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# ENVIRONMENTAL EFFECTS OF DAMS AND IMPOUNDMENTS

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## INTRODUCTION

Most of the primary civilizations of the world emerged in or near river valleys. The construction of dams and other hydraulic structures is, therefore, one of the oldest branches of engineering (e.g. 11, 105).

The earliest dams were probably built for the purposes of irrigation, flood control, and water supply. Later, water was impounded so that its subsequent controlled release could provide a source of energy, first by the use of waterwheels and later by the use of hydroelectric generators. Other purposes include the maintenance of an adequate river flow through the year for navigation, and the provision of facilities for recreation. Most modern reservoirs are designed for two or more of these purposes. Usually "the role of water storage reservoirs . . . is to impound water in periods of higher flows so that it may be released gradually during periods of lower flows" (135), but sometimes the sole purpose of the impoundment is to provide a new body of standing water for use as such; for example, for fishing or boating, or for waste-heat dissipation from a thermoelectric generating plant.

The earliest dams were probably constructed by blocking the stream with earth. Such dams are still constructed. In its simplest form, an earth-fill dam is a pile of compacted earth extending across a stream with a fairly gentle slope both upstream and downstream. Similar to earth-fill dams are rock-fill dams composed of quarried rock or natural boulders or gravel with a layer of impervious material on the upstream face.

A later development in dam construction was the invention of the masonry dam, probably in Spain (150). The earliest masonry dams were of the gravity type. Such dams are held in place by their own weight pressing against their foundations, and usually have a long sloping downstream toe to prevent overtipping.

Arched masonry dams are convex upstream with their ends abutting against the walls of the stream valley or against suitable artificial structures. Such dams are held in place by thrust against their abutments, and are steeply sloping or vertical both upstream and downstream. Dams may also be built of structural masonry, or less commonly, of steel or timber.

In almost all dams, provision must be made for the safe discharge of excess water by the construction of a spillway, and in most instances, provision is made to control the rate of discharge. In dams constructed for hydroelectric purposes, there is also a discharge of water through a penstock to the turbines, and dams for irrigation or water supply must have outlets to the irrigation canals or water supply system. Penstocks and other outlets may draw water from well below the surface of the water in the reservoir.

The water level in a reservoir is usually manipulated according to the purpose for which it was built within the constraints imposed by the prevailing climatic conditions. Reservoirs built solely for flood control are usually emptied as soon as possible after a flood. Reservoirs for other purposes, however, are usually filled at times of high flow and either drawn down gradually during the rest of the year, or maintained for several months at a fairly constant level, then drawn down rather quickly in anticipation of the next period of high flow (143).

The amount of water impounded by a dam differs greatly from one site to another. In run-of-the-river hydroelectric projects, the purpose of the dam is essentially to direct and control the flow of the stream and little water is impounded. At the other extreme, a major new lake may be formed with a retention time measurable in years.

Dams may be built on streams that leave natural lakes so that the level of these becomes subject to some degree of regulation and they may be regarded as reservoirs. The effect on large lakes is slight. The conversion of smaller lakes to reservoirs may have very considerable effects on their ecology (94).

Most commonly, impounded water is retained directly behind the dam in an on-channel or mainstream reservoir, but occasionally water may be diverted from the stream to a suitable natural or artificial basin to form an off-channel reservoir.

A special form of hydroelectrical generating station of increasing importance is the pumped storage plant (4). In such a plant, some of the generated electrical power is used to pump water to a higher level to be used to generate electricity at a later time. Essentially, this is a means of storing energy. The reservoirs used in such projects are usually small.

Man is, of course, not the only dam-building animal. The dams of beavers, although smaller than many of those made by man, can cause spectacular changes in certain areas. Streams may also become dammed temporarily or permanently by various accidents, such as clogging with masses of floating vegetation or obstruction by landslides or lava flows. Lake Tana in the Ethiopian Highlands, the source of the Blue Nile, is an important example of a lake formed by the damming of a stream by the flow of lava (19).

The most dramatic environmental effects are those associated with the very large impoundments, especially perhaps those in Africa: Lake Volta, in Ghana, the largest in the world; Lake Nasser on the Nile, in Egypt and the Sudan; Lake Kariba on the Zambezi, between Zambia and Rhodesia; and the newest, also on the Zambezi, behind the Cobora Bassa Dam in Mozambique (56, 74). The many large reservoirs in the USSR, such as the Kuybyshev, Rybinsk, and Gorkii Reservoirs on the Volga, have received a great deal of attention. One South American reservoir, Lake Brokopondo in Surinam, has been studied by ecologists (90, 91). The largest North American reservoir is the Smallwood Reservoir in Labrador, Canada. The James Bay Hydroelectric Project in Quebec, Canada, will involve the construction of several large reservoirs (23, 48, 76, 137). In the United States, the best known is probably Lake Mead, on the Colorado River, although at least two others cover larger areas: the Garrison Reservoir and the Oahe Reservoir, both on the Missouri River. A more extensive list of large reservoirs of the world has been compiled (34).

Many studies have also been made on small reservoirs, such as those under the jurisdiction of the Tennessee Valley Authority (e.g. 172). Such countries as Rumania (40) and Spain (104) are dotted with small reservoirs. The study of reservoirs in Spain and in Czechoslovakia (64, 66, 67) has been a major activity of the limnologists of those countries in recent years.

The control of water for the benefit of man has been traditionally regarded as a particularly noble activity. According to one interpretation of Goethe's *Faust, Part Two,* it was Faust's hydrological endeavors that ultimately saved him from damnation. In our own time, such projects as the Tennessee Valley Authority have been rightly regarded as marvellous accomplishments. At the same time, the possible dangers of manipulating the flow of water have been recognized in moral and legal codes; the Negative Confession in the Egyptian Book of the Dead (16) contains the words "I have not turned back water at its springtide. I have not broken the channel of running water." The traditional Ethiopian law code, the Fetha Negast, recognizes the duty of people in the highlands to let waters flow to people in the lowlands (35). Doubtless, many more such examples could be found. Large modern projects have made provision to avoid at least the most obvious objectionable side effects; for example, the operating schedule of the TVA reservoirs includes periodic fluctuations in the water level to destroy the larvae of malaria-transmitting mosquitoes (143).

An attitude of optimism and enthusiasm still survives; it has recently been said (162) that "dams are the only solution to Man's angst." This attitude, however, is by no means universal. In recent years some very large projects have been undertaken to produce man-made lakes approaching in size all but the biggest of natural lakes. Some of these projects have had effects that were not anticipated or were ignored by their planners, and these have given rise to widespread concern. The literature on reservoir ecology is extensive, and is scattered through journals devoted to a wide range of disciplines, reports from various agencies, and books. Entry to this literature has been greatly facilitated by previous reviews (32, 41, 94, 106, 113, 138) and by the published reports of several symposia (1, 3, 33, 96, 118, 121). Translations of a number of Russian works are available (146, 147, 166, 175).

It has been pointed out more than once that a large impoundment may be regarded as a large-scale ecological experiment that may reveal or at least illustrate certain general ecological principles. The emphasis in this review is on the peculiarities of reservoirs and how they differ from natural lakes. Much excellent work on reservoirs has advanced our general knowledge of limnology rather than our specific knowledge of reservoirs. For the most part, I have not referred to this.

