Effects of an Arctic Environment on the Origin and Development of Freshwater Lakes

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ABSTRACT

Thaw lakes beyond the glacial boundary in northern Alaska may be quiescent, with elliptical saucer-shaped basins, or they may be actively expanding, with deeply pocked basins. Glacial lakes of the usual types are found in the glaciated southern part of the region. The lakes freeze to a depth of almost 2 meters in winter and warm without stratifying to about 13°C in summer. Of the annual heat budget of some 28,000 cal/cm² only 6,000 cal is wind distributed. Total dissolved solids are known to range from 35 to 159 ppm, and the water is of a calcium bicarbonate type except where sea-spray influence is strong. The silica content is very low. A shore community is poorly-developed or absent, apparently because of ice-push, and the standing crop of benthos varies from an indetectable amount to 89.4 kg/ha. Remains of the midge Dryadotanytarsus are found throughout the sedimentary column of one lake, indicating that this genus, which is known only as a late-Pleistocene fossil, lives there today. The sediments of lakes receiving the products of the widespread processes of arctic weathering are very inorganic, with few and poorly-preserved microfossils. Computations based on a radiocarbon-dated pollen chronology suggest a net community productivity averaging less than 2 mg of organic matter/cm²/yr, and Bosmina and tendipodid productivities of less than 10/cm²/yr during the past 6,000 years. Further computations involving the data of other authors suggest that of the solar energy fixed by a temperate or arctic lake about one-quarter is preserved in the sediments, one-half is dissipated by the decomposing organisms and one-quarter is dissipated by all the other plants and animals. The arctic environment appears to influence lakes principally through physiographic processes affecting origin, sedimentation, and drainage.

INTRODUCTION

This paper is the result of two summers spent in the Brooks Range and Arctic Coastal Plain of northern Alaska. Observations made in the field and laboratory examination of the samples collected have provided more questions than answers, and the findings are presented as an introduction to rather than a complete monograph of the limnology of a very interesting region.

The area with which we are concerned lies north of the Arctic Circle. It is very cold and very dry. Weather stations are scarce, but at Point Barrow on the arctic coast, where records have been kept for over thirty years, the mean annual temperature is −12°C, and the mean annual precipitation 10.7 centimeters (U. S. Weather Bureau 1943). At Anaktuvuk Pass, in the Brooks Range, where a weather station has been maintained for two years, the mean annual temperature is −10.8°C, and the mean annual precipitation 34.6 centimeters (U. S. Weather Bureau 1956).

The dryness of the coastal plain and the foothills is so severe that they have never been glaciated. The Brooks Range was covered by ice at least four times during the Pleistocene, and it supports a few small
The cold dry climate of the coastal plain is ideal for the accumulation of ground ice, and perennial freezing temperatures prevail to a depth of several hundred meters (Payne et al. 1951). Only the upper few decimeters of the land surface thaw out in summer, not only on the coastal plain but in the mountains and foothills as well.

The bedrock of the coastal plain is covered in most places to a depth of over thirty meters with the Pleistocene Gubic formation which consists largely of silt (Payne et al. 1951). So much ice has accumulated in the silt (Leffingwell 1915) that it constitutes a considerable fraction of the total volume of the formation.

The vegetation of northern Alaska varies from a subarctic mixture of boreal forest and tundra to an arctic tundra of herbs and prostrate shrubs. South of the Brooks Range divide most of the river valleys have stands of the Picea-Populus-Betula forest that covers the interior of Alaska (Hulten 1941). On the north side of the divide spruce seems to be almost absent, although there are local stands of Populus in a number of sheltered valleys (Leffingwell 1919, Spetzman 1951).

METHODS

Core samples were taken from one or two pneumatic rubber dinghies with a Hiller sampler modified according to a suggestion by Erdtman (in Wodehouse 1935) to hold a removable metal liner, or else with a modified Kullenberg piston sampler (Livingstone 1955a). Microfossils were separated from their silty matrix by bromoform flotation according to the method of Frey (1951), and were counted at 100× magnification.

Relative chlorophyll contents were determined by measuring in a Beckman spectrophotometer at 6630 Å the absorption of the pigment extracted from one milliliter of wet lake mud by five milliliters of acetone.

ORIGIN AND MORPHOMETRY

Most of the lakes visited during this study owe their origin to the action of ice. The mountain lakes are of glacial origin. Some of them occupy kettles formed by the melting of buried glacier ice (see Fig. 12), while others lie in basins formed in part by glacial scours and in part by the damming action of moraines and fans.

The lakes on the coastal plain were formed in a rather different way. They are thaw lakes, resulting from the melting of large masses of ground ice (Hopkins 1940, Black and Barksdale 1949, Wallace 1948). In the foothills between the Brooks Range and the coastal plain there are some lakes of other types, such as the numerous ox-bow ponds in the river valleys, but the only lake covered in the present study that was not clearly a thaw lake or a glacial lake or some combination of the two was Swallowtail Lake near Umiat, which appears to occupy a depression behind some material that has slumped off the hillside.

In the glaciated part of northern Alaska it is sometimes rather difficult to distinguish between thaw lakes and kettles. A lake
that is primarily a kettle may be enlarged from time to time by the melting of ground ice in the surrounding material. Slumping and mudflow on the shores of a kettle may give it the superficial appearance of a thaw lake, and it is very difficult when examining an actively expanding lake in a body of till or outwash, to tell whether it is expanding at the expense of ground ice that has formed in situ or at the expense of buried remnants of glacier ice. Even though the outwash body may be very old the possibility that some glacier ice persists cannot be ruled out, because climatic conditions are extremely favorable for prolonged ice preservation.

Rough contour maps of a number of lakes appear in Figure 1, and representative profiles across a few thaw lakes and kettles are shown in Figure 2. The shape of the glacial lakes is not extraordinary, but that of the thaw lakes calls for some comment.

The profile of Ikrowik is characteristic of most of the mature oriented thaw lakes on the Arctic Coastal Plain in the vicinity of Point Barrow. Its outstanding property is remarkable uniformity. Once away from the shallows near shore one finds that the depth hardly varies by more than a decimeter over a distance of more than a kilometer.

Some aspects of the shape of these lakes have been discussed in an earlier paper (Livingstone 1954). It appears that they owe their great regularity, in profile as well as in plan view, to the system of circulation currents set up in them by the prevailing northeasterly winds. These currents take silt dislodged from the bank by the pounding waves and distribute it over the basin, filling in the hollows and producing a regular, shallow, saucer-shaped depression.

Lakes of the Ikrowik type lie in the low part of the coastal plain, where the relief and the elevation above sea level are only a few tens of meters. At the present time they appear to be draining about as fast as they are forming, and the processes of lake formation and drainage have been going on for some time, so that the land area of this part of the coastal plain seems to consist almost entirely of the drained basins of elliptical lakes. These drained basins are covered with a polygonal pattern consisting of low-centered polygons, which are young, and high centered polygons, which are old. Black (1952), estimating the ages of some of the ice-wedges between these polygons by extrapolating present rates of growth, has come to the conclusion that some of them are about 3000 years old. The method is open to objection but it indicates an order of magnitude for the minimum time since the process of ice-wedge formation began around Point Barrow.

Away from the coast in the transition zone between the coastal plain and the foothills conditions are rather different. Here the altitude is greater, and there is a local relief of 15 or 25 meters. Instead of a simple plain the countryside consists of a pocked and dissected plateau. The surface of this plateau is covered with cottongrass tussocks rather than polygonal ground.

Set about 15 meters into the plateau are occasional stream valleys and many thaw lakes. At present most of the lakes do not completely occupy their basins, so that there is a certain amount of ground as well as water occupying the lower level 15 meters below the surface of the tussock-covered plateau. On this low ground a polygonal pattern has developed, but all the polygons are low-centered young ones.
Fig. 3. Age of willows on the shore of East Oumalik Lake as a function of distance from the edge of the water.

