# The Ecology of Tundra Ponds of the Arctic Coastal Plain: A Community Profile

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# THE ECOLOGY OF TUNDRA PONDS OF THE ARCTIC COASTAL PLAIN: A COMMUNITY PROFILE

by

John E. Hobbie
The Ecosystems Center
Marine Biological Laboratory
Woods Hole, MA   02543

Project Officer

Edward Pendleton
National Coastal Ecosystems Team
U.S. Fish and Wildlife Service
1010 Gause Boulevard
Slidell, LA   70458

Performed for
National Coastal Ecosystems Team
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# PREFACE

The Arctic Coastal Plain is a flat or gently rolling area of tundra which covers the entire coastal region of northern Alaska. The grasses, sedges, and waterbodies are covered with ice, snow, and silence for 9 months of the year, but lakes, ponds, marshes, and birds abound for the brief summer. This entire region is almost pristine today, but only because the mountains of the Brooks Range isolated northern Alaska from the roads and development of the rest of the state. Before the recent oil boom, only a few Eskimo villages and radar sites were present along the coast and the population was less than 3,000 people in an area the size of Lake Superior.

Changes have come with the development of oil fields at Prudhoe Bay. An all-weather highway, completed in 1975, carries tractor-trailers to the Arctic Ocean and may soon be opened to the public. While only two oil spills of consequence have occurred since the trans-Alaska pipeline began operation, many hectares of the coastal plain have been covered by roads, airfields, gravel drilling pads, and pipelines. The roads have changed drainage patterns in many places and created and destroyed wetlands. These changes will continue as new oil fields are sought and developed on the coastal plain and under the Arctic Ocean.

Ecological scientists have long been attracted to the Arctic both because of the excitement of exploration where wildlife is abundant and because of the opportunity to study environments unaffected by man. Investigators have also used arctic habitats to test hypotheses about general ecological principles and to analyze the effects of certain environ-

mental factors that may vary together in temperate regions. As a result of the scientific interest and of the presence of oil development, there is a great deal known about the wetlands of the Arctic Coastal Plain.

This community profile synthesizes much of the information on the ecology of these coastal plain wetlands. It will provide background and information needed by government planners and environmental scientists whose decisions will influence the future of this vast region. In addition, it will provide students, scientists, and laymen a better understanding of how arctic ponds and wetlands function.

The profile emphasizes the environmental conditions and ecological interactions that produce these particular wetland communities. The communities are described here, but we now know enough about their ecology that the controls of processes and species can also be discussed. It is usually the disruption of these controls, such as changing the water movement in a salt marsh or the nutrient cycle of a lake, that causes unplanned or unexpected changes.

The text includes descriptions of the communities as well as of ecological processes. An introductory description of the Arctic Coastal Plain is followed by a discussion of the types of wetland habitat found there. Next, the physical and chemical environment is described with special emphasis on the controlling influence of the permafrost and of the phosphorus cycle. The following chapter gives details of the plants and animals and of their seasonal abundance. After this, the food chains, the cycling of carbon, energy flow, and the controls

acting on these wetland ecosystems are discussed. Finally, human effects on ponds, wetlands, and their processes are described.

Most of the detailed scientific studies of arctic wetlands have dealt with small ponds in the coastal plain and, of necessity, so does this community profile. Although rivers and large shallow lakes are also important parts of the wetlands of the Arctic Coastal Plain, they are not discussed in this profile.

This report is one in a series of community profiles on important coastal ecological communities of the United States. Community profiles are designed to provide comprehensive reviews and syntheses of current research results and scientific literature and to assist Fish and Wildlife Service personnel and others in making sound and informed management decisions on issues affecting our nation's natural resources.

Any questions or comments about or requests for this publication should be directed to:

Information Transfer Specialist
National Coastal Ecosystems Team
U.S. Fish and Wildlife Service
NASA--Slidell Computer Complex
1010 Gause Boulevard
Slidell, LA 70458

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## Metric to U.S. Customary

| Multiply | By | To Obtain |
|---|---|---|
| millimeters (mm) | 0.03937 | inches |
| centimeters (cm) | 0.3937 | inches |
| meters (m) | 3.281 | feet |
| kilometers (km) | 0.6214 | miles |
| square meters (m$^2$) | 10.76 | square feet |
| square kilometers (km$^2$) | 0.3861 | square miles |
| hectares (ha) | 2.471 | acres |
| liters (1) | 0.2642 | gallons |
| cubic meters (m$^3$) | 35.31 | cubic feet |
| cubic meters | 0.0008110 | acre-feet |
| milligrams (mg) | 0.00003527 | ounces |
| grams (g) | 0.03527 | ounces |
| kilograms (kg) | 2.205 | pounds |
| metric tons (t) | 2205.0 | pounds |
| metric tons | 1.102 | short tons |
| kilocalories (kcal) | 3.968 | British thermal units |
| Celsius degrees | 1.8(C°) + 32 | Fahrenheit degrees |

## U.S. Customary to Metric

| | By | To Obtain |
|---|---|---|
| inches | 25.40 | millimeters |
| inches | 2.54 | centimeters |
| feet (ft) | 0.3048 | meters |
| fathoms | 1.829 | meters |
| miles (mi) | 1.609 | kilometers |
| nautical miles (nmi) | 1.852 | kilometers |
| square feet (ft$^2$) | 0.0929 | square meters |
| acres | 0.4047 | hectares |
| square miles (mi$^2$) | 2.590 | square kilometers |
| gallons (gal) | 3.785 | liters |
| cubic feet (ft$^3$) | 0.02831 | cubic meters |
| acre-feet | 1233.0 | cubic meters |
| ounces (oz) | 28.35 | grams |
| pounds (lb) | 0.4536 | kilograms |
| short tons (ton) | 0.9072 | metric tons |
| British thermal units (Btu) | 0.2520 | kilocalories |
| Fahrenheit degrees | 0.5556(F° - 32) | Celsius degrees |

# CHAPTER 1.

# INTRODUCTION

## 1.1 DEFINITION AND DESCRIPTION OF THE ARCTIC COASTAL PLAIN

The Arctic Coastal Plain of Alaska is a marshy grassland extending for 900 km along the Arctic Ocean from Canada to the Chukchi Sea (Figure 1). As this figure shows, northern Alaska is physiographically divided into the mountains of the Brooks Range, the foothills, and the coastal plain. The plain is the flat to rolling area rising gently from the edge of the ocean to the 75-m contour where the foothills abruptly begin. In places, the Arctic Coastal Plain is up to 175 km wide from the ocean south to the 75-m contour; its total area, 70,900 km$^2$, is about the same as the state of South Carolina. Small streams are rare but rivers do flow across the plain from the mountains north to the sea. Innumerable small ponds are scattered over the plain along with some larger lakes (Figure 2). These ponds and lakes are the breeding grounds of ducks, geese, swans, and shorebirds. About 90% of the coastal plain is suitable habitat
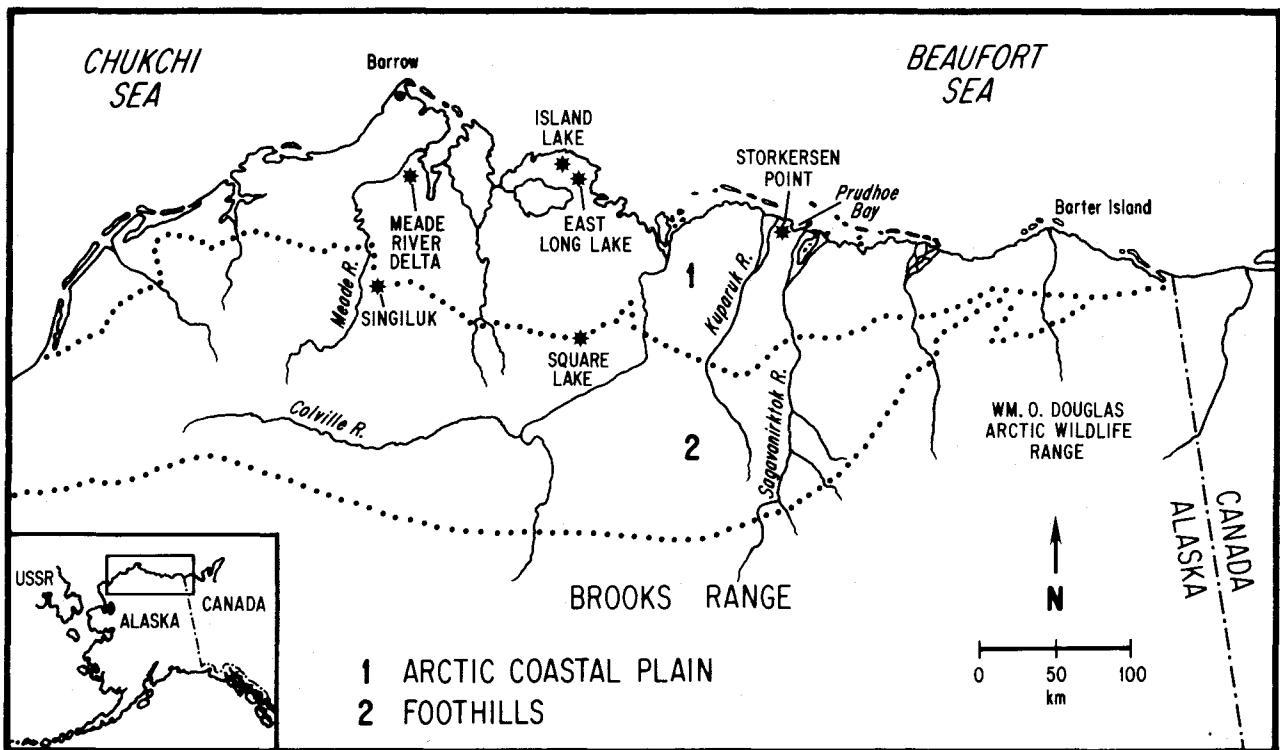


Figure 1. Map of the Arctic Coastal Plain and location in Alaska. The asterisks are locations studied by Derksen et al. (1981). The National Petroleum Reserve - A covers the area west and south of the Colville River.

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for waterfowl. Moose are occasionally found in the willow thickets of the larger rivers and herds of caribou often reach the coast. The most abundant mammal, however, is the brown lemming (Lemmus trimucronatus), whose dramatic population peaks occur about every 3 to 5 years (Batzli et al. 1980).

Despite the desert-like precipitation, 10-30 cm per year, the ground is wet or moist throughout the short summer, which lasts from June until mid-September. Low temperatures and frozen ground limit evaporation and prevent the water from sinking into the soil. Under these conditions, grasses and sedges grow well but decomposition does not keep pace and the whole plain is underlain by peaty, organic-rich soils.



Figure 2. Aerial view of the Arctic Coastal Plain (photo provided by J. Brown). The center of the large lakes (each several kilometers long) is covered by ice. Several former lake basins are visible but ponds are too small to be seen.

For 8 months of the year, the Arctic Coastal Plain is frozen and covered by about 40 cm of snow. In early June the snow begins to melt and soon water covers much of the ground. By mid-June the ice has melted in the shallow ponds but may linger until mid-July in the large lakes. Birds arrive in mid-May to early June as soon as there is any open water, and congregate in flocks. The flocks soon disperse as ducks, geese, and swans move to the small ponds for nesting. In June, the coastal plain is a flat brown landscape, but later in the summer the new shoots of grasses and sedges push above last year's dead stalks and the tundra becomes green. Along the slightly higher riverbanks, flowering plants are abundant and some willows may even be found, but these usually lie flat on the ground. By mid-August many ponds have dried up and soon the tundra plants begin to turn brown. Freezing of ponds begins in early September and the snow begins to accumulate by mid-September.

The continuous sunlight during May, June, and July is one unique feature of the Arctic. Another is the presence of permafrost, or permanently frozen ground, underlying the entire coastal plain. The permafrost is present because the annual average temperature (around -12°C) is below freezing. During the summer, when air temperature reaches 10°-15°C, the upper 40 cm or so of soil thaws. Below this thawed zone, called the active layer, the permafrost extends for hundreds of meters (400 m thick at Barrow, Brewer 1958).

1.2 CLASSIFICATION AND DISTRIBUTION OF TUNDRA PONDS AND WETLANDS ON THE ARCTIC COASTAL PLAIN

The classification scheme of Bergman et al. (1977) is used here (Table 1), although it does not include rivers and most types of streams. Also, it does not include areas with saturated soil during the growing season (e.g., the scheme of Cowardin et al. 1979); most of the Arctic Coastal Plain may well have saturated soils because of the poor drainage caused by permafrost. In the Bergman et al. (1977) scheme, ponds are smaller than 20

ha in surface area and lakes are larger. Another important criterion is the presence or absence of the water sedge (Carex aquatilis) and pendant grass (Arctophila fulva), emergent plants that often dominate these wetlands. The eight classes of wetlands are as follows:

CLASS I: Flooded Tundra. Very shallow ponds formed when melt water from the spring thaw or, rarely, from rain, spreads over shallow, vegetated depressions. The depth of the water is 10 cm or less; these ponds often dry up during July. The basins are poorly defined because they are entirely covered with Carex.

CLASS II: Shallow--Carex. Shallow, well-defined ponds containing both a fringe of C. aquatilis and a central open-water zone. The maximum depth ranges from 10 to 30 cm.

CLASS III: Shallow--Arctophila. Ponds containing A. fulva in the central zone and A. fulva or C. aquatilis in the shoreward zone. The shores deepen more rapidly than in Class II and maximum depths are 20-50 cm. Sometimes these ponds are formed in beaded streams.

CLASS IV: Deep--Arctophila. Ponds or lakes with open central zones and A. fulva near the shore. The maximum depths exceed 40 cm. These wetlands are often formed in drained lake basins.

CLASS V: Deep--Open. Large, deep lakes with abrupt shores and a deep central zone. A. fulva is present over less than 5% of the lake and may be completely absent. Maximum depth of this class of lakes was reported as 1.1 m in Bergman et al. (1977) but is actually 2.0 m. Fish are present in lakes deeper than about 1.7 m, the thickness of the ice cover.

CLASS VI: Basin--Complex. Large, partially drained basins covered with water in the spring. By midsummer, the water has partially receded leaving Carex-covered depressions and

Table 1. Classification of wetlands (modified from Bergman et al. 1977).

| Wetland designation | Dominant emergents | | Common size |
| | Shore zone | Central zone | |
| --- | --- | --- | --- |
| Flooded tundra (Class I) | Carex aquatilis or Eriophorum angustifolium | C. aquatilis or E. angustifolium | Pond |
| Shallow-Carex (Class II) | C. aquatilis | Semiopen to open | Pond |
| Shallow-Arctophila (Class III) | C. aquatilis or Arctophila fulva | A. fulva | Pond |
| Deep-Arctophila (Class IV) | A. fulva | Open | Pond or lake |
| Deep-open (Class V) | Open | Open | Lake |
| Basin-complex | Basin interspersed with C. aquatilis, A. fulva, and open water | Basin interspersed with C. aquatilis, A. fulva, and open water | Lake |
| Beaded streams (Class VII) | C. aquatilis, A. fulva, or Open | Open or A. fulva | Pond= Bead |
| Coastal wetlands | C. subspathacea, Open, or Puccinellia phryganodes | Open | Pond or lagoon |

deeper ponds with Arctophila along the edges.

CLASS VII: Beaded Streams. Small, intermittent streams containing pools formed by melting of ice within the permafrost. The pools can be deep and resemble Classes III or IV.

CLASS VIII: Coastal Wetlands. Brackish habitats along the ocean. These include lagoons confluent with the sea and ponds periodically inundated by the tide. The vegetation along the margins is characteristically Carex subspathacea and Puccinellia phryganodes (creeping alkaligrass).

The classification scheme used in this profile is quite specific for the Arctic Coastal Plain and was, in fact, developed there for studies of waterfowl (Bergman et al. 1977). However, a more general scheme does exist (see Table 2 for comparison) and applies to the entire United States (Cowardin et al. 1979). The general scheme is hierarchical with "riverine", "lacustrine" (greater than 8 ha of water surface), "palustrine" (marshes, bogs, prairies, less than 8 ha, less than 2 m deep), and "estuarine" (salinity greater than 0.5 part per thousand, more land than marine influence) as the system descriptors that apply here. Class descriptors include "emergent wetland" (erect hydrophytes) and "unconsolidated bottom". Next, the subclass descriptors include "persistent" and "nonpersistent", depending on whether or not the plants remain standing until the beginning of the

Table 2. Comparison of nomenclature used in Arctic Coastal Plain and national wetland classification systems. When Bergman et al. (1977) wetlands contain more than one category of the Cowardin et al. (1979) hierarchial system, components are shown in parentheses (from Derksen et al. 1981).

| Class (Bergman et al. 1977) | Cowardin et al. (1979) | | | |
| | System | Subsystem | Class | Subclass |
| --- | --- | --- | --- | --- |
| Flooded tundra (Class I) | Palustrine | None | Emergent wetland | Persistent |
| Shallow-Carex (Class II) | Palustrine | None | Emergent wetland (Unconsolidated bottom) | Persistent (sand, organic) |
| Shallow-Arctophila (Class III) | Palustrine | None | Emergent wetland | Nonpersistent |
| Deep-Arctophila (Class IV) | Palustrine (Lacustrine) | None (Limnetic littoral) | Emergent wetland (Unconsolidated bottom) | Nonpersistent (sand, organic) |
| Deep-open (Class V) | Lacustrine | Limnetic | Unconsolidated bottom | Organic (sand) |
| Basin-complex (Class VI) | --a | -- | -- | -- |
| Beaded stream (Class VII) | Riverine | Lower perennial | Emergent wetland | Nonpersistent |
| Coastal wetland (Class VIII) | Estuarine | Intertidal | Emergent wetland | Persistent |

a Class VI basins may contain the other seven wetland types of the Bergman et al. (1977) classification system. There is no equivalent unit in the Cowardin et al. (1979) classification system.

next growing season. Finally, a modifier is added to describe elements like the water regime and water chemistry. For the Arctic Coastal Plain, the modifiers "seasonally","semipermanently", "permanently", or "irregularly" describe flooding.

The relative abundance of the different types of wetlands has only been determined in a few areas of the Arctic Coastal Plain. Sellman et al. (1975) surveyed the abundance of large lakes from LANDSAT photos while Derksen et al. (1981) reported all classes at six sites (Table 3; see Figure 1 for locations). The wetlands made up 31% to 86% of the surface area and large lakes dominated the northern and coastal sections of the Arctic Coastal Plain. In the eastern part of the Coastal Plain, Walker et al. (1982) estimated that wetlands (lakes, ponds, wet sedge tundra) made up 20%-36% of the total area (6,640 km$^2$) surveyed.

1.3  RESEARCH ON ARCTIC ALASKA WETLANDS

Expeditions have traversed the Arctic Coastal Plain since the 1820's when Sir John Franklin and his men rowed from the MacKenzie River in Canada west to Barrow and named major rivers, lagoons, and islands. Scientific expeditions in the early 1900's collected plants and aquatic animals in this area, but travel was extremely difficult and intensive studies did not begin until after World War II. In 1947, the Naval Arctic Research Laboratory was opened at Barrow and served as a center for physiological, ecological, and geophysical research until its closing in 1980.

The wetlands near Barrow consist of marshy grasslands; small, shallow ponds; and large, shallow lakes. The origin (Carson and Hussey 1960), chemistry (Howard and Prescott 1973), and algal produc-

Table 3. Percentage composition of wetlands at six Arctic Coastal Plain sites[*] (modified from Derksen et al. 1981).

| | East Long Lake | Island Lake | Meade River | Square Lake | Singiluk | Storkersen Point |
|---|---|---|---|---|---|---|
| I Flooded tundra | 48.1 | 63.3 | 51.3 | 43.0 | 46.6 | 51.2 |
| II Shallow -- Carex | 16.2 | 14.5 | 15.7 | 7.1 | 2.1 | 32.4 |
| III Shallow -- Arctophila | 6.1 | 7.9 | 1.4 | 1.4 | 0.5 | 4.5 |
| IV Deep -- Arctophila | 4.7 | 0.8 | 1.7 | 48.4 | 45.5 | 2.9 |
| V Deep -- open | 24.1 | 13.4 | 29.8 | 0.0 | 2.1 | 6.6 |
| VII Beaded stream | 0.8 | 0.1 | 0.1 | 0.1 | 3.2 | 2.4 |
| Wetland surface area (ha) | 790.5 | 1,334.2 | 756.9 | 839.5 | 489.5 | 650.3 |
| Percent of study site in wetlands | 50.8 | 85.8 | 48.7 | 54.0 | 31.5 | 41.8 |

[*]Each study site was 15.54 km$^2$ (1,554 ha).

tivity (Kalff 1967) of the lakes and ponds were well studied in the 1960's and several ponds were exhaustively studied from 1971 to 1973 when Barrow was the site of a multidisciplinary ecological study (the International Biological Programme, IBP).

These IBP studies are summarized in large books on aquatic (Hobbie 1980a) and terrestial (Brown et al. 1980a) ecosystems.

The need to understand the effects of oilfield development on the wetland biota has led to several recent studies. Birds were studied near Prudhoe Bay by Bergman et al. (1977) and at six sites on the Arctic Coastal Plain by Derksen et al. (1981). The sites are identified by asterisks in Figure 1. Effects of devel-

opment on plants were studied at Prudhoe Bay by Walker et al. (1978, 1980).

