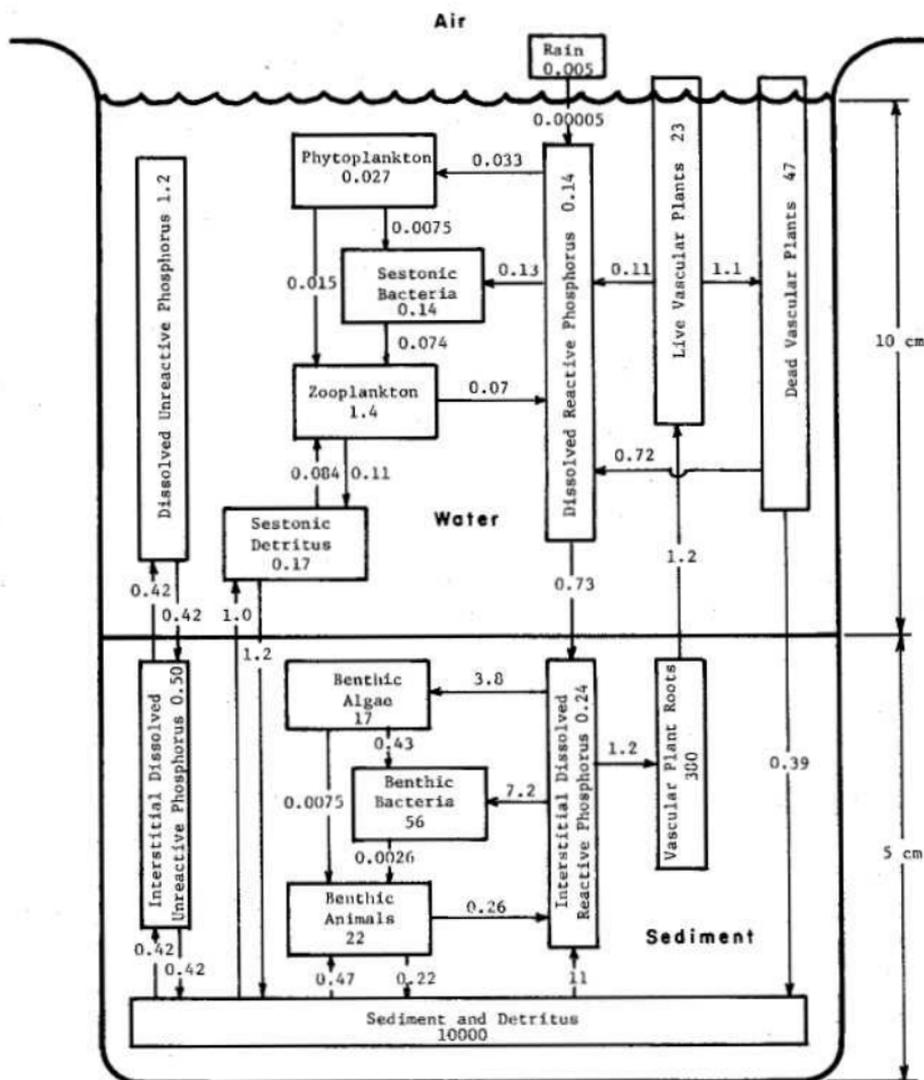


FIGURE 1-7. Phosphorus flow diagram in a tundra pond for 12 July 1971. Units are mg P m^{-2} and $\text{mg P m}^{-2} \text{ day}^{-1}$. Fluxes were measured whenever possible (Prentki 1976) or were based on the carbon flux data (Figure 1-5).

0.001 and 0.002 mg P liter⁻¹. This is the form of phosphorus that is available to algae and higher plants; their primary production can be enhanced over several weeks by adding phosphorus to a pond. Even in the fertilized ponds, however, the concentrations of inorganic phosphorus rapidly decline to 0.001 to 0.002 mg P liter⁻¹. Why are these phosphorus concentrations so low and why are there such small changes over the summer?