## MORPHOLOGY AND PHYSICAL AND CHEMICAL LIMNOLOGY OF MAN-MADE LAKES

### *General Morphological Characteristics of Reservoirs*

When a new lake is formed by damming a stream, its shape will usually be different from that of most natural lakes (68). The shoreline development (the ratio of the length of the shoreline to the circumference of a circle of the same area as the lake) is almost always higher than for natural lakes. If the river is confined between high banks, the new lake will be long and narrow; if there are tributaries, the water will back up into them, giving the new lake a dendritic form. If the river flows through flat terrain and has low banks, the water will spread over the plain forming what Russian scientists (175) call a lobed reservoir. The Manicouagan Reservoir in Quebec is ring-shaped, having been constructed by blocking the outlet of a meteorite crater with an elevated center (79, 148). It has, perhaps, the greatest insulosity of any large body of water in the world. When a reservoir is formed by damming the outlet of a lake, the change in morphology is less pronounced; but here too, the new shoreline will be more developed than the old. Off-channel reservoirs, on the other hand, being often completely artificial constructions, may be unusually regular in shape.

Reservoirs formed by damming rivers frequently differ from natural lakes in the shape of their longitudinal profiles. Whereas natural lakes are normally deepest somewhere near the middle, river reservoirs are almost always deepest just upstream from the dam. They have been referred to as "half-lakes" (32). One consequence of this is that surface currents passing down the reservoir will not dissipate themselves in shallow water as they do in natural lakes, but may be deflected downward or reflected backward at the dam.

The new shoreline, a shoreline of submergence in Johnson's (77) terminology, will not persist. It is acted upon by waves, by currents, and in cold regions, by ice; it is modified at a rate depending on the energy available, the shape of the reservoir and the surrounding terrain, and the resistance of the material. Ultimately the development of the shoreline is reduced, although in the earlier stages it may increase (159).

The extent of shoreline modification in a reservoir is likely to be greater than in a comparable natural lake because the annual drawdown exposes a larger area to the effects of shore processes.

Empirical equations exist (81, 85, 95) for calculating the available wave energy and the amount of material that will be eroded, but attempts to predict the changes that will occur have not been very successful (25).

In high latitudes where the inundated area may consist of muskeg overlying permafrost, shoreline changes may be particularly extensive and prolonged as the permafrost melts. The time required to establish a new shoreline of moderate permanence under such conditions may be more than 30 years (115).

Although the modification of the shorelines of reservoirs is usually a fairly gradual process, on at least one occasion it has been catastrophic. In October 1963, a large landslide fell into the newly filled reservoir behind the Vaiont Dam in Italy, spilling an equal volume of water over the dam into the valley below with the loss of more than 2000 lives. This disaster was probably due in part to seismic activity, perhaps induced by the filling of the reservoir (141).

### *Sedimentation*

Most of the material eroded from the banks of the reservoir will probably be deposited elsewhere within it. How it is deposited will depend on the morphometry of the lake and the currents in it. If the bottom has a low slope and there are strong currents along the shore, the material may be deposited near the shore, forming spits or sand bars. If the bottom slope is high, and nearshore currents are weak as, for example, in Lake Diefenbaker on the South Saskatchewan River in Canada (22), the material will be transported to the deeper parts of the lake and deposited there.

If the reservoir is on a river that carries a heavy load of sediment, this material will also contribute to the modification of the morphology of the lake. The sediment load of a stream may be produced either by sheet erosion of the surrounding land or by erosion of the banks of the stream itself or its tributaries. Of these, sheet erosion is usually the more important. Its extent depends on rainfall, slope, soil, and the vegetational cover; it may be greatly modified by land use.

Material carried by a stream may be divided into relatively coarse material pushed or rolled along the bottom (bed load) and finer, suspended sediment. When a stream carrying such material enters a body of standing water and its flow rate decreases, the material may be deposited, forming a delta. The coarsest material is dropped first, forming the foreset bed. As the delta grows, the rate of flow of water over it is further reduced, and material is deposited on top of it, forming a topset bed. Finer material may be deposited beyond the leading edge of the growing delta as a bottomset bed. Delta formation in reservoirs is complicated by the practice of drawdown. Material deposited when the water is high may be eroded away again when the level drops. Consequently, the shape and position of the delta are constantly changing, and the nature of these changes is not easy to predict.

If the gradient in the river is not very steep, the deposition of material will not be confined to the reservoir itself, but may extend upstream, sometimes for many miles. This leads to reduction in the capacity of the river channel and a consequent danger of flooding at high flows.

### *Physical Limnology*

The retention time of water in many reservoirs is fairly short, so that its circulation is likely to be dominated by near-field effects, i.e. those associated with the inflow and outflow, rather than the far-field effects (thermal circulation and currents generated by winds) that are dominant in most natural lakes. The situation in reservoirs is rendered still more complex by the fact that the discharge is frequently effected from a point at some depth below the surface. This depth may be varied. Discharge may be effected from more than one level at the same time. If the water in the reservoir is stratified, the outgoing water will be drawn from a relatively thin layer at the level of the outlet, so that internal currents (withdrawal currents) are set up and little vertical movement occurs (174).

The water entering a reservoir frequently differs from the water already present in temperature, or in content of dissolved or suspended solids, or in some combination of these, and consequently, in density. The incoming water does not then mix immediately with the water of the reservoir, but moves downstream and laterally above, below, or within it, as an overflow, underflow, or interflow. Such flows are referred to as density currents. A convergence line often appears where the inflowing water plunges below the surface. A compensating upstream current is generated, carrying back debris which is immobilized where the two currents meet, making a convergence line visible even if its position has not already been revealed by a difference in turbidity between the inflowing and the surface water. The first density currents to be observed in a reservoir were apparently those in the Norris Reservoir, the largest of the storage reservoirs of the Tennessee Valley Authority (171).

When the inflowing water owes its greater density in whole or in part to suspended material, the resulting underflow is known as a turbidity current. The difference in density may be only a few percent; or the water may be so loaded with silt as to form a virtual slurry, so that the distinction between a turbidity current and a sliding mudflow may be almost obscured. The differences have been discussed by Kuenen (87). Turbidity currents caused by very dense suspensions are important in the sea (78) but in lakes and reservoirs, the density difference is usually rather small. Formulas exist for the calculation of the flow rates of turbidity currents (151).

The best known turbidity currents are those in Lake Mead which may extend for the whole length of the lake—about 160 km (51). Turbidity currents are important not only for their contribution to the flow patterns within a reservoir, but because they can carry silt for a long distance into it, depositing some of it on the way, and so contribute to the formation of bottomset deposits.

Slapy Reservoir on the Vltava River in Czechoslovakia provides a good example of the complexity of the flow and stratification patterns in reservoirs of relatively short retention time (65). This reservoir is 42 km long and 313 m in mean width and has a maximum depth of 53 m. Water is withdrawn from it at a depth of 35 m. The filling time at the mean flow rate of the river is 38.5 days. From February or March until August, the outflow water is cooler than the inflow, and during the rest of the year, the inflow is cooler. Through most of the year, the surface water is warmer and less dense than either the inflowing or outflowing water, so that the inflowing water plunges beneath the surface, mixing, to some degree, with hypolimnic water but not to any great extent with surface water. The consequence is that the renewal time for surface water is very considerably higher than the mean renewal time for the reservoir as a whole, the reverse of the usual situation in natural lakes. This tendency of the inflowing water to pass under the epilimnic water has been accentuated by the construction upstream of another reservoir (the Orlik Reservoir), the cool outflowing water of which becomes the inflow of Slapy.