In comparison with the ponds and lakes, little is known of the limnology of rivers and streams of the coastal plain. Chemistry of the Colville and Sagavanirktok Rivers has been investigated (Kinney et al. 1972, Carlson et al. 1974). The zooplankton (Reed 1962), fish and insects (Craig and McCart 1975), and discharge (Arnborg et al. 1966) of other rivers and streams have also been studied.

To put the Alaska studies into the perspective of arctic limnology, the reader should consult reviews by Livingstone (1963), Kalff (1970), and Hobbie (1973, 1984).

# CHAPTER 2.
## PHYSICAL AND CHEMICAL CONDITIONS

The wetlands of the Arctic Coastal Plain exist because the climate is cold enough to maintain continuous permafrost and wet enough to keep basins filled. A colder and drier climate would likely result in dry deserts with scattered vegetation and low productivity similar to those of Canada's Arctic Archipelago. A warmer climate would not allow permafrost to exist; the result would be better drainage and fewer wetlands.

## 2.1 CLIMATE

The only long-term weather records for the Arctic Coastal Plain come from Barrow and Barter Island, both coastal stations and both with very similar temperatures (Table 4). Prudhoe Bay, also a coastal station, has a similar annual mean temperature but is warmer in the summer and colder in the winter than the other two stations. At this station, the summer temperatures are above freezing but the air is kept cool by coastal cloudiness and by cool winds from the Arctic Ocean. Early in the summer the ocean is still covered with ice, but by August there are open-water areas which may extend 30-100 km from the coast. Even so, the ocean temperature is only about 3°C.

During the summer, coastal fogs occur about one day in three but these dissipate inland and the air temperatures increase with distance from the coast. For example, the July average air temperature at

Table 4. Mean monthly and annual temperatures (°C) for Barrow, Prudhoe Bay, and Barter Island (U.S. Dept. Commerce, from Brown et al. 1975).

| | 1970-1973 Mean | | | (1941-1970) | 30-Year normals |
| Month | Barrow | Prudhoe | Barter Island | Barrow | Barter Island |
|------|------|------|------|------|------|
| Jan | -26.3 | -29.2 | -27.1 | -25.9 | -26.2 |
| Feb | -28.2 | -31.8 | -29.4 | -28.1 | -28.6 |
| Mar | -28.5 | -31.0 | -29.2 | -26.2 | -25.9 |
| Apr | -19.8 | -20.2 | -19.6 | -18.3 | -17.7 |
| May | -7.6 | -6.7 | -6.5 | -7.2 | -6.1 |
| June | 0.8 | 2.6 | 1.4 | 0.6 | 1.2 |
| July | 4.6 | 6.4 | 4.7 | 3.7 | 4.4 |
| Aug | 2.9 | 4.8 | 4.1 | 3.1 | 3.8 |
| Sept | -0.8 | -0.8 | -0.7 | -0.9 | -0.2 |
| Oct | -10.1 | -12.5 | -10.7 | -9.3 | -8.7 |
| Nov | -17.2 | -19.0 | -17.3 | -18.1 | -17.7 |
| Dec | -21.8 | -25.3 | -23.1 | -24.6 | -24.7 |
| Annual | -12.7 | -13.6 | -12.8 | -12.6 | -12.2 |

an inland site was 5.9°C warmer than 100 km to the north at Prudhoe Bay; a similiar increase was measured south of Barrow (Brown et al. 1975; Walker et al. 1980; Haugen and Brown 1980). Thus, there are large differences in air temperatures within the Arctic Coastal Plain. However, at inland stations the extra warming in summer is likely balanced by extra cooling in winter, so the average annual temperature for the whole of the Arctic Coastal Plain is close to -13°C. Summer temperatures probably average 6°C in June, 10°C in July, 9°C in August, and 5°C in September.

Precipitation (Table 5) is much more variable than temperature and some of the records are open to question. At Barrow, for example, Dingman et al. (1980) found the winds during July to be between 2 and 10 m sec$^{-1}$ 60% of the time, and that winds cause the measured precipitation to be an underestimate. They believe that the actual precipitation at Barrow is 170 mm and at Barter is 248 mm. Precipitation increases inland, so the average for the Arctic Coastal Plain is about 350 mm. Almost half of the annual precipitation falls as rain from June through September.

Blowing snow during late September rapidly fills in surface irregularities. Along the coast, accumulation is 20 cm in the first 3 weeks, followed by a slow buildup to 40 cm by the end of the winter. The foothills and mountains receive up to three times this amount; the average

accumulation on the Arctic Coastal Plain is probably 80 cm.

## 2.2 HYDROLOGY

The Coastal Plain is crossed by many north-flowing rivers (Figure 1) with well-developed channels and high flows during the summer. Yet these are mostly maintained by flow from the foothills and mountains. Drainage on the coastal plain is poorly developed and only a few small streams lie completely within the Coastal Plain. The hydrologic cycle for these streams, described by Dingman et al. (1980), is remarkable in that half of all the runoff occurs in 3 to 9 days in June when the snowpack melts. At this time, water floods most of the low-lying areas, and fills up pond and lake basins; some enters the streams. Within a week or so the streams virtually stop flowing for the remainder of the summer, although an exceptionally wet summer will cause flooding and eventually increase the stream flows.

The runoff in the four Coastal Plain streams considered by Dingman et al. (1980) averaged 11 cm, but there are only a few measurements. These authors also state that evaporation might be 14 to 21 cm. The results, which show that about 50% of the precipitation runs off, may be very misleading because hydrologists use well-defined watersheds for their measurements and these are rare on the Coastal

Table 5. Mean monthly and annual precipitation (mm) for Barrow and Barter Island (U.S. Dept. Commerce, from Dingman et al. 1980).

| Site | J | F | M | A | M | J | J | A | S | O | N | D | Annual |
|------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|--------|
| Barrow | 5.8 | 5.1 | 4.8 | 5.3 | 4.3 | 8.9 | 22.4 | 26.4 | 14.7 | 14.0 | 7.6 | 4.8 | 124.1 |
| Adjusted[a] | 9.3 | 8.2 | 7.7 | 8.5 | 6.9 | 9.8 | 24.6 | 29.9 | 23.5 | 22.4 | 12.2 | 7.7 | 169.8 |
| Barter Island | 13.9 | 8.4 | 6.6 | 5.8 | 7.9 | 13.5 | 28.5 | 32.5 | 22.6 | 20.6 | 11.4 | 7.4 | 179.0 |
| Adjusted[a] | 22.2 | 13.4 | 10.6 | 9.3 | 12.6 | 14.8 | 29.6 | 35.8 | 36.2 | 33.0 | 18.2 | 11.8 | 247.5 |

[a]Values adjusted to compensate for underestimation due to wind.

Plain. Most of the precipitation in this area undoubtedly does not run off and is eventually lost by evaporation. There has been no study of the water balance of a large area of the Arctic Coastal Plain where surface flow may be the dominant process.

Some evidence for the low runoff of much of the Coastal Plain comes from a water budget of a small pond (Class III) studied during the IBP studies at Barrow. Miller et al. (1980) measured average inputs to Pond B of 9.3 cm of water in snow, 6.7 cm in rain, and 5.8 cm as melt-water input during the spring. Outputs were 5.8 cm as spring runoff to a tempo-rary stream and 21.4 cm as evapotranspira-tion (from a standard evaporation pan placed next to the pond). The extra water needed to balance the equation, 6 cm, came from slow input from the drainage basin and from calculation errors (perhaps from using evaporation pan data which have to be reduced by 40% in temperate regions). In some wet summers the ponds will over-flow and flood the whole drainage basin. In the IBP Pond the water level fell 16 cm during a typical summer.

The IBP data lead to the conclusion that when ponds are abundant, most of the water that would ordinarily run off in the spring instead goes to fill up the pond basins. Evaporation, not runoff, accounts for most of the water loss from much of the Arctic Coastal Plain.

## 2.3 WATER TEMPERATURES AND ICE COVER

The water temperatures of the ponds are much more influenced by the solar radiation than by the air temperature. A few sunny days can raise pond temperatures up to 16°C; several cloudy days may cause the pond temperature to decrease to 2°C the next week (Figure 3). In this Class III shallow pond (maximum depth 40 cm), the average temperature was 7.1°C in 1971 (Miller et al. 1980); a nearby Class IV lake (maximum depth of 70 cm) had an average temperature of 4°C, so the depth of the water is also important. Large Class IV lakes with depths up to 2 m seldom warm above 9°C.
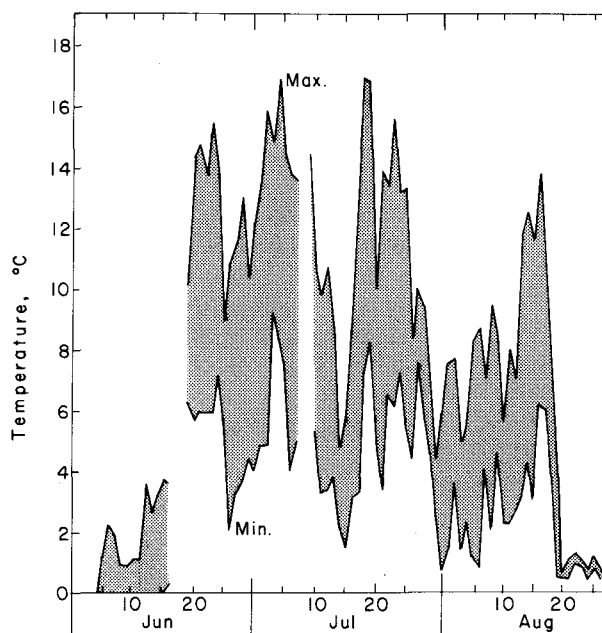


Figure 3. Daily maximum and minimum pond temperatures at Barrow, 1971 (from Miller et al. 1980).

The ponds and lakes are so shallow and the summer winds so strong (average 6.2 m sec$^{-1}$ at Barrow, June-September) that no temperature stratification is found.

The duration of the ice cover influ-ences the temperature of the larger lakes but has little effect on the pond temper-atures. Ponds and lakes at Barrow first become ice-covered between 7 and 16 Sep-tember (1963-1973). The maximum thickness of the ice is 1.7 m but the actual thick-ness attained depends upon the snow cover. Ponds, which freeze completely, will have only 20-40 cm of ice while lakes, which may or may not freeze completely depending on their depth, will often have 1.7 m. Obviously, the thin ice of the ponds thaws in a few days while the thick lake ice may take a month more to thaw. Near Barrow, the ponds thaw between 6 and 18 June (1963-1973), while Imikpuk Lake (2.8 m maximum lake depth) thaws in mid- to late July (Miller et al. 1980). Large lakes (1.1 m maximum depth) near Prudhoe Bay thaw in late June or early July (Bergman et al. 1977).

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## 2.4 WATER CHEMISTRY

The chemistry of lakes and ponds in the Arctic Coastal Plain is largely controlled by the surrounding soils but is also influenced by meltwater dilution and evaporation. The soils around Barrow are acid and highly organic, reflecting in part the poor drainage and the lack of carbonates in the soil. The rivers to the east of the Colville River - for example, the Kuparuk and Sagavanirktok Rivers at Prudhoe Bay - run from the mountains to the ocean and deposit carbonates on the coastal plain (Brown et al. 1980b, Walker et al. 1980). In contrast, the Colville River intercepts rivers running from the mountains north towards Barrow and prevents deposition of carbonates in that region (Figure 1). Ponds at Barrow have around 4 ppm $Ca^{++}$ and conductivities of 160 $\mu$mho $cm^{-1}$, while those at Prudhoe Bay have 20-40 ppm $Ca^{++}$ and conductivities of 500 $\mu$mho $cm^{-1}$ (Prentki et al. 1980, Douglas and Bilgin 1975). In spite of this difference, the pH of the Barrow ponds was around 7.2 while Prudhoe Bay ponds had pH's of 7.5 to 8.0 (Bergman et al. 1977).

In the spring, the ponds are flooded with meltwater and the ions in the original pond water are diluted (Figure 4). After this, evaporation of the water and re-solution of ions from sediments causes ionic concentration to increase as much as four fold. During freeze-up, ions are excluded from the ice and reach high concentrations in the remaining water. Finally, as the freezing front moves downwards, many of the ions move into the sediments.

The only other chemical difference between these coastal plain ponds and the majority of temperate ponds is the high NaCl content in ponds within a kilometer or so of the coast. Some ponds may receive seawater during storms or high tides while others will receive wind-blown spray and salts.

### 2.4.1  Iron and Phosphorus

In ponds of the Arctic Coastal Plain, the nutrient concentrations and rates of supply are controlled by interactions with the sediments. These are iron-rich peats
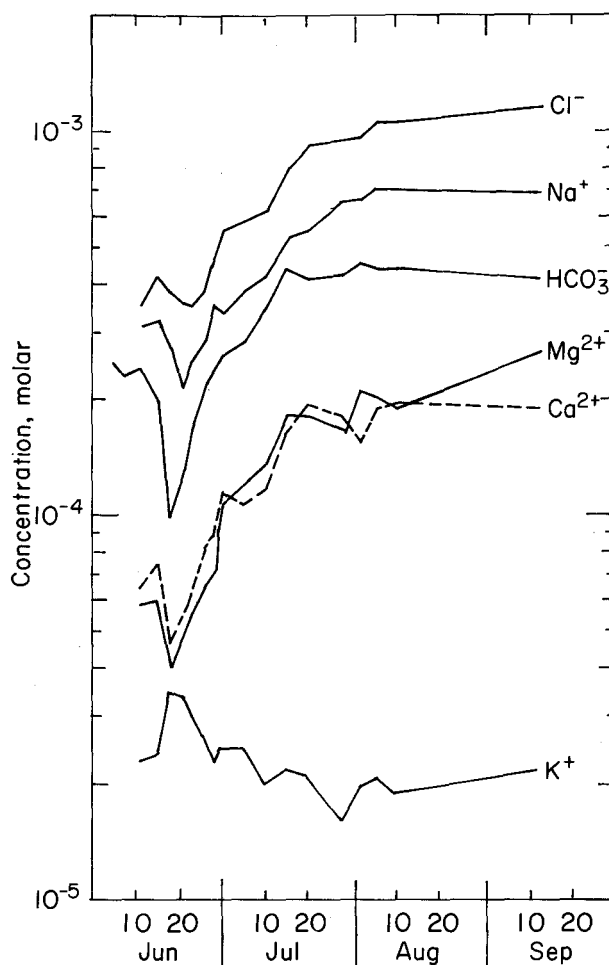


Figure 4. Concentration of major ions in Pond B, Barrow, 1970 (from Prentki et al. 1980).

with an oxygenated zone restricted to the top 1 cm. The iron concentrations control the phosphorus concentrations and these in turn control the growth of algae. Both iron and phosphorus are high in the sediments (Table 6) although iron concentrations in pond water are about the same as found in soft-water Wisconsin lakes. The organic content is very high as well; sometimes lenses of sand or ice occur deep in the sediments but these are not typical (e.g., <30 cm in Pond C, Table 6).

A detailed picture of the iron-phosphorus relationships in the ponds at Barrow has been developed (Prentki et al. 1980). Iron reaches the pond after being leached from the soils and sediments; especially high concentrations in the

Table 6. Chemical composition of sediments in ponds near Barrow, 1970 (from Prentki et al. 1980). Total P was determined on digests.

| | mg P (g dry wt)$^{-1}$ | mg Fe (g dry wt)$^{-1}$ | Organic (%) |
|---|---|---|---|
| **Pond C** | | | |
| 0-1 cm, organic | 1.2 | 43 | 83 |
| 0-10 cm, organic | 0.68 | 21 | 70 |
| 10-20 cm, organic | 0.64 | 20 | 60 |
| 20-30 cm, organic | 0.59 | 17 | 37 |
| 30-40 cm, organic + ice | 0.54 | 23 | 22 |
| 40-50 cm, sand | 0.39 | 18 | 2 |
| **Pond D** | | | |
| 0-10 cm, organic | 0.72 | 24 | 67 |
| 20-30 cm, organic + sand | 0.34 | 12 | 65 |
| 50-60 cm, peat + ice | 0.32 | 9 | 60 |

water, up to 0.7 mg liter$^{-1}$, were measured after summer rain storms. This dissolved iron quickly combines with organic matter either by chelation or by complexing (possibly as ferric hydroxide) and settles out as a floc. When dissolved reactive phophorus enters the pond from snowmelt or rainfall, it sorbs to the iron oxide-organic matter complex and is removed from the water column. While the sorption is really a dynamic equilibrium, the equilibrium is strongly shifted towards the sediments. Even when large quantities of phosphorus are added to a pond, the sediments sorb it and come into equilibrium with the water within the sediment, which will contain 1 to 5 μg P per liter. Some idea of the tremendous amount of phosphorus trapped in the sediments comes from the fact that in a 20-cm-deep pond, the P concentration in the water column was 1.5 mg m$^{-2}$; in the sediment water, 2.0 mg m$^{-2}$; and in the sediments (top 10 cm), 25,000 mg m$^{-2}$, of which 3,600 mg was sorbed and the remainder organic.

The result of this large sediment buffer is a very low concentration of reactive phosphate in the water of tundra ponds and lakes (Table 7). Prentki et al. (1980) reported that near Barrow the P content of 15 ponds was 0.9 to 3.0 μg liter$^{-1}$ on one date in August, while in a deep lake it was 0.5 to 4.4 μg on 17 different collection dates. In four lakes near Prudhoe Bay, P content was 0.2 to 1.9 μg liter$^{-1}$. The ponds at Barrow also illustrate a large difference between different types of ponds. The three ponds on the left side of Figure 5 are not

Table 7. Concentrations and annual phosphorus budget for Pond B, Barrow, 1971. The DRP is dissolved reactive phosphorus, DUP is dissolved unreactive phosphorus (organic), and PP is total particulate phosphorus (from Prentki et al. 1980).

| | Form | μg P liter$^{-1}$ | μg P m$^{-2}$ yr$^{-1}$ |
|---|---|---|---|
| Winter snow (collected May 1971) | DRP | 1.5 | 87 |
| | DUP | 1.1 | 64 |
| | PP | 1.4 | 81 |
| | | | 232 |
| Spring runoff entering pond | DRP | 2.4 | 1820 |
| | DUP | 13.6 | 10340 |
| | | | 12160 |
| Spring runoff leaving pond | DRP | 2.5 | -1900 |
| | DUP | 15.4 | -11700 |
| | | | -13600 |
| Summer precip. | DRP | 7.2 | 468 |
| | DUP | 0.7 | 46 |
| | | | 514 |
| Net balance | | | -694 |
| Summer 1971, water in Pond B | DRP | 2.0 | |
| | DUP | 10.6 | |
| | PP | 7.1 | |

polygon ponds (Class II or III) but are deep and irregular ponds formed when ice wedges melted. In this case, repeated trips of a tracked vehicle destroyed the insulating layer of tundra and caused the melt. The resulting newly formed ponds are low in iron (by 30%) and, as a consequence, the reactive phosphorus is high.

As described later, the algal productivity is also very high in these new ponds. It is not known if this scenario occurs in other types of newly formed ponds.