An indication of just how young some of this young surface is can be obtained from an analysis of the age of willow shrubs growing on it.

A series of willow shrubs was collected along a transect of the low plain along the west shore of East Oumalik Lake (69° 50' N, 155° 27' W). The age of the shrubs was determined by counting the annual rings, and the age of the plants was then plotted against their distance from the water's edge (Fig. 3). For the first 90 meters the age of the oldest willow at each sampling station bears a direct relationship to the distance of the station from the water. Apparently the level of the water has been gradually falling, and the age of the shrubs growing on any spot is dependent upon the length of time since the spot was uncovered by the retreating lake.

Farther away from the shore the straight-line relationship breaks down completely for reasons that were obvious in the field. Beyond the 90-meter station the ground is broken up into polygons, and willow bushes are scarce. The few that do occur have a precarious existence on the dykes dividing the low-centered polygons, where they are at the mercy of frost-churning which kills them before they reach a very great age.

If we extrapolate the rate of lake retreat indicated for the stable ground near shore over the entire distance from the present water's edge to the steep bank where the water stood when the lake occupied its basin completely, we arrive at a figure of 150 years, more or less, for the length of time since the lower level of the landscape was exposed by the retreating lake. Some parts of the lake basin may be somewhat older than this, but such rapid evolution suggests that East Oumalik Lake is rather young. Apparently lake formation in the transition zone around East Oumalik is a rather recent phenomenon. Around Point Barrow, on the coastal plain proper, it has been going on for a long time.

The bottom profile of East Oumalik Lake (see Figs. 1 and 2) shows its youthfulness. Over most of the lake smooth contours are prevalent, as they are over all of Ikrowik. In the northern part of the Oumalik basin, however, there are numerous deep pits. These pits all occur in the vicinity of rapidly eroding parts of the shoreline. They are in the part of the lake that appears youngest and almost certainly are the cavities left by melted ice wedges. Such ice wedges are exposed at several places in the Oumalik neighborhood.

The growth of East Oumalik Lake appears to have proceeded in steps. Each step consists of a stage of active growth, during which ice wedge holes appear in the lake bottom, then a period of quiescence, during which the contours are smoothed out. At the present time the lake is in an active phase and is expanding toward the north. It must be admitted that if the active phases are short and the quiescent phases long, then
the lakes may be much older than is indicated by the ages of the willows on the shore at East Oumalik. The foregoing computation, which yielded a figure of 150 years, probably deals only with events during the current active phase.

If we assume that lakes form at random over the countryside, the lake bottom contours give us a means of estimating the amount of ground ice contained in the upper layers of the country material. Consider the volume contained by the surface area of East Oumalik Lake between the level of the plateau and the level of the deepest hole in the bottom. At the present time this volume is occupied by air, water, and silt. Before the formation of the lake it was occupied by silt and ice. Very little of the original silt has left the basin, because of the depth of the lake and the weakness of the drainage from it. At present there is no outlet stream at all, but there is physiographic evidence that in former times when the lake level stood higher, water did spill over into a small brook joining the Oumalik River. This stream can scarcely have removed much silt from the basin, but it may have removed a good deal of water. More water may, of course, have evaporated.

At the present time, silt occupies about the same fraction of the total volume that it did before formation of the lake. The original ice has been replaced by the water in the lake and by the air above it. These various volumes computed from the contour map with the aid of a planimeter indicate that about 70 per cent of the volume was originally occupied by ground ice:

<table>
<thead>
<tr>
<th>Description</th>
<th>Volume</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height of plateau above water</td>
<td>16 m</td>
</tr>
<tr>
<td>Maximum depth of water</td>
<td>12 m</td>
</tr>
<tr>
<td>Total depth of basin</td>
<td>28 m</td>
</tr>
<tr>
<td>Surface area of original lake</td>
<td>$1.93 \times 10^6$ m$^2$</td>
</tr>
<tr>
<td>Total volume</td>
<td>$54.04 \times 10^3$ m$^3$</td>
</tr>
<tr>
<td>Present air volume</td>
<td>$30.88 \times 10^3$ m$^3$</td>
</tr>
<tr>
<td>Water volume</td>
<td>$6.00 \times 10^3$ m$^3$</td>
</tr>
<tr>
<td>Mud volume</td>
<td>$17.16 \times 10^3$ m$^3$</td>
</tr>
<tr>
<td>Original ice volume = present water volume +</td>
<td>Original ice</td>
</tr>
<tr>
<td>present air volume</td>
<td>volume = $36.88 \times 10^3$ cubic meters</td>
</tr>
<tr>
<td>Original ice volume as percent of total volume</td>
<td>$36.88 \times 100 = 68%$</td>
</tr>
</tbody>
</table>

This proportion is rather high but not surprisingly so. Casual observation of the amount of ice exposed in cut-banks and slump scars indicates that it is of the correct order of magnitude. Although subject to various errors it probably provides the best estimate of ground-ice volume that is currently available—a much better estimate than core-drilling, for example, which covers a much smaller volume and is apt to melt some of the ice while the sample is being taken.

These actively-growing lakes fill a role that is rather unusual for small bodies of standing water. They are the most effective erosional agents in the district and are rapidly reducing the countryside to a local base level about 15 meters below the top of the plateau. One tends to think of small lakes as passive and temporary basins of sedimentation; it is rather surprising to find them actively devouring the landscape in this way.

Morphometric data also provide one character that usually distinguishes thaw lakes from kettles. The important difference is in the size of the holes left when ice masses melt. Coalescence of ice-wedge holes may produce a basin many miles in extent, but the individual pits are only about ten meters in diameter. In an active ice-wedge lake these pits are easily detected with the sounding line, although they are too small to show up on a map of ordinary scale. Most kettle-holes are much more than ten meters in diameter, and so kettle lakes lack this pattern of fine bottom pitting.

Before leaving the difference between kettles and thaw lakes it would be well to draw attention to two of the ways in which the erosional processes of permafrost regions can modify the morphology of a real kettle. White Lake, in the Brooks Range, lies in a till body of Itkillik (Early Wisconsin?) age (Livingstone 1955b, Péwé et al. 1953), so that, barring a very exceptional lingering of a buried ice mass all through the mid-Wisconsin interval, it must be a very old kettle. Yet a considerable amount of mudflowing is taking place on its banks (see Fig. 4). This erosion produces a series of cusps between the scours of successive mudflows that might, after the passage of a few centuries, be confused with crevasse fillings. In this way the sculpturing of the shores of a kettle may
be rejuvenated every time the climate becomes cold enough for the establishment of permafrost.

While it is rejuvenating the visible parts of the kettle this process may mask part of the sedimentary record. The silt, sand, and gravel delivered to the lake by mudflow may be distributed over the bottom and might form a layer impenetrable to standard sediment samplers. A mild example of this sort of thing is, of course, very well known from the Upper Dryas deposits of western Europe. What we have in mind is a much more severe development of solifluction, leading to the formation of a deposit massive enough and coarse enough in texture to be confused with basal till.

**Physical Limnology**

The characteristic features of the physical environment of an arctic lake are its low temperature and the extreme seasonal variation in insolation. Because our field work was restricted to the summer months, information is lacking about the interesting long winter night with its thick ice cover. Dr. Wiggins of the Arctic Research Laboratory at Point Barrow very kindly measured the ice thickness of Ikrowik during the spring of 1951, but even this elementary datum is missing for most of the lakes. The depth of spring ice on Ikrowik, however, was 1.85 meters, which indicates a considerable depth of freezing for lakes in the area.

Some summer temperatures are available (see Table 1), and since most of them were obtained during August they can be accepted as an approximation to the maximum temperature attained during the year.