Slapy Reservoir also displays a degree of horizontal zonation not usually found in natural lakes. The upstream region of relatively high flow has a length of 10–15 km and merges through a transition zone of 5–10 km with a relatively stagnant section of about 20 km. Finally, there is a zone of about 5 km where the reservoir is directly influenced by the turbines. The biological consequences of this horizontal zonation are discussed below.

If a reservoir is formed in a wooded area and the trees are not removed before flooding, they may have a significant effect on the circulation pattern of the reservoir. In the Nam Ngum Reservoir in Laos, standing trees almost completely abolish wind-generated turbulence and consequently reduce the extent of mixing. This gives rise to a complex pattern of stratification with a surface layer of warm water and an intermediate cooler layer from which water is drawn to the turbines, and a still cooler bottom layer apparently consisting of water that has been brought in by streams from the mountain during the coolest part of the year (W. M. Lewis, in preparation). Standing trees also interfere with mixing in the Brokopondo Lake in Surinam (90).

The exposed parts of flooded trees are quickly destroyed by wind and waves combined with biological action. The fully submerged parts, however, persist for a long time. In the Gouin Reservoir in Quebec (latitude 48 degrees N), the wood of submerged trees showed little change 55 years after the reservoir had been filled (28). In warmer climates, the process of decomposition is presumably more rapid; but even there, submerged trees may be expected to persist for many years.

### *Chemical Limnology*

The chemical composition of the water of natural lakes and mature man-made lakes, particularly the concentrations of conservative constituents, is largely determined by the chemistry of inflows and of precipitation into it. However, in new impoundments it may be influenced by the leaching of soluble material from the flooded ground. If the amount of soluble material is small and the retention time of the water is short, this effect may be brief. If the amount of soluble material is large, as in Lake Mead (63), and especially if the retention time is long, the chemistry of the impounded water may continue to differ from that of the inflow for a long time. The presence of density currents may lead to unusual and complex patterns of chemical stratification if the chemical composition of the inflowing water is different from that of the water already present in the reservoir (152, 153, 171).

The decomposition of submerged vegetation often leads to a depletion of oxygen in the depths of the reservoir. The peculiar profile of most reservoirs, as compared with natural lakes, may permit the accumulation of a mass of stagnant water in the deepest part against the dam (165). This bottom layer can become anoxic (36), and reduced substances such as sulfide, ferrous, and manganous ions may accumulate. Nutrient substances may be leached from the underlying soil or released by the decomposition of submerged vegetation. The biological consequences of this are discussed in the next section.

Impoundment by itself usually improves the quality of water for domestic and industrial use (134); suspended solids have an opportunity to settle, the bacterial population decreases, the dissolved oxygen concentration may increase, and the color of the water may decrease [probably by photo-oxidation of the dissolved humic substances (155)]. In a new reservoir, however, many of these effects may be more than balanced by the depletion of dissolved oxygen and the leaching of humic substances from the soil (46). As the reservoir matures, the quality of the water gradually improves. To hasten improvement, it has sometimes been the practice to strip the area to be flooded (i.e. remove the vegetation and top soil) before the reservoir is filled (155). The usefulness of this practice depends among other things on the nature of the soil, climatic conditions, and the retention time of the reservoir. In a group of reservoirs in New England, water over the unstripped soil attained normal conditions in an average of six years (145). In experiments carried out in southeastern Quebec using several types of soil in small basins, the concentrations of most constituents over unstripped soils approached those over stripped soils in a year or so (18).

Often the construction of dams on a river is only one aspect of increasing industrial activity in a region; to the effects of impoundment are thus added the effects of domestic and industrial effluents. In the Saint John River in New Brunswick, Canada, the construction of dams has reduced the rate of flow of the river, and consequently, its ability to become oxygenated; and at about the same time, the establishment of industries along the river has contributed effluents of high biochemical oxygen demand (29).

The flooding of previously dry ground may lead to the release into the water of toxic substances there either naturally or as a result of human activity. The alteration of the pattern of erosion and sedimentation may lead to the release of pollutants (such as mercury) which are known to accumulate in sediments.

## BIOLOGY OF RESERVOIR ECOSYSTEMS

### *Some General Principles*

An ecosystem consists of a biological community and the habitat in which it lives. The two interact so that both change. The formation of a new lake provides a new habitat for the development of a new ecosystem. This section considers the biological factors that come into play when a new lake is created, and traces the way the biological community develops.

A number of general biological principles have been discerned by ecologists which make it possible to predict, in its broad outlines, the course of development of a new ecosystem and to provide a general conceptual framework for interpreting the observed events. The epistemological status of these principles is a matter of question (127). At least, however, they are helpful in organizing and systemizing large numbers of diverse observations. Among the most useful of these are the following:

THIENEMANN'S RULES 1. The greater the diversity of conditions in a locality, the larger the number of species in the biological community. 2. The more conditions in a locality deviate from the normal, and thus from the optimum for most species, the smaller the number of species and the greater the biomass of each. 3. The longer a locality has been in the same condition, the richer its biological community (160).

THE CONCEPT OF SUCCESSION Students of terrestrial botany have long recognized that the development of a new plant community follows a recognizable pattern (e.g. 84). This concept has been generalized and refined by Odum (119, 120) with an emphasis on certain characteristic changes that an ecosystem exhibits as it matures. Among the most important are the following: A balance is approached between gross production and community respiration (in a new ecosystem either may exceed the other); there is an increase in species diversity and spatial heterogeneity, in the complexity of food chains, and in orderliness (a decrease in entropy, an increase in information content).

THE CONCEPT OF PULSE STABILITY This concept, also Odum's (119, 120), argues for the maintenance of an ecosystem in a relatively immature state by the periodic or quasi-periodic imposition of a physical perturbation. In the present context, periodic flooding is the perturbation of interest. Many of the most dramatic ecological effects of impoundment can be interpreted as results of the interference with previously existing pulse-stabilized ecosystems, or the establishment of new ones.

THE CONCEPT OF THE ECOTONE As the concept of pulse stability concerns the ecological consequence of variability in time, so the concept of the ecotone comprehends the consequences of variability in space. An ecotone is a transition between two communities or environments. It is usually narrow and characterized by a greater diversity of species than the communities or environments on either side. The littoral zone of a lake or river may be regarded as an ecotone (102, 120).

THE THEORY OF ISLAND BIOGEOGRAPHY A lake is in some ways the aquatic equivalent of an island (83). The concepts of island ecology (98) are of value in understanding the ecology of lakes, especially the colonization of new ones. Specifically, the distinction between $K$-selection and $r$-selection first proposed by MacArthur & Wilson (98) and subsequently developed by a number of authors (e.g. 131) appears useful. The terms $K$ and $r$ refer to the parameters of the logistic equation: $N = K/(1+e^{a-rt})$, which generally describes the growth of populations. $N$ is the number of individuals at time $t$, and the parameters $K$ and $r$ are respectively the maximum population possible in the given habitat and the specific growth rate of the species in question. $K$-selected species have a high capacity for maintaining their numbers under competitive conditions, whereas $r$-selected species can increase their numbers rapidly. New ecosystems are usually colonized by $r$-selected species.