When Prentki et al. (1980) made a detailed study of the concentration of dissolved reactive phosphorus (DRP) in
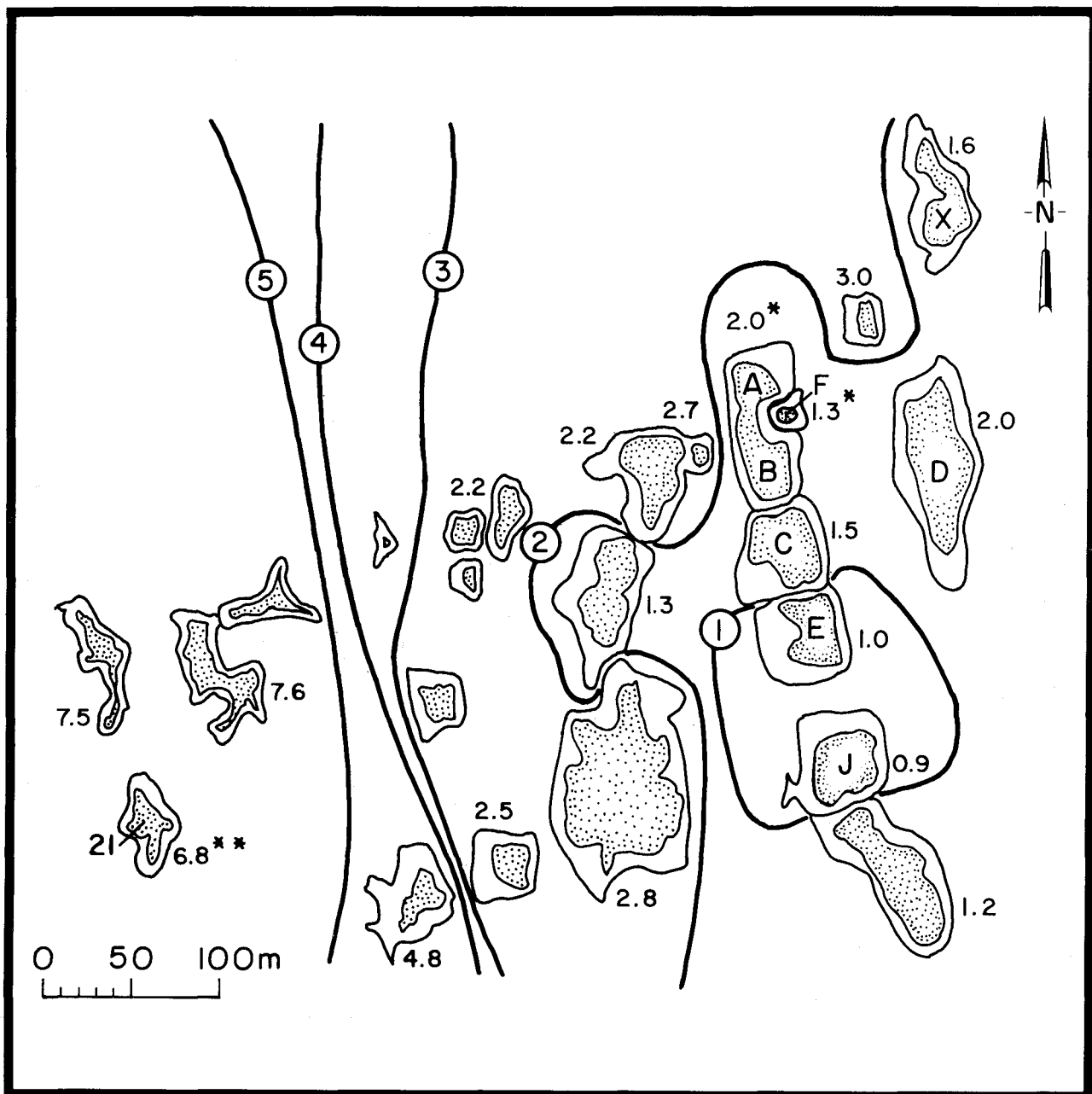
Figure 5. Concentration of reactive phosphorus ($\mu$g P liter$^{-1}$) in Barrow ponds in August, 1970 (Prentki et al. 1980). The contour lines connect areas of equal P concentration.

the water of Barrow ponds over three summers, they found 4-6 μg liter$^{-1}$ in the meltwater from the tundra, 2-3 μg in the water column during the summer, and less than 1 μg liter$^{-1}$ in the water column during peaks of algal production in late June and August. These numbers cannot convey the rapidity of the phosphorus cycling but, for example, concentrations changed by 1.5 μg in 4 hours in a 2-day series of observations. This rapidity was confirmed with radioisotope experiments; uptake rates of $^{32}PO_4$ into the plankton gave a P range of 13 to 320 μg liter$^{-1}$ day$^{-1}$ corresponding to turnover times of 0.23 to 4.6 hr. It is typical of freshwaters in general that this uptake was much more than the amount needed for algal growth; in the Barrow ponds it was 200 times greater.

Where does this phosphorus come from? For this short term cycling, DRP is excreted by zooplankton (13 μg m$^{-2}$ day$^{-1}$), lost from plants (860 μg m$^{-2}$ day$^{-1}$), and released from sediments (170 μg m$^{-2}$ day$^{-1}$). Over an entire year, the ponds appear to be just about in balance or even may lose a little phosphorus through runoff (Table 7). The loss is only 0.003% of the phosphorus in the top 10 cm of the pond. Based on this budget, most of the phosphorus in the ponds must come from the soils that were there before the ponds were formed. Small amounts enter from the winter and summer precipitation, but the ponds may even give up a little phosphorus to the spring meltwater that moves through the system.

## 2.4.2 Nitrogen

Although phosphorus is the most important nutrient limiting algal and plant growth in freshwaters, nitrogen is also necessary (for algal growth, the weight ratio of N:P is 7:1). In the Barrow ponds (see Prentki et al. 1980 for details), nitrate and ammonia are both abundant early in the summer but nitrate concentrations become extremely low during August (Table 8, Figure 6). As is typical for all waters, the dissolved organic nitrogen (DON) makes up the largest quantity of nitrogen but it is likely that this is relatively inert material that cannot be easily broken down by bacteria. The concentrations of

Table 8. Average concentrations (μg N liter$^{-1}$) of various forms of nitrogen in a pond and lake near Barrow, 1971 (Prentki et al. 1980).

| Location | June | July | August |
|---|---|---|---|
| Pond B | | | |
| Nitrate | 25.0 | 33.0 | 1.0 |
| Nitrite | 0.3 | 0.2 | 0.2 |
| Ammonia | 27.0 | 25.0 | 23.0 |
| Dissolved organic nitrogen | | 920 | 870 |
| Particulate nitrogen | 108 | 36 | 39 |
| Ikroavik Lake | | | |
| Nitrate | | | 0.0 |
| Ammonia | | | 14 |
| Dissolved organic nitrogen | | | 996 |
| Particulate nitrogen | | | 100 |
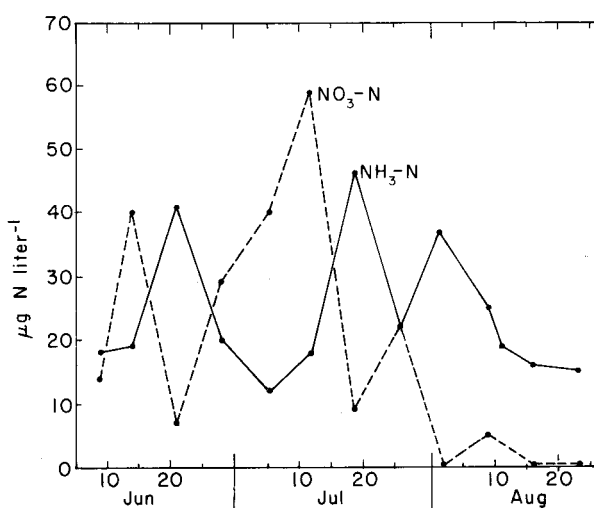


Figure 6. Concentrations of nitrate and ammonia nitrogen in Pond B, 1971 (from Prentki et al. 1980).

nitrogen in the lakes are about the same as in the ponds.

The inorganic nitrogen does recycle in the water but the turnover times are much longer than those for phosphorus and are tied to algal needs. For example, the uptake of ammonia-$^{15}N$ is 15-40 times higher than the uptake of nitrate-$^{15}N$ and the turnover time of ammonia is about 150 hours. The total planktonic uptake of both forms of N was 0.16 μg liter$^{-1}$ hr$^{-1}$, which agrees with the nitrogen necessary to support algal production (0.17 μg N liter$^{-1}$ hr$^{-1}$).

Ammonia is abundant in the sediments (up to 3.2 mg N liter$^{-1}$) and there is an

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equal amount of dissolved organic nitrogen ($1-6$ mg N liter$^{-1}$). However, the ammonia is used by plants so rapidly that the concentrations within plant beds are practically zero (Figure 7). Uptake of N by plant roots is 18 mg m$^{-2}$ day$^{-1}$; by benthic algae, 12 mg; and by plankton, 1.2 mg m$^{-2}$ day$^{-1}$.

The fixation of nitrogen occurs in the pond sediments but the rates are very low (Prentki et al. 1980). Two of four ponds sampled near Barrow showed fixation at an average rate of 0.31 mg m$^{-2}$ day$^{-1}$. This is small compared to the amount of ammonia nitrogen present in sediments (168 mg m$^{-2}$ in the top 8 cm) and is about half of the nitrogen fixation rate in the tundra (Barsdate and Alexander 1975). This low rate implies that N supplies are adequate.

Denitrification, the transformation of nitrate to nitrogen gas, occurs in the anaerobic sediments at low rates. This could account for the low concentrations of nitrate in the sediments, but the denitrification rate of 0.032 mg N m$^{-2}$ day$^{-1}$ is a tenth of the fixation rate.

It is obvious from the uptake rates and concentrations that ammonia is rapidly regenerated in the ponds. Regeneration has been measured only in the plankton where the rate of 1.9 µg N liter$^{-1}$ hr$^{-1}$ is ten times higher than the algal uptake rate. In addition, there should be a high rate of regeneration in the sediments and some transfer from sediments to the water column; thus nitrogen should never be limiting to algal and other plant production.

The annual budget for a pond (Table 9) indicates that most of the dissolved inorganic nitrogen (DIN) enters the pond during summer rainfall while most of the DON enters by nitrogen fixation and spring runoff. There was a net N input of about 60 mg m$^{-2}$, which is small compared to the
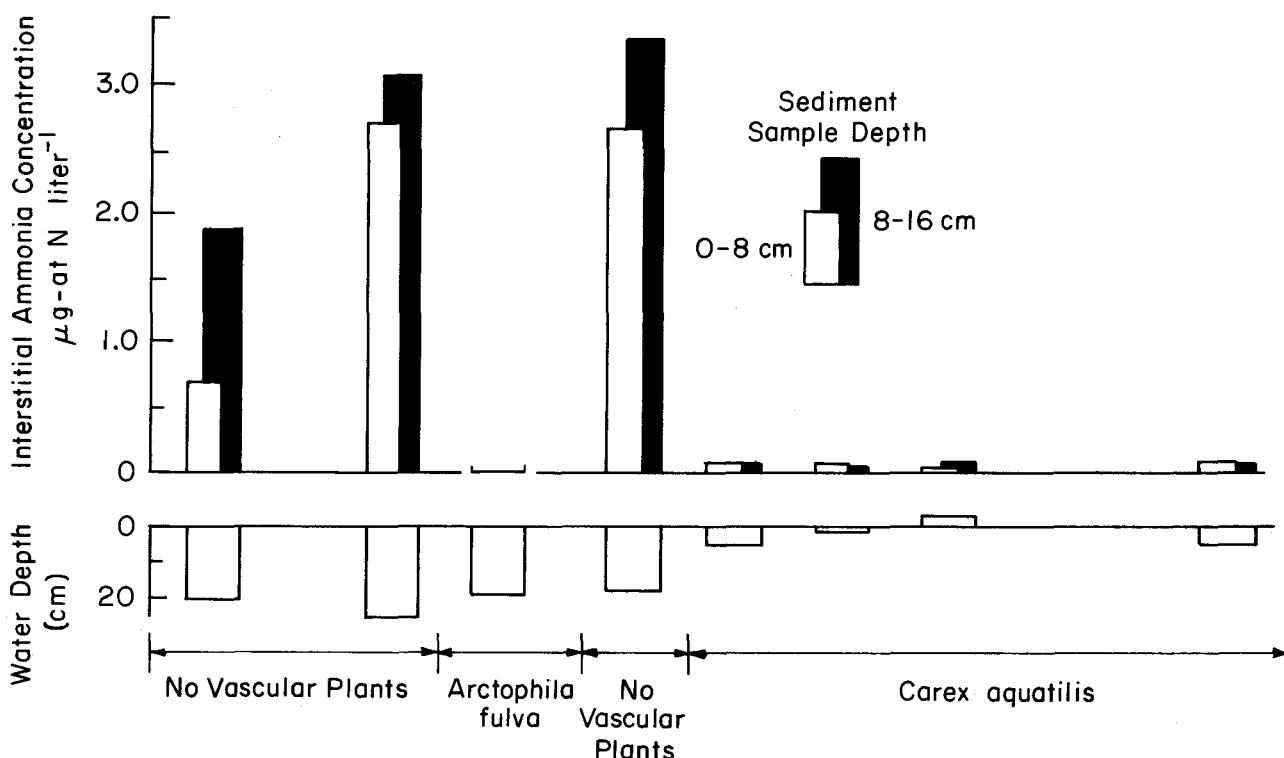


Figure 7. Concentrations of interstitial ammonia N (mg liter$^{-1}$) in sediments of Pond J, 1973. The center of the pond, with no vascular plants, is at the left and the shore is at the right (Alexander et al. 1980).

Table 9. Nitrogen budget for Pond B, Barrow (Prentki et al. 1980).

| | DIN (mg $m^{-2}yr^{-1}$) | DON (mg $m^{-2}yr^{-1}$) |
|---|---|---|
| Nitrogen fixation in sediments | | +28.0 |
| Summer rainfall | +11.5 | + 2.5 |
| Runoff, spring (amount retained) | + 0.9 | +20.6 |
| Denitrification | - 2.8 | |
| Net input | + 9.6 | +51.1 |

accumulation of 400-1300 mg $m^{-2}$ in temperate lakes.

## 2.5  THE ORIGIN OF PONDS AND LAKES, THE THAW-LAKE CYCLE, AND PERMAFROST

Ponds and lakes are abundant in the Arctic Coastal Plain because the permafrost prevents both drainage and the development of streams and because the landscape is very flat. The flat land is a result of marine-sediment deposition in near-shore areas in the mid to late Quaternary. After a number of advances and retreats, the ocean finally receded to approximately its present location (at least at Barrow) about 14,000 years ago (Brown et al. 1980b). Quaternary glaciers did not extend onto the coastal plain although they were (and are) present in the mountains.

After the ocean receded, permafrost formed in the fine-grained sediments. Cracking of the soil occurred due to contraction during rapid winter cooling. (Similar cracks, on a much smaller scale, are seen when a mud puddle dries up.) These soil cracks are subsequently filled by melt water and this soon freezes. Over centuries, a network of ice wedges forms in the ground; the wedges may penetrate for many meters and can be from a few centimeters to 8 m in width (Figure 8).

The network of wedges forms polygons some 15 to 40 m across (Figure 9A). Above each ice wedge the ground is heaved up to form a rim around the polygon. This rim may trap water to form a pond (Figure 9B) or the ice wedge may melt and a pond form in the trough between polygons (Figure 9B). When ponds form, there is a drastic change in the heat flow into the soils as the insulating layers of surface vegetation are replaced by dark pond sediments. As a result, ice in the permafrost melts (Sellman et al. 1975 found that ice made up 70% of the soil volume at 0.5 m and 50% at 4 m) and ponds coalesce to form lakes (Figure 9C, 9D). These lakes are usually oriented north-south by erosion of wind-driven currents. The last stages of this thaw-lake cycle (Hopkins 1949; Britton 1957) begin when the divides between lakes are breached by erosion or when streams form and headward erosion drains the lake (Figure 9E). Ice wedges and polygonal ground soon form in the drained lake bottom and the thaw-lake cycle begins again (Figure 9F).

Permafrost seals off the soil of the coastal plain and prevents subsurface drainage. Permafrost also moves into every raised road or gravel drilling pad which then becomes a barrier to surface runoff. This is the cause of the many new ponds along the road servicing Prudhoe Bay (Figure 8).

Figure 8.  A. Aerial view of tundra ponds in polygonal ground near Prudhoe Bay.
           B. Flooded tundra and gravel road, Prudhoe Bay.
           C. Small lake near Prudhoe Bay.
           D. Ice wedge along eroding shore of Lake Colleen, Prudhoe Bay.
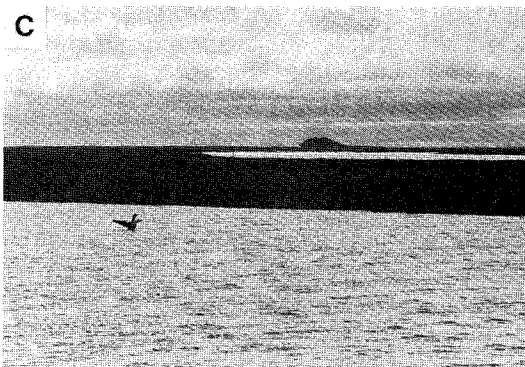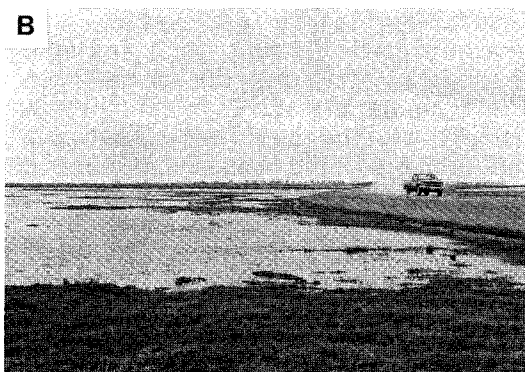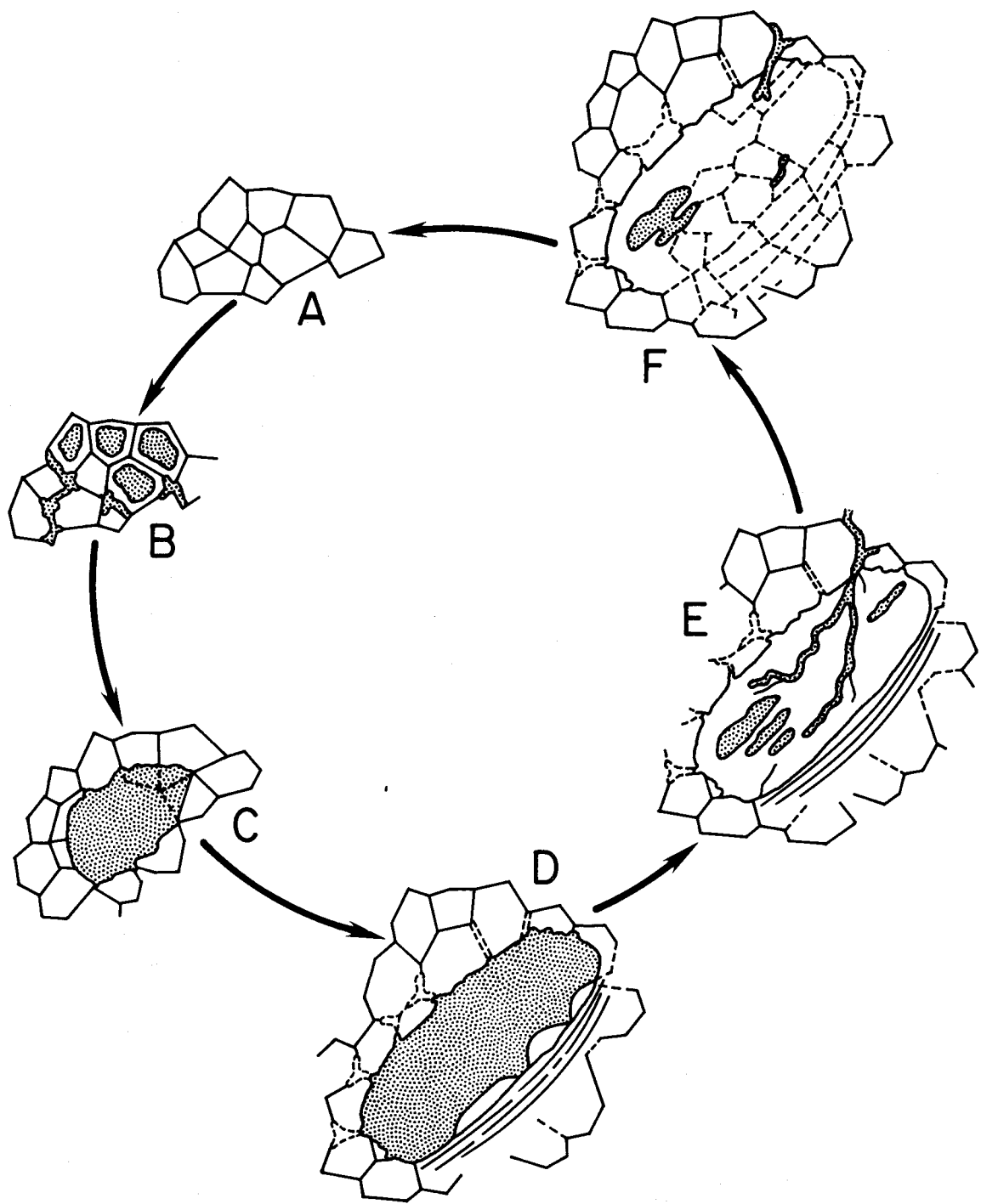
Figure 9. The thaw-lake cycle from polygonal ground (A) to drained lake basins (F) (after Walker et al. 1980). See text for explanation.