The first thing that is apparent from the available temperature data is that no arctic lake examined shows summer stratification. It is unfortunate that stormy weather prevented temperature measurements on White Lake, which is over twice as deep as the deepest temperature record in Table 1. Perhaps this lake does show some summer stratification, but the others, even Chandler Lake at 18 meters (temperature readings
were not taken in the 21-meter hole of Chandler) and the small 12-meter pit in East Oumalik Lake, were circulating. This is not very remarkable, although temperate lakes of similar size and shape would be expected to show some stratification. The deep Alaskan lakes attain a summer temperature of only 12 or 13°C. They warm through the range of slight density change of water, and only a moderate amount of work is required to mix the warmed surface water into the depths. Because the lakes are unprotected by trees the summer wind is in an ideal position to perform this moderate amount of work.

The work of the wind in distributing water warmed above 4°C has been calculated for Chandler Lake by the method of Birge (1916). It is 175 cal/cm² of Lake surface. This is to be compared to a value for Lake Mendota in Wisconsin, a lake of comparable depth, of 1209 cal/cm². The difference is not due to the strength of the prevailing summer wind, which is much greater in the Brooks Range than it is in Wisconsin, but simply to the low summer temperature of the Brooks Range.

In the absence of good winter temperature data, and especially of data on the thickness of ice, it is impossible to construct an accurate heat budget for Chandler Lake. By making a few reasonable assumptions about the state of affairs in winter, however, we can calculate a rough heat budget that will not be too far from the true one. Suppose we assume a depth of freezing of two meters and assume further that the upper meter of this ice is cooled to a temperature of -10°C, while the lower meter is cooled only to 0°C. No data are available for the water temperature at the time of freezing, but it will be less than 4°C throughout the lake and probably, because of the very high winds, quite close to 0°C.

Accepting these assumptions, the heat budget of Chandler Lake is as follows:

<table>
<thead>
<tr>
<th>work of the wind in distributing water warmed above 4°C</th>
<th>864 X 10¹² cal</th>
</tr>
</thead>
<tbody>
<tr>
<td>warming, 0-4°C</td>
<td>600 X 10¹² cal</td>
</tr>
<tr>
<td>melting 2 meters of ice</td>
<td>2480 X 10¹² cal</td>
</tr>
<tr>
<td>warming upper meter of ice</td>
<td>150 X 10¹² cal</td>
</tr>
<tr>
<td>total heat income</td>
<td>4154 X 10¹² cal</td>
</tr>
</tbody>
</table>

Dividing total heat income by the surface area of 15 X 10⁹ cm² we get 27,800 cal/cm² of which 5800 cal is wind-distributed heat.

It is evident that the largest item in this
The thickness of the winter ice has a profound effect on the thermal balance of the basin in which a lake lies. Dry land in arctic Alaska is underlain by perennially frozen ground and the same is true of land covered by shallow water. Lakes too deep to freeze solid in winter, however, have a bottom temperature that is above freezing throughout the year. Should such a lake form over frozen ground there is a flow of heat from the water to the mud so that a body of unfrozen ground accumulates. Ultimately an equilibrium condition results in which the body of unfrozen ground is as large as can be maintained by the heat flux through the bottom, and the temperature of the upper layers of mud rises and falls with seasonal change in water temperature.

We have a few data concerning the extent of the unfrozen ground. Chandler Lake sediments, under 21 meters of water, are thawed to a depth of at least 7 meters, and East Oualalik Lake sediments, under 12 meters of water, are thawed to a depth of at least 4 meters. In Skimo Lake near Barrow Village, with one meter of water, solid ice persists in midsummer less than one meter below the mud-water interface. Presumably the sediments of such a lake are completely frozen during the winter, and this presumption is borne out by the fact that a well-developed polygonal pattern beneath the shallow water is visible from the air.

It should be noted that the net flow of heat from the water to the mud in deep arctic lakes is in accord with such data as are available for temperate lakes. Birge, Juday, and March (1928) found that there was a slight but appreciable net transfer of heat from the water to the mud of Lake Mendota in the course of a year.

A less important effect that the ice of an arctic lake exerts on its basin is that of ice-push. This is a phenomenon to be found in the temperate zone wherever there is severe freezing in winter, but in arctic lakes it is quantitatively more important and is one of the dominant processes sculpturing the beaches. On the lakes of the Chandler River system exposed deltas have ice-push ridges four or five meters high which are so substantial they are not reduced even by the heavy gales of summer.

Because of the thermal capacity of a deep lake the ice cover forms in the fall and disappears in the spring more slowly than it does on shallow ones. This must be of considerable importance in the illumination of
the water, for it keeps the deep lakes ice-covered until July. More than half the season of 24-hour sunlight has passed by the time the ice disappears. The millions of separate crystals of melting spring ice reflect a good proportion of the incident light, and this must have a very great effect on the annual light income of the deep lakes.

Such color and transparency data as are available are presented in Table 2. It may be seen that the transparency was neither very great nor very variable. Measurements were not made on a thaw lake while it was circulating under a strong wind. Under such circumstances many thaw lakes are very turbid and the transparency might be much lower. Color is extremely variable, even in the small series of lakes examined. The shallow lakes tend to be brown, many of them, like Ikrowik, rather deeply stained, while the deep lakes are (lightly) colored a characteristic translucent gray-green. This color never failed in our experience as an indicator of considerable depth.

CHEMICAL LIMNOLOGY

Chemical tests for a few major ions were carried out in the field. In addition, samples of unfiltered water were collected in pyrex bottles and sent to Dr. Whetstone, Alaska District Chemist, who analyzed them within six months. His results, which are more reliable than the field tests, are presented in Table 3.

The most obvious generalization that can be drawn from the results is that Ikrowik, which is only seven km from the coast, is predominantly a sodium chloride lake, while calcium and bicarbonate ions predominate in the inland lakes, with lesser quantities of magnesium and sulphate.

The two analyses of Ikrowik water span the period of disappearance of the ice. We expected that the summer water would be more dilute than the spring water because of the addition of relatively pure ice meltwater. Apparently the blown sea-spray of summer is sufficient to nullify the effect of meltwater and make the summer water more concentrated than the water in the spring.

East Oumalik Lake and the small lake northeast of it are substantially more concentrated than the others. East Oumalik Lake is without an outlet, but since the other is a drainage lake the high concentration cannot be the result of evaporation. Presumably it is due to bedrock control.

Chandler Lake and Eight Lake are rather high in sulphate. This, too, is probably the result of bedrock control, but we cannot substantiate this belief with analyses of the bedrock in either case.

It is evident from the table that the water chemistry of these Alaskan lakes is not extraordinary. The only feature that may have regional significance is the low silica content. Silica analyses of waters stored in glass bottles are notoriously unreliable, and it may be worth while to note in this connection that we were unable to detect silica in any of our field tests, using a Taylor comparator and a method sensitive to one milligram per liter. The silica-sesquioxide ratio of cold-climate soils is high (Robinson 1936), and it is to be expected that the waters leach-
ing such soils would be low in silica. The observations of Böcher (1949), however, who found several parts per million of silica in dilute Greenland lake water after it had been stored in glass for many months, prevent us from generalizing to any great extent about the silica content of arctic waters.

**BIOLOGICAL LIMNOLOGY**

The most striking biological characteristic of arctic Alaskan lakes is the absence of a well-developed shore community. In the smaller lakes there is sometimes a good stand of *Arctophila fulva*, a coarse aquatic grass, and in the shallow ponds there is often a good growth of *Hippurus vulgaris* or *Ranunculus pallasii*. Spetznarm (1951) lists a total of only thirteen species of vascular plants from aquatic communities on the North Slope. In general, though, the dense stands of emergent and floating vegetation that are found around the shores of so many temperate zone lakes, particularly shallow ones, are lacking in most lakes of northern Alaska.