These concepts are not independent. The high diversity in spatially variable environments to which Thienemann's first rule refers could be attributed, in part, to the large number of ecotones in such environments. Poorly diversified yet relatively productive ecosystems such as hot springs (15), highly saline waters (173), or soda lakes (158) to which the second rule applies may be considered immature ecosystems that are unable to develop because the few species able to live in them cannot bring about any modification of their physical and chemical characteristics. Thienemann's third rule calls attention to one of the most prominent features of the process of maturation of ecosystems.

DIFFERENCES BETWEEN STREAMS AND LAKES When a stream is dammed, the new lake provides a very different habitat from that provided by the stream (71). Because flow is always turbulent in a stream, thermal stratification rarely develops and oxygen depletion rarely occurs unless the stream is grossly polluted. Because floating organisms are being swept away continually, the population of plankton is low, whereas the benthic population may be high. The benthic organisms of streams often display morphological adaptations to life in flowing water.

An even more fundamental difference between the biological communities of streams and those of lakes is the source of the energy needed to maintain them. The communities of standing waters rely for the most part on photosynthesis. In streams, however, the ultimate energy source is allochthonous organic material that is heterotrophically metabolized (72). Part of this is in particulate form and is utilized by benthic organisms either directly or after being attacked by microorganisms (7); and part is in the form of dissolved organic compounds, mostly leached from the soil. These together may provide more than 99% of the utilizable energy input (38). Although a few predominately heterotrophic lakes exist, especially in the tropics (9), the concept of lakes as fundamentally autotrophic systems and streams as heterotrophic ones appears useful and generally valid.

Since in streams respiration always exceeds production, it might be thought that a stream is a permanently immature ecosystem. In fact, it is not meaningful to regard a stream as an ecosystem (72); this term can only be usefully applied to the entire watershed.

When a river is dammed and a new lake is formed, two things may therefore be expected to happen: (*a*) the lotic benthos will perish to be replaced eventually by lentic organisms; and (*b*) plankton populations will develop, so that the importance of photoautotrophic processes will increase. Ultimately, the amount of heterotrophic activity will probably decrease as the area of water increases relative to the length of shoreline providing litter. Initially, however, there will almost always be a burst of intensified heterotrophic activity as organic matter in the drowned vegetation and flooded soil is utilized.

### *Development of the Benthos*

Among the first very large reservoirs to be constructed were those on the Volga in the USSR. The development of the benthic populations of the Gorkii and Kuybyshev reservoirs has been described in some detail (110). These reservoirs were filled in the autumn. By spring, most of the organisms originally present had perished and so the benthic fauna was very sparse. Beginning in July, larvae of the chironomid *Chironomus* (*Tendipes*) *plumosus* appeared and reached such numbers that when the midges emerged they interfered with navigation (175). Several other species of chironomids subsequently appeared in smaller numbers, along with motile aquatic arthropods and the freshwater mussel, *Dreissena,* which has motile larvae. Other molluscs, and oligochaetes such as tubificids, remained confined to the old river bed. During the following season, the chironomid population declined and the solely aquatic species continued to spread into the newly flooded area. This trend continued during the third season and the benthic population approached that of a natural lake.

Chironomids are well adapted to be the first colonizers of newly flooded areas. They may reach the area either as the winged adults or as larvae (26). Their fecundity is high; they may be regarded as typical *r*-selected organisms. Furthermore, some species can endure the low oxygen concentrations that are likely to occur in new impoundments. It is scarcely surprising, therefore, that chironomids have been among the first organisms to appear in new impoundments under a considerable range of conditions. Thus, a beaver dam in Algonquin Park, Ontario, was constructed in the early summer, and the insect fauna almost immediately changed (154). The numbers of Ephemeroptera, Trichoptera, and Plectoptera decreased, and the number of chironomids increased. This trend was even more pronounced in the following year. The study was carried out by trapping emerging adults. No information was obtained about other components of the benthic fauna.

In a broader study on a small impoundment in southern Ontario (123), the reservoir was filled in the spring and the major component of the benthic fauna was initially oligochaetes that invaded the flooded area from the original stream bed. However, during the summer, chironomid larvae became dominant. The chironomid population was smaller during the second season, and the species distribution showed a shift from species characteristic of a highly eutrophic lake to those favored by less eutrophic conditions. During much of the study period, oribatoid mites were the third largest group (after oligochaetes and chironomids) in the population.

In Barrier Lake, a reservoir on the Kananaskis River in Alberta, Canada, the population of chironomids developed very quickly after filling; during the next two years, chironomids made up most of the benthic biomass (116). Here, too, a succession was observed from organisms favored by eutrophic conditions to those preferring relatively oligotrophic conditions. A decade later, chironomids had decreased and the benthic fauna now included substantial numbers of pisidia and oligochaetes (117). In the reservoir formed by the Goczalkowice Dam on the Vistula River in Poland, a similar succession (chironomids to oligochaetes to molluscs) was observed (86).

It seems reasonable to suppose that in the temperate regions, small areas of newly flooded land will be colonized first by oligochaetes from the former stream; but if the area flooded is large, the first to arrive will be chironomids, and oligochaetes and other purely aquatic organisms will invade the area later. Occasionally, however, the damming of small lakes has been followed by a decrease in the population of chironomids (149).

The development of the benthic populations of Lakes Volta and Kariba has recently been reviewed (106). As in large temperate impoundments, the first colonizers were chironomid larvae; in Lake Volta one species, *Chironomus transvaalen-*

*sis,* was predominant. In Lake Kariba, the population after filling was more diverse, but when the water level rose again after the first drawdown, *C. transvaalensis* became dominant here too. In Lake Volta, the chironomid population became smaller but more diverse as the lake filled. This was attributed to changes in the bottom material along the shore when the shoreline was subjected to increased wave action owing to the increased wind fetch over the lake (130). In both lakes, the benthos was initially confined to a narrow strip along the shore because of the absence of oxygen in the deeper water. As the depth of oxygenation increased, the organisms moved outward and downward. In contrast to what was observed in temperate impoundments, the population of oligochaetes never became very high. This has been attributed to the greater rate of decomposition in the tropics, which prevents organic matter from accumulating below the mud–water interface, so that little food was available for burrowing organisms (106).

There is frequently considerable longitudinal variation in the benthos of reservoirs. In Barrier Lake, the largest population was found in the upper part of the reservoir where sediment rich in organic material was regularly deposited and the area of bottom laid bare at drawdown was relatively small (116). Likewise, in Lake Volta, after the benthic biomass in the lake as a whole began to decline, a higher population was maintained in the areas most directly influenced by inflows (128).