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# CHAPTER 3.
# BIOLOGICAL COMPONENTS

The ponds of the Arctic Coastal Plain contain phytoplankton, zooplankton, and benthic organisms similar to those of temperate ponds (Figure 10) but certain animals are missing. There are no amphibians, dragonflies, mayflies, true bugs, leeches, or crayfish. At Barrow there are no mosquitos, clams, or amphipods (scuds), but these are found inland. Fish are present only in waters deeper than 1.7 m, the maximum ice thickness, so are absent from all ponds and most of the lakes. The fish, insects, and zooplankton that are present are represented by few species compared with assemblages in temperate ponds. For example, Ikroavik Lake near Barrow has only two species of whitefish (Coregonus) and the ninespined stickleback (Hobbie 1973). Butler et al. (1980) reported 35 species of chironomids (midges) from Barrow ponds, whereas temperate ponds might have more than a hundred. This simplicity makes it somewhat easier to study each organism or community but does not make any process or interaction easier to understand.
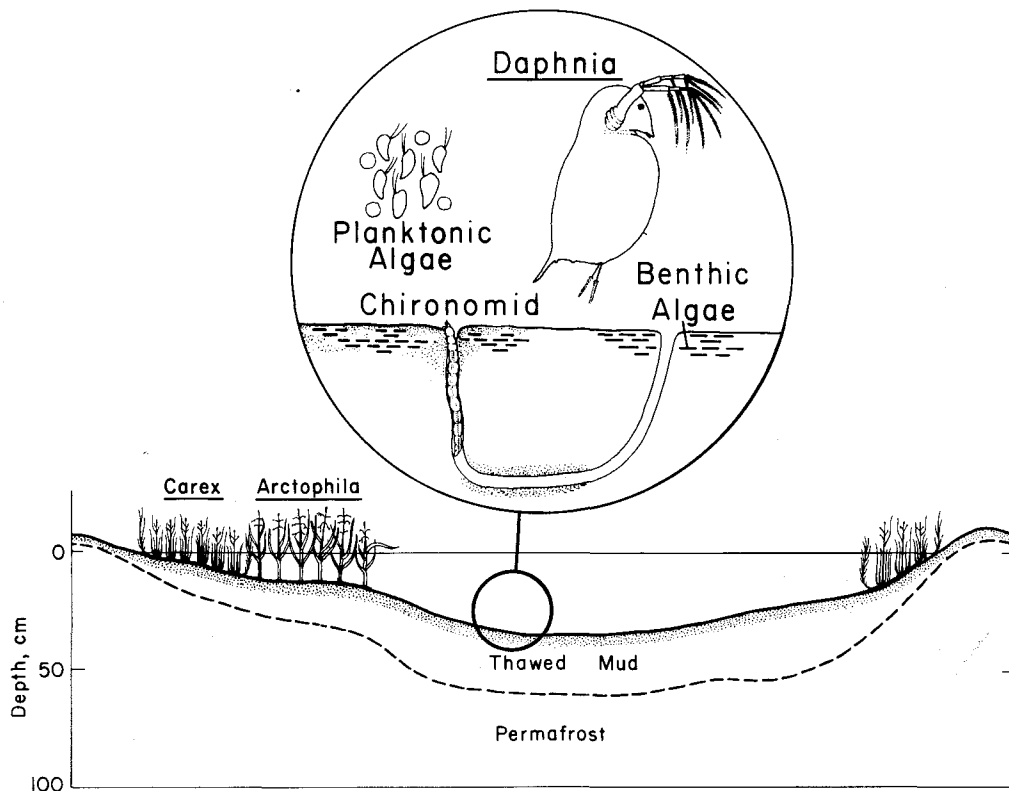


Figure 10.   A cross-section of a typical pond (from Hobbie 1980).

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## 3.1 PHYTOPLANKTON

In contrast to the special adaptations of the vascular plants, the planktonic algae show no arctic adaptations; they are the same species with the same physiology found in temperate ponds and lakes in the spring (Alexander et al. 1980). The 105 species found are almost all nanoplankton, that is, cells smaller than 20 μm. Chrysophytes (Chromulina and Ochromonas) and Cryptophytes (Rhodomonas minuta, Cryptomonas, and Chroomonas) dominated, although 4-μm and 6-μm unidentified flagellates were often the most abundant forms.

There are 1 to 6 million algae cells per liter throughout the summer in the ponds of the coastal plain (five or six sites) (Alexander et al. 1980). However, these cells are so small that their biomass of 25-400 mg wet wt liter$^{-1}$ is low compared with the 400-6,000 mg in a moderately productive temperate lake. The amount of chlorophyll in these algae, another measure of biomass, lies between 0.4 and 1.2 μg liter$^{-1}$ (Figure 11). Lakes at Prudhoe Bay contained 0.13-1.46 μg and Ikroavik Lake near Barrow had 0.03-2.37 μg liter$^{-1}$. The early rise in chlorophyll after the spring melt (Figure 11) was made up of Chrysophyta, but these forms were replaced by Cryptophyta around 1 July. Although this was true for almost all of

the Barrow ponds, there was one pond with diatom dominance and one with dominance of the blue-green alga Microcystis.

The rates of primary production of these nanoplankton follow the seasonal curve of the chlorphyll (Figure 12). Although the production per liter is reasonably high, the ponds are so shallow and the ice-free season so short that the annual production of 1 g C m$^{-2}$ is one of the lowest ever measured. Ikroavik Lake near Barrow, had a production of 2.2 g C m$^{-2}$ because of its greater depth (2.2 m maximum). All these waters fall at the low end of the productivity scale and are considered extremely oligothropic.

As noted above, the nanoplankton are the same as those found in the spring in temperate ponds. They are adapted to cold water; their optimum temperature for photosynthesis is 15°-20°C. These low temperatures do not limit the algae and, in fact, an experimental rise in the temperature by 4°C did not increase photosynthesis at all (Alexander et al. 1980). The ponds are so shallow that light was more than adequate; algal photosynthesis was at a maximum most of the time. During June and the first half of July there was even enough light for
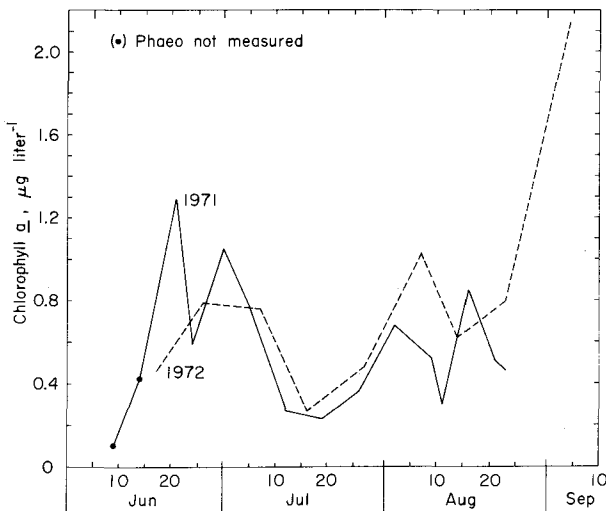


Figure 11. Chlorophyll a in the water of Pond B, Barrow, 1971 and 1972 (from Alexander et al. 1980).
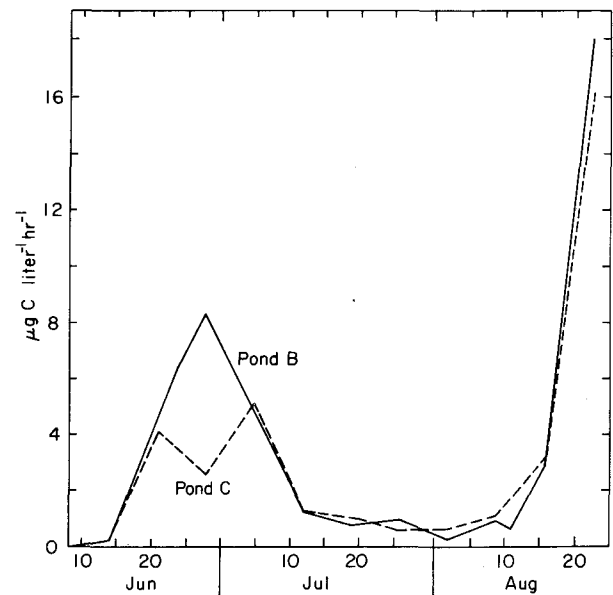


Figure 12. Rates of planktonic primary productivity in Ponds B and C, Barrow, 1971 (Alexander et al. 1980).

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photosynthesis to proceed all night. Throughout the summer, the photosynthesis rate was so rapid that the cells reproduced every 1/3 to 3 days. Yet the number of cells and the chlorophyll in the water changed very slowly (Figure 11). What is the explanation?

The answer is that zooplankton grazing removes algae fast enough to control the population. The dominant zooplankter, Daphnia middendorffiana, filters 2-6 ml of water per hour at 11°C (Chisholm et al. 1975); the population of Daphnia filters the entire volume of a pond every 2 days. There is some proof of this control; when the zooplankton are removed, either by an oil spill or by setting up an artificial pond, the phytoplankton increase dramatically (Figure 13). Zooplankton grazing also controls the species composition, for the dominant algal species could be changed from Rhodomonas to Uroglena by the removal of zooplankton (Alexander et al. 1980).

The most important control of the phytoplankton is by phosphorus limitation of photosynthesis and growth. The spring bloom shown in Figure 11 begins to decrease in early July shortly after the phosphate concentrations fall to less than 1 mg liter$^{-1}$. In a test of this theory by Alexander et al. (1980), the addition of phosphorus alone to a pond rapidly quadrupled the rate of photosynthesis (Figure 14). This proves that sufficient nitrogen for algal needs was present in the pond. The phosphorus concentrations and supply rates are controlled by the iron-organic matter complex in the sediments (Section 2.4). In newly formed ponds, where the iron-organic complex was not abundant, the phosphorus concentration was 20 times as great, and algal photosynthesis was 200 times that in old ponds. In old ponds, the slight changes found naturally in the phosphorus-buffering capacity of sediments is reflected in the changes in algal photosynthesis (Figure 15). This demonstration of the mechanism of the control exerted by small changes in P concentration over chlorophyll production is unique in limnology.

## 3.2 BENTHIC ALGAE

Large numbers of small algae are also found in the top 4 cm of the sediments; most are attached to particles. The majority of these benthic algae are, like the phytoplankton, less than 10 μm in size, but are completely different species. In the sediments, the dominant



| Graph | Treatment | |
| | Zoop. | Oil |
| 1 | yes | no |
| 2 | no | no |
| 3 | no | yes |
| 4 | yes | yes |
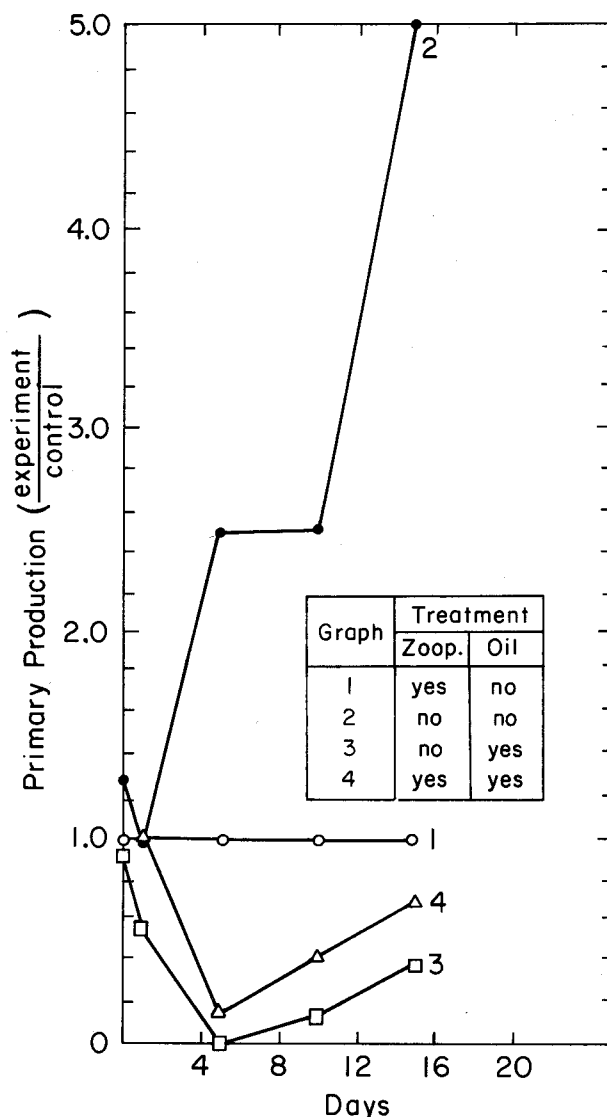
Figure 13. The ratio of phytoplankton biomass in subponds at the start of the experiment to that 5, 10, and 15 days later. The treatments were as follows: 1) zooplankton present (control); 2) zooplankton absent; 3) zooplankton absent, oil added; 4) zooplankton present, oil added (from Alexander et al. 1980).

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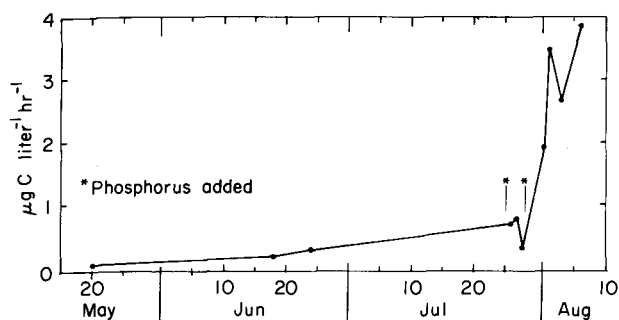
Figure 14. Photosynthesis of phytoplankton in Pond D, Barrow, before and after the addition of 46.5 g P on 25 July and 232 g P on 28 July, 1970 (Alexander et al. 1980).

forms of the 45 species are Chlorophyta (Chlamydomonas, Closterium, Ankistrodesmus) and Cyanophyta (Microcystis, Gomphonema, and Aphanozomenon). The dominance varies from pond to pond and even diatoms (Navicula, Cymbella) are sometimes important. Details of the biology of this community are given in Stanley (1976).

Even though these algae are abundant, up to $4 \times 10^{10}$ cells m$^{-2}$, they are so small that their mass is only about 0.5-1.0 g C m$^{-2}$ (Figure 16). Yet this is 250-500 times the phytoplankton biomass, 2 mg C m$^{-2}$. Over the season, there is a steady increase in the number and mass of the benthic algae, while the productivity peaks in July (Figure 16). This is quite different from the early and late summer phytoplankton peaks (Figure 12). Annual production estimates range from 410 to 10 g C m$^{-2}$, about 10 times the planktonic production. In deeper lakes, the benthic algae are not so productive because of the shorter ice-free period, lower light intensity, and lower temperatures. Ikroavik Lake, a 2.2-m-deep lake near Barrow, had a production of 2.3 g C m$^{-2}$, which was about the same as the planktonic production (Alexander et al. 1980).

In spite of the saturating light at the sediment surface, the sediments rapidly absorb light, so only 10% of the light penetrates to 1 mm in the sediments (1% reaches 2 mm). For this reason the production of the benthic algae is light-limited and photosynthesis is restricted
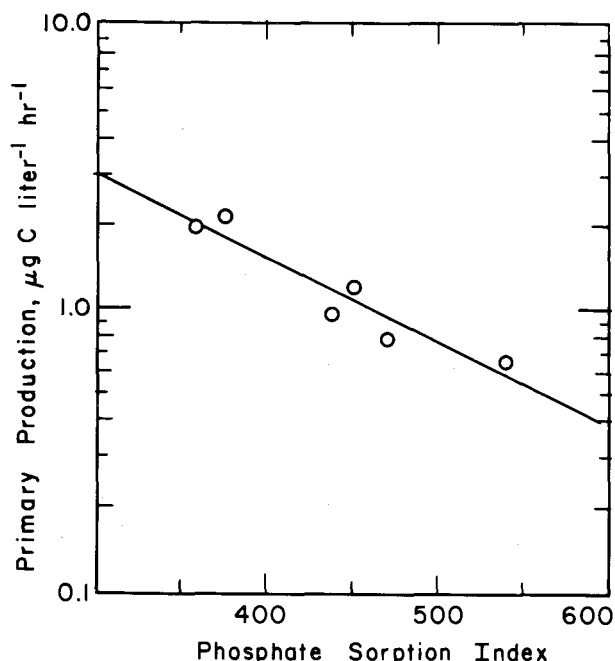


Figure 15. Algal photosynthesis in the water column of tundra ponds at Barrow at various buffering capacities of the sediment (phosphate sorption index) (from Hobbie 1980b).

to the top 2 mm of sediments. But the algae are distributed throughout the top 4 cm of the sediment. Why does this happen? The answer developed by Stanley (1976) is that algae are mixed down into the sediment by the activities of animals, particularly chironomid larvae and tadpole shrimp. This stirring is difficult to observe directly but a thin layer of sand spread on the sediment surface was buried within several days. This burial of algae severely limits the population, as most of the cells cannot photosynthesize. They do, however, survive for months by the slow respiration of storage products and can immediately photosynthesize when brought into the light. The stirring also prevents the formation of algal mats that can build up in shallow ponds when animals are absent (for example, antarctic ponds described by Hobbie 1983).

Grazing of algae by animals in the sediments is minor. The protozoans and micrometazoans, (rotifers, gastrotrichs, small nematodes) graze selectively on the algae, removing at a maximum rate of 8 mg C m$^{-2}$ day$^{-1}$ in these ponds (Fenchel

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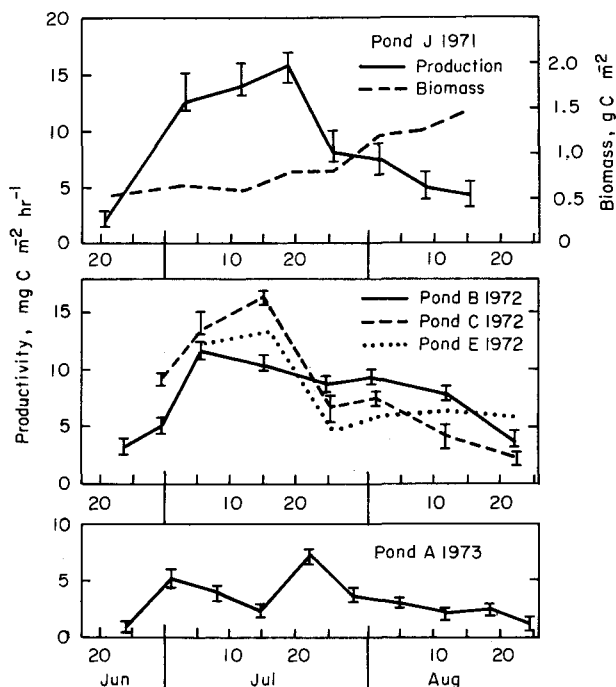
**Figure 16. Productivity and biomass of benthic algae, Barrow, 1971-1973 (Alexander et al. 1980).**

1975). Nonselective grazers, such as chironomids, oligochaetes, and larger nematodes ingest both algae and organic detritus, but the sediments are composed of 99.7% detritus, 0.06% algae, and 0.17% bacteria. Even if there were a 5-fold selectivity for algae over detritus, the consumption would be only 1 mg C m$^{-2}$ day$^{-1}$. This total feeding of 9 mg C day$^{-1}$ is only about 2% the 500 mg C m$^{-2}$ in benthic algae.

The benthic algae are limited by nutrient availability as well as by light. In view of the abundant ammonia in the sediments, nitrogen should never be limiting (Section 2.4). Phosphorus, in contrast, is no more abundant in the interstitial water than in the water column, so that phosphorus should be limiting algal growth here as in the water column. This was confirmed by an experimental addition of phosphate to a pond: production doubled within a month (Alexander et al. 1980). A special case of nutrient limitation is the silica-diatom interaction. In these waters, the silica is so low (averages 0.1-0.3 mg liter$^{-1}$) that diatoms do not thrive.

None are found among the plankton, while only a few are found in the sediments (Alexander et al. 1980).

## 3.3 EMERGENT PLANTS

Two rooted aquatic plants dominate the vegetation of the shallow ponds throughout the Arctic Coastal Plain. The water sedge Carex aquatilis is a dominant terrestrial plant on the Arctic Coastal Plain (Webber et al. 1980), but is also a facultative hydrophyte found to 20 cm depth in ponds (Table 1). The pendant grass Arctophila fulva is found up to a depth of 70 cm in deeper ponds (Bergman et al. 1977). Other aquatic plants include Hippuris vulgaris, Caltha palustris, Cardamine pratensis, Ranunculus pallasii, Utricularia intermedia, Sparganium minimum, and the mosses Drepandocladus and Scorpidium scorpiodes (Bergman et al. 1977, Spetzman 1959).

Both Carex and Arctophila (Figure 17) reproduce vegetatively through a network of horizontal rhizomes and stems connecting mother and daugther plants (see Alexander et al. 1980 for details). Every fall there is almost complete die-back of aboveground leaves and stems; in early to mid-June the growth begins again from the stem base. The leaves, 0.3 cm wide for Carex and 8-11 cm wide for Arctophila, live for 40-50 days; seven leaves may be produced over the growing season. The roots of Carex are long-lived (up to 7 years) and contain 90%-95% of the total plant weight. In contrast, the roots of Arctophila die back each year and contain 57%-78% of the total plant weight during the growing season. The plants reach their maximum growth by the first week in August and their mass declines rapidly thereafter. At Barrow, the maximum mass for Carex was 292 g dry wt m$^{-2}$ aboveground and 3119 g belowground. From these and other observations, a total net production of 300-400 g C m$^{-2}$ yr$^{-1}$ was calculated by Alexander et al. (1980). This estimate is for the plant stand, which is 30% of the pond area. The production rates for Arctophila depend upon the density of the stand; in the intensively studied Barrow ponds the production was about 20 g C m$^{-2}$ but where the plants cover the surface, a more typical value is 150 g C m$^{-2}$ yr$^{-1}$.
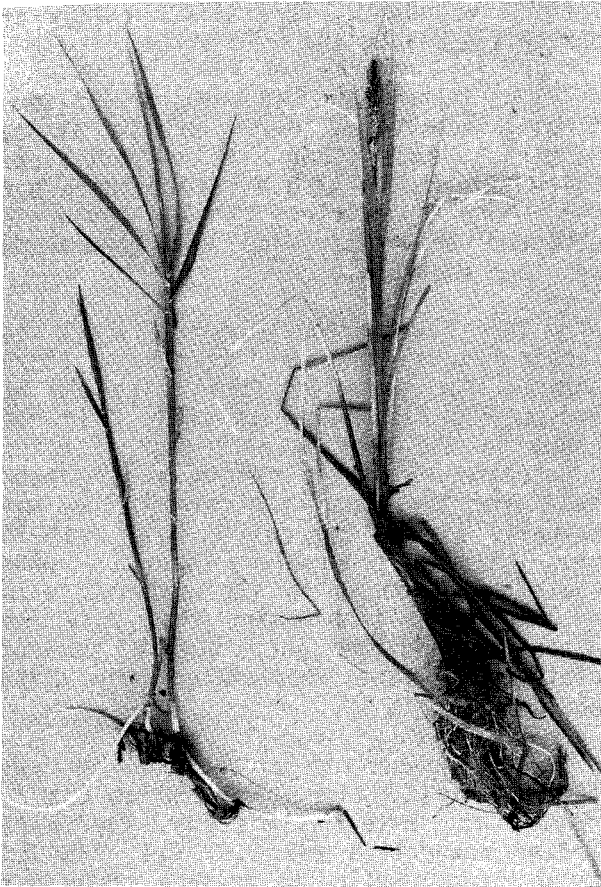
Figure 17. Arctophila fulva (left) and Carex aquatilis from northern Alaska.