A part of the answer is that the dissolved reactive phosphorus (DRP) cycles very rapidly in the ponds (Figure 1-7). For example, there is 0.14 mg P m⁻² in the water on the day illustrated in the figure while the bacteria and algae take up 5.8 mg P m⁻² day⁻¹. At the same time, there is also a transport of 0.73 mg P m⁻² into the DRP pool of the interstitial water; the DRP thus turns over 50 times per day in the ponds. During the rapid turnover of the small amount of DRP in the water, the large quantities of phosphorus in the sediment turn over very slowly and actually buffer the whole system.

The other part of the answer lies in the chemical properties of the sediment. When DRP enters the pond, it quickly moves to the sediment where much of it is sorbed onto a hydrous iron complex. The concentration of DRP and the release rate of the sorbed phosphorus are controlled by a chemical equilibrium; ponds with different amounts of iron and inorganic phosphorus in the surface sediments will have different

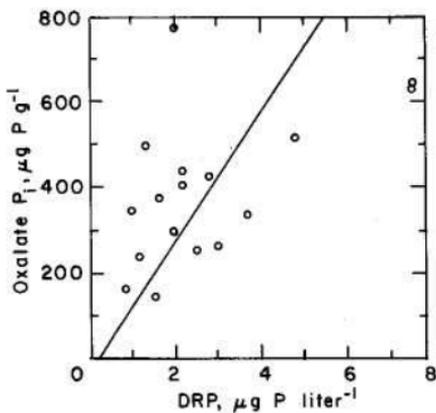


FIGURE 1-8. Oxalate extractable phosphorus in the sediments of five tundra ponds of similar origin plotted against the dissolved reactive phosphate (DRP) of the overlying water column.

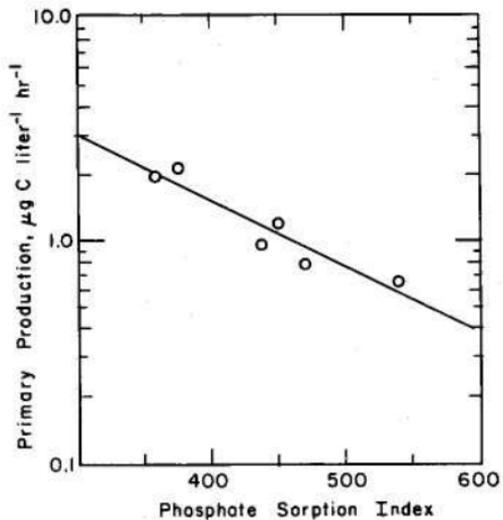


FIGURE 1-9. Algal photosynthesis in the water column of a series of tundra ponds plotted against the phosphate sorption index of the underlying sediments (9 August 1973). (Data are from Prentki 1976.)

amounts of DRP in the water. In a series of intensively-studied ponds (Figure 1-8), the concentration of DRP in the water column could even be predicted from a single measurement of the sediment phosphorus that could be extracted with oxalate. In the same ponds, the oxalate-extractable phosphorus appeared to be directly related to the photosynthesis rate of planktonic algae (Figure 1-9). Thus, we conclude