The great variety of animals usually inhabiting the shore zone of lakes is missing too. There appear to be no freshwater sponges, no Notonectidae, Corixidae, Gyrinidae, Dytiscidae, and no Amphibia north of the Brooks Range. The lack of a shore community, combined with the scars of heavy ice-push, gives to even the most permanent arctic lake a barren, raw, and temporary aspect. The shoreline looks like that of a spring puddle or temporary ditch rather than a lake.

It is not easy to determine the reasons for lack of a shoreline community. Undoubtedly the ice plays an important role. The mere physical disruption which it causes must inhibit the formation of a proper community, just as heavy wave action does in the temperate zone. It is evident, however, that this is not the whole story. On the south side of the Brooks Range, where winter temperatures are almost as low as on the north slope, but where the summer is much warmer, many of the elements of a shore community are present. At Death Valley near Bettles, for example, both Notonectidae and Gyrinidae were observed. Although no living sponges were seen spicules are common in the sediments of this lake. At Bettles there are frogs (personal communication from Mr. James Bee), and in all the lakes of the vicinity there is a dense growth of water lilies (*Nuphar sp.*). It appears that some of these species are being governed in their distribution by the same factors that govern the distribution of the timberline. Summer temperature is particularly likely to be important in the case of poikilothermous animals.

It should be noted that although lack of a shore community is characteristic of most lakes on the tundra we cannot say with assurance that all lakes with an arctic thermal regime will be without one. Although the necessary data on summer temperature and thickness of winter ice are not available, it seems likely that Death Valley Lake and others like it in the interior of Alaska which have a well-developed shore zone would be classified as arctic on the basis of the thermal scheme proposed above.

Whether or not a lake freezes to the bottom in winter is, of course, a matter of very great biological importance. Fish, in our experience, are to be found only in lakes that are deep enough to have a considerable body of water under the ice in winter, or else in lakes that are connected with deep lakes, rivers, or the sea. It is widely believed that the Alaskan blackfish, *Dallia pectoralis*, is able to withstand freezing, or at least temperatures below the freezing point of pure water (Jordan and Evermann 1896, p. 621). Attempts to verify this in the laboratory have failed consistently (Scholander et al. 1953).

At East Ounalik many sticklebacks (*Pungitius pungitius*) were found in small pools and tractor ruts on the floodplain of the lake. It was apparent from the location of these ruts and puddles that the fish could have reached them at any time the water level was raised by a few decimeters, or at any time snow meltwater was flowing into the lake. The surface of the tundra is wet at all times and well provided with pools and puddles. Small fish such as sticklebacks and young blackfish would have little difficulty moving across it from deep lakes to
Table 4. Net weight of dredgings from some Alaskan lakes

<table>
<thead>
<tr>
<th></th>
<th>Depth of dredgings m</th>
<th>Sphaeridiae g</th>
<th>Tendipodid g</th>
<th>Oligochaeta g</th>
<th>Gastropoda g</th>
<th>Miscellaneous</th>
<th>Total g</th>
<th>Total weight g/m²</th>
<th>Weighted mean for entire lake kg/ha</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chandler Lake</td>
<td>14</td>
<td>0.000</td>
<td>0.017</td>
<td>0.000</td>
<td>0.000</td>
<td>Copepoda, cyclic diatoms, Ostracoda, ephippia</td>
<td>0.017</td>
<td>0.85</td>
<td>6.99</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>0.010</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>Cyclic diatoms, ephippia, oligochaete cocoons</td>
<td>0.010</td>
<td>0.50</td>
<td></td>
</tr>
<tr>
<td></td>
<td>21.5</td>
<td>0.010</td>
<td>0.016</td>
<td>0.011</td>
<td>0.000</td>
<td>Copepoda, ephippia, oligochaete cocoons</td>
<td>0.037</td>
<td>1.85</td>
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<td>21.5</td>
<td>0.004</td>
<td>0.005</td>
<td>0.020</td>
<td>0.000</td>
<td>Insect cases</td>
<td>0.038</td>
<td>1.90</td>
<td></td>
</tr>
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<td>Little Chandler</td>
<td>12</td>
<td>0.002</td>
<td>0.032</td>
<td>0.000</td>
<td>0.000</td>
<td>Nematoda, insect cases</td>
<td>0.012</td>
<td>0.60</td>
<td>11.5</td>
</tr>
<tr>
<td>Lake A</td>
<td>12</td>
<td>0.001</td>
<td>0.024</td>
<td>0.000</td>
<td>0.000</td>
<td></td>
<td>0.025</td>
<td>1.25</td>
<td>9.5</td>
</tr>
<tr>
<td>Lake A</td>
<td>6</td>
<td>0.001</td>
<td>0.012</td>
<td>0.000</td>
<td>0.000</td>
<td></td>
<td>0.013</td>
<td>0.65</td>
<td></td>
</tr>
<tr>
<td>Lake A</td>
<td>6</td>
<td>0.001</td>
<td>0.012</td>
<td>0.000</td>
<td>0.000</td>
<td></td>
<td>0.025</td>
<td>1.25</td>
<td></td>
</tr>
<tr>
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<td>10.5</td>
<td>0.054</td>
<td>0.007</td>
<td>0.007</td>
<td>0.007</td>
<td>Characeae, insect cases</td>
<td>0.025</td>
<td>1.25</td>
<td></td>
</tr>
<tr>
<td>Lake A</td>
<td>4</td>
<td>0.004</td>
<td>0.046</td>
<td>0.000</td>
<td>0.052</td>
<td>Ostracoda, Hydracarina, Nematoda, Musci, Characeae, gelatinous algae, insect cases</td>
<td>0.068</td>
<td>3.40</td>
<td></td>
</tr>
<tr>
<td>Lake A</td>
<td>4</td>
<td>0.123</td>
<td>0.242</td>
<td>0.000</td>
<td>0.004</td>
<td></td>
<td>0.102</td>
<td>5.10</td>
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<tr>
<td>Lake A</td>
<td>1</td>
<td>0.083</td>
<td>0.005</td>
<td>0.080</td>
<td></td>
<td>0.378</td>
<td>18.00</td>
<td>80.4</td>
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</tr>
<tr>
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<td>0.005</td>
<td>0.080</td>
<td></td>
<td>0.168</td>
<td>8.40</td>
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<td>Ikrowik</td>
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<td>0.000</td>
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<td></td>
<td>0.000</td>
<td>0.00</td>
<td>0.0</td>
</tr>
</tbody>
</table>

shallow ponds where their presence would be cause for surprise. It is, of course, possible that these fish may be able to withstand freezing temperatures, but until such time as they have survived freezing in the laboratory or been collected alive in the ice it is not wise to accept the circumstantial evidence of occasional occurrence in shallow ponds.

However it may affect fish, Andersen (1946) found that winter freezing had no adverse affect on the chironomids of northeast Greenland. On the contrary, there was a heavier population in the shallows, where the animals were submitted to annual freezing, than in the deeper water, where they were submitted to the effects of oxygen depletion while in an active state.

In Alaska there does not seem to be any such enhancement of the bottom fauna in the shallows. Although a fertile lake such as East Oumalik maintains a good population of bottom animals in the one-meter zone, the crop is even heavier in water of moderate depth. This difference is probably due to the greater size and consequent greater ice-push of the Alaskan lakes. Eight Lake, the only one comparable in size to Andersen's, was not dredged for bottom animals, but it had, as already mentioned, a fair amount of rooted vegetation in the shallows. On large lakes the physical disruption due to ice expansion probably prevents the establishment of a good bottom fauna in the littoral zone, just as it prevents the establishment of a shore community generally.

Prescott (1953) found considerable difference in the algal floras of the various thaw lakes near Point Barrow. A particularly striking difference is that between the acid
EFFECTS OF ARCTIC ENVIRONMENT ON FRESHWATER LAKES

203 desmid-dominated lakes and the basic diatom-dominated ones. Failing to find any consistent chemical differences other than pH between the two types of lakes Prescott suggested that accidents of colonization might be responsible for the floral differences. To the present authors it seems rather likely that a chemical difference involving some ion or ions not measured by Prescott does exist and that the differences are due to the chemical composition of the sediments in which the lake basins lie.