Where aquatic plants cover more than about 10% of the area of ponds, they will be the most imporatnt primary producers. The contribution of benthic and planktonic algae together is about 11 g C m$^{-2}$ yr$^{-1}$. In fact, the plant production in the ponds is actually higher than that of the adjoining tundra (Alexander et al. 1980). This may be the result of higher phosphorus availablity in the ponds than in the terrestrial soils, or it may be the result of better light conditions for plants in the pond. On the tundra, the dead leaves from the previous year remain standing for most of the summer and block much of the light. In the ponds, the dead leaves fall over.

Tundra plants are so well adapted to arctic conditions that their production is as high as that of temperate plants (Brown et al. 1980a). In part this high produc-

tion rate is due to the 24 hours of sunlight; the plants have positive net photosynthesis continuously from early June until the sun begins to set in August. Their main adaptation is their ability to function at low temperatures. Photosynthesis, root growth, the translocation of carbohydrates, and phosphate absorption all begin when the Carex warms to 0°C. However, temperature may still be an important limiting factor for plant growth through its effect on the regeneration rate of phosphorus.

The leaves of Carex are adapted to the low angle of the sun; the leaves are erect and angled perpendicularly to the sun's rays. As a result of their orientation, the leaves intercept nearly all of the low-angled solar radiation (average of 25° from the horizontal on 21 June). In spite of the adaptation, the solar radiation is rarely strong enough at Barrow to saturate the photosynthetic mechanism.

3.4 ZOOPLANKTON

Crustaceans dominate the zooplankton of ponds and lakes (Figure 18). Rotifers are present but rare. In general, the species are similar throughout the Arctic Coastal Plain (Reed 1962). Where fish are absent, the very large (1-4 mm in length) Daphnia species (D. pulex and D. middendorffiana) and the fairy shrimp (Branchinecta and Polyartemiella) (15 mm in length) dominate. In deep lakes with fish, these Daphnia species and the fairy shrimp are replaced by the small, transparent D. longiremis (e.g., in Ikroavik and Sungoroak Lakes near Barrow) (Stross et al. 1980). Imikpuk, a deep lake without fish, contains the large forms shown in Figure 18. From this evidence, it is likely that size-selective predation by fish may control the species composition of the zooplankton.

All crustaceans except for Daphnia have but one generation per year. Usually, the animals overwinter as eggs, but in the case of the cyclopoid copepods (Cyclops), a preadult form overwinters in the frozen sediments. These overwintering forms begin to reproduce shortly after the

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## Polygon Pond



*Cyclops vernalis*

*Cyclops magnus*

*Daphnia middendorffiana*

*Branchinecta paludosa*

*Polyartemiella hazeni*

*Heterocope septentrionalis*

*Diaptomus glacialis*

*Diaptomus bacillifer*
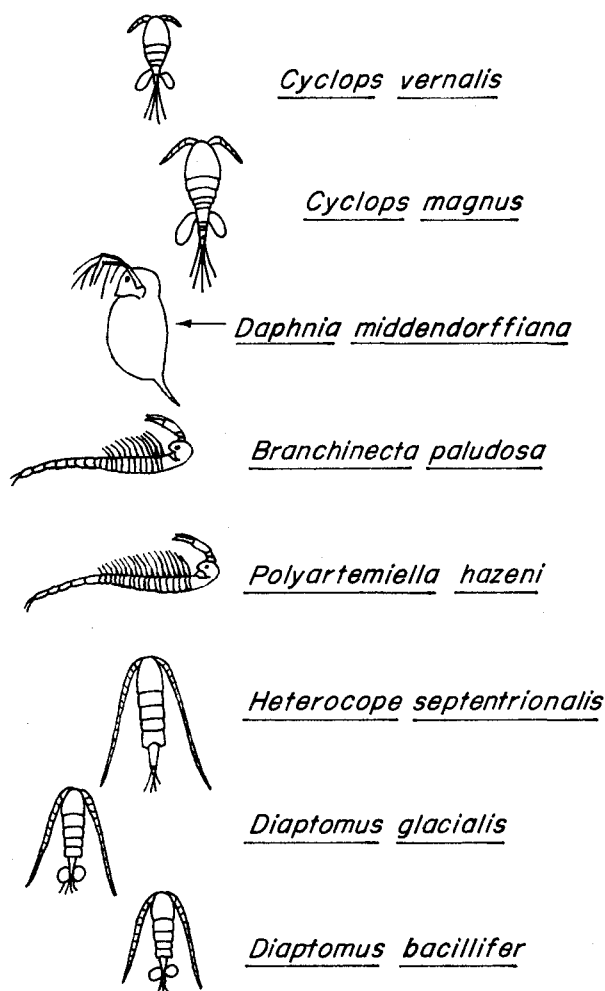
Figure 18. Crustacea found in the plankton of ponds and pools. at Barrow (Stross et al. 1980).

ice melts in June while the other copepods (Diaptomus, Heterocope) and the fairy shrimp (Branchinecta and Polyartemiella) do not reproduce until late July. Daphnia has a more complicated life history. The overwintering eggs (ephippial eggs) hatch shortly after the ice melts. The hatchlings, all female, reach maturity in mid-July and release a brood of young (12-14 eggs are incubated and hatched in a brood pouch). After this brood is produced, the females begin to produce overwintering eggs (two at a time). The brood of young may also produce overwintering eggs but only when the summer is very warm and food is abundant. This occurs rarely at Barrow but may be the rule inland.

The Daphnia and Diaptomus are filter-feeding herbivores that feed on algae, bacteria, and other small particles. Fairy shrimp are also filter feeders but use large particles, while cyclopoid copepods and Heterocope are predaceous on other zooplankton.

The zooplankton are difficult to sample because they tend to clump. Fairy shrimp, for example, form pairs during mating and all the pairs collect in one place in the pond. Large Daphnia often congregate along the margin of the pond away from the sun; in midsummer they may actually circle the entire pond over 24 hr. The sampling problems lead to strange peaks and troughs in the seasonal data on abundance, considering that only one generation is present, but a general picture is that zooplankton are quite abundant (Table 10).

The production of zooplankton was about 1 mg C liter$^{-1}$ or 200 mg C m$^{-2}$. During the 3-year IBP study, the fairy shrimp production was 0.8, 0.1, and 0.1 mg C liter$^{-1}$ while the Daphnia production was 0.2, 0.8 and 0.5 mg C liter$^{-1}$ in the same year (Stross et al. 1980).

There are no fish in the ponds, so the only important predation is by other zooplankton. Dodson and Egger (1980) found that phalarope predation on Daphnia was not enough to control the Daphnia population. The invertebrate predatory web in the Barrow ponds was studied in a series of glass jars incubated on the bottom of a pond (Dodson 1975). This is an artificial situation, but the results do indicate the probable strength of the interaction (Figure 19, Table 11). Table 11 shows that the higher the predation coefficient (K) value, the stronger the interaction. Cyclops had a high K for nauplii (its own or those of other cyclopoids) and for Heterocope nauplii. Heterocope had a high K for young Daphnia and probably killed all the young of the year. This was possible because by mid-July, when the Daphnia hatch, the Heterocope are adults. They were not large enough to prey on the Daphnia that hatched in June from the overwintering eggs.

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In addition to predation, another limit is the food supply. Daphnia are efficient feeders and become more efficient as they increase in size. The pond animals appear to be filtering at their maximum rate of 8 ml hr$^{-1}$ for a 2.6 mm animal (Chisholm et al. 1975). Still, if the algae are sparse, as is the case in these ponds, then the Daphnia growth and reproduction rate will be lower. Still, the animals in the ponds were not growing at their maximum rate; Daphina grown in isolated, plastic-lined pondlets on the tundra did have higher production rates (Stross et al. 1980). This effect could have resulted from a larger total food supply or by the same quantity of algae and bacteria (good quality food) along

Table 10. Abundance of zooplankton in Barrow ponds (individuals per liter).

| Type | June | July | August |
|---|---|---|---|
| Cyclopoid copepods | excyst; 5 copepodids then adults | early, 5 eggs; then 35 nauplii | 10 nauplii |
| Calanoid copepods | late, 40 copepodids | mid, 6 adults | 6 adults |
| Fairy shrimp | mid, hatch; 2 nauplii | early, 0.3 adults | 0.3 adults |
| Daphnia | late, hatch; 2-5 young | 2-5 adult; 1-3 young of the year | 2-5 adults |
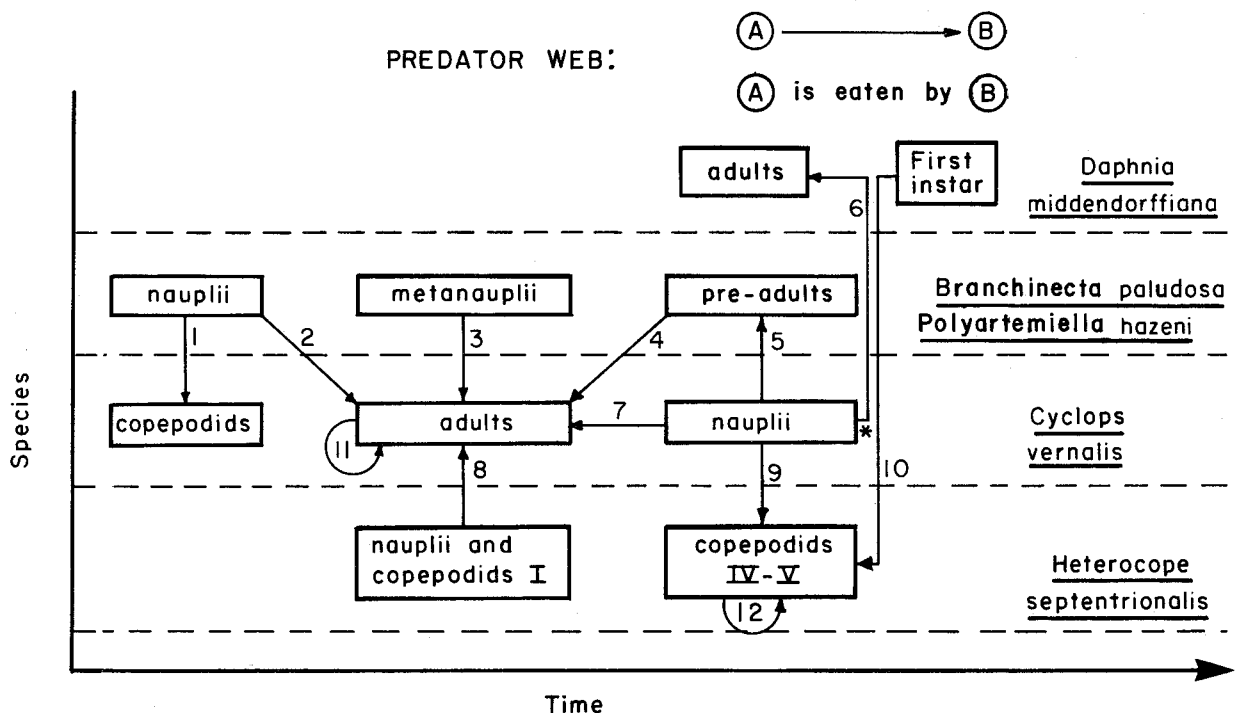


Figure 19. Predatory web of the planktonic crustacea in Pond C, Barrow (Stross et al. 1980).

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Table 11. Sizes of predator and prey and predation coefficients for the inter-
actions shown in Figure 19 (Stross et al. 1980, modified from Dodson 1975).

| Experiment dates | Predator length (mm) | Prey length (mm) | K value[a] | Interaction[b] |
|---|---|---|---|---|
| June 20 | 1.08-1.17 | 1.23 | 0.0040[c] | 1 |
| June 20 | 1.50 | 1.23 | 0.0145 | 2 |
| June 26 | 1.50 | 1.67-3.42 | 0.0101 | 3 |
| July 3 | 1.50 | 2.53-4.16 | 0.0051 | 4 |
| July 6 | 5.33-6.66 | 0.28-0.80 | 0.0225 | 5 |
| July 12 | 2.32-2.92 | 0.32-1.08 | 0.0205 | 6 |
| June 30 - July 3 | 1.50 | 0.28-0.68 | 0.100 | 7 |
| June 26 - 30 | 1.50 | 0.66-0.80 | 0.0722 | 8 |
| July 4 - 12 | 2.20-2.66 | 0.28-1.08 | 0.250 | 9 |
| July 12 | 2.32-2.92 | 0.32-1.08 | 0.236 | 10 |
| July 12 | 1.50 | 1.50 | 0.0026 | 11 |
| July 13 | 2.25-2.66 | 2.25-2.66 | 0.0144 | 12 |

[a] K = predation coefficient, liters day$^{-1}$.
[b] Interactions are those shown in Figure 19.
[c] An underestimate, because at least half the copepodites were the nonpredaceous
C. strenuus.

with a smaller quantity of particulate
detritus (poor quality food). This
hypothesis was proposed by M. C. Miller
and R. J. Daley (in Stross et al. 1980),
who noticed that the maximum zooplankton
mass (a measure of production) in a pond
during one year was highest when the POC
(particulate organic carbon) was lowest
(Figure 20). They believe that the algal
and bacterial carbon mass is about the
same from year to year (100 mg liter$^{-1}$)
but that the POC (mostly poor quality
food) changes drastically from one year to
the next (250-800 mg C liter$^{-1}$). Daphnia
have to filter all the particles making up
the POC and thus obtain fewer algae and
bacteria in years when the POC is high,
because their food handling apparatus is
clogged with POC. Certainly the
correlation is excellent, but it is
impossible to determine if the zooplankton
were abundant because the POC was low or
if the POC was low because the zooplankton
was abundant.

In any case, the zooplankton do not
appear to be limited by the cool summers,
at least not directly. As discussed in
Section 3.1, however, the low temperatures
may well ultimately control productivity
by the effect on phosphorus regeneration.

3.5 BENTHIC ANIMALS

The larger benthic animals, mostly
insects, are extremely important to the
ecology of the ponds. Not only is their
biomass and productivity larger than those
of any other group of animals, but they
also continually change the structure of
the sediments by their feeding and
burrowing. The circulation of water
through their burrows mixes oxygen into
the sediment and increases the exchange
of dissolved substances. The benthic
animals also eat zooplankton, microfauna,
benthic algae, and each other and are in
turn food for birds and even zooplankton
(see Butler et al. 1980 for a detailed
discussion).

In the center of the ponds (Figure
21), the dominant animals are Chironomidae
(midge larvae) such as Chironomus,
Procladius, and Tanytarsus; oligochaete

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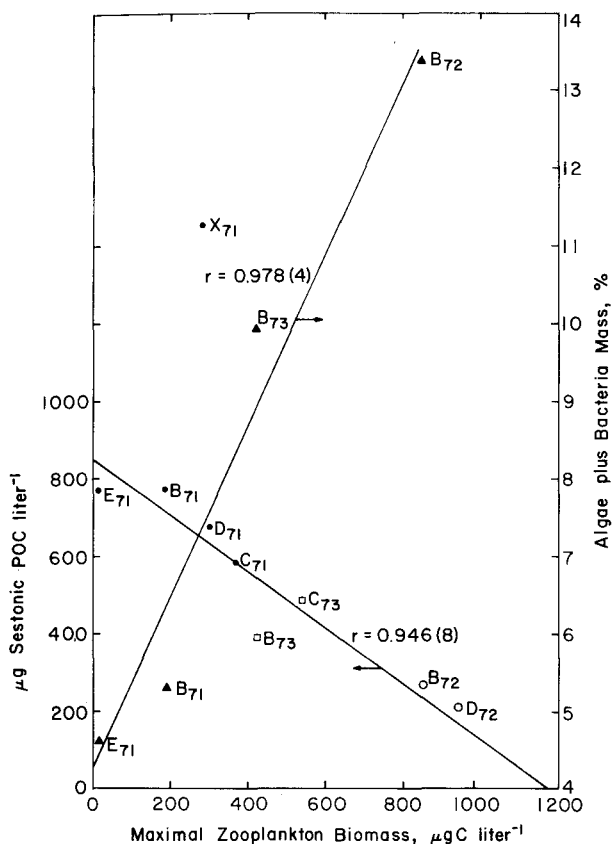
Figure 20. POC and percent algae and bacteria as a function of zooplankton density in Barrow ponds, 1971-1973. The value for Pond X in 1971 was omitted from the regression as it was heavily fertilized with phosphorus (from Stross et al. 1980). The letters are pond names, subscript is the year, and the triangles refer to the four points for the right-hand axis.

worms (Tubifex) account for the remainder of the biomass (5-25%). The large (3-4 cm) tadpole shrimp (Lepidurus), is present at about 1 m⁻². Along the edge of a pond, among the emergent plants, are found caddisflies (Limnephilus and Micrasema), a stonefly (Nemoura), predaceous dytiscid beetles (Agabus and Hydroporus), chironomids (Corynoneura, Paratanytarsus, and Trichotanypus), a mite (Libertia), an enchytraeid worm (Propappus), a snail (Physa), and a turbellid worm. Ponds further inland from the coast may also contain amphipods and pelecypod clams (Bergman et al. 1977). In all ponds the insects and molluscs are so large that

their mass outweighs the chironomids along the edge of the ponds, at least on an areal basis.

Most of the benthic animals in the pond are detritivores and most of these are deposit feeders. Within the chironomids there are several types of feeders including carnivores. Because the aquatic plant zones make up only a small percent of the pond area, the chironomids are by far the dominant group and will be considered in more detail along with the tadpole shrimp.

Over 36 species of chironomids have been collected from the Barrow ponds. Several of these have adapted to the windy environment by dispensing with the normal adult swarming behavior. Instead, mating takes place on the pond surface in early to mid-July. For all species, egg are laid below the water surface and larvae hatch within 3 days (at 15°C) to 14 days (at 5°C). The larvae then take years to pass through four instar stages to a pupal stage and then emerge as adults. Males of most species form aerial swarms and mating and egg laying quickly occur. When temperatures begin to fall in the late summer, the larvae spin cocoons and spend the winter frozen in the mud. The whole development cycle in these arctic ponds can occur as rapidly as 2 years or as slowly as 7 years (in temperate ponds it takes a few weeks). The life cycle of Chironomus pilicornis is illustrated in Figure 22; the IV instar, pupae, and adults are large (pupae are 16-18 mm long) and are harvested to some extent by birds.

The larvae occupy the top 6 cm of sediments with most in the top 2 cm. Total numbers of larvae can reach 15,000 m⁻² and up to 5,000 adults m⁻² can emerge each year. Estimates of benthic-insect production are about 1 g C m⁻² yr⁻¹, well within the range for temperate-zone midge populations.

Within the chironomid community there is a diversity of trophic types. Most are detritivores and, like Chironomus, feed on material either gathered from near the surface of sediments or filtered from the water with nets. Trichotanypus and Corynoneura feed on fine detritus and

## Peripheral Macrophytes

d) Agabus sp. (adult)
e) Hydroporus sp. (larva)
o) Physa sp.
a) Limnephilus sp.
n) Tubifex sp.
**Pond Center**
q) Lepidurus arctica
k) Tanytarsus inaequalis
l) Libertia sp.
b) Micrafema scissum
p) Turbellaria
c) Nemoura arctica
j) Procladius vesus
h) Trichopanypus alaskensis
f) Corynoneura sp.
g) Paratanytarsus penicillatus
i) Chironomus pilicornis
m) Propappus sp.

Corex / arctophila
Thawed Mud
Permafrost
Depth, cm
0
50
100

Figure 21.   Habitats  and   principal  taxa  of  benthic  animals  in  a  tundra  pond   (adapted from Butler et al. 1980).

algae adhering to the vascular plants. One chironomid, Procladius, is the most common invertebrate predator. There are 900 to 1800 Procladius m$^{-2}$ in the pond centers; each eats one Instar III chironomid every 2 days. This is about 300-600 prey day$^{-1}$ for a Barrow pond.