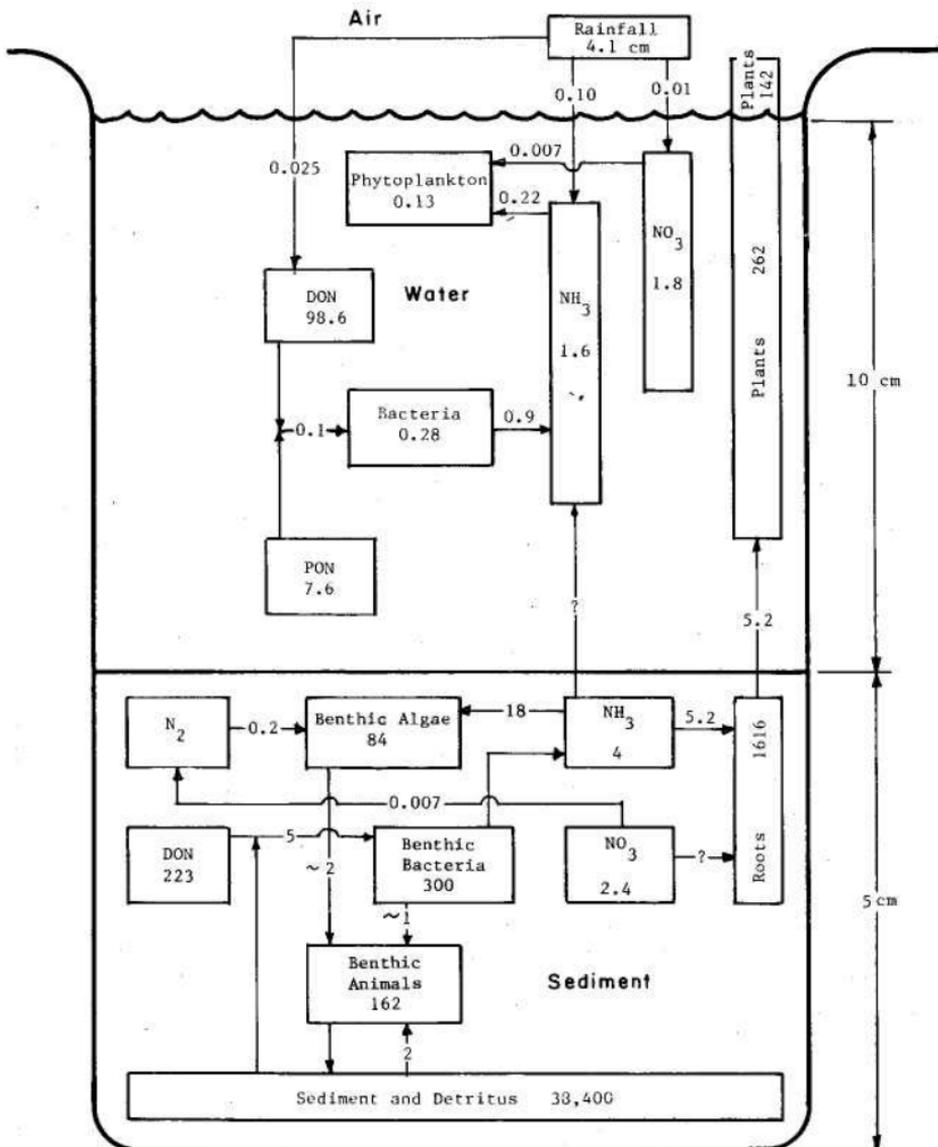


FIGURE 1-10. Nitrogen standing crop and fluxes in the water and sediments of a tundra pond on 12 July 1971. Units are mg N m^{-2} for the concentrations and $\text{mg N m}^{-2} \text{ day}^{-1}$ for the fluxes. The amounts and flux rates were measured whenever possible; some are calculated from the data in Figure 1-5.

that chemical reactions in the surface sediments, especially those reactions involving iron, set the concentration of DRP in the water and in this way control the productivity of the ponds.

Flux of Nitrogen

The main inputs of nitrogen to the pond came from the rain water ($11.5 \text{ mg inorganic N m}^{-2} \text{ yr}^{-1}$) and from nitrogen fixation ($28 \text{ mg N m}^{-2} \text{ yr}^{-1}$). The ponds appear to accumulate some nitrogen each year but the total, somewhat less than $80 \text{ mg N m}^{-2} \text{ yr}^{-1}$, is very small compared to the $38,400 \text{ mg N m}^{-2}$ stored in the top 5 cm of sediment. In the water column, ammonia was more abundant than nitrate, 20 to $40 \mu\text{g NH}_3 \text{ N liter}^{-1}$ vs. 2 to $13 \mu\text{g NO}_3\text{-N liter}^{-1}$. Uptake in the plankton was slow (Figure 1-10) so that turnover times ranged from 30 to 100 days for the inorganic nitrogen. Measurements with $^{15}\text{NH}_3$ indicated that the rate of supply of ammonia from within the water column was high enough to replace the NH_3 in 6 to 48 hr. As expected, we found no evidence of nitrogen limitation upon the primary production of the algae in the pond. When the uptake of nitrogen was used to calculate primary productivity, by taking the ratio of C uptake to N uptake as 100 to 12, the results exactly matched the ^{14}C primary productivity measurements.