This part of the coastal plain has had a very complicated Pleistocene history. After any good August gale when the sea cliffs are well exposed, the churned and interfingering layers of terrestrial, aeolian, marine, lacustrine, and fluviatile material that compose the upper part of the Gubic formation around Point Barrow can be seen. As mentioned above, the surface of the coastal plain bears witness to a very complex history of lake formation, drainage, and reformation, so that various lakes on the coastal plain are apt to have had very different histories and be surrounded by materials of very different chemical nature. A lake that is actively eroding a shallow calcareous sea deposit will have a different water chemistry from one that is expanding into windblown sand or one that is shrinking.

One chemical substance not measured by Prescott that seems to us very likely to be involved in the difference between a diatom flora and a desmid flora is silicon. Lund (1950) has shown for Asterionella that 0.5 ppm of silicate is essential to growth. Non-planktonic species probably require considerably more than this. Hutchinson (1957, pp. 797-8) cites a number of laboratory investigations in which diatoms were found to grow best at concentrations up to 30 ppm of silicate. It may be significant, therefore, that Ikrowik, the only lake we have both worked on, was found by Prescott to have no diatoms at all and by us to have too little silicate to be detected by our field method.

The results of dredgings taken in a variety of lakes are summarized in Table 4. The bottom fauna is low, but not remarkably so. The data for these lakes when plotted against mean depth on a graph with data from a large number of lakes, such as that of Deevey (1941), fall near the bottom of the range of scatter but do not appear to form a separate group. This is in agreement with the findings of Comita and Edmondson (1953) who concluded after an intensive study of the productivity of Imikpuk near Point Barrow that the summer productivity and the summer standing crop of the lake did not differ markedly from those of temperate lakes. A great deal of solar energy enters a high latitude lake during the summer. It is the shortness of the growing season that limits the annual production of arctic lakes.

PALEOLIMNOLOGY

Gross stratigraphic features

Conditions of sedimentation in arctic lakes are under the close control of climate and its associated physiographic processes. It is evident from what has been said about the origin and development of thaw lakes that the sediments laid down in an actively expanding thaw lake are derived in very large measure from the silt and peat of which the banks are composed. For this reason it is difficult, if not impossible, to apply the standard stratigraphic methods to the investigation of thaw lake history. The chemistry and fossils of the sediments that have been deposited on the lake bottom are very likely to have been derived from older beds surrounding the lake basin. What is more, in most cases it is impossible to separate such derived fossils from autochthonous ones.

The danger of secondary deposition was underlined in the summer of 1951, at East Oomalik Lake, when the bones of an extinct elephant were found lying on the surface of the lake mud a short distance from shore. The bones were disarticulated fragments, and even if they had been found deeper in the sediment they would not have been accepted as indicators of conditions at the time the bone-bearing bed was laid down. There is no obvious way, however, in which cladocera, tendipodids and pollen grains washed out of old lake deposits in the shore can be discriminated from the much younger
fossils of organisms that lived during the lifetime of the present lake.

A further difficulty is to be found wherever lakes lie in an unconsolidated formation that is itself partly lacustrine in origin. It is impossible, in taking the core samples, to know when one has pierced through the sediments of the present lake and entered the underlying beds of some extinct lake that may be many thousands of years older.

In the rocky basins of the Brooks Range we always knew when we had penetrated the lake sediments: further progress was impossible. Out on the coastal plain, with its thick unconsolidated mantle, there was no way of telling when the bottom of the lake deposit had been reached. It is quite possible that the cores taken in the deepest part of East Oumalik Lake, in the recently thawed ice-wedge pits, did not go through sediments of the present lake at all, but only through the underlying Gubic formation.

Because of this difficulty in deciphering the fossil record of the coastal plain lakes, consideration will be restricted to the glacial lakes of the Brooks Range.

Pertinent observations were made on four lakes in the mountains: Death Valley Lake near Bettles; Chandler Lake north of the Brooks Range divide; and two smaller lakes near Chandler Lake, Eight Lake and Lake A.

The time scale used in the paleolimnologic computations is based upon pollen analysis of cores from the lakes. The detailed results of these analyses have already been published (Livingstone 1955b). For present purposes it is sufficient to state that three pollen zones can be recognized in the longest profile, from Chandler Lake, but only the upper two of these can be recognized in the other lakes. These zones, which have been arbitrarily designated I, II, and III, consist of an herbaceous pollen zone, a birch pollen zone, and an alder pollen zone, respectively. Three of the lakes are so close together that the II/III transition, the only identifiable horizon found in all three sections, is certainly synchronous in these lakes. Death Valley Lake is so far away, however, and situated in a region of such different climate and vegetation, that there is every likelihood that its II/III transition is not synchronous with that in the Chandler region, but dates from a much earlier time.

Undated pollen zone boundaries are of limited usefulness in dealing with the history of lakes. Unfortunately the organic content of most of the Brooks Range Lakes is so low as to make direct carbon dating difficult, so one is forced to rely on correlations with the nearest carbon-dated pollen
profile, from a valley fill near Umiat, 134 km to the north of Chandler Lake (Livingstone 1957a). This profile consists of three pollen zones. The upper two correspond vegetationally to the upper two at Chandler, and as the distance and vegetational difference between these two localities is not great, it is very likely that the II/III boundary is synchronous or nearly so at Umiat and Chandler Lake. At Umiat this boundary has a carbon age of 5900 ± 200 years.

The lowest zone at Umiat bears many similarities to Zone I at Chandler Lake but it also has some important differences, mainly the presence of a considerable amount of birch pollen throughout the zone. For this reason some considerable doubt arises about the synchrony of this transition with the I/II transition at Chandler Lake, but nevertheless the carbon age of between 7500 ± 250 and 8100 ± 250 years may be taken as an estimate of the age of the I/II transition at Chandler Lake. This estimate is likely to be too low if the Umiat Zone I is, as its high birch content suggests, contemporary with Chandler Zone II instead of Chandler Zone I.

**Organic and inorganic matter**

Per cent-loss-on-ignition curves have been drawn in the conventional manner for the four mountain lakes (Fig. 5). These curves are rather featureless, and, with the possible exception of Death Valley Lake, lack any indication of the dramatic sigmoid increase in organic content apparently typical of temperate-zone lakes (Hutchinson and Wollock 1940, Deevey 1942). It is the opinion of one of us (Livingstone 1957b) that the sigmoid increase of temperate zone lakes is a result of the change from arctic to temperate weathering conditions, a change that has not yet occurred in northern Alaska, so one would not, perhaps, expect to find a sigmoid increase in our three northernmost lakes nor more than a very questionable indication of it in our subarctic lake from Death Valley.

Some explanation can be offered for the differences between the loss on ignition curves of the various lakes. Chandler and Lake A have similar curves: loss on ignition is low, and it undergoes a slow but steady increase from bottom to top of the section. The sediment in these lakes is only to the smallest degree autochthonous. It is clayey
silt, brought in by viscous creep and stream action. The source of this material is the thin active layer, a few decimeters thick, that thaws out in summer and slides slowly over the smooth underlying frozen sub-stratum of the countryside to the depressions containing the lakes and streams. The material of which this mantle is composed is clayey silt with some included peat, and it bears on its surface the living tundra vegetation.

At Death Valley the delivery of material by viscous creep is not so important. The sediment filling the lake is a silty gyttja. A certain amount of allochthonous material is being added to the lake, however, by localized thawing and slumping of the shores.

Eight Lake does not receive such massive amounts of allochthonous material from any source at the present time. It lies in a rocky till-body, where viscous creep is not active, and its shores are not slumping nor do they bear recognizable slump scars. A small stream enters it, and this probably accounts for a considerable percentage of the small amount of inorganic material entering the lake basin.