It is amazing that these midges are able to do so well in these arctic ponds. What are their adaptations to this environment? One adaptation, already mentioned, is the reduction in the aerial swarming behavior because of the windiness of the Arctic Coastal Plain. Another adaptation, perhaps a preadaptation, is the ability of the larvae to survive the winter frozen in the sediments. However, there are limits

even to this, as Scholander et al. (1953) found that larvae from Barrow did not survive temperatures below about -30°C. In the laboratory, Butler et al. (1980) found that larvae would not grow and molt at 5°C but would at 10°C; thus, there is a threshold for these Barrow animals, but it is also true that certain species are adapted to even colder summer temperatures and grow and emerge from Char Lake, a deep arctic lake that does not thaw every year (Welch 1976). The conclusion must be that these chironomids are well adapted to the cold winters and the cool summers.

It may also be the case that these midges do well because some predator is absent. Procladius is certainly there, but perhaps the absence of fish or dragon-

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fly larvae allows a relatively high percent of the larvae to survive.

Ultimately, the general level of production of chironomids may be set by food availability resulting from the primary production in the system. In fact, Welch (1973) found that the emerging insect biomass is a constant proportion (0.6%) of the total primary production in lakes. If the primary production value of 50 g C m$^{-2}$ yr$^{-1}$ is used, and this

is 80% vascular plants (Alexander et al. 1980), then chironomid production of 0.2-0.4 g C m$^{-2}$ is 0.4 to 0.8%. This agrees with Welch's constant.

The source of the food for chironomids is difficult to determine. These larvae are so large that they cannot selectively devour the benthic algae and bacteria which make up, respectively, 0.06% and 0.17% of the organic matter of the sediments. The feeding rate of the
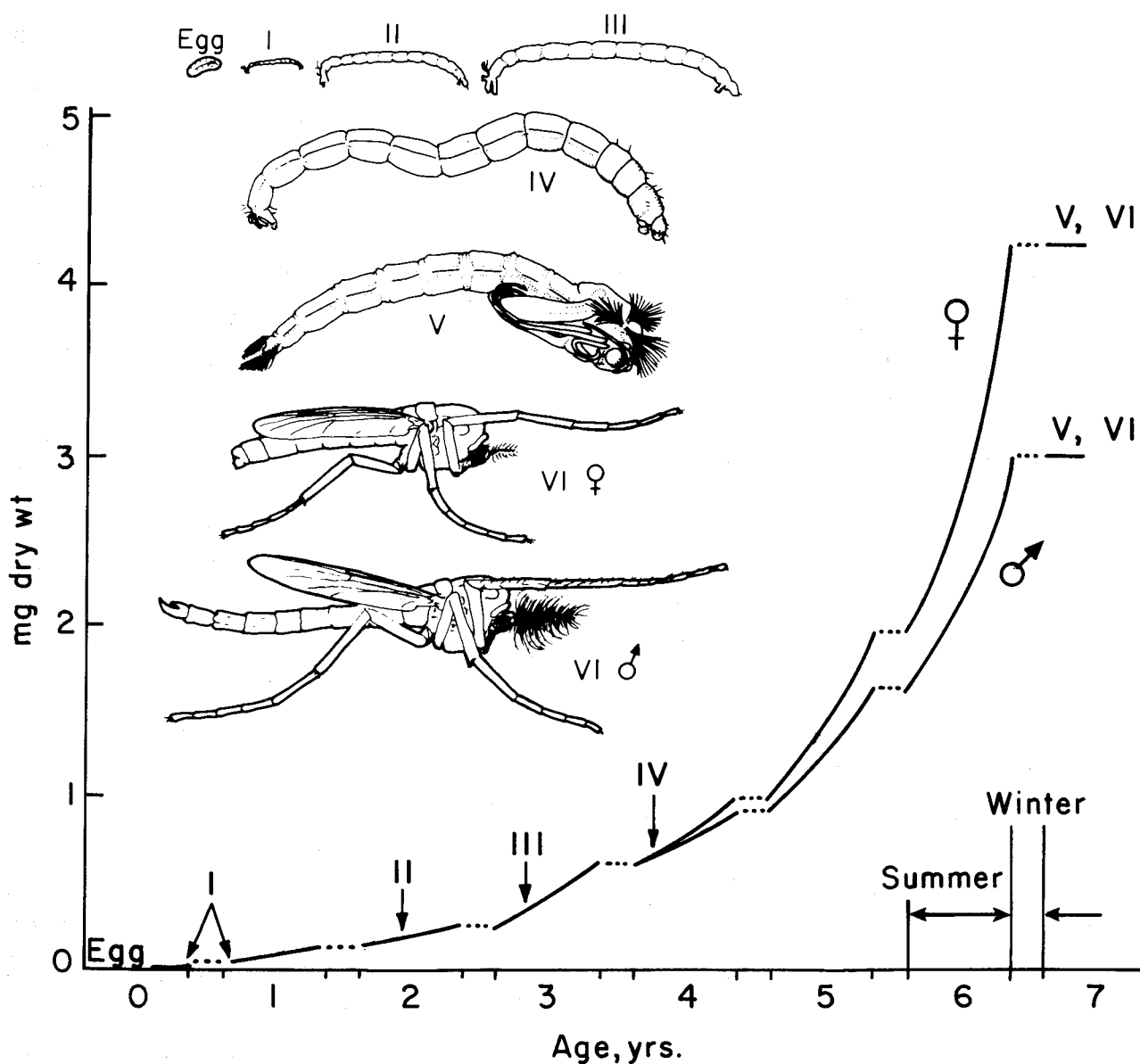


Figure 22. Life cycle of Chironomus pilicornis. The arrows indicate the time of molting to the next instar (Butler et al. 1980).

chironomids is 7.5 cm$^3$ m$^{-2}$ day$^{-1}$, measured by the incorporation of $^{32}$P-labelled detritus. Yet this 7.5 cm$^3$ contains only 0.21 mg of algal organic carbon and 0.6 mg of bacterial carbon. This is less than 4% of the carbon requirements of the larvae. The conclusion is that the chironomid larvae must get a large proportion of their food from detritus. One source of this detritus is the vascular plants along the edge of the pond, but the link here is based only on the production rates; there is enough production by these plants to support the chironomid production.

A second source is the peat in the sediments which was laid down when the pond site was land many thousands of years ago. Support for this theory comes from the work of Schell (1983), who determined from $^{14}$C dates that the average age of peat of the Arctic Coastal Plain is 8,100 years while the Carex and Arctophila have the same $^{14}$C content as the modern atmosphere. The surface sediments of two large oriented lakes and particulate carbon from the Colville River had ages of 2,000 to 3,000 years He also found that an oldsquaw duck had an apparent age of 1,300 years shortly after leaving its pond breeding area in early August. Schell thought it likely that the bird was eating organisms (insect larvae?) that had obtained carbon and energy from the old peat. The theory is interesting and will be tested soon when Schell is able to measure the $^{14}$C ages of chironomids and other detritivores.

A very large benthic crustacean, the tadpole shrimp (Lepidurus arcticus), inhabits only bodies of water with no fish. The adult looks very much like a miniature horseshoe crab. In temperate regions it is limited to ephemeral ponds; on the Arctic Coastal plain it inhabits ponds and shallow lakes. This animal is important in the pond because it moves continuously in the top few centimeters of sediment at an average speed of 10 cm min$^{-1}$ and thus mixes the sediment. Stross et al. (1980) calculated that during August these animals mix all the sediments of a pond each day. The life history of the tadpole shrimp is like

that of the fairy shrimp; they both over-winter as eggs and have but a single generation per year. Eggs hatch in late June and planktonic nauplii are found in the water until early July (Table 12). Then at the time of molt to Instar V the animals move into the sediment and become very difficult to sample. When they reappear at the surface of the sediment in early August, they have grown from 2.6 mm to 17 mm in length and the abundance has dropped by 95%. Nothing is known about the cause of this mortality but it is an important control on production. In mid-August, animals longer than 17.3 mm begin to carry 30-80 eggs internally. Each animal is self fertilizing. One to three eggs at a time are carried externally for 3 days and finally released to the sediments. About 20 eggs are deposited by the time of freeze in mid-September.

When they reappear at the surface of the sediments, the animals' sizes are indirectly related to the area and depth of the body of water (Table 12). This is caused by water temperature; animals are largest in the shallow ponds where the hatching date is early and water temperature high compared to lakes.

The planktonic nauplii are not effective filter feeders, so are likely predaceous. The same is true for the preadult sediment-dwelling stage but the only firm data comes from experiments with adults. These preyed on large zooplankters but their preferred prey was flatworms. Butler et al. (1980) concluded that the production of Lepidurus is only 0.011 g C m$^{-2}$ yr$^{-1}$. Yet, top carnivores often do have effects and the tadpole shrimp should not be dismissed as an insignificant curiosity.

## 3.6 THE DETRITAL FOOD WEB

As the emergent plants and the algae grow, they release dissolved organic matter (DOC). When plants and algae die, about 20-40% of their organic matter is leached as DOC within the first week or so, and the remaining particulate organic matter (POC) is slowly broken down by the enzymes of bacteria and fungi. The food web that utilizes the DOC and POC from these sources is called the detrital web.

Table 12. Mean length (mm) and density (individuals m$^{-2}$) of <u>Lepidurus arcticus</u> in Pond A (PA), North Meadow Lake (NML), and North Meadow Pond (NMP) in 1973 (Butler et al. 1980).

| Date of observation | PA | | NML | | NMP | |
|---|---|---|---|---|---|---|
| | Length | Density | Length | Density | Length | Density |
| June 27 | 1.96 + 0.04 | 14.6 | | | | |
| June 29 | 1.93 ∓ 0.03 | 14.6 | | | | |
| July 2 | 2.44 ∓ 0.07 | 30.6 | | | | |
| July 4 | 2.45 ∓ 0.19 | 30.6 | | | | |
| July 5 | 2.62 ∓ 0.05 | 2.0 | | | | |
| July 30 | | | 6.79 + 0.45 | 7.0 | | |
| Aug. 3 | 17.16 + 0.72 | 0.3 | | | | |
| Aug. 6 | | | 10.75 + 3.26 | N.D. | | |
| Aug. 8 | | | | | 27.78 + 1.16 | 0.12 |
| Aug. 11 | 18.61 + 0.59 | 0.5 | | | | |
| Aug. 13 | | | 15.89 + 1.74 | 7.3 | 28.94 + 3.73 | 0.15 |
| Aug. 16 | 21.45 + 1.59 | 1.4 | 21.07 ∓ 1.04 | N.D. | | |
| Aug. 20 | 24.56 ∓ 1.66 | 1.6 | 21.96 ∓ 3.06 | 7.3 | 31.30 + 3.51 | 0.07 |
| Aug. 24 | 25.10 ∓ 1.79 | 1.3 | | | | |
| Aug. 25 | | | | | 33.27 + 1.67 | 0.06 |
| Aug. 26 | 25.63 + 2.64 | 1.3 | | | | |

The bacteria and fungi have one characteristic that makes it difficult to study their ecology, and that is their ability to turn their activity off and on. For this reason, their presence does not mean that they are respiring. Another problem is that all the species look alike under the microscope and only a small proportion (less than 1%) of those seen will grow in the laboratory. The ecological studies in these ponds are really studies of what the whole community of microbes is doing.

In the Barrow pond studies (Hobbie et al. 1980) the numbers of bacteria in the water column were mostly between 2 and 3 x 10$^6$ ml$^{-1}$ throughout the summer except for a rise to 4-6 x 10$^6$ in early August (Figure 23). However, this rise may be the result of stirring of the sediment by wind. This early August population peak corresponds to 2-5 mg C m$^{-2}$. Peaks in numbers and biomass were observed in the sediment in June and in late July; numbers were 1-3 x 10$^{10}$ cells (g dry wt)$^{-1}$, or around 1.3 g m$^{-2}$ to a depth of 5 cm (the amount per square meter is about 400 times higher in the sediments than in the water column). The early season peak of numbers in the water column is caused by bacteria from the soil in the meltwater entering the pond. An early season peak in the sediment reflects a burst of microbial activ-
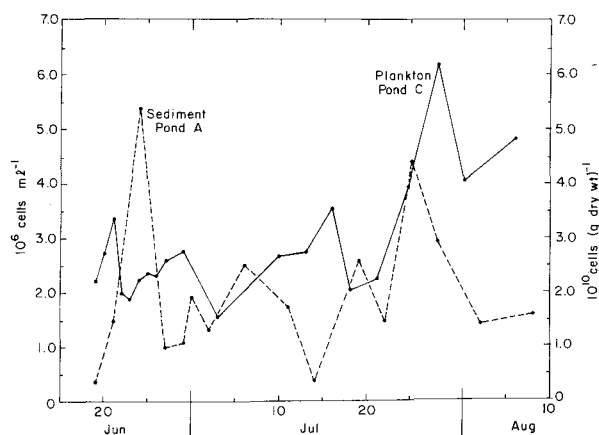


Figure 23. Numbers of bacteria in the sediment of Pond A and the plankton of Pond C, 1973 (from Hobbie et al. 1980).

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ity immediately after the thaw. This may be caused by organic compounds released from dead microbes during the freezing and thawing. These numbers for the water and sediment are slightly high compared with values from temperate lakes (10-20%).

Fungi are also present in the sediments of the ponds A single direct count by G. Laursen (quoted in Hobbie et al. 1980) revealed 1000-1700 m of hyphae per gram dry weight of sediment at 1-2 cm depth and 140-300 m at 6-7 cm. This translates into a carbon content of 3.5 g $m^{-2}$, or 3.3 times the bacterial biomass. The value is similar to those for temperate soils, but there have been no other counts made for ponds anywhere.

One measurable effect of microbial activity is the decomposition of the leaves of Carex aquatilis, the dominant primary producer of the ponds. This was measured in the Barrow ponds by incubation of leaves in litter bags made of nylon mesh (Hobbie et al. 1980). By the end of the first summer (8 weeks of actual incubation time) 75.6% of the leaves remained (Table 13). At the end of the fourth summer, the leaves were completely decomposed. Other types of experiments showed that about 25% of the loss was by leaching of DOC, 16% by microbial action (hydrolysis), and the rest (59%) was lost by breaking up into very fine POC (trituration). These fine particles are later broken down by microbes, eaten by insect larvae, or incorporated into the sedi-

ments. Compared with rates in temperate ponds, the decomposition is slow but can be explained by the short period of microbial activity (only 3 months per year) and the low temperatures.

A larger scale measure of microbial activity is the respiration rate of the sediment community. Here, the rate of production of $CO_2$ from the entire community is measured by the incubation of cores and partitioned into the microbial and nonmicrobial parts. Miller and Reed (1975) found that there was 2.5 times more respiration in the plant stands than in the center of the pond, apparently caused by root respiration or the increased decomposition caused by the addition of organic matter (dead roots) into the sediment. Total respiration averaged 20 g C $m^{-2}$ $yr^{-1}$ over the entire pond (3 years of measurements). The chironomid respiration was 3.0 g C $m^{-2}$ $yr^{-1}$, benthic algal respiration was 1.5 g C $m^{-2}$ $yr^{-1}$, and microbenthos about 1.4 g C $m^{-2}$ $yr^{-1}$. The remainder, 14.1 g C, was mostly bacterial respiration but some root respiration may also have occurred.

The total respiration in a Barrow pond was also calculated by measuring the movement of $CO_2$ from the water to the air. Coyne and Kelley (1974) used gas analysis of $CO_2$ to establish the partial pressure gradient from the water to the air (nearly 400 ppm) and the evasion coefficient (the rate of movement of $CO_2$ from the water to the air per atmosphere of gradient). They

Table 13. Time course of the percent of decomposition of Carex aquatilis leaves incubated in 0.02 mm nylon mesh bags in a Barrow pond (Hobbie et al. 1980).

| Incubation time (yr) | Fraction of initial weight remaining (%) | Loss by leaching (%) | Loss by hydrolysis (%) | Loss by trituration (%) |
|---|---|---|---|---|
| 1 | 70.5 | 20.7 | 8.8 | 0 |
| 2 | 59.0 | 4.0 | 7.4 | 0 |
| 3 | 23.9 | 1.0 | 0 | 34.7 |
| 4 | 0 | 0 | 0 | 24.1 |

calculated the loss to be 45 g C m$^{-2}$ yr$^{-1}$. This is about twice the value derived from the sediment incubations, but does confirm the magnitude of the loss. In contrast to this 20-45 g, the loss from soil from a nearby wet meadow was 160 g C m$^{-2}$ yr$^{-1}$ (Flanagan and Bunnell 1980).

The annual production of bacteria was calculated by Hobbie and Rublee (1975) from respiration, changes in biomass, loss to predation, and methane production. They estimated a gross production of 22.5 g C m$^{-2}$ yr$^{-1}$ and a net production of 13.1 g C m$^{-2}$ yr$^{-1}$. The predation term was divided into 1.0 g C m$^{-2}$ yr$^{-1}$ of chironomid grazing and 2.0 g C m$^{-2}$ yr$^{-1}$ of microbenthos grazing.

In part because of the large amounts of bacterial production and the difficulty of accounting for its fate, a study was made at Barrow of the microbenthos and its effect on the sediment algae and bacteria (Fenchel 1975). The microbenthos consists of protozoans (zooflagellates and ciliates) and micrometazoans (turbellarians, nematodes, harpacticoid copepods, ostracods, rotifers, gastrotrichs). These were almost all restricted to the upper 2 cm of sediment by the anoxic conditions in the deeper layers. In one pond (Figure 24) the small zooflagellates were numerically the most important part of the microfauna ($10^{10}$-$10^{11}$ m$^{-2}$) while micrometazoans were present at $10^5$-$10^6$ m$^{-2}$; however, the biomasses of the two groups were equal. Nematodes, rotifers, and harpacticoid copepods have approximately equal numbers at 20-40 x $10^3$ m$^{-2}$. These values are typical of temperate marine and freshwater shallow sediments.

Most of the grazing of bacteria is by zooflagellates and most of the grazing of algae is by the micrometazoa (Figure 25). All of the grazing removes only 1% of the biomass of bacteria and algae in the sediments per day; this is about 20% of the bacterial and 5% of the algal daily production so grazing may exert some control on these populations.



Figure 24. Numbers and biomass of zooflagellates, ciliates, and micrometazoa in the sediment of Pond B, Barrow (from Hobbie et al. 1980).
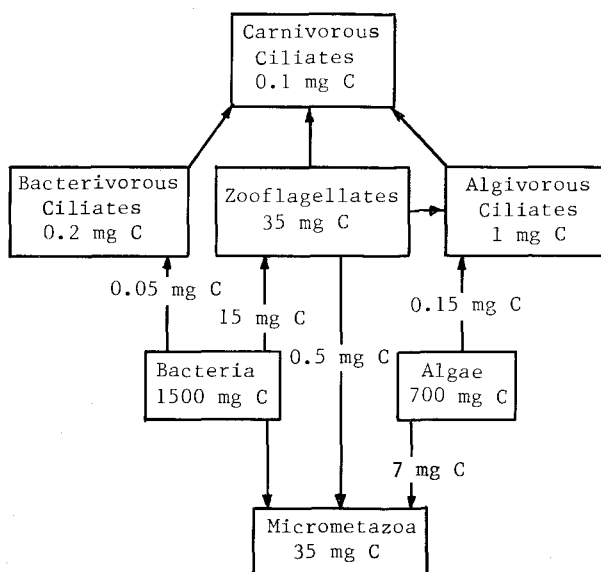


Figure 25. Carbon flow through the protozoans and micrometazoans of the sediment of a Barrow pond. Units are mg C m$^{-2}$ day$^{-1}$ for the fluxes and mg C m$^{-2}$ for the standing crops (from Hobbie 1980b after Fenchel 1975).

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# CHAPTER 4.
## PRODUCTION AND CARBON FLUX IN A COASTAL POND

There are a number of approaches to ecological studies of wetlands such as the Arctic Coastal Plain. Results of some of these approaches, such as descriptions of environmental influences, descriptions of the roles of individual populations, or the determinations of factors controlling populations, have been presented in the previous chapters. The carbon flux of an ecosystem is also a useful way to describe the ecology of wetlands. It has the advantage that there are internal checks of the accuracy of measurements; the carbon moving through any part of the ecosystem must agree with the amount available from lower trophic levels. It also has the advantage that it forces ecologists to examine parts of ecosystems that are difficult to work on or are otherwise unpopular or unglamorous. This is the reason that, in the 1960's, limnology studies at Barrow were devoted to the zooplankton and phytoplankton whereas the intensive studies in the early 1970's focused on the benthic algae, microbes, and chironomids.

The values for production or net growth of microbes, plants, and animals in a single Barrow pond (Pond B) are summarized in Table 14. However, the production of fungi is missing and it must be at least equal to that of the bacteria. Primary production is dominated by the vascular plants, which are Carex aquatilis in Pond B. The value in Table 14 is only one-third of the production in the plant stands as the Carex occupies only one-third of the pond. Still, it is amazing that Carex is able to achieve the same productivity as temperate-zone plants.