In the sediments, the interstitial water contained high amounts of ammonia except where plant roots were present. For example, there were 0.7 to $2.7 \text{ mg NH}_3\text{-N liter}^{-1}$ in the sediments in the plant-free center of the pond but only 0.01 to $0.08 \text{ mg NH}_3\text{-N liter}^{-1}$ inside a *Carex* bed at the pond edge. Based upon production calculations, the *Carex* may turn over all the ammonia each day. Despite this relatively high rate of removal, the *Carex* appears not to be limited by nitrogen concentrations.

The only evidence for a limitation by nitrogen was that nitrogen fixation by sediment algae began when the ponds were continually fertilized with phosphorus. It is likely that the algae were phosphorus-limited; when excess amounts of P were added, the uptake rate of both nutrients increased and eventually the N became limiting. At this point, the blue-green algae gained a competitive advantage by fixing nitrogen.

Effects of the Arctic Environment

The annual primary production of the ponds is low, but this is largely a result of the short ice-free season. When compared to the daily production of other ecosystems the ponds are reasonably productive. Thus, food supply is adequate in spite of the low temperatures. There is, of

course, a general slow-down of metabolism because of the cold temperatures and this will affect all ecosystem processes from decomposition to predation. Yet, low temperatures (2 to 8°C) are also found in all temperate ponds; in fact, a majority of months will be cold-water months. The unique properties of arctic ponds are: (1) they never warm, (2) they are frozen for 8 1/2 or 9 months of the year, (3) there is continuous light from late April until mid-August (although the intensity does vary greatly over 24 hours).

The smallest life forms of the ponds do not seem to have any special adaptations to the Arctic. Bacteria, for example, are just as abundant in the Arctic as in the water and sediments of any temperate pond; their activity is low but it is about the same as for a temperate pond in the spring when the water is cold. Phytoplankton species are almost identical to the species found in temperate ponds in the spring. There is not even a reduction of species number as 105 species were found in the ponds. These same species, by the way, are found throughout the world and even reach the Antarctic. The physiology of the algae was also normal except that at low temperatures photosynthesis was strongly inhibited by high light levels. This is not adaptive; it may be a result of the low temperatures slowing the rate of repair of chlorophyll. It has been suggested that photosynthesis is less affected than is respiration by low temperatures and for this reason, biomass production would be very efficient in the Arctic. We were not able to measure algal respiration or biomass changes very well so we cannot say if this is true.

Protozoans were also found to have the same species and total abundance as temperate pond communities. Some forms that do not have resistant resting stages might be absent, for so little is known of protozoan life history that this could not be detected. Thus, it was surprising to find *Paramecium* in the pond, for this species has never been known to form resistant cysts.

Metazoans are affected in a number of ways by the arctic environment. The obvious way is by exclusion of some forms because of physiological limitations. Amphibia and sponges are absent while Hemiptera, Odonata and Megaloptera are rare. Ephemeroptera, Trichoptera, and Coleoptera are represented by only a few families or genera.

Another way that organisms are affected is by exclusion from certain habitats. For example, fish are found in deep lakes but not in ponds or lakes shallower than 2 m; they are excluded by the 2-m-thick ice cover in arctic fresh water. This absence of fish allows large zooplankton to exist such as the large *Daphnia middendorffiana* which reaches 3 mm in length and the fairyshrimp which can be 20 mm long. These large animals, in turn, affect the species composition of the algae. We first noticed this effect when all the zooplankton were killed in a pond by the addition of oil. The same shift in the dominant algae, a replacement of the *Rhodomonas* by *Uroglena*, also occurred when we removed the zooplankton by net.