If the flooded area contains standing trees, these will provide a substrate for a variety of invertebrates. In the reservoirs of the Volga, the first invertebrates were almost exclusively chironomids (109). Later, mussels attached themselves to the trees and accounted for most of the biomass (97). In Lake Volta, the situation was entirely different; although some chironomids were present, the predominant form was the larva of the burrowing mayfly, *Povilla adusta*, which excavates holes in wood where it hides (129). In Lake Kariba, the submerged trees were of species having harder wood than those at Lake Volta, and they apparently resisted the attack of the mayfly nymphs (106). Consequently, after the lake filled, the fauna of the trees consisted largely of chironomids and oligochaetes. When the lake was drawn down the now exposed dead trees were attacked by the larvae of wood-boring beetles, which tunnelled between the bark and the wood. When the lake was filled again, substantial numbers of *Povilla* nymphs and smaller numbers of other insect species appeared, living in the tunnels that had been made by the beetles.

Organisms like *Povilla* do not use wood as food; they make tunnels only as places of refuge. Indeed, no freshwater invertebrates seem to eat wood the way teredenid molluscs do in the sea and many insects do on land. The decomposition of submerged wood is only brought about by the slow action of bacteria and fungi, which no doubt accounts for wood lasting a long time in fresh water, even if it is well oxygenated.

The conditions of gentle flow of relatively clean water that prevail in many reservoirs and their associated structures appear particularly favorable to certain sessile organisms, notably bryozoans and sponges. Thus they may occur in large numbers particularly near the outlet pipes; they have long been referred to as "pipe moss" by water engineers (111).

### *Development of the Plankton*

Impoundment may influence the plankton population of a body of water in a number of ways. Reduction of the rate of flow of a stream will allow the sparse plankton already present to multiply before it is swept away. Often a large plankton population develops when the reservoir is filling and there is little outflow (106). Even after the reservoir is full and outflow becomes substantial, a fairly large plankton population may persist.

Various authors have attempted to define the conditions of flow under which the transformation of a stream ecosystem to a lake ecosystem may occur. Margalef (101) has suggested that the conditions under which a flowing, rather than a static, ecosystem will exist may be defined by the inequality: $V^2 > 4A'r$, where $V$ is the rate of flow, $A'$ is the coefficient of eddy diffusivity, and $r$ is the rate of increase of the plankton. This relationship is based on an expression relating to the development of the plankton of the sea (139), where cells are being removed not by horizontal flow but by vertical settling. Russian scientists (164) suggest an even simpler criterion; in Russian reservoirs a lacustrine plankton population develops if the rate of flow is less than 0.2 m $sec^{-1}$. It seems unlikely that any simple criterion is universally applicable. Typically, many reservoirs contain regions of fairly rapid flow where the plankton populations will be small, and other regions of slack water where considerable populations may develop.

Where the development of a plankton population is mainly due to the decrease in flow rate without addition of nutrients, as in the temporary reservoirs of the Nile, a decrease in the concentration of nutrients in solution is likely (133). However, if the impoundment causes the flooding of a considerable area, the growth of phytoplankton may be increased by the nutrients made available by leaching from the soil and by decomposition of drowned vegetation. The first effect to be observed may be an increase in primary productivity rather than of standing crop. In these cases, the nutrients made available may be taken up so quickly that little or no increase in their concentrations may be observed (140).

When a lake is impounded, the earliest effect to be observed may be a decrease in phytoplankton standing crop, as a result of dilution, especially if the inflowing water is highly colored (122). Artificial lakes frequently are relatively eutrophic at the beginning. Blooms of blue-green algae are often observed, although their development may be suppressed if the water is highly turbid (105). However, under the flow conditions prevailing in many reservoirs, eutrophy is unlikely to persist. In stratified natural lakes with fairly long retention times, the behavior of nutrients is controlled to a large extent by biological processes. These processes are probably less significant in many reservoirs because of their low retention times, which permit nutrients to be flushed away fairly quickly (161). Nutrient loss will be hastened by discharge from the hypolimnion, since the concentration of nutrients is higher in the hypolimnion than in the epilimnion for much of the year.

Large variations in the water levels of reservoirs may hasten the return of nutrients from the sediments in the areas that are laid bare. This certainly happens in tropical impoundments. In temperate regions, the normal drawdown regime exposes large areas of the bottom only during the cold part of the year when the release of nutrients from the sediments will be slow. However, if an area is kept exposed for a year or more and then reflooded, significant amounts of nutrients can be released to the water (161).

The zooplankton of reservoirs, like the zoobenthos, changes in species distribution following impoundment, but the change is less dramatic. Species typical of rivers decrease in numbers or disappear, whereas characteristically lacustrine species appear or increase.

Conditions in reservoirs appear to favor the development of certain unusual zooplankters. Thus, the copepod *Arctodiaptomus ibericus* is widely distributed in Spanish reservoirs but has not yet been found in natural waters (103). Even more surprisingly, a previously undescribed species of water mite (*Piona limnetica* Biesiadka) was found to constitute a substantial part of the zooplanktonic biomass in a thirty-year-old reservoir in the Canal Zone of Panama (47). Water mites are not usually an important part of the zooplankton (69) and the presence of these predacious organisms influenced the general composition of both the zooplankton and phytoplankton communities.

If a river is regulated over a considerable range of latitude, the series of reservoirs may provide a series of stages by which northern species of zooplankton may be introduced into the more southerly regions, as in a number of rivers in the USSR (30).

A longitudinal zonation of plankton, similar to that observed with benthos, occurs in many reservoirs. In Slapy Reservoir, the area most influenced by the inflowing river has a higher population of green algae, and a lower population of blue-green algae than has the central, more lake-like zone. All forms of phytoplankton decrease in the area directly influenced by the outflow. The zooplankton population is relatively sparse in the upper region as compared with the main body of the reservoir. There is also some lateral variation with local concentrations of plankton in bays and inlets (65).

In Lake Volta, blue-green algae predominated at first in the upper and diatoms in the more lake-like lower part. Subsequently, diatoms have established themselves more widely throughout the reservoir (12).

### *The Littoral Region*

The ecotone between land and water is normally a productive and interesting region. Its nomenclature is complex (68); for the present discussion, following Pieczynska (132), the term *eulittoral* will designate the area between the highest and lowest waterlines, together with the part of the land that is splashed by waves and the area below the lowest water level that is intermittently uncovered by waves. The terrestrial zone immediately above the eulittoral will be referred to as the *epilittoral.*

The characteristics of the plant communities of eulittorals, subjected to a variety of flood regimes, have been summarized (60). The development of reservoir eulittoral ecosystems is dominated above all by the practice of drawdown. In natural lakes, the zones between the highest and lowest waterlines are commonly subjected to a short period of flooding in the spring or during the rainy season, followed by a long period of exposure. Many organisms adapted to this regime have evolved;

diversified and productive pulse-stabilized communities usually exist in such regions. In reservoirs, the situation is commonly reversed, there being a long period of flooding and a short period of exposure. This fundamentally unnatural regime stabilizes an ecosystem of a degree of immaturity which in high latitudes amounts virtually to barrenness; indeed, Swedish ecologists have proposed a new term, *aridal,* to designate the drawdown zone of reservoirs (94). In tropical regions where growth of terrestrial vegetation is possible during the period when the drawdown zone is exposed, the situation is somewhat different. The littoral regions of pumped storage reservoirs are subject to particularly severe conditions. Here the period of fluctuation of the water level may be as short as a day, often with a superimposed weekly fluctuation, since water is usually pumped into the reserves at night and during weekends (4).