There is no insect herbivore in the pond that grazes on the Carex. As a

Table 14. Annual C production (g C m$^{-2}$) of Pond B communities at Barrow (Hobbie 1980b). The values are for the entire pond divided by the pond area.

| Type of community | Production (g C m$^{-2}$) |
|---|---|
| Phytoplankton | 1.1 |
| Benthic algae | 8.4 |
| Vascular plants | 96 |
| Zooplankton | 0.2 |
| Benthic animals | 1.65 |
| Microbenthos | 0.2 |
| Planktonic bacteria | 0.01 |
| Benthic bacteria | 8-20 |
| Protozoa | 0.3 |

result, all of the production enters the detrital food web. Production of benthic animals and of bacteria is high; it is not known how much the benthic animals use the high-quality food resource of the benthic algae and how much they use the plant detritus directly. As noted earlier, Schell (1983) believes that the benthic animals are able to use some of the ancient peat deposits for food.

In contrast to the high productivity of the plants and the detrital food web, the planktonic food chain is low in productivity. Algal production is low in the water column and this, in turn, leads to low zooplankton production.

Ultimately, almost all of the carbon fixed by both algae and vascular plants is decomposed by microbes. One might think that the detailed measurements of

the major production and decomposition processes would allow a determination of whether or not the Pond B sediments accumulated organic matter during the IBP study period. However, it is clear that belowground processes are the dominant ones in this pond and the accumulation and release of carbon in the roots of Carex is poorly known. This uncertainty, plus the normal +10% or so errors in any biological measurement, make it impossible to say if the estimates of two large

numbers, production and decomposition, are significantly different. Thus, the question about the possible accumulation of organic matter in the sediments cannot be answered despite the detailed IBP study.

Another way to look at the various interconnections within this pond ecosystem is by a carbon flux diagram (Figure 26). This type of diagram illustrates how fast various stocks are turning over and their relative sizes. Similar
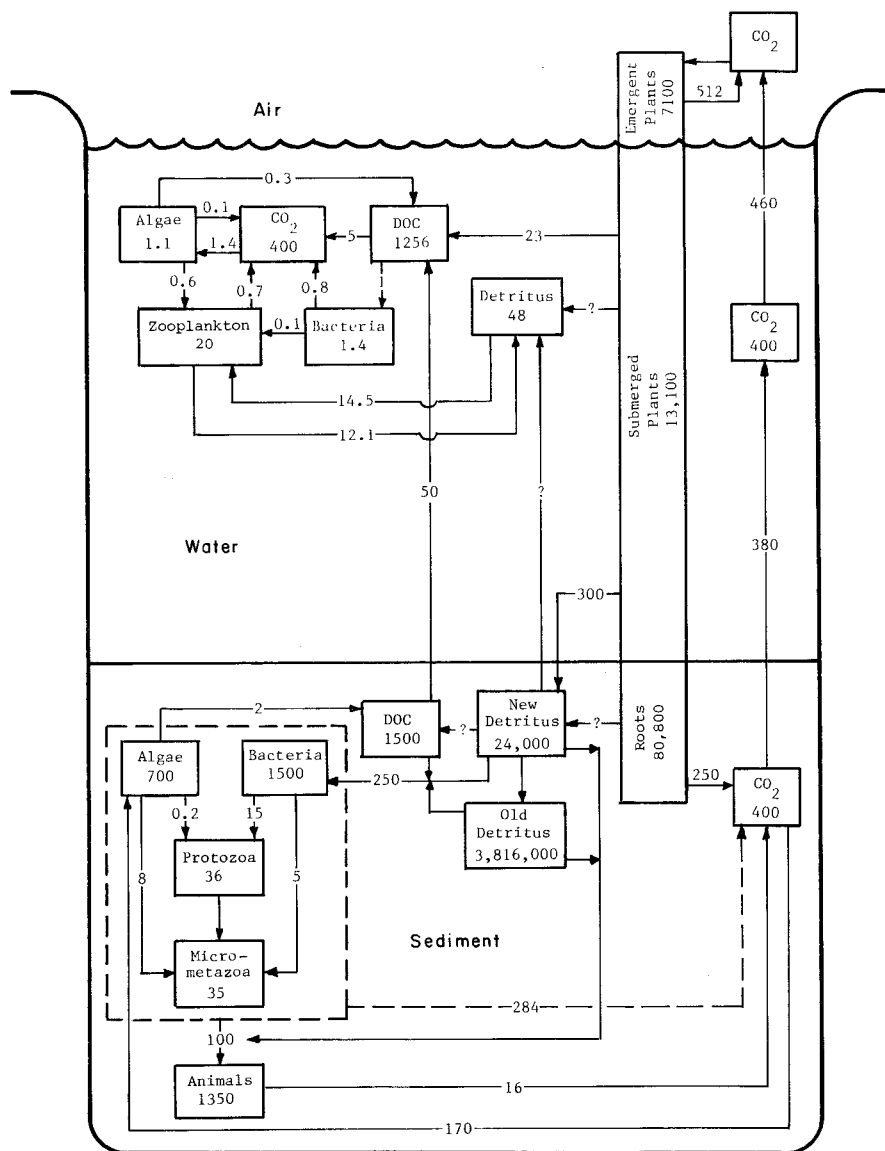


Figure 26. Carbon flux through a typical tundra pond. All data were calculated for a single day, 12 July 1971. On this date the average depth of the water was 10 cm and the depth of the sediment was taken as 5 cm. Units of the standing crop (in boxes) are mg C m$^{-2}$ and of transfer rates (arrows) are mg C m$^{-2}$ day$^{-1}$ (Hobbie 1980b).

diagrams for this tundra pond were published for phosphorus and nitrogen (Hobbie 1980b).

The flux diagram immediately confirms that processes related to the Carex dominate the carbon and energy flux of this pond. For example, the two largest fluxes of carbon in the water column are the release of DOC from the submerged leaves and stems of Carex and the transfer of DOC from the new detritus of the sediment surface to the water column. In the sediment, the carbon is transferred from the plant by excretion from roots as DOC (very difficult to measure), by death of root hairs and small roots, by death of larger roots, and by root respiration. Little is known of these transfers from the roots because in any measurement in the field it is impossible to separate microbial from root activity. In the laboratory the conditions are so artificial that the rates of root growth, root hair death, or release of DOC may be experimental artifacts. Root respiration is undoubtedly a large part of the total sediment respiration but the exact value is uncertain.

The best known part of the carbon flux is the transfer from the water to the air. (In Figure 26 it is 460 mg C m$^{-2}$ day$^{-1}$.) As mentioned in Section 3.6, the partial pressure of $CO_2$ was measured continuously in the pond water and consequently a continuous record of efflux from a Barrow pond was calculated (Coyne and Kelley 1974). The total, 45 g C m$^{-2}$ yr$^{-1}$, is less than the vascular plant production of 96 g C m$^{-2}$ yr$^{-1}$ (Table 14). The conclusion is that the pond sediments are likely to be accumulating some organic matter each year. This does not rule out some use of the old peat.

The major part of the metabolic activity of the pond biota, aside from that in the Carex, is in the sediments and in the organisms of the detrital food web (Figure 26). This activity, as shown by carbon flux, is driven by the energy from the decomposition of Carex as well as by the production of the benthic algae. The detritus provides a tremendous reservoir of food for animals and a steady supply of nutrients for the benthic algae and for

the Carex. The flux diagram also reveals that the algae and bacteria of the sediments have large biomasses but low rates of growth per unit. Average generation times may be about 7 days. Despite these relatively large biomasses of algae and bacteria, the kilogram quantity of detritus is so great that larger animals use large amounts of this low quality food. Small animals such as protozoans and nematodes, can select the high quality algae and bacteria as food.

The contrast between the sediment and water divisions of the pond ecosystem is dramatic (Figure 26); the living mass of organisms and their activity are 150 times higher in the sediments than in the water. The amount of detritus in the water is very low, but this particulate matter moves back and forth from water to sediments depending on the wind-driven turbulence. One material that is present in about the same quantity in both water column and in the interstitial water of sediments is the DOC. The turnover of a very small fraction of this DOC was measured for the plankton; this rapidly cycling fraction is probably about 20 mg C out of the 1,250 mg C m$^{-2}$, or about 2%. The remainder of the DOC is probably biologically inert and this is the reason that the concentrations are so similar in the water and in the sediments.

The planktonic part of the pond ecosystem is strongly affected by the sediments. For example, the planktonic bacteria obtain an important portion of the DOC they use from the sediment detritus. This particular link is confirmed by comparison of the bacterial activity and phytoplankton productivity in ponds and lakes around the world (Hobbie and Rublee 1975); the bacterial activity in the Barrow ponds is at least 10 times higher than expected from the algal production. Another important link could be the feeding of zooplankters (Daphnia) at the surface of the sediment (Stross et al. 1980). However, the most important effect is through the sediment control of the concentration of phosphate in the water (Prentki et al. 1980); this results in a very low rate of planktonic production and carbon flux (Figure 26).

# CHAPTER 5.

## WETLANDS AND BIRDS

The birds that use the wetlands of the Arctic Coastal Plain are predominantly migratory and many are important game birds. These birds are at the top of both the grazing food chains and the detritus food chains, but have been omitted from the discussion up to this point because their biomass is insignificant per square meter. For example, if there are 50 birds $km^{-2}$ (Derksen et al. 1981), and each weighs 100 g (dry wt), then the bird biomass is about 2 mg C $m^{-2}$ or about the same insignificant amount as the planktonic algae in a pond. Yet, the somewhat rare animals at the top of the food chains can affect the structure of that chain by, for example, selectively preying on large organisms.

### 5.1 DISTRIBUTION AND ABUNDANCE OF BIRDS

The literature on the birds of the Arctic Coastal Plain has been recently reviewed by Derksen et al. (1981). They also give weekly censuses of birds for six sites (see Figure 1 for locations). Two of these sites, Singiluk and Square Lake, are inland near the foothills in flat to gently rolling terrain. Two are coastal (Meade River delta and Storkersen Point) and two are in a region of large lakes. The percentage composition of the wetlands at these six sites is given in Table 3.

The wading shorebirds, in particular the pectoral sandpiper and the dunlin, are the most abundant birds using the wetlands (Appendix 1). King (1970, quoted in Derksen et al. 1981) estimated that 4.6-4.8 million shorebirds made up 91-93% of the waterbirds in the National Petroleum

Reserve-A in July 1977 and 1978. (This is about 80% of the area of the Arctic Coastal Plain.) However, when they feed the wading shorebirds utilize the tundra itself and exposed sediments of temporary wetlands rather than the ponds or lakes.

Phalaropes, both red and northern, are the next most common group. These shorebirds eat the large planktonic and sediment animals stirred up by their characteristic behavior of swimming in tight circles in the shallow ponds.

Ducks make use of the ponds for food and for breeding. The most abundant is the pintail followed by the oldsquaw and the three species of eiders.

Geese are locally abundant but only the white-fronted geese and black brant breed in considerable numbers on the Arctic Coastal Plain. King (1970) estimated 50,000 white-fronts on the Arctic Slope, dispersed widely across the Coastal Plain. As many as 17,000 brant breed along the coast. Canada geese occur locally in the upper Colville River and Prudhoe Bay areas and Alaska's only snow goose colony is near the Sagavanirktok River delta.

### 5.2 BIRD ENERGETICS

Most of the food of the wading shorebirds is insects from the soil. MacLean (1980) calculated that food needs of the shorebirds at Barrow is about 0.1 g C $m^{-2}$ $yr^{-1}$; he believed the birds are so dependent upon the insects that the timing of breeding is determined by the emergence of adult dipterans. Prior to the emergence

of the dipterans, adult birds feed heavily on dipteran larvae from beneath the soil surface. About 40% of their prey is larvae and adults of the cranefly (Tipula carnifrons) and another 20% is two other cranefly species. About 23% of the total cranefly emergence is eaten by avian predators.

Another group of shorebirds, the red and northern phalaropes, eat the pond invertebrates. Both adult and larval chironomids and Daphnia are taken (Holmes and Pitelka 1968, Dodson and Egger 1980). The effect of this predation on the chironomids was thought to be small by Butler et al. (1980) but Dodson and Egger (1980) concluded that Daphnia populations and population dynamics could be affected. They studied the feeding of caged red phalaropes and found that the normal density of 2.5 birds per ha (at Barrow) would not affect the Daphnia populations. However, a flock of actively feeding phalaropes might remove so many of the large Daphnia that the population structure would shift to small species (similar to the effect of planktivorous fish). The only estimate of the food requirements of the red phalarope is $0.01$ g C m$^{-2}$ yr$^{-1}$, made by MacLean (1980). This is only a small percentage of the invertebrate production of $1.85$ g C m$^{-2}$ yr$^{-1}$ (zooplankton 0.2, benthic animals 1.65). While it is possible that a high concentration of birds in one place could have an impact, all the ponds ever sampled are dominated by the large zooplankton species so any drastic impact of these birds must be very localized.

Loons use the edges of ponds and islets for nesting, but arctic loons prefer large ponds with stands of Arctophila while red-throated loons prefer small, partially-drained basins (Bergman and Derksen 1977). These authors found that arctic loons fed their young pond invertebrates such as tadpole shrimp (Lepidurus), fairy shrimp, and caddis fly larvae (Trichoptera). In contrast, the red-throated loons carried marine fish, such as arctic cod, back to the young.

Geese and swans mostly graze on vegetation, especially rhizomes and young shoots. There have been only a few reports of food habits of these birds on the Arctic Coastal Plain; for example, Derksen et al. (1982) mentioned that Canada geese, white-fronted geese, and brant grazed on fine grasses and sedges adjacent to large lakes during their molt near Teshekpuk Lake (Figure 1).

## 5.3 WETLAND USE

The percentage use of the various classes of wetlands is given in Table 15. The table also indicates when the number of birds using a particular class of wetland was significantly greater than the number expected (based on the total area of wetlands and the area of the particular class). The following information is from Bergman et al. (1977).

CLASS I: Flooded Tundra. The primary use is by red phalaropes, although there was some use by pintails before and after their molt in July.

CLASS II: Shallow -- Carex. Most of the species in Table 15 occurred on Shallow--Carex ponds, but only adult oldsquaws and king eider hens with broods fed there and used the ponds significantly.

CLASS III: Shallow -- Arctophila. The shallow water and the extensive stands of the grass provided feeding habitat and cover. There was extensive use by pintails before and after the molt.

CLASS IV: Deep -- Arctophila. These were the principal habitats for all waterfowl except for white-fronted geese and pintails. Swans also nested next to this type of pond and used Arctophila wetlands for concealment. King eiders used these wetlands before, during, and after nesting and virtually all observations of adult spectacled eiders were on this class of wetland. Black brant and loons also used these wetland areas for nesting. There was also significant use by loons.

CLASS V: Deep -- Open. There was some use of these lakes by arctic loons after nesting, but most use was

Table 15. The locations of loons and waterfowl at Storkersen Point. Data are reported as percentage of the total sightings. Parentheses give the numbers of birds observed or the number of broods of the king eider (from Bergman et al. 1977). The chi-square values refer to differences between the observed numbers of birds using a wetland class and the numbers expected from the total numbers of birds if they were distributed across all classes according to the relative areas of the classes.

| | Flooded tundra (I) | Shallow Carex (II) | Shallow Arctophila (III) | Deep Arctophila (IV) | Deep open (V) | Basin complex (VI) | Beaded stream (VII) | Coastal wetland (VIII) |
|---|---|---|---|---|---|---|---|---|
| **Arctic Loon** | | | | | | | | |
| Pre-nest (31) | - | - | - | 52** | - | 36** | 6 | 6 |
| Nest (79) | - | 5 | 3 | 59** | 5 | 18 | 5 | 5 |
| Post-nest[a] (57) | - | 9 | - | 52** | 16* | 16 | 2 | 5 |
| **Red-throated Loon** | | | | | | | | |
| Pre-nest (55) | - | 2 | 3 | 22** | - | 73** | - | - |
| Nest (115) | - | 6 | 8 | 33** | - | 51** | 2 | - |
| Post-nest[a] (65) | - | 2 | 3 | 24** | 3 | 65** | 3 | - |
| **Black Brant** | | | | | | | | |
| Pre-nest (55) | - | - | - | 9 | - | 18 | - | 73** |
| Nest (22) | - | 9 | - | 91** | - | - | - | - |
| Post-nest[a] (12) | - | - | - | - | - | - | - | 100** |
| **White-fronted Goose** | | | | | | | | |
| Post-nest (189) | - | - | 3 | - | 94** | 3 | - | - |
| **Pintail** | | | | | | | | |
| Pre-molt (544) | 8 | 7 | 26** | 14 | 1 | 37** | 5 | 2 |
| Molt (270) | - | - | 6 | 2 | - | 92** | - | - |
| Post-molt (871) | 9 | 14 | 12** | 13 | - | 46** | 3 | 3 |
| **King Eider** | | | | | | | | |
| Pre-nest (23) | - | 14 | 7* | 30** | - | 39** | 3 | 7** |
| Nest (188) | - | 22 | 8* | 42** | 8 | 9 | 3 | 8** |
| Post-nest[b] (87) | - | 26 | 8 | 52** | 6 | 5 | - | 3 |
| Brood | - | 64** | 5 | 26** | - | 5 | - | - |
| **Spectacled Eider** | | | | | | | | |
| Pre-nest (20) | - | - | - | 90** | - | 10 | - | - |
| Nest (9) | - | - | - | 89** | 11 | - | 0 | - |
| Post-nest[b] (7) | - | - | - | 100** | - | - | 0 | - |
| **Oldsquaw** | | | | | | | | |
| Pre-nest (223) | - | 31** | - | 40** | 2 | 10 | 8* | 4 |
| Nest (261) | 1 | 28** | 3 | 36** | 10 | 9 | 10** | 3 |
| Post-nest[b] (345) | - | 5 | - | 9 | 85** | - | 1 | - |
| **TOTAL (3,763)** | 3 | 12 | 10** | 22** | 14** | 32** | 3 | 4 |

[a] Adults and young.
[b] Adults only.
* Chi-square value significant (P < 0.05).
**Chi-square value highly significant (P < 0.01).

by white-fronted geese and Canada geese during their wing molt in the last half of July and in August. Oldsquaws, females and broods, also gathered on deep-open lakes during their molt.

CLASS VI: Basin -- Complex. Pintails preferred ponds in these basins throughout the summer and spent much of their time feeding. King eider also used these ponds as gathering places for large flocks in early June. Both species of loon used these ponds for nesting and brood-rearing.

CLASS VII: Beaded Streams. All species of loons and ducks in the area occasionally used beaded streams.

CLASS VIII: Coastal Wetlands. These coastal lagoons and brackish ponds were mostly used by pintails, wigeon, and migrating black brant; also, black brant moved to coastal salt marshes a few days after their young hatched.

# CHAPTER 6.
## EFFECTS OF HUMANS ON WETLANDS

## 6.1 OIL-SPILL EFFECTS

The production of oil at Prudhoe Bay has stimulated research on effects of an oil spill on coastal plain wetlands. Because the intensively studied ponds at Barrow could be used as controls, an experimental spill was made in a pond in July of 1970 and the recovery followed for 7 years. (Details are given in Barsdate et al. 1980.)

The spill was four barrels of crude oil or 1.6 liter m$^{-2}$. The wind immediately moved the oil to the edge of the pond where most became trapped in the vegetation and litter. Some oil floated for about a month but by the end of the summer most of it had sunk. After several years at least half the oil was still present,

covered by debris and organic matter; it still welled up and created a scum when disturbed. After 5 years the oil remaining had virtually the same chemical composition as the oil in the fresh spill except for the loss of low molecular weight hydrocarbons.

The zooplankton community was the most strongly affected by the oil. A second test spill in 1975 revealed that fairy shrimp were all killed after 1 day, Daphnia after 3 days, and Heterocope after 5 days (Table 16). Daphnia and fairy shrimp did not return to the 1970-spill pond until 1976.

The phytoplankton community responded to the oil by a 50% reduction of primary productivity for several weeks followed by

Table 16. Sequence of disappearance of zooplankton species from Pond Omega following an oil spill of 0.24 liter m$^{-2}$ on 9 July 1975 (Barsdate et al. 1980).

| Species observed | Observed presence after spill[a] | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 7/10 | 7/11 | 7/12 | 7/14 | 7/16 | 7/18 | 7/21 | 7/23 | 7/29 |
| Fairy shrimp (both species) | X | O | O | O | O | O | O | O | O |
| Daphnia middendorffiana | X | X | X | O | O | O | O | O | O |
| Heterocope septentrionalis | X | X | X | X | X | X | X | X | X |
| Cyclops spp. | X | X | X | X | X | X | X | X | X |

[a] An "X" indicates that a representative of that species or group of species was found alive on that day. An "O" indicates that no individual of that species or group was found alive on that day. Source: O'Brien 1978.

an apparently complete recovery. There were, however, other changes and the dominant nanoplankton algae, Rhodomonas minuta, was replaced by Uroglena sp. (Figure 27). The Rhodomonas did not return to this pond until 1976, the same year the Daphnia and fairy shrimp reappeared (Federle et al. 1979). Other tests showed that this replacement is caused by the removal of the zooplankton, not by the toxicity of the oil. The exact mechanism of this interaction is unknown but it could be grazing pressure or the enhancement of the nutrient cycling rate by the zooplankton.

