Summary: Reservoirs in Relation to Man—Fisheries

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Reservoirs are created primarily for irrigation, water storage, flood control, or hydroelectric power and rarely for fisheries, but the rapidly increasing demands for protein, especially in developing tropical countries, and for sport fishing in the more affluent societies now call for the fullest use to be made of man-made lakes for fisheries development. Far above the often considerable cash value of the fish caught and of the numerous ancillary services associated with the fishing industry is the immense value of fishery development for the physical and mental health of the people in the countries concerned.

At present, some 60% of the people living in less-developed countries have nutritionally inadequate diets, and, to meet estimated protein and calorie needs throughout the world in 1985, at least 50% more food will be required [*Stroud*, 1970]. When *Holt* [1967] summarized world needs for protein, he pointed out that the best prospects for increased fish production now come from small lakes, reservoirs, and ponds, where management is possible. The increasing demands for sport fish in the United States have been assessed by *Jenkins* [1964]. In 1963, 1200 large reservoirs provided 86 million days of angling, and an 85% increase was expected by 1976. Management is therefore aimed at a 30% increase in fish yield, from 17.2 kg/ha/yr to 23 kg/ha/yr.

Some types of reservoirs lend themselves to fish production better than others do. Irrigation reservoirs, which run very low in dry years, obviously need different management from deep hydroelectric power lakes. The reservoir fishery biologist is concerned with finding out how best to manage each type of water.

The aim of fisheries management is to obtain the maximum sustained yield of desired fish species, be they food fish (which are often herbivorous plankton or benthos feeders) or sport fish (which are most often piscivorous species). For sport fishing the quality of the fishing is also important. In developing countries it may be more important to make employment available for a large number of fishermen than to aim purely at the highest fish production, but this paper is concerned with the more technical aspects of getting a good crop of fish.

For fisheries management in a new lake we need to be able to forecast the fish yield before the dam is completed. This yield will depend on the biological production of fish (which is dependent on the species present, the latitude, and the limnological conditions in the new lake) and on the fishing effort (which will involve sociologic and technological problems, such as the availability of able fishermen, gear and craft, transport, and markets). When the lake is formed, we have to be able to assess the fish stocks present (this assessment is generally based on age and growth rate data in temperate lakes) and to regulate the fishery to crop an amount equivalent to the fish flesh produced over a given period of time.

The biological production is the rate at which fish flesh is produced in contrast to the standing crop or biomass of fish in the water body, and the yield or catch (often miscalled 'production' in fishery publications) represents the proportion of fish removed from the lake as a result of the fishing effort. In a balanced fishery the annual yield should be made to approximate the annual production.

In addition to fishery development within a new reservoir we also have to consider how damming the river may affect fisheries already in existence in the river, both above and below the dam, and in the estuaries and neighboring seas. Damming a river will obviously stop fish movements upstream and downstream unless fish passes are provided, but subtler effects will also exist: changes in water level regime below the dam may affect both fish spawning rhythms and feeding and breeding areas, nutrients may be cut off from downriver stretches right to the sea, or salinity changes may affect marine fishes that come into the estuaries to spawn.

SEQUENCE OF BIOLOGICAL EVENTS AFTER A RIVER IS DAMMED

The general sequence of biological events after a river is dammed is now well known for temperate lakes, but each case presents its own problems and calls for preimpoundment surveys and continued monitoring of fish populations for successful fishery management. For large tropical reservoirs, which are relatively new phenomena, there is as yet rather little biological information.

As the dam is closed, the rising water level drowns the surrounding vegetation. This rots, and the resulting nutrients lead to an outburst of production among the bacteria, flora, and fauna. Fish populations expand rapidly, the abundant food and cover allowing high survival rates among juvenile fishes spawned at this time, and the fish grow fast. In temperate zone lakes, production slows down after 2–3 years, when nutrients are exhausted and fish are abundant. This 'trophic depression phase' lasts 25–30 years at high latitudes (north of 55°N in the USSR) but is over correspondingly quickly in 6–10 years in lakes further south (south of 55°N in the USSR) [*Lapitsky*, 1968]. Production increases slightly as the lake settles down. Lakes might stabilize more rapidly at the high temperatures of the tropics, where events proceed so fast, but data on this point are needed. Lake Kariba appears to be through this trophic depression phase 12 years after dam closure.