Both aquatic and terrestrial organisms adjacent to the periphery of the reservoir are adversely affected. During the period of high water, organisms enter the drawdown zone only to perish when the water level falls. The effect drastically reduces the diversity of the benthos in temperate regions (70, 117). In a tropical reservoir, Lake Kariba, chironomid larvae are stranded by the falling water, but the population in the water is maintained because adult females are always available to lay eggs below the receding water line (106). There is evidence, however, that even in the tropics drawdown reduces the diversity of the benthic population (106).

In the tropics, terrestrial grasses may grow on the drawdown zone when it is uncovered. Around Lake Kariba, this grass provides grazing for many large animals. When the water rises again, nutrients are leached from their dung, which probably increases the productivity of the aquatic ecosystem (106). In the temperate regions, however, since the drawdown zone is usually exposed at the coldest time of the year, little growth is possible. Despite attempts to plant amphibious trees or shrubs, such as willow, on the edges of reservoirs (44) or, in fairly mild regions, to seed the drawdown zone with cereals (39), these regions will remain unattractive at best. The prospect of the transformation of the eulittoral of a lake into a near-barren mud flat has often aroused very bitter opposition among biologists, as for example in Tasmania where the flooding of Lake Pedder became a major political issue (126).

When the water level of a lake or stream rises following impoundment, the existing epilittoral will be flooded and destroyed. This, like the eulittoral, constitutes an interesting and productive ecotone, providing food and shelter for many animals, including birds and mammals both large and small. Eventually a new epilittoral will establish itself above the new eulittoral, although the large variations in water level may prevent it from ever becoming as productive as the original. In warm climates but not in colder regions, the new epilittoral should establish itself fairly quickly. Since this zone is particularly important in cold regions, the destruction of the epilittoral has been a matter of particular concern in such developments as the James Bay project (48, 76).

## *Fish and Other Vertebrates*

It has long been known that new impoundments frequently provide excellent fishing, both for sport and on a commercial scale (32). More recently, high fish yields have been obtained in the large African reservoirs (106). A factor that contributes to this plenty is undoubtedly the availability of large numbers of benthic organisms as food. In temperate regions, the high population of fish usually declines after a few years. Soviet scientists (5) have observed three phases in the development of many of their reservoirs. The first phase of high productivity, based largely on benthic organisms feeding on drowned vegetation, is followed by a phase of trophic depression when this material is exhausted or rendered unavailable by silting. This phase, which may last for several decades, gradually leads to a slow increase in productivity as the growth and settling of plankton provide a new layer of organic sediment. In Lake Volta, fish catches have declined in the 10 years since the dam was closed, but they are still good (49).

The high fish yields in new impoundments are probably not due solely to the abundant food supply, but also to the cover provided for young fish by the flooded vegetation. Increased fish yields in Lake Mead in years following unusually high water levels have been attributed at least in part to this (61).

However, impoundments may also be harmful to fish. In temperate and tropical regions many species spawn in nests in the shallow water near the shore, and these may be laid bare when the water level drops, so that the eggs or young perish (94, 144). There is also a danger of large numbers of fish being killed if the bottom water of the reservoir has become anoxic and is then mixed quickly with the surface water as a result of a change in weather conditions (32).

The impoundment of a river often leads to changes in the kinds and numbers of fish parasites; sometimes the level of infestation may become very high. A number of factors are involved in this. The number of zooplankters that serve as intermediate hosts increases, and the feeding habits of the fish may change (8, 62, 89).

The long-term effects of impoundments on populations of nonmigratory fish, therefore, depend on a large number of factors, including habits of the particular species affected, the drawdown regime of the reservoir, and the prevailing climate (which, in turn, imposes constraints on the drawdown regime). The many dams constructed by the Tennessee Valley Authority have greatly benefited the fisheries in the area involved, both in terms of numbers of fish and in terms of the species available (172). These dams were built in a region where the climate is relatively mild. During most of the summer, the water levels are kept constant (except for fluctuations to control malaria). In higher latitudes, the situation may be different. In lake reservoirs in Sweden, populations of littoral species have declined, whereas pelagic species have not been greatly affected (94). The time of spawning may be delayed if the time of autumn cooling or spring warming of the water is changed (100). Flooding of spawning grounds may discourage breeding although fish may continue to spawn in the same places after the water level rises (24).

Methods proposed for reducing the harmful effects of drawdown on the fish populations include the construction of sub-impoundments that retain water when the level in the main impoundment drops (54), the construction of floating nesting platforms (175), and a drawdown regime which avoids laying bare the littoral at the most critical times (61).

The rapid fluctuations of water level in pumped storage reservoirs probably have less direct effect on fish than the long-term fluctuations in conventional reservoirs.

Apparently the selection of sites for nest construction and spawning takes several days, so that the eggs are not likely to be laid in the drawdown zone (57).

In general, impoundment is not likely to be disastrous to the fish populations of any body of water. The species composition of the population may be changed to some degree.

Many mammals are trapped and drowned during the filling of large new reservoirs. In some instances, large operations have been mounted to rescue them. At least one such operation, at Lake Brokopondo in Surinam, has provided interesting new zoogeographical information (91). After the initial loss, the effect of an impoundment on wildlife depends on the prevailing conditions. In some areas, river valleys provide the best wildlife habitat; if one of these is flooded, there will be a permanent decrease in the animal population. Elsewhere, however, flooding may favor wildlife by providing water and opportunities for grazing on the drawdown zone.

Similar considerations apply to birds. Many nests are destroyed when a reservoir is filled during the nesting season, and the amount of suitable habitat for some species is permanently reduced. However, reservoirs may provide significant new habitat for waterfowl in areas where natural standing water is scanty, and may lead them to modify their migratory and nesting habits to some degree (6). Where vegetation has an opportunity to grow on the drawdown zone, it is used by birds as well as by mammals, e. g. around the Koka Reservoir in Ethiopia, where large numbers of Egyptian geese, spur-wing geese, and other waterfowl are often seen on the drawdown zone (personal observation). In Kariba Reservoir, birds feed on chironomid larvae stranded when the water level drops (106).

## DOWNSTREAM EFFECTS OF IMPOUNDMENTS

Many of the effects produced by dams on the stream below them are the reverse of those produced on the lake above them. What is retained in the lake (heat, silt, inorganic or organic nutrients) is lost to the stream. Moreover, the large annual variation in the water level of the lake will almost certainly be associated with a decrease in the annual variation of water level in the stream. All these, in turn, may have certain biological consequences, sometimes far away.

Other effects may be caused by the mere existence of the dam as a barrier to free passage up and down stream, and by the induction of a precipitous fall of water or, alternatively, by the elimination of a precipitous fall of water when water is diverted upstream from a waterfall. This may lead to the destruction of interesting local spray-zone ecosystems (14, 82).