A rough estimate of the chlorophyll content of the sediment in the four lakes was obtained by extracting samples of sediment in acetone and measuring the optical density of the solution. The results are plotted in Figure 6. The curves bear a general similarity to the ones for per cent-loss-on-ignition, with the principal difference being the extremely low chlorophyll content of Chandler Lake sediment.

This difference is due in part to a relatively small contribution of chlorophyll-rich autochthonous organic matter and a relatively large contribution of peaty terrestrial material to the total loss on ignition for Chandler Lake, but it may partly be due also to a more severe mineralization of the settling seston in Chandler Lake, which is much deeper than the others.

Per cent-loss-on-ignition curves are apt to be rather misleading, for they are influenced by changes in the rate of organic sedimentation and also changes in the rate of mineral sedimentation. They make no allowance for differences in the water content of the sedi-

![Fig. 8. Ash content of lake sediment.](image)

ment. Thus the loss-on-ignition curves might indicate that the organic content of Eight Lake sediment was much higher than that of any of the other lakes, but when the data are plotted in terms of grams lost on ignition by each cubic centimeter of sediment, as in Figure 7, a rather different result emerges. On this basis the four lakes are rather similar. Per cent loss on ignition is a function of both mineral content and organic content and the differences in per cent ignition loss between these lakes result from differences in mineral content (see Fig. 8). Eight Lake, except at 0.4 meters, has an unusually low mineral content by arctic standards. Much of the sediment volume in this lake is composed of water. Viewed in this light the difference in chlorophyll content of the lakes appears even more striking.

**Microfossils**

Of the Chandler lakes only Eight Lake was rich in morphological fossils. Tendipedin (chironomid) head capsules, jaws, and exuviae, including many specimens of *Dryadotanytarsus* and "Tanytarsus" (i.e., one of the Calopsectrini), were abundant, as were fragments of *Bosmina* carapaces and turbellarian cocoons. Desmids (*Cosmarium, Euastrum, Staurostrum, Desmid-
Il'rc:. !I. l'ediashma conlcnt of lakc sediment. (ium), filamentous algae (cf. Stigeoclonium), in some levels with recognizable cytoplasmic constituents still intact, and brown moss leaves were also present. *Pediastrum boryanum* was common, especially in the upper levels, and a few pennate diatoms were encountered.

The other lakes also contained *Pediastrum boryanum*, though in smaller quantities. Lake A had a measurable quantity of *Bosmina* and tendipedid fragments, but in Chandler Lake tendipedids were very scarce and *Bosmina* was not recognized at all. Death Valley Lake has a rather rich fossil fauna and flora, including diatoms, which were scarce elsewhere, and sponge spicules, which were not encountered at all in the more northern lakes; no detailed counts, however, have been made on its sediments except for things such as *Pediastrum* which are found on the pollen slides.

In all four lakes (see Fig. 9) *P. boryanum* shows an increase from bottom to top, although little significance can be attached to this increase in Chandler and Lake A, where the total numbers involved are very low. It is interesting to note that the highest *P. boryanum* content is found in the shallowest lakes. In further support of this tendency may be mentioned the fact that Footprint Lake near Point Barrow, which contained only about one meter of water until artificially drained a few years ago, laid down a sediment so rich in *Pediastrum* that the colonies cannot be counted by the standard method. *P. boryanum* is an extremely variable species and a tycho-plankton. There is no reason known to the authors for considering it as a plant of shallow waters in general, but it appears to be in Alaska. If this is so then the progressive increase it shows in the sedimentary column of each individual lake may simply reflect shoaling as the lake filled in.

Of other microfossils only Eight Lake has numbers high enough for reliable counting. This lake shows a very striking decline of *Bosmina* carapaces and tendipedid fragments from initial high values to later low values (Figs. 10 and 11). This is the opposite of what one usually finds (Deevey 1942), and taken at face value it indicates a decline in productivity since the early history of the lake. *Pediastrum* shows that the situation is not so simple as this, as do the brown moss leaves that form the bulk of the sediment in the upper 0.4 meters. We are really not justified in drawing a conclusion of diminished productivity from such conflicting evidence.

We may, however, be justified in drawing conclusions about a change in the nature of the material produced, though even here we must be cautious. The decline in *Bosmina*, for example, may not reflect a decrease in

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Fig. 9. *Pediastrum* content of lake sediment.

Fig. 10. *Bosmina* content of lake sediment.
overall zooplankton production, but simply a replacement of cladocerans by copepods as dominant members of the zooplankton community. Copepods do not fossilize under ordinary conditions and they were certainly the most important animals in the zooplankton when we visited the lake and took plankton tows. The decrease in tendipedids, however, is not so easily explained by such special pleading, and the general impression that emerges is one of a decrease in the relative amount of animal production. The great increase of mosses suggests that the lake is passing from an initial rather eutrophic condition into a dystrophic one; the brown color of the water at the present time lends support to this suggestion.

If this is the case then the peculiar edaphic features of the drainage basin may be involved. Eight Lake lies in a rocky till-body that is free of active mass-wasting of any sort that would expose a continuing supply of fresh soil. In addition, it is perennially frozen below a depth of a few decimeters, so there can be no flow of ground water to the lake. It seems quite likely that under such conditions the supply of mineral nutrients has been drastically reduced since the years immediately after formation of the lake. The connection between dystrophy and dissolved mineral salts is not fully understood, at least by the authors, but it is evident that dystrophy arises under conditions of low base and nutrient content in the water. We do not feel that the occasional examples of moderately calcareous lakes that are dystrophic (Ohle 1934) are sufficient to obscure this general tendency, although they do show that the situation is not a simple one. We offer the suggestion that this lake is becoming dystrophic because of a progressive restriction of the supply of water-soluble mineral substances.

**Fig. 11.** Tendipedid content of lake sediment.

**Fig. 12.** Lake A, Alaska. View looking north in early August, 1952. Notice how the contours of the tillbody in which this kettle lies have been smoothed by viscous creep. Kames cannot be recognized.
TABLE 5. Absolute sedimentation rates of Linsley Pond, Conn., and some Alaskan lakes

<table>
<thead>
<tr>
<th>Time interval</th>
<th>Loss on ignition mg/cm²/yr</th>
<th>Ash wt. mg/cm²/yr</th>
<th>Bosmina fragments/cm²/yr</th>
<th>Tendipedid fragments/cm²/yr</th>
</tr>
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<tbody>
<tr>
<td>Lake A</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zone III, 6000 yrs</td>
<td>1.66</td>
<td>19.36</td>
<td>6.00</td>
<td>1.2</td>
</tr>
<tr>
<td>Eight Lake</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zone III, 6000 yrs</td>
<td>0.88</td>
<td>5.86</td>
<td>0.75</td>
<td>6.6</td>
</tr>
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<td>Chandler Lake</td>
<td></td>
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<td></td>
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<tr>
<td>Zone III, 6000 yrs</td>
<td>1.71</td>
<td>24.59</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>* Zone II, 2000+ yrs</td>
<td>4.64</td>
<td>65.45</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Death Valley Lake</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>* Zone III, 6000+ yrs</td>
<td>6.82</td>
<td>58.52</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Linsley Pond</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C 2 &amp; C 3, 5200 yrs</td>
<td>8.31</td>
<td>9.14</td>
<td>6000</td>
<td>2.2</td>
</tr>
<tr>
<td>C-1, 3100 yrs</td>
<td>6.81</td>
<td>6.19</td>
<td>4177</td>
<td>0.7</td>
</tr>
<tr>
<td>† A &amp; B, 3100 (? yrs)</td>
<td>3.04</td>
<td>36.07</td>
<td>433</td>
<td>0.4</td>
</tr>
</tbody>
</table>

* Because of uncertainty about the length of time represented by Zones II and III, absolute sedimentation rates calculated for these zones are likely to be too high.
† Absolute sedimentation rates for Zones A & B may be too high or too low.