Metazoans which are found in arctic ponds do not appear to have any particular adaptations to arctic conditions because the same forms are often found in temperate ponds as well. Rather, many of the adaptations or abilities they already possess that permit them to survive freezing or other stresses permit survival in the Arctic as well. For example, in temperate lakes, cladoceran zooplankton overwinter as diapausing eggs or embryos and the cyclopoid copepods overwinter as diapausing subadults (copepodids); the same species has a copepodid diapause stage in temperate lakes where it moves into the sediment for several months. They utilize the same methods for longer periods in the Arctic.

Many of the arctic forms of midges have adults which have reduced wings. After hatching, the adults move about on the water surface rather than make the typical laying swarms. This behavior keeps them from being blown away by the constant winds. The life histories of many higher animals are affected by the low temperatures. Zooplankton grow so slowly that there is time for but a single generation per year in most species. This puts a very specific upper limit on annual production of zooplankton because the number surviving the winter may be the single most important factor determining annual production. Chironomids, which live in the top several centimeters of sediment where the annual average temperature in the summertime is only about 3°C, are most affected by the environment. They grow very slowly; one species of *Chironomus* takes 7 years to pass through the four instar stages. In spite of these difficult conditions for growth, the number of midge species found in the ponds, around 35, is not very different from the number in a temperate pond. Many of these species have been found only in the Arctic or only in the Barrow area.

The sedge, *Carex aquatilis*, that grows in the pond is well adapted to a variety of habitats from dry meadows to the shallow water. Perhaps the most obvious adaptation to the arctic environment is its ability to begin growth when the air temperature is still close to 0°C. It also takes up phosphorus through the roots at these very low temperatures.

Modeling

A part of the original plan of the U.S. IBP was to construct predictive mathematical models of various ecosystems. This pond study offered several advantages for this approach; the ecosystem is somewhat simplified and physical factors (circulation and stratification) could be ignored; the active life of the pond organisms is completed in only 100 days each year; all the investigators worked on a common pond; controlled experiments could be carried out in replicate ponds and in the nearby laboratory. Our conclusion is that modeling is a very helpful approach but that the construction of a large, complicated predictive model is not possible with the existing gaps in our knowledge of aquatic ecology.

Even in the pond ecosystem, the number of interactions is too great and most cannot be included in any model. We decided what to include on the basis of the carbon flow results (Figure 1-5). The modeling helped by forcing all the workers to sample just one pond and by forcing us to work on some processes which were virtually unknown (e.g., the detritus food web). It quickly became obvious that we simply did not understand many of the controls of the pond ecosystem. Despite this, the deterministic model which resulted did an excellent job of mimicking or simulating the annual cycles of carbon flow through the plankton and benthic systems. For example, the submodel of benthic algal photosynthesis (Figure 1-11) was developed with physiological data from 1973 but the simulation fits the 1971 and 1972 field data very well. Unfortunately, there were several assumptions that had to be included, in spite of our attempts to measure every parameter, and the results of the calculations were very sensitive to