The fish fauna of the new lake will depend on the species present in the river (which will vary with biogeographic zone and latitude) and their response to the changed conditions. A new lake generally has far fewer fish species than the river did. The fishes have to face changes in (1) physical and chemical conditions (temperature, turbidity, current flow, and so on and deoxygenation as the submerged vegetation rots), (2) available food, and (3) spawning conditions.

Spawning under the new conditions presents great challenges. Stream spawners have to find a tributary stream in which to spawn, and the young fish have to be able to return to the lake. Among the lake spawners, fish with buoyant or semibuoyant eggs (such as the sciaenid freshwater drum) are able to spawn successfully, and year classes tend to be regular [*Benson*, 1968]. Fish that spawn deep enough not to be affected by water level fluctuations may spawn successfully too, but the many species that spawn in the littoral zone either on the bottom (cichlids and centrachids) or among aquatic plants (many forage fish) will be very much affected by water level fluctuations, and year classes will tend to be very irregular. Indeed, water level fluctuations can be used to control unwanted spawning in these species.

In many tropical fishes, spawning is triggered by rising water levels, and so water level fluctuations are likely to have correspondingly greater physiological effects on tropical fishes than on temperate zone fishes, which spawn according to water temperature or day length.

Riverine fishes tend to be facultative feeders, and so can often adapt to new foods within their trophic group. The increased plankton in the new lake presents special opportunities, and lakes that have plankton-feeding species in their riverine fauna (such as *Tilapia*, which feed on phytoplankton, and sardine clupeids, which feed on zooplankton) get a good start. The bottom fauna is much changed as the former riverbed is drowned. In thermally stratified lakes, much of the bottom will be deoxygenated and so will be unfit for habitation by fish. The establishment of a littoral flora and fauna depends very much on water level fluctuations. Drowned trees and bushes present important substrata for a flora and fauna of food organisms, as has happened in Volta Lake, where periphytic algae and the burrowing nymphs of the ephemeropteran *Povilla adusta* have had vital roles in the productivity of the new lake [*Petr*, 1971]. As the lake stabilizes, various niches will be filled by different species of fish. If a niche remains vacant, such as that for plankton feeders in open water, the lake will not be as productive as it would otherwise be. The establishment of new lake faunas has been well studied in temperate lakes (in the USSR particularly), and there is an extensive literature. In tropical lakes, such studies are in their infancy.

DIFFERENCES BETWEEN TROPICAL AND TEMPERATE LAKES

Most fishery research has been carried out in temperate waters, but how far can the management techniques worked out for these lakes be applied in tropical conditions?

First, events move much faster at the higher temperatures of the tropics. Fish grow faster and mature earlier (many commercial species maturing in <1 year), populations build up much more quickly, and good and bad spawning years show their effects sooner in the catchable population (and conversely their effects do not last as long). Also, production represents a higher proportion of the biomass (standing crop) of fish. For example, in Cuba, production was three quarters of the biomass, whereas in European reservoirs it was only about one third [*Holčik*, 1970*a*].

Second, tropical communities are very complex. Numerous species that look very much alike live together, and it is often difficult to identify the young stages. The fisheries are generally for fishes of diverse sizes and shapes, which complicate fisheries management and legislation.

Third, conditions are less seasonal. Many species spawn throughout the year, and so fish enter the catchable population continuously. This together with the lack of seasonal growth checks, which register the age on the scales and bones of temperate fish, makes the determination of fish ages and growth rates very difficult in many tropical waters. As such age and growth data are basic tools for population assessment in temperate lakes, new methods of stock assessment need to be devised for tropical waters.