Among the microfossils discovered in the sediments of Eight Lake were the head capsules and exuviae of Dryadotanytarsus. This genus of midge is known only as a late-Pleistocene fossil. It was described by Andersen (1943) from the Upper and Lower Dryas deposits of Denmark, and found independently by Deevey (1955) in the lake facies of the moa swamp deposit at Pyramid Valley, New Zealand. The Danish species, D. edentulus, is restricted in its stratigraphic range to cold-climate deposits, but the New Zealand one, D. daffi, is found in temperate deposits, indicating that the genus is not restricted to a narrow range of climate.

We first found Dryadotanytarsus remains in the midge rich lower layers of Eight Lake. A systematic search revealed their presence from top to bottom of the core, and so the organism presumably is living in the lake today. This supports the suggestion of Deevey (1957) that the animal is probably known as an adult by some other name. The rather bizarre feeding apparatus of this midge, with toothless jaws and labium rolled into a tube around the hypopharynx, have given rise to some speculation about its feeding habits. The presence of nucules in both the Danish and the New Zealand deposits prompted the suggestion that it lived by crushing Characeae with the toothless jaws or sucking out their juices with the hypopharynx and labium. The complete absence of nucules from the Eight Lake deposit argues very strongly against a strictly characeous diet, at least for the Alaskan species.

Remains of this midge were not found in any other Alaskan deposit nor in any of the dredgings, despite a keen search for them. Entomologically inclined travellers in the Brooks Range might be well advised to keep an eye cocked for this very characteristic midge and to rear some of the larvae to adulthood if they are found.

We have also found Dryadotanytarsus in some material from Whitrig Bog, Scotland, which was very kindly provided for examination by Dr. Anne Conolly. It seems likely that the genus is very widespread as a fossil, and only the unfamiliarity of most palynologists with the Tendipedidae has prevented its discovery in other places.

Dynamics of ecosystem development

Paleolimnologic computations based on estimates per unit volume are basically unsatisfactory because, to translate them into biological terms, one must make some unverified assumption about the rate of sedimentation—usually, that it has been constant. It is much more satisfactory (Livingstone 1957b) to make the computations in terms of time rather than volume of sediment, and for this one must have an absolute time scale of some sort.

The time scale available for the Alaskan lakes is a rather poor one, bearing only two or three gradations of mixed reliability, but it is infinitely better than no absolute time scale at all. In Table 5 loss on ignition, ash weight, Bosmina fragments, and tendipedid fragments preserved per square centimeter per year are presented, along with similar data for three sections of the sedimentary column of Linsley Pond. For reasons mentioned above in the section on stratigraphy,
the lengths of time represented by Zone II at Chandler and Zone III at Death Valley are both likely to be seriously underestimated, so that the corresponding rates may be expected to be too high. The length of A and B time in Devey's Linsley Pond core L10 is also uncertain, the bottom of the core being equated with Valders time in accordance with some suggestions by Valentyn and Swabey (1955). The lengths of C-1 and C-1 + C-2 are much more secure, being based on pollen-correlation from the carbon-dated profile of Upper Linsley Pond (Flint and Devey 1951).

The column listing loss on ignition per square centimeter per year is perhaps of the greatest interest, for rate of deposition of organic material gives a measure of the rate of net productivity of the entire community. Unfortunately, as we have already seen, there is reason to believe that a good deal of the organic matter in the sediments of Chandler Lake, Lake A, and Death Valley Lake is allochthonous and so cannot justifiably be included in the production of the lake. All that can be said about the estimates obtained—1.71, 4.64, 1.66, and 6.82 mg/cm²/yr—is that they are probably much too high. Chronological uncertainties also make it likely that the figures 4.64 and 6.82 are too high, so we can conclude only that the net community production for these lakes is probably less than 1 milligram per square centimeter per year.

With Eight Lake and Linsley Pond we are on somewhat surer ground. There is no indication of massive allochthonous organic sedimentation, although we must be prepared to expect some influx of wind-blown material, especially leaves, and the figures for these lakes in Table 5 may be taken as first approximations to net community productivity. It is evident that the net productivity of Eight Lake has been lower than that of contemporary Linsley Pond by almost a complete order of magnitude, and that it is even lower than the net productivity of Linsley Pond during the unproductive early stages of its history.

It is not possible to obtain an estimate of past gross production, or even past net plant production, that is independent of the figures for net community production, although there is hope that a careful study of the proportions of stable and unstable components in the sediment may make it possible to arrive at an estimate of changes in diagenetic efficiency. For the time being we must content ourselves with comparing the present-day gross productivity with the net community productivity of the upper layer of sediment.

The light and dark bottle method gives an estimate of the gross productivity of the plankton community in a lake. We did not carry out such determinations in Alaska, but Comita and Edmondson (1953) have reported some determinations carried out on Imikpuk, a lake on the arctic coast at Point Barrow which is about the same depth and somewhat larger than Eight Lake. During the summer, from July 22 to September 6, 1952, Imikpuk had a daily production of fixed carbon averaging 0.030 milligrams (as glucose) per square centimeter per day. Annual figures are not available, but it is likely that this production rate was maintained for only three or four months, and that during the rest of the year there was very little photosynthesis. If this rate were maintained for 120 days the annual productivity would be 3.6 milligrams per square centimeter. If the productivity of Eight Lake has been about the same for the past six thousand years as the present productivity of Imikpuk, an efficiency of utilization of gross production of about 75 per cent is indicated.

Some comparable figures for photosynthetic activity of Linsley Pond have been obtained by Riley (1940) during the months of September to June. They indicate a productivity of about 0.089 milligrams (as glucose) per square centimeter per day, which is not appreciably different from the rate in Imikpuk. The Imikpuk measurements, however, were made during the summer season, while the Linsley Pond measurements are for ten months of the year, omitting July and August. If those months were as productive as June and September, Riley's annual mean might be raised to about 0.11 milligrams per square centimeter per day, or 40 milligrams per square
centimeter for an entire year. If this rate held throughout C2 and C3 time, the diagenetic efficiency of Linsley Pond must have been about 80%. This is slightly more than the efficiency calculated for Eight Lake, which is only two meters deep as opposed to 15 meters for Linsley Pond. Deep lakes should, in general, have a higher efficiency than shallow ones. The settling seston is subject to decomposition in the epilimnion of a deep lake that is comparable to the decomposition in the entire water column in a shallow one. In addition a certain amount of decomposition may be expected in the hypolimnion, despite the possible inhibitory influence of the low hypolimnetic temperature and oxygen tension that prevail there.

The figures for the amount of material preserved in the mud enable us to make some calculations concerning the relative importance of the energy flow through the decomposing organisms in a lake community. If we accept the respiration values, culled from the literature by Lindeman (1942), then 26% of the gross productivity of a lake is used by producers and consumers in respiration. The balance of 74% is preserved in the sediments or used by decomposing organisms such as bacteria and fungi. If this proportion holds for our lakes as well, then the percentage of the gross production that passes through the decomposing organisms is about 54% in Linsley Pond and about 49% in Eight Lake. This is somewhat higher than the figure of 24% which can be derived from the data of Odum (1957) from Silver Springs, Florida. Odum's estimate of bacterial energy flow depended on in situ measurements of bacterial activity in the mud. If bacterial activity in the periphyton is not, as he assumed in his calculations, equal to activity in the mud, but is higher, then his estimate is too low. We cannot, however, make any very great adjustments in the estimated energy flow through producers in Silver Springs without upsetting the community energy budget, nor does any general expectation that the role of decomposers in all ecosystems should be quantitatively similar constrain us to do so. We feel that quantitative analysis of the relative importance of decomposers, consumers, and storage or export will yield results of great importance to ecology, i.e., to the problems of terrestrial and aquatic paludification, and we regret only that the accuracy of our estimate does not enable us to pursue the subject any further.