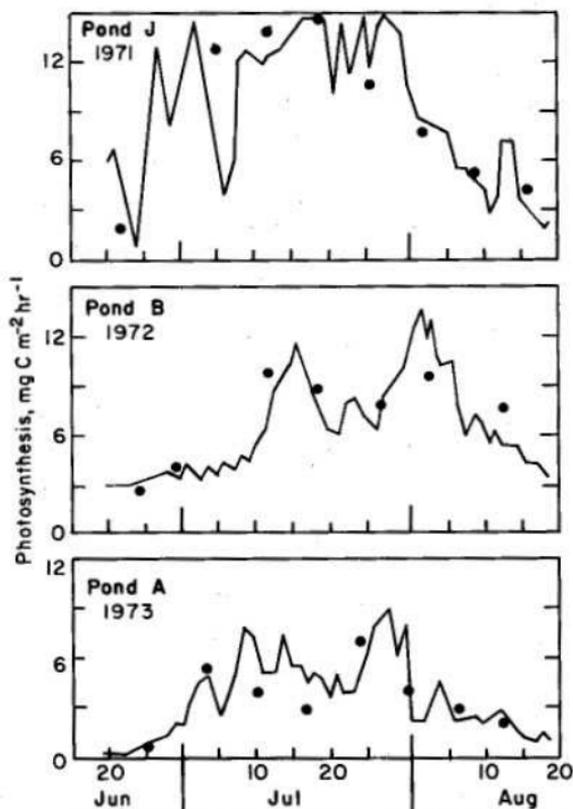


FIGURE 1-11. Model simulation (solid line) and measured estimates (circles) of the photosynthesis of epipelagic algae ($\text{mg C m}^{-2} \text{hr}^{-1}$). (Redrawn from Stanley 1974.)

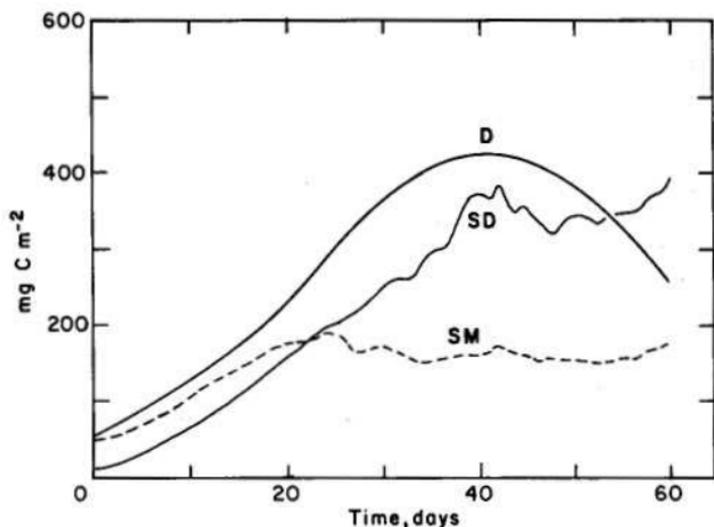


FIGURE 1-12. Model simulation of epipellic algal biomass. The lines represent the deterministic model (D), the mean of nine runs of the stochastic version of the same model (SM), and the standard deviation of the stochastic mean (SD). (After Tiwari et al. 1978.)

some of these. Therefore, the result shown in Figure 1-11 can be easily changed in an extremely drastic way by changing the algal respiration coefficient from 0.25 to 0.30. Even if we did have a good way of measuring algal respiration, in the field it would not distinguish between these two values. In a similar fashion, if the rate of maximum photosynthesis is changed from 0.05 to either 0.04 or 0.06, the algal biomass rapidly approaches zero. Yet we know that this maximum photosynthesis rate does change over the year in our pond.

The next step was to see what would happen to the model if all the coefficients and parameters were varied slightly. This stochastic model is probably more realistic, as variability is a property of every biological measurement and interaction. Unfortunately, we did not have the data on the mean and standard deviation of every measurement that would be necessary to implement this approach. However, when we incorporated reasonable variability into the benthic model, the mean values (Figure 1-12) were quite different from the deterministic model values.

In only a few cases could the model be used to test hypotheses. For example, we did examine the hypothesis that the mixing of the sediments was an important control of the growth of benthic algae. This mixing could not be measured directly in the field or laboratory but the modeling exercise helped to put reasonable limits on this rate.

Our conclusions from the modeling effort were that we knew too much about the pond ecosystem to be satisfied with fine-tuning a model

which contained several untested assumptions. It was obvious that the interactions which controlled the results of the model were not necessarily the same ones acting to control the real ecosystem. In spite of our failure to construct a predictive model, the modeling exercise was very worthwhile and should be a part of every large-scale ecosystem project.