SECTION PAPERS

The papers presented in this section on various aspects of fisheries come from both tropical and temperate waters, and each may be taken to illustrate a different problem. From Africa the paper from Kainji Lake on the River Niger is concerned mainly with preimpoundment and postimpoundment surveys. Another African paper comes from Lake Nasser on the Egyptian Nile, which has basically the same fish fauna as Kainji Lake, and is concerned with catches in the early years of the impoundment. Then, from Asia, there is a paper from Ceylon, where introduced exotic fish have greatly boosted the catch, and another from the Mekong River that raises questions on the importance of migrant fishes and on possible effects of the planned impoundments on the very valuable fisheries that already exist, both in the river and associated lakes and in the delta and the neighboring sea. From the United States, there are four papers, one that examines the effects of water level fluctuations on fish populations in Missouri main stem impoundments, another from Lake Apopka in Florida that deals with eutrophication, a third from the South Lake Tahoe area that demonstrates sophisticated treatment of waste waters to enable them to be used for sport fishing, and a fourth that concerns the gas bubble disease of fish, which results from exposure to an environment that is supersaturated with nitrogen, as experienced at the lower Columbia and Snake River reservoirs.

OTHER SOURCES OF INFORMATION

Reservoir fish studies in the United States. The United States had >1300 reservoirs (each >200 ha) by the end of 1968 totaling >3½ million ha with >50 types of fish. A bibliography of reservoir fishery biology for North America [*Jenkins*, 1965] indicates the large amount of research in progress: surveys, studies of fish population dynamics, age and growth, food habits, life histories and ecology, and management techniques. Some of the studies have been in progress for decades. Further research needs and techniques to obtain the desired information were discussed by *Jenkins* [1964]. More recently, the influence of environmental factors on standing crops has been explored by extensive multiple regression analyses using a computer. The results of these analyses have been summarized by the director of the National Reservoir Research Program [*Jenkins*, 1968*a*, *b*, 1970].

Data based on recovery following rotenone treatment and on sport and commercial fish harvests [*Jenkins*, 1968*a*, *b*] indicate that in 1968 the mean standing crop in 127 U.S. reservoirs was 204 kg/ha/yr, the mean sport harvest in 121 reservoirs was 24.8 kg/ha/yr, and the mean commercial harvest in 46 reservoirs was 11.2 kg/ha/yr. The environmental factors that appeared to exert the greatest positive influences were found to be dissolved solids, which influenced the standing crop and the sport fish harvest; the age of the reservoir, which influenced the commercial harvest and the clupeid standing crop; the storage ratio (i.e., lower water exchange rate), which influenced the sport harvest; and the shore development, which influenced the standing crop and the sport harvest. Factors of greatest negative influence were the age of the reservoir, which influenced the sport harvest; the storage ratio, which influenced the clupeid standing crop and the commercial harvest; the area, which influenced the sport harvest; and the mean depth and the shore development, which influenced the commercial harvest [*Jenkins*, 1968*a*].

In later analyses, factors such as outlet depths, growing seasons, and drainage areas were tested, and distinctions were made between reservoirs with or without a thermocline. Interspecific correlations between the standing crops of various fish species were also made [*Jenkins*, 1968*b*, Table 3], and were useful for designing stocking programs. As the environment changes, so will the interactions between the species.

Among the relationships that *Jenkins* [1970] considers most useful for fisheries predictions and management are the positive effects of increasing outlet depth, shore development, and dissolved solids on standing crops, of growing season and storage ratio on clupeid crops in hydropower reservoirs with a thermocline, of increasing shore development on total crops in nonhydropower reservoirs, and of the age of the reservoir on the total crop.