The figures for rate of inorganic sedimentation given in the third column of Table 3 call for little comment. Their principal importance is that they show that the rate of silting in arctic lakes is greater, in general, than it has been in temperate Linsley Pond since its early history, but that Eight Lake, as is apparent from every other line of evidence as well, forms an exception and has lower rate of deposition of mineral sediment than Linsley Pond since the beginning of C-2 time.

The figures for Bosmina fragments indicate a much lower productivity in the Arctic than in Linsley Pond. The extremely low value for Eight Lake is to some extent a reflection of the fact that the lake had passed through its phase of high Bosmina productivity before the beginning of the time under consideration in these computations, but the concentration per cubic centimeter at the lower levels is only about 100 times as great. Even a Bosmina production of 75 instead of 0.75 per square centimeter per year would be a good deal below the lowest value computed for Linsley Pond. Unfortunately the reality of this difference must be slightly suspect, for the arctic Bosmina consisted of poorly preserved fragments instead of the half-carapaces so common in Linsley sediment.

With tendipedids, however, the story is different. Eight Lake appears to have had a productivity three times as great as that of Linsley Pond at its highest. The results cannot be regarded as conclusive because of the very great variation in the production, or at least the standing crop, of tendipedids in the temperate zone (Deevey 1941).

**DISCUSSION**

The principal characteristics of the arctic environment are its cold, with long severe winters and short cool summers, and the very marked seasonal distribution of insola-
tion. To a very considerable extent low precipitation is characteristic of the arctic regions as well.

The question that we had in our minds throughout this investigation is to what extent, if at all, these peculiar properties of the Arctic influence the workings of its lakes. We believe that we have found that the regional limnology of the Arctic is peculiar, but not always in the way that one would expect.

In the first place, the extreme cold of the far north does not seem to have a very great direct effect, except perhaps at the shore, upon life in the water. The lakes we have studied are not very large ones, and they attain summer temperatures of 12 or 13°C. This is no colder than the summer temperature of many deep lakes much farther south. For example, Lake Superior, at a latitude of about 48°, attains a maximum open water surface temperature of only about 10°C., although isolated bays and shallow water near shore may be somewhat warmer (Millar 1952). The well known thermal properties of water act to buffer aquatic organisms against the regional thermal environment, and the actual temperatures to which aquatic organisms are subjected are as much a function of lake size and shape as of latitude.

This is not to say that the length of the growing season is not affected by the shortness of the arctic summer; it is, but a short growing season is not restricted to the far north. In ephemeral lakes of the temperate and tropic zones the length of the growing season is limited by summer drought, and most aquatic organisms, at least of the smaller kinds, are adept opportunists, able to take advantage of favorable circumstances when they offer and to endure long resting phases of very low activity with little ill effect.

The seasonal distribution of insolation seems to influence mineralization. Although Eight Lake has a diagenetic efficiency somewhat less than that of Linsley Pond, the state of preservation of fossils in the sediment of the various lakes leads us to believe that the diagenetic efficiency of other Brooks Range lakes, particularly Chandler Lake, is very much greater. This is to be expected, for not only does the seston of a deep lake like Chandler have to fall a greater distance before it is preserved in the bottom mud, but a much greater reserve of dissolved oxygen is trapped under the winter ice to be available for oxidizing the organic component of the seston during the season of darkness.

The secondary characteristic of the arctic climate, low precipitation, has even less effect on life in the lakes. For most of the year the temperature remains below freezing and the light snowfall accumulates. Summer temperatures are so low that evaporation is not high and the frozen ground prevents subsurface run-off. As a result water is not scarce, despite low precipitation, and the arctic lakes do not show the striking seasonal variations in level so characteristic of lakes in other arid and semiarid lands.

Although the direct effect of the arctic environment on the biology of lakes does not seem to be pronounced, the effect on their physiography, and through it on all aspects of lake metabolism, is very great indeed. On the coastal plain the very existence of lakes, as well as their peculiar shape, their growth, and their ultimate disappearance, are due to the physiographic effects of the arctic climate. Even in the mountains, where the lakes owe their existence to past climatic phenomena that are not unique to high latitudes, the effect of climate on lake physiography is profound, not only in such minor things as the sculpturing of beaches but also in such important ones as the nature and amount of allochthonous sedimentation.

SUMMARY

1. Thaw lakes in northern Alaska occupy elliptical basins with a regular bottom, which appear to be in equilibrium with the environment, and irregular basins with pocked bottoms, which appear to be actively expanding and reducing the level of the landscape by about 15 meters.

2. Computations based on the shape of the active lake basins indicate that about 70% by volume of the upper 15 meters of the countryside consists of ice.

3. Active thaw lakes can be distinguished
from kettle lakes by the fineness of the bottom pitting. Quiescent thaw lakes can be distinguished from kettles by their smooth bottom contours.

4. The water of the Alaskan lakes freezes to a depth of almost two meters in winter and warms to about 13°C in summer. The lakes are unstratified during the summer months.

5. Although prevailing wind velocities are high the work of the wind in warming Chandler Lake, which is 21 meters deep, is only 175 cal/cm² of lake surface. The annual heat budget is about 28,000 cal/cm², of which only about 6,000 cal is wind-distributed heat.

6. There is a net flow of heat from the water to the earth in the case of lakes too deep to freeze solid in winter.

7. The total dissolved solids of the lakes investigated ranged from 35 to 159 ppm. At the seacoast Na⁺ and Cl⁻ were the dominant ions. Elsewhere Ca²⁺ and HCO₃⁻ were more important.

8. Silica was not detected in field tests, but up to 1.9 ppm of silica was found in samples that had been stored in pyrex bottles for several months.

9. The shore community is poorly developed or lacking in most arctic Alaskan lakes.

10. Standing crops of benthic organisms are low but not markedly so. Benthos ranged up to 89.4 kg/ha.

11. Most of the arctic lakes receive a very large contribution of allochthonous sediment.

12. Dryadotanytarsus is found throughout the sedimentary column of Eight Lake in Alaska and presumably lives there today.

13. In all the lakes investigated Pediacastrum boryanum increases in abundance from the bottom to the top of the sedimentary column. This increase appears to be associated with shoaling.

14. Eight Lake, which has a good fossil record, appears to have passed from an early eutrophic stage with high productivity of Bosmina and tendipedids to a later dystrophic stage with low animal productivity and high productivity of mosses. This change is attributed to exhaustion of the available base supply in the watershed.

15. Using a radiocarbon-dated pollen chronology, estimates have been made of the net community productivity of the Alaskan lakes. It appears to have averaged less than 2 mg of organic matter/cm²/yr during the past 6,000 years, as compared to 8 mg/cm²/yr for Linsley Pond, Connecticut, during a comparable period of time, and 7 and 4 mg/cm²/yr during earlier times.

16. On the basis of several more or less reasonable assumptions the efficiency of utilization of gross production is calculated to be 80% for Linsley Pond, Connecticut, and 75% for Eight Lake, Alaska. It is probably somewhat higher for the other Alaskan lakes.

17. On the basis of the same assumptions plus the respiration percentages of Lindeman, it is calculated that about 50-55% of the energy fixed by producing organisms passes through the decomposer level in a lake food chain.

18. Less than 10 Bosmina fragments have been preserved per square centimeter per year during the past 6,000 years in the Alaskan lakes as compared to 400, 700, and 4,000 per year for various stages in the development of Linsley Pond. Corresponding figures for tendipedid fragments are less than 1, 1, and 7 for the Alaskan lakes and 0.4, 0.7, and 2.2 for Linsley Pond.

19. The arctic environment appears to influence lakes principally through physiographic processes affecting origin, sedimentation, and drainage.

REFERENCES