If sediment is deposited in the reservoir, the clear water leaving it may pick up a new load of sediment, eroding the shores and stream bed below the dam as it does so. The loss of organic detritus from the stream may reduce the level of heterotrophic activity, at least until a new source of detritus is provided by the plankton of the reservoir. The amount of primary production in the stream will be favored by the decrease in turbidity; it will tend to be decreased, however, if the growth of plankton following impoundment has led to a depletion of nutrients from the water. On the other hand, if the amounts of nutrients introduced into the water by flooding are in excess of what can be taken up by the plankton of the reservoir, primary productivity downstream may increase, at least for a time (88).

The complex flow pattern in many reservoirs may have an important influence on the downstream temperature regime. In summer, solar radiation on the reservoir will be converted to thermal energy that will heat the epilimnion but have little effect on the hypolimnion. Thus, the epilimnion serves as a trap for heat that would otherwise have served to warm the water of the stream. In winter, after stratification has broken down, some of this heat will enter the outflow. The overall effect, therefore, makes the stream below the dam cooler in summer and warmer in winter than it was before the dam was built.

This can give rise to density currents flowing upstream in tributaries entering the main stream below the dam. These will flow on the bottom of the streambed during the summer, and over the surface of the tributary streams during the colder part of the year. Among other effects, such upstream density currents can adversely affect water quality in the tributaries (20).

The biological effects of the change in the temperature regime may be quite severe. In the South Saskatchewan River below Lake Diefenbaker, the benthos has been found to be impoverished as much as 110 km downstream (93). Below the dam of a mountain reservoir in Colorado (169) the diversity was less than that in similar but unregulated streams, but the biomass was higher. (Compare Thienemann's second principle.)

The construction of a dam usually leads to a decrease in the amplitude of long-period, especially annual, variations in water level downstream. However, if the dam has been built to generate electrical power, the operation of the plant may introduce small-amplitude short-period variations as the discharge is varied in accordance with the demand for electricity. These variations can be destructive of benthic organisms and cause a considerable reduction in diversity (37, 163).

At higher trophic levels in particular, it is exceedingly difficult to predict the net effect. Decreased turbidity may increase primary productivity (thus perhaps increasing the available food supply) and will make it easier for fish to find food; but it will also make it easier for predators to find fish. Cooling of the stream may make it possible for cold-water fish, such as salmonids, to survive where they were unable to before (172). At the same time, however, it may decrease the supply of benthic food organisms whose numbers may be still further reduced by a decrease in heterotrophic metabolism and by the destructive effects of short-term variations in the water level.

Another danger for fish and other aquatic animals below dams is gas-bubble disease (58, 112, 142, 156), which resembles the "bends" in divers (27). If a fish ingests water supersaturated with gases, the excess gas may come out of solution as bubbles. These lodge in various parts of the fish's body and cause, depending on their size and location, injury or death. Water may become supersaturated with gases in two ways that are relevant to the present discussion. When air and water are mixed in a turbine, the pressure may be great enough to force gas into solution (99). When water plunges over a spillway into a deep basin, entrained air bubbles may be carried to a considerable depth where the hydrostatic pressure may be great enough to force gas into solution (10). The degree of supersaturation required to cause gas-bubble disease depends on the age and species of the fish, but as little as 18% supersaturation may be sufficient (142).

Dams may pose a serious obstacle to the upstream movement of anadromous fish, as well as to the downstream movement of the smolts. Of the two, the former is probably the more serious. Since some species of Pacific salmon spend as little as two years in the sea, blockage of streams for this short a time as, for example, during the construction of a dam, could effectively eliminate the population of these species from the stream. Even a partial blockage could obscure the olfactory and tactile clues by which the fish are guided to their spawning grounds (59). Pacific salmon do not feed on the way to their spawning grounds, and the energy reserve in their bodies is little more than sufficient to bring them to their destination (73). Hence, time lost wandering in a region of slack water above a dam could reduce their chances of reproducing.

Dams also pose an obstacle to the downstream movement of catadromous fish, of which eels are the most important. The fate of eels in the hydroelectric turbines at Cornwall on the Saint Lawrence Seaway has been gruesomely described (92). However, young eels (elvers) can negotiate obstacles that would be impossible for adult salmon, and there is no evidence that elvers seek out the streams from which their parents came, so that the danger of the depletion of eel populations as a consequence of hydroelectric development does not appear serious.

The construction of fish ladders and other devices to permit fish to pass dams is a well-developed branch of engineering (21). Doubt has been expressed, however, (41) whether such structures are adequate in all cases. Alternatively, fish may be caught below the dam and transported by truck to the undisturbed higher parts of the river.

Some of the most dramatic effects of impoundments, good or bad, result from the change of the downstream flood regime. One purpose of building dams is to reduce annual variations in water level, making the floodplain habitable throughout the year and allowing its ecosystem to become more mature; or, more commonly perhaps, causing it to be replaced by a different ecosystem maintained in a state of immaturity by the practice of agriculture.

Reduction of this variation is not an unmixed benefit; one consequence of the building of the Aswan Dam is that agriculture in the Nile Valley now requires fertilizer, whereas in the past the soil was fertilized naturally by the deposition during the flood period of silt from the Ethiopian Highlands. Elsewhere, the fertilization of the river by the floodplain may be more important than the fertilization of the floodplain by the river. This seems to be an important factor in maintaining the fish populations of many African rivers (170).

A good example of unplanned large-scale alteration of a pulse-stabilized ecosystem is provided by the effect on the Peace-Athabasca Delta in the Canadian province of Alberta of the construction of the W. A. C. Bennett Dam on the Peace River (124, 125, 136). This region was usually flooded in the spring by the water of the Athabasca River that entered it from the south. Water from the Peace River, which passes to the north of the Delta to join the Slave River, contributed little to the actual flooding, but for flooding to occur it was necessary for the level of Peace River to be high enough to cause the water of the Athabasca River to back up into the Delta. When the flow of the Peace River was regulated, the Delta began to be transformed from marshland into meadow. This was considered undesirable, particularly because the local inhabitants subsisted on trapping and fishing in the marsh (136). A weir has now been built which will hold back the water sufficiently to permit flooding as before.

Dams on northward-flowing rivers in high latitudes are a cause for particular concern. Gill (45) has discussed the possible consequences of damming the MacKenzie River, which flows from Great Slave Lake to the Beaufort Sea through the Canadian Territory of MacKenzie. Present ecological conditions in the Delta of the MacKenzie are maintained by pulse stabilization, so regulation of the river flow would almost certainly cause considerable changes in this region. Moreover, the spring breakup of ice in the lower reaches of the river is hastened by the hydrostatic pressure generated by flood waters from the more southerly part of the river flowing under it. Consequently, a reduction in the maximum flow of the river would probably delay the beginning of spring. Somewhat similar concerns have been expressed with regard to a proposed hydroelectric project on the Ob River in Siberia (167).

If a river runs into the sea, regulating the river will probably have an effect in and around its mouth. Since the construction of the Aswan High Dam, the area of the Nile Delta has been reduced because of the disturbance of the equilibrium between erosion by the sea and deposition of sediment by the river (2). The sardine catches in the Mediterranean near the mouth of the Nile have decreased, owing either to the absence of nutrients formerly provided by the river or to the dispersal of the fish over a wider area (43).