Management accomplishments in U.S. reservoirs summarized by *Jenkins* [1970] include stocking, liberalizing the angling season to allow year-round fishing for warmwater fish, control of forage fish (using rotenone) and of 'rough' fish (by netting, electrofishing, and so on), using the drawdown to ameliorate limnological conditions (and also to control the reproduction of undesirable species), timber clearing, and installing fish passes for migrating salmonids. In some places, fish are eradicated completely; then cooler waters are restocked with trout, or centrachids are reintroduced into warmwater impoundments.

Reservoir fish studies in the USSR. The USSR has more large reservoirs, due to hydropower development, than any other country. Fishery development is regarded as an important part of the use of these reservoirs, and so an immense amount of work is being done on the hydrobiological conditions, the establishment of new fish faunas, and fishery management to give maximum yields of high-quality food fish. Fortunately, the extensive Russian literature has been summarized in papers in English prepared for study tours of fisheries research and management in the USSR [*Food and Agriculture Organization*, 1968]. The reservoirs in the USSR totaled 5 million ha in 1968, and, when planned projects are completed, this area should be doubled. The Volga, Don, and Dnieper rivers are being transformed into cascades of reservoirs along their entire courses. Another large reservoir complex has been completed west of Lake Baikal on the Angara and Yenisei rivers, which drain to the Arctic Ocean. (These may one day be linked by the suggested huge Omsk and New Siberia reservoir and by canals to the northward flowing River Ob and west to the Caspian Sea.) By 1968 the USSR reservoir catch was circa 44,000 metric tons/yr, although only some of the reservoirs were in commercial use. On the basis of present catches the target is 20–30 kg/ha/yr of high-quality fish products, which, if it is achieved, should give circa 170,000 metric tons/yr of fish from these reservoirs. The USSR reservoirs are classified according to their hydrobiological characteristics and fish faunas by *Melnikov* [1962].

The development of fisheries and ways of raising fish productivity in big reservoirs were considered by *Lapitsky* [1968], who summarized what is known about patterns of ichthyofauna formation in reservoirs and reservoir management in the USSR. (He cited the history of fishery development in the Tzimljanskoye Reservoir on the River Don formed in 1952 as an example.)

The Russians have paid great attention to shaping hydrobiological conditions in large reservoirs [*Pirozhnikov and Miroschneichenko*, 1968]. They have done much work on fish passes and fish lifts for anadromous fishes, protection facilities to keep fish out of turbines, and so on [*Nusenbaum*, 1968]. They have also made great strides with induced spawning and rearing of migratory fishes for stocking when a river is completely blocked [*Vovk*, 1968]. Induced spawning has made possible the introduction of plant-eating silver carp or white tobilisk (*Hypophthalmichthys molitrix*) from the Amur River into the European part of the USSR [*Konradt*, 1968]. The grass carp is now breeding in the Kara Kum canal in Turkmenia. Sometimes the Russians advocate wiping out the indigenous fauna and stocking with a new fauna of more productive fish. Chemical methods of rehabilitation and propagation of new fish faunas are described by *Burmakin* [1968]. Stocking with invertebrates (crustacean mysids, mollusks, and polychaetes) is also advocated to boost fish food supplies during the trophic depression phase [*Lapitsky*, 1968].

In the USSR, where fish mature relatively slowly at the low temperatures, great stress is laid on encouraging the right fish populations to develop as the reservoir fills, for the fishery will be based on these populations for many years to come. Management measures taken include stocking the reservoir with spawners of valuable food fish, which are transferred from other waters to strengthen spawning stocks during the first year of filling, since an overwhelming abundance of fry can then inhibit the growth of trash fish; construction of fish hatcheries at the reservoirs to stock the new lake with the fry of valuable species; and planned fishing with protection of valuable species during the early stages of stock formation by a complete ban on fishing for them for 2 years prior to filling and during the first years after impoundment. This saves spawner stocks for use under favorable propagation conditions in the first year to obtain huge populations of fry. Trash fish are inhibited by selective fishing. Other measures include the acclimatization of food organisms to overcome the trophic depression phase, the preparation of the reservoir bottom for commercial fishing, ascertaining optimum water level regimes, and so on. Fishing for the valuable species may remain 'closed' until the first generation of lake fish matures.