The spills had little effect on the numbers and production of chironomids but one genus, Tanytarsus, was nearly eliminated from the ponds. Beetles, caddisflies, stoneflies, and snails were also drastically affected; most of these animals live only in the plant beds and may have become trapped in the oil on plant stems. These insects were still absent 6 years after the spill.

There is also information on effects of crude oil on Carex from the studies of Walker et al. (1982) at Prudhoe Bay. The plants in wet sites were less susceptible than those of drier sites and all plants were much more affected by refined oil (gasoline and diesel fuel) than by crude oil.

When an oil spill is relatively light, as in these experiments at Barrow,
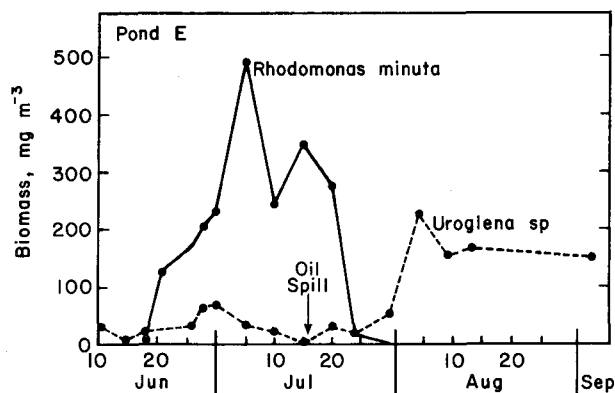


Figure 27. Biomass (wet weight) of Uroglena sp. and of Rhodomonas minuta in oil spill pond, 1970 (Barsdate et al. 1980).

the best treatment of a spill would be to absorb the floating oil (e.g., with straw or plastic sponge absorbers), then to flood the marsh to float the oil away from littoral plants, and then to absorb the floating oil again. The biota of the pond will recover in a few years with this simple treatment. Drastic cleanup measures are likely to induce greater changes in the ecology of these coastal plain ponds.

## 6.2 EFFECTS OF OFF-ROAD VEHICLES AND ROADS

Oil spills and physical destruction of wetlands are obvious and dramatic effects of human activity on the Arctic Coastal Plain. But there are also less obvious and subtle interactions as well and these produce serious local effects. The effect of various types of vehicles on the tundra surface illustrates the possible range of effects.

The smallest effect is produced by air cushion vehicles (ACV). The sequence of events begins with removal of standing dead leaves and stems and ends with an increase in plant production (righthand side of Figure 28). The change is well within the natural variation produced by lemming population highs.

A more noticeable change is triggered by balloon-tired vehicles (Rolligons). These have extremely large tires with low bearing pressure, yet the depression of the vegetation reduces insulation and leads eventually to an effect on plant productivity that takes 5 to 15 years to disappear (see lefthand side of Figure 28).

The most severe effect is a result of vehicles with tires or tracks driving across tundra. The organic layers overlying the mineral soil are compacted and the vegetation may be destroyed (center of Figure 28). Eventually, the ice in the permafrost may melt; the volume of soil decreases and a pond may form in the resulting depression. This thawing and formation of a depression has been called a thermokarst phenomenon; it is named after the limestone Karst region of the Dalmatian coast (Yugoslavia) where solu-

tion lakes are common. When vehicle tracks cross ice wedges, these may melt and ponds several meters deep may form. On slopes, vehicle tracks intercept sheet flow and stream channels may form. It may take centuries or thousands of years to form stable new communities (see Abele et al. 1978 for more information).

While new ponds are formed in this way, the conversion of shallow ponds and grass and sedge wetlands to muddy tracks and deep ponds is certainly a net loss of wildfowl habitat and food.

A different series of events ensue when roads are built. The roads are usually built of gravel and are 2 m thick (Figure 8). In the climate of the Arctic Coastal Plain, the center of the gravel becomes frozen and the road acts as a dam to normal drainage unless many culverts are provided. Klinger et al. (1983) identified snowbank formation, flooding, and road dust deposition as the main effects of roads on the tundra. For ponds, only flooding has been shown to have any significant effect during the few years of study; the main result of

```
                    ┌─────────────────────────────────────────────────────┐
                    │   Original terrestrial community in equilibrium      │
                    └─────────────────────────────────────────────────────┘
                                          │
                                    ┌──────────┐
                                    │  ACCESS  │
                                    └──────────┘
                                          │
                              ┌─────────────────────┐
                              │  Offroad vehicles    │
                              └─────────────────────┘

    ┌───────────────┐         ┌───────────────────┐          ┌───────┐
    │ Balloon tire  │         │ Wheeled and track │          │  ACV  │
    └───────────────┘         └───────────────────┘          └───────┘

    ┌───────────────┐                                    ┌───────────────┐
    │  Depressed    │         ┌───────────────────┐      │  Removal of   │
    │  vegetative   │         │ Soil compaction:  │      │ standing dead │
    │     mat       │         │depressed soil surface│   │  from canopy  │
    └───────────────┘         └───────────────────┘      └───────────────┘

  ┌───────────────┐     ┌──────────┐  ┌───────────────┐  ┌───────────────┐
  │Increased soil │     │ Modified │  │Increased soil │  │Slightly increased│
  │ temperature   │     │ drainage │  │ temperature   │  │ soil temperature │
  └───────────────┘     └──────────┘  └───────────────┘  └───────────────┘

   ┌───────────┐      ┌──────────┐    ┌───────────┐        ┌───────────┐
   │ Increased │      │ Erosion  │    │ Increased │        │ Increased │
   │   thaw    │      └──────────┘    │   thaw    │        │   thaw    │
   └───────────┘                      └───────────┘        └───────────┘

  ┌───────────┐                    ┌───────────────┐     ┌───────────┐
  │ Increased │                    │ Thermokarst   │     │ Increased │
  │ nutrient  │                    │ and ponding   │     │ nutrient  │
  │availability│                   └───────────────┘     │availability│
  └───────────┘                                          └───────────┘

┌───────────────┐        ┌───────────────────┐        ┌───────────────┐
│Increased plant│        │ Aquatic or emergent│       │Increased plant│
│  production   │        │    community       │       │  production   │
└───────────────┘        └───────────────────┘        └───────────────┘

   5-15 years            100's to 1000's of years          2-4 years

                    ┌─────────────────────────────────────────────────┐
                    │  New terrestrial communities in equilibrium     │
                    └─────────────────────────────────────────────────┘
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Figure 28. Impact of air cushion vehicles (ACV) and wheeled and tracked vehicles on the tundra of the Arctic Coastal Plain. The numbers are recovery times (Webber et al. 1980).

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flooding is likely to be the replacement of numerous and diverse shallow ponds and wetlands by larger and deeper water bodies that are of lower value for breeding birds.

The future effects of humans on the ponds and other wetlands that make up the Arctic Coastal Plain will depend greatly upon the amount of planning and control exerted by various State, local, and Federal agencies. At present, much of the Coastal Plain is under the jurisdiction of the Federal government. (As seen in Figure 1, the western part of the Coastal Plain is in the National Petroleum Reserve and the eastern part in the National Wildlife Range.) The North Slope Borough and the State of Alaska also control large areas. Minimal change will occur only if travel is restricted to roads and if roads are constructed with adequate culverts. The key to preservation of adequate and diverse habitat for wildfowl is the preservation of the permafrost and its natural insulating layer of vegetation.

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# APPENDIX

Species composition, status[a], and mean[b] seasonal densities (birds km$^{-2}$) of birds at Arctic Coastal Plain sites in 1977 and 1978[c] (from Derksen et al. 1980).

| | Large lake regime | | | | | Delta | | Near foothills | | | | Coastal | | |
| | East Long Lake | | | Island Lake | | Meade River | | Singiluk | | Square Lake | | Storkersen Point | | |
| | Status | 1977 | 1978 | Status | 1978 | Status | 1977 | Status | 1977 | Status | 1978 | Status | 1977 | 1978 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Common loon (Gavia immer) | - | | | - | | - | | - | | - | | CV | | |
| Yellow-billed loon (G. adamsii) | CV | | | CV | | CV | | UB | | UB | 0.1 | CV | | |
| Arctic loon (G. arctica) | CB | 1.5 | 1.2 | CB | 0.8 | CB | 2.1 | UB | 0.6 | CB | 1.5 | CB | 1.9 | 1.6 |
| Red-throated loon (G. stellata) | CB | 1.3 | 0.5 | UB | 0.1 | UB | 0.2 | - | | CV | | CB | 0.5 | 0.6 |
| Whistling swan (Olor columbianus) | UB | 0.2 | 0.2 | RV | | UB | 0.2 | RV | | RV | 0.2 | UB | 0.3 | 0.1 |
| Canada goose (Branta canadensis) | RV | 3.7 | 1.4 | RV | 6.6 | - | | CV | | CV | | UB | - | - |
| Black brant (B. bernicla) | CB | 5.4 | 9.1 | CB | 9.6 | CB | 0.3 | - | | - | | UB | 0.3 | 0.7 |
| White-fronted goose (Anser albifrons) | CB | 1.1 | 1.0 | CB | 0.9 | CB | 0.7 | CB | 2.7 | CB | 0.8 | CB | 1.0 | 2.2 |
| Lesser snow goose (A. caerulescens) | UB | | | RV | | RV | | CV | | - | | M | | |
| Mallard (Anas platyrhynchos) | CV | | | - | | CV | | - | | - | | CV | | |
| Pintail (A. acuta) | UB | 17.1 | 6.5 | RV | 2.3 | UB | 5.1 | CB | 3.2 | UB | 1.1 | RV | 14.1 | 6.2 |
| Green-winged teal (A. crecca carolinensis) | - | | - | | | CV | | - | | UB | | CV | | |
| American wigeon (A. americana) | CV | | | CV | | CV | | CV | | CV | | CV | | |
| Northern shoveler (A. clypeata) | CV | 0.1 | - | - | | CV | | CV | | - | | CV | | |
| Greater scaup (Aythya marila) | CV | | | - | | CV | | UB | 0.5 | CB | 0.8 | CV | | |
| Common eider (Somateria mollissima) | M | | | CV | | - | | - | | - | | RV | | |
| King eider (S. spectabilis) | CV | - | 0.3 | CV | 0.3 | CV | 0.1 | UB | 0.2 | CB | 0.2 | CB | 2.4 | 1.9 |
| Spectacled eider (S. fischeri) | CB | 0.6 | 0.5 | CB | 0.1 | CB | 0.3 | CV | | - | | UB | 0.2 | 0.2 |
| Steller's eider (Polysticta stelleri) | - | | | - | | - | | CV | | - | | - | | |
| Oldsquaw (Clangula hyemalis) | CB | 3.2 | 3.3 | CB | 2.3 | CB | 1.1 | CB | 3.5 | CB | 4.6 | CB | 2.3 | 1.8 |
| White-winged scoter (Melanitta deglandi) | - | | | - | | - | | - | | CB | 1.0 | - | | |
| Surf scoter (M. perspicillata) | CV | | | - | | - | | - | | CV | | CV | | |

Continued

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| | Large lake regime | | | | | Delta | | Near foothills | | | | Coastal | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | East Long Lake | | | Island Lake | | Meade River | | Singiluk | | Square Lake | | Storkersen Point | | |
| | Status | 1977 | 1978 | Status | 1978 | Status | 1977 | Status | 1977 | Status | 1978 | Status | 1977 | 1978 |
| Red-breasted merganser (Mergus serrator) | - | | | - | | - | | - | | CV | | CV | | |
| Marsh hawk (Circus cyaneus) | - | | | - | | - | | - | | - | | CV | | |
| Rough-legged hawk (Buteo lagopus) | CV | | | - | | - | | - | | CV | | - | | |
| Golden eagle (Aquila chrysaetos) | - | | | - | | CV | | - | | CV | | CV | | |
| Gyrfalcon (Falco rusticolus) | - | | | - | | - | | - | | CV | | - | | |
| Peregrine falcon (F. peregrinus) | CV | | | - | | - | | - | | CV | | CV | | |
| Willow ptarmigan (Lagopus lagopus) | UB | | | - | | UB | 0.1 | CB | 1.1 | CB | 3.8 | UB | | |
| Rock ptarmigan (L. mutus) | - | | | - | | - | | - | | RV | 0.1 | CV | 0.1 | - |
| Sandhill crane (Grus canadensis) | - | | | CV | | CV | | - | | CV | | CV | | |
| American golden plover (Pluvialis dominica) | CB | 3.5 | 1.6 | CB | 0.6 | UB | | UB | 1.3 | CB | 4.1 | CB | 5.4 | 4.7 |
| Black-bellied plover (P. squatarola) | CB | 4.4 | 1.1 | CB | 1.7 | UB | 6.3 | UB | 3.2 | CB | 2.8 | CB | 1.9 | 1.9 |
| Semipalmated plover (Charadrius semipalmatus) | - | | | - | | - | | - | | CV | | CV | | |
| Whimbrel (Numenius phaeopus) | - | | | - | | - | | - | | CV | | CV | | |
| Bar-tailed godwit (Limosa lapponica) | CV | - | 0.1 | - | | - | | UB | 11.2 | RV | 1.2 | CV | | |
| Buff-breasted sandpiper (Tryngites subruficollis) | UB | | | CV | | - | | - | | UB | 0.3 | CB | 0.6 | 3.7 |
| Stilt sandpiper (Micropalama himantopus) | CV | | | CV | | - | | - | | CB | 3.3 | RV | | |
| Long-billed dowitcher (Limnodromus scolopaceus) | UB | 4.0 | 1.5 | CV | 0.4 | UB | 3.7 | CV | | UB | 5.8 | RV | 1.2 | 0.8 |
| Ruddy turnstone (Arenaria interpres) | UB | - | 0.2 | UB | 0.3 | UB | 0.2 | - | | - | | UB | 1.1 | 2.4 |
| Pectoral sandpiper (Calidris melanotos) | CB | 36.3 | 18.5 | CB | 13.0 | CB | 22.9 | CB | 24.1 | CB | 11.6 | CB | 24.3 | 20.1 |
| Red knot (C. canutus) | - | | - | | | - | | - | | - | | CV | | |
| Dunlin (C. alpina) | CB | 12.8 | 16.0 | CB | 12.8 | CB | 21.1 | UB | 0.5 | CV | 0.2 | CB | 15.5 | 15.7 |
| Sanderling (C. alba) | - | | | - | | - | | - | | - | | CV | | |
| White-rumped sandpiper (C. fuscicollis) | - | | | - | | - | | CV | | - | | CV | | |

Continued

| | Large lake regime | | | | | Delta | | Near foothills | | | | Coastal | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | East Long Lake | | | Island Lake | | Meade River | | Singiluk | | Square Lake | | Storkersen Point | | |
| | Status | 1977 | 1978 | Status | 1978 | Status | 1977 | Status | 1977 | Status | 1978 | Status | 1977 | 1978 |
| Baird's sandpiper (C. bairdii) | RV | 0.1 | - | - | | - | | - | | - | | UB | 0.9 | 2.8 |
| Least sandpiper (C. minutilla) | - | | | - | | - | | CV | | - | | | | |
| Semipalmated sandpiper (C. pusilla) | CB | 6.3 | 3.1 | CB | 1.4 | CB | 7.0 | CB | 6.9 | CB | 15.5 | CB | 11.6 | 17.2 |
| Western sandpiper (C. mauri) | - | | | - | | - | | - | | CV | 0.1 | CV | | |
| Red phalarope (Phalaropus fulicarius) | CB | 32.5 | 25.7 | CB | 13.7 | CB | 20.6 | UB | 4.0 | RV | 0.3 | CB | 26.5 | 26.4 |
| Northern phalarope (P. lobatus) | CB | 13.3 | 9.8 | RV | 1.0 | RV | 4.2 | CB | 9.7 | CB | 16.8 | UB | 1.6 | 3.6 |
| Common snipe (Gallinago gallinago) | - | | | - | | - | | - | | RV | 0.3 | - | | |
| Parasitic jaeger (Stercorarius parasiticus) | UB | 0.4 | 0.4 | UB | 0.4 | UB | 0.4 | UB | 0.3 | UB | 0.4 | UB | 0.5 | 0.5 |
| Pomarine jaeger (S. pomarinus) | M | | | M | 0.1 | M | 0.2 | CV | | M | 0.1 | M | | |
| Long-tailed jaeger (S. longicaudus) | RV | 0.2 | 0.1 | RV | | UB | 0.2 | UB | 0.4 | UB | 0.3 | RV | 0.2 | 0.1 |
| Glaucous gull (Larus hyperboreus) | UB | 0.7 | 0.4 | UB | 1.4 | UB | 1.1 | CV | | UB | 0.3 | UB | 0.6 | 0.5 |
| Bonaparte's gull (L. philadelphia) | - | | | - | | - | | CV | | - | | CV | | |
| Sabine's gull (Xema sabini) | UB | 0.3 | 0.3 | RV | | CB | 0.7 | CV | | CV | | CV | | |
| Arctic tern (Sterna paradisea) | UB | 0.8 | 0.5 | RV | 0.1 | UB | 0.7 | UB | 0.9 | UB | 1.3 | RV | | |
| Short-eared owl (Asio flammeus) | CV | | | CV | | CV | | CV | | UB | | CV | | |
| Snowy owl (Nyctea scandiaca) | RV | | | CV | 0.1 | CV | | CV | | CV | | RV | | |
| Say's Phoebe (Sayornis saya) | - | | | - | | - | | - | | - | | CV | | |
| Horned lark (Eremophila alpestris) | - | | | - | | - | | - | | - | | CV | | |
| Barn swallow (Hirundo rustica) | - | | | - | | - | | - | | - | | CV | | |
| Common raven (Corvus corax) | - | | | - | | - | | CV | | RV | | CV | | |
| Bluethroat (Luscinia svecica) | - | | | - | | - | | - | | CV | | - | | |
| Ruby crowned kinglet (Regulus calendula) | - | - | | - | | - | | CV | | - | | - | | |
| Yellow wagtail (Motacilla flava) | - | | | - | | - | | UB | 0.8 | UB | 0.4 | - | | |

Continued

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| | Large lake regime | | | | Delta | | Near foothills | | | | Coastal | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | East Long Lake | | | Island Lake | Meade River | | Singiluk | | Square Lake | | Storkersen Point | | |
| | Status | 1977 | 1978 | Status | 1978 | Status | 1977 | Status | 1977 | Status | 1978 | Status | 1977 | 1978 |
| Rusty blackbird (Euphagus carolinus) | - | | | - | | - | | - | | CV | | - | | |
| Redpoll (Carduelis sp.) | - | | | - | | CV | 0.3 | UB | 0.1 | CB | 1.5 | UB | | |
| Savannah sparrow (Passerculus sandwichensis) | CV | | | - | | CV | | UB | 12.0 | UB | 2.7 | - | | |
| Tree sparrow (Spizella arborea) | - | | | - | | - | | - | | CV | 0.4 | - | | |
| Lapland longspur (Calcarius lapponicus) | CB | 64.2 | 47.6 | CB | 24.3 | CB | 24.1 | CB | 42.3 | CB | 42.5 | CB | 20.4 | 36.7 |
| Snow bunting (Plectrophenax nivalis) | CV | | | CV | | CV | | - | | - | | UB | 0.6 | 1.1 |
| Species breeding | 25 | | | 16 | | 23 | | 23 | | 27 | | 25 | | |
| Species total | 45 | | | 36 | | 40 | | 41 | | 53 | | 62 | | |

[a] Status: CB = Common Breeder; UB - Uncommon Breeder; M = Migrant; RV = Regular summer visitor; CV = Casual or accidental visitor; - = Not present.

[b] Means were determined from weekly surveys, June through August.

[c] Meade River and Singiluk sites were studied in 1977, East Long Lake and Storkersen Point in 1977 and 1978, and Island Lake and Square Lake in 1978.

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15. Supplementary Notes

16. Abstract (Limit: 200 words) The Arctic Coastal Plain is a flat or gently rolling area of tundra which covers the entire coastal region of northern Alaska. This profile synthesizes data on the ecology of the thousands of small shallow ponds that form an important wetland community on the tundra.

These polygonal ponds are formed by the freezing, thawing, and cracking of the permafrost. Nutrient concentrations and rates of supply to the water column are controlled by interactions with the iron-rich peat sediments. Iron concentrations control phosphorus concentrations and these in turn control the growth of algae.

Two fringing emergent vascular plants, Carex and Arctophila, are often the most important primary producers in the ponds. Most algae and higher plant biomass is decomposed by microbes in a detrital food web concentrated in the pond sediments. Chironomid larvae, oligochaete worms and other insects are the dominant benthic animals. Because the ponds freeze to the bottom each winter they contain no fish; however, the community is important for many species of migratory waterfowl and shorebirds that use the ponds for feeding and breeding.

Activities associated with oil production, including spills, roads, and off-road vehicles, are the major issues facing managers of this wetland community.

17. Document Analysis  a. Descriptors

Ecology, primary productivity, invertebrates

b. Identifiers/Open-Ended Terms

Arctic tundra ponds, waterfowl, nutrient cycling, carbon flux

c. COSATI Field/Group

| 18. Availability Statement<br><br>Unlimited | 19. Security Class (This Report)<br>Unclassified | 21. No. of Pages<br>52 |
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