An estuary is a complex and productive ecotone, maintained over the long term by a complex flow pattern known as a haline circulation (114). Fresh water from the river flows seaward over salt water flowing landward. Nutrient-rich seawater is entrained in the fresh water, leading to a high level of productivity in the upper layer (42). Any change in the flow pattern of the river will influence the haline circulation and the salinity gradient. This can have dramatic biological consequences. The influence of the Volta Dam on the bivalve mollusc *Egeria radiata* (9) may serve as an example. This freshwater mollusc requires a slight salinity of about 1‰ for reproduction. Construction and operation of the dam caused shifts of the spawning grounds many kilometers up and down the river.

In higher latitudes where estuarine and nearshore marine environments are more variable than in the tropics, such dramatic effects are perhaps not to be expected. Thus, the marine zooplankton in James Bay is largely composed of euryhaline and eurythermal species that will probably not be much affected by regulation of the inflowing rivers (52, 53). There are grounds for believing, however, that regulation of rivers entering such areas as the Strait of Georgia (42) and the Gulf of Saint Lawrence (114) will influence their fish populations. To what extent is difficult at present to predict.

## OTHER CONSEQUENCES OF IMPOUNDMENTS

Both during its construction and afterwards, a large dam has various frequently undesirable side-effects. These consequences are common to many large industrial or technical projects. The following discussion is limited to effects peculiar to the construction of dams and the impoundment of water.

The presence of a new body of standing water produces changes in the climate in its vicinity; these are proportional to its size (17). There may be changes in the annual precipitation pattern, an increase in low stratus clouds and fog, a decrease in air temperatures in spring and an increase in the fall, all leading in high latitudes to a delay in the beginning and end of the growing season. The range of diurnal air temperature will decrease. Changes of this nature have been predicted in the vicinity of the reservoirs of the James Bay project (13).

Recently it has become apparent that large impoundments may induce seismic activity in their neighborhoods (50, 55, 80, 108). The shocks that occur are fortunately usually small, and there is considerable difficulty in attributing any given shock to the effect of impoundment. The stresses set up by the weight of water impounded even in very large reservoirs are too small by one or two orders of magnitude to exert any geophysical effect by themselves. The effect therefore is either one of increasing the pressure of groundwater in fissures in the rocks, thus enabling slippage to occur under the influence of preexisting geophysical forces, or perhaps of the addition of a critical increment to pre-existing stresses.

The incidence of certain diseases associated with water may increase in the vicinity of new impoundments. Schistosomiasis almost always increases in the vicinity of impoundments in the tropics (31, 168), partly because of the enlarged habitat made available for the snails that are its intermediate hosts. Malaria may also increase because of the enlarged breeding areas made available to the mosquitoes that transmit the various forms of this disease. The breeding of malaria-transmitting mosquitoes in the reservoirs of the Tennessee Valley Authority is prevented by periodic changes in the water level, but this is not always practicable. The malaria vectors in some regions, such as Lake Volta, would be favored by fluctuating water levels (168).

On the other hand, onchocerciasis, or river blindness, is likely to decrease as a consequence of impoundment. This disease is transmitted by a black fly that breeds in running water. Many of the rapids where it breeds will be flooded by impoundment, although new breeding areas may become available below the dam (31, 168).

Among the most distressing consequences of large reservoir construction has been the disruption of the everyday lives of the people of the region. Unlike small reservoirs for such purposes as irrigation and flood control, large hydroelectric reservoirs often contribute little in any direct way to the well-being of those most affected. This has been a particularly serious problem where the people involved have been living in closely knit tribal communities, or where their livelihood has been dependent on hunting, fishing, or trapping. The large impoundments in Africa have, unfortunately, caused a good deal of distress (168). Much of this probably resulted from inefficient and insufficiently planned resettlement schemes and it may be hoped that past experience will provide a guide to future arrangements of this sort. In other instances, people have shown considerable ingenuity in adapting, as for example, by planting crops on the drawdown zone or by changing their fishing techniques.

In northern Canada, which is becoming an increasingly important source of hydroelectric power as the potentialities of more southerly sites become exhausted, similar considerations apply. In these regions communities of indigenous peoples, largely Cree and Inuit (Eskimo), have maintained viable social and economic systems based on traditional patterns of fishing, trapping, and hunting. The disruption of the indigenous community in the vicinity of the Peace-Athabasca Delta has already been mentioned. Similar concerns have been expressed in connection with a large hydroelectric development in northern Manitoba (115, 157) and particularly with the James Bay development (76, 137). Such concerns have led to considerable research in the latter area (23) and to the signing of a detailed agreement between the governments of Canada and Quebec and the representatives of the indigenous communities (75).

## SUMMARY AND CONCLUSIONS

Although reservoirs have sometimes been referred to as "embryo lakes" (106), they are probably better regarded as a distinct type of freshwater ecosystem differing from both streams and lakes. Many are characterized by a highly developed shoreline, a longitudinal profile with its maximum depth near the downstream end, a complicated flow pattern often involving discharge from the hypolimnion, and a pattern of seasonal variation in water level involving a long period of flooding and a short period of exposure. Because reservoirs are frequently built on streams carrying a heavy sediment load, the deposition and distribution of this material within the reservoir are often more important in reservoirs than they are in natural lakes. Therefore constraints on the nature of the developing biological community are imposed when a new reservoir is constructed.

The environmental changes below a dam may be no less dramatic than those above it. The two sets of events show a certain symmetry; each is to a large extent the inverse of the other. Below the dam, as above, the change in flow regime is the immediate cause of many other changes. This symmetry may be remarkably precise. For example, it has been estimated (144) that the increase in annual yield of fish from the Nasser Reservoir above the Aswan Dam may correspond closely to the decrease in annual yield from the Nile Delta and the eastern Mediterranean following the closure of the dam.

After the completion of some of the large African dams during the 1960s, many observers expressed surprise at the environmental consequences. This surprise may appear naive in retrospect, but certain of the consequences still seem remarkable—for example, the enormous populations of mayfly nymphs that developed in Lake Volta.

Large impoundments now exist under a variety of climatic and geographical conditions. Since not all the hydraulic head of the world's rivers has yet been utilized, it seems likely that more remain to be built. Certainly the rate of construction of smaller reservoirs shows no sign of diminishing (107). Will there be further ecological surprises?

The first great African impoundments were genuine novelties; nothing like them had ever existed before, and there was no basis in experience on which to predict their consequences. Subsequent tropical impoundments will not be novelties and their effects should be predictable, in their broad outlines, from earlier experience.

The development of reservoirs in the temperate regions has been more gradual. Experience with smaller reservoirs has consequently been applicable, within limits, to larger ones. Moreover, the generally lower rate of biological processes at higher latitudes has made their effects less dramatic, and perhaps has allowed more time to arrest and reverse undesirable effects before they became irreversible, as for example, the drying up of the Peace-Athabasca Delta. It seems unlikely that subsequent impoundments in the temperate regions will give rise to any large-scale surprises.

On the more detailed scale likely to be of importance to man, much remains to be learned. How the flooding of a certain area will influence the populations of furbearing animals in it, or how the damming of a certain river will influence the runs of salmon up it, are likely to be matters of intense concern to the people whose livelihood depends on these resources. Such questions can only be answered by a careful and thoughtful investigation of all possible aspects of the ecology of the region.

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