Reservoir fish studies in India. India is a land of big rivers and small streams, which are in spate during the two monsoons and become straggling streams during the rest of the year. To conserve monsoon floods, most of the rivers (large and small) have been dammed at suitable places, and the waters have thus been stored for irrigation, water supply, pisciculture, and hydroelectric power. By 1969, India had 295 major reservoirs (211 of them >400 ha) [*David and Gopinathan*, 1970]. These Indian reservoirs are major ones formed by damming rivers and minor ones formed by damming vast depressions at their lowest level. These depressions are filled during the monsoon rains by rainfall and surface runoff and almost dry up during the hot weather. These two types of reservoirs are found scattered throughout India, and they are stocked with the fry and fingerlings of major Indian carps (*Catla catla, Cirrhina mrigala, Labeo rohita,* and *L. calbasu*).

At a seminar held in India at the Central Inland Fisheries Research Institute, Barrackpore, in 1969 on the ecology and fisheries of freshwater reservoirs, >50 papers were presented. Measures adopted for the development of reservoir fisheries in India were summarized by *Jhingran and Tripathi* [1970]. Other published abstracts indicate that the supply of fish fry 'seed' to stock the many reservoirs is of major concern. The rivers in which the major carps spawn have been mapped [*David*, 1959, Figure 1], and their spawning seasons and biology are summarized by *Qasim and Qayyum* [1961]. Some species migrate upriver from the new lakes and move out laterally to spawn [*David*, 1959]; some spawn in the headwaters of the new dams (as they do in Lake Bhakra [*Bhatnagar*, 1964]). Yields of >45 kg/ha/yr are recorded from several reservoirs, though average yields may be much smaller (7.5 kg/ha/yr). The desirability of replacing 'wild' fish by more productive carps is advocated [*Bhimachar*, 1970], as is the importance of protecting the spawners of the valuable species, which are often fished heavily as they move into the shallows to spawn [*Jones*, 1970]. Fish yields in relation to primary production and various limnological conditions in Madras reservoirs have been studied by *Sreenivasan* [1970].

Reservoir fish studies in Indonesia. Some of the earliest studies on fish production in tropical man-made lakes were made in Indonesia, where herbivorous fishes contribute to very high yields. *Vaas and Sachlan* [1952] report 500–600 kg/ha/yr from a 25-km artificial lake in west Java (mainly *Cyprinus carpio, Puntius javanicus,* and *Helostoma temmincki*). A reservoir in central Java had previously been found to yield 250 kg/ha/yr [*Vaas and Schuurman*, 1949].

Reservoir fish studies in South America. Since South America has such a rich natural freshwater fish fauna with more endemic species than any other continent and since there are as yet so few large reservoirs, few studies of fisheries in man-made lakes have been made. In Lake Brokopondo, Surinam, the forest was not cleared, and no attempt was made to develop a commercial fishery, though the fish fauna was studied and collected intensively at the time of impoundment [*Leentvaar*, 1967]. In the Andes, rivers are being harnessed for hydroelectric power. Introductions of salmonids into these rivers were followed by the decimation and virtual disappearance of the endemic species flocks of large cyprinodontoid poeciliids. These were of the greatest scientific interest and also of considerable value as food fish for the indigenous Indian peasants. The salmonids were found to have carried a sporozoan parasite to the indigenous *Orestias* [*Villwock*, 1972]. Studies in Brazil [*de Godoy*, 1959] and Argentina [*Ringuelet et al.*, 1967] show that some of the important commercial fish make very long migrations upriver and downriver. Fish passes are likely to be needed here if rivers are dammed. The South American fish fauna is so complex that ecological studies need to be made well in advance of any impoundment schemes to gage the effects on the fish.

Marine areas turned into freshwater lakes. The development of freshwater fisheries in lakes that were formerly arms of the sea raises different problems. These are being studied mainly in Holland at the Delta Research Division of the Hydrobiological Institute, and their progress is reported in their annual reports [*Vaas*, 1968]. Feasibility studies on estuarine storage in the Morecambe Bay area of the United Kingdom are considered by *Gibb and Corlett* [this volume]. A freshwater reservoir has been created from an arm of the sea for Hong Kong.

SPECIAL PROBLEMS

Forecasting fish yields from reservoirs. In the early days of man-made lakes, predictions of yields had to be based on yields from natural lakes of comparable morphometry and at comparable latitudes. *Roundsell* [1946] working on this basis pointed out the decline in yield as the lakes increased in area and that overoptimistic estimates were often based on small areas. (The total fish population was likely to fall from around 300 kg/ha/yr in 0.4-ha ponds to 35 kg/ha/yr in 80-ha lakes, and between these sizes the annual yield of sport fish might vary from 82 to 10 kg/ha/yr.) The commercial fish catch can be much higher than the sport fish catch in large reservoirs. The yield per hectare, Roundsell suggested, is probably correlated with the relative area of fertile shallow water, which is larger in small lakes than in large lakes. He also noted that other factors, such as chemical nutrients, the fish species present, and the balance between them, will also affect fish production.

In recent years, many attempts have been made to find indices to predict yields from reservoirs. Some of these were reviewed by *Ryder* [1965], who reckoned that the 'morphoedaphic index,' i.e., the total dissolved solids divided by the mean depth of the lake, as a simple regression on fish production allowed him to predict yields for lakes of various sizes in the temperate zone of North America, and he has since attempted to apply this method to African lakes. The multivariate computer analyses of data from U.S. reservoirs [*Jenkins*, 1968*a*, 1970], already considered above, also help predictions to be made.

In the tropics, there is as yet far less comparable work to provide base lines for predictions. *Holden* [1969], who has reviewed problems of forecasting yields for tropical lakes, suggested that the growth of indicator species (such as *Tilapia nilotica*) might be helpful. For Lake Kariba the highest annual catch, circa 5400 metric tons in 1963–1964 [*van der Lingen*, this volume; Zambia Republic, unpublished report, 1968], was far short of the least optimistic estimate of circa 8200 metric tons (quoted by *Jackson* [1960], who also mentioned another estimate of 28,000 metric tons). The low yields in Lake Kariba seemed to be the result of a combination of human and biological factors. Fishermen evidently returned to their gardens instead of fishing owing to marketing difficulties, controversy over fish prices, and poor roads. *Salvinia* cover over the mouths of tributary streams [*Begg*, 1969] might have affected spawning runs and the recruitment of fish.

Volta Lake, on the other hand, has been much more productive than was expected. About twice the area of Lake Kariba, Volta Lake has produced 10 times the amount of fish (>60,000 metric tons in 1969–1970). As a shallower lake it was likely to be relatively more productive, but the happy accident of the presence of both *Povilla adusta* and clupeid fishes seems to have contributed greatly to its productiveness. As the lake rose gradually, new areas were flooded year by year, and so production remained high. *Petr* [1971] observed that production will fall when the trees rot and are no longer able to support large *Povilla* populations. Indeed, catches have already fallen (to circa 38,000 metric tons according to *Kalitsi* [this volume]), and, if Ryder's morphoedaphic index predictions are applicable to tropical lakes (which is by no means yet certain), they may fall to about one-half this amount again before they stabilize.

The extent to which the predicted yield can be realized depends on whether the new lake is fishable with the gear available and whether preparations have been made to develop and regulate the fisheries [*Holden*, 1969]. At present, many opportunities are probably being missed. Helping the fishermen to exploit species of fish other than the usual commercial ones would assist them during the inevitable period of decline after the initial burst of production.

The extent to which the potential yield should be cropped in the early years of impoundment needs consideration in each individual case. In the USSR, as was already mentioned, great care is taken to protect the spawners of desirable fish species until stocks have had time to build up. In tropical lakes, on the other hand, the desirability of cropping the fish hard during the initial high production phase has been advocated not only to make use of the fish and to demonstrate to the indigenous people the advantage to be gained from having a lake but also to remove the excess nutrients from the system, which might lead to an outburst of weed growth.

Nutrient buildup will depend on other factors, such as the flushing rate of the lake, the speed with which the lake fills, and so on. In tropical waters, fish populations can build up so quickly that there will probably be less need to prohibit fishing for valuable species for some years than there is in the USSR. However, selective fishing for undesirable species should be encouraged in the early years, less desirable predators, such as *Hydrocynus*, be fished hard. *Bowmaker* [this volume] suggests that they can be cropped as they migrate up to spawn. The large predator *Lates*, on the other hand, is a valuable food fish, capable of adding greatly to the yield from a lake. The uncleared bush-covered areas provide protection for fish such as *Tilapia* in many lakes (as they do in Kainji Lake).

The rate of fish production is dynamic and will itself change according to the numbers of fish in the lake. Fish grow faster when populations are sparse in relation to food supply, and production is reduced as a lake gets overcrowded and growth slows down. The situation is, however, complex. *Beauchamp* [1958] pointed out that, since breakdown of plant matter in the bottom mud of tropical lakes is slower than breakdown through herbivores, the removal of large numbers of herbivores, such as *Tilapia*, from a lake will itself decrease productivity by slowing down production cycles.

Bush clearance and fisheries. At the time that the Volta Dam was being built, bush clearance in the area of the new lake was considered advisable if it could be afforded to enable fishing nets to be used; to avoid a high level of nutrients, which might lead to an aquatic plant cover problem, as it had in Lake Kariba, where *Salvinia* growth was so high after the decomposition of the bush; and to avoid deoxygenation, which might have damaging effects on fish stocks.

As it happened, only small areas of bush were cleared because of the high cost of clearing. It now seems from *Petr*'s [1971] studies that one of the main reasons for the unexpectedly high fish production in Volta Lake is that the uncleared bush offers a substratum for periphytic algae and the wood-burrowing nymphs of the ephemeropteran *Povilla adusta*. These have both provided extensive food resources for the fish, the periphyton for *Tilapia* and other algal feeders and the *Povilla* (which itself feeds on periphyton) for fishes that were formerly bottom feeders (such as *Schilbe*) and also for the small clupeid sardines (*Pellonula*), which have multiplied fast in the new lake.

The ability of bushes to increase the yield of fish from these tropical lakes might have been predicted from (1) experiments in fishponds in which screens used to increase the growth of periphytic algae improved the growth rate of herbivorous fish, (2) the use of the 'acadja' or fish park indigenous fishing method in the lagoons of the coastal areas of Dahomey, west Africa, which consists of planting bare branches in an area of lagoon to increase the algal area and provide cover for the fish, the result being greatly increased yields of fish, mainly *Tilapia* [*Welcomme*, 1972], and (3) observations in the Great Lake of the Khmer Republic, where *Hickling* [1961] noted that production was spectacularly high because the fishes fed in the submerged forest on periphytic plant matter on the trees.

Clearing the bush does help fishing operations and is very necessary for some of them, but the Volta Lake experience suggests that clearance might be done in lanes, as was suggested by *Bowmaker* [1970], areas of bush being left for increased fish production. In Kainji Lake, there are reports of shoals of large *Tilapia* in the bush-covered area, but it is very difficult to catch them. New fishing methods need to be devised to do so.

Introductions: transplants and exotics. To get the maximum yields from a new lake, it may be necessary to supplement the fish fauna either by stocking with fry, fingerlings, or spawners of indigenous fish (transplants) or by introducing exotic species from outside the drainage basin. The introduction of an exotic species may boost the yield from a new lake (as it did in Ceylon), but it carries many dangers with it, and each case needs careful examination both of the limnological conditions and of the biology of the fish to be introduced. There are numerous examples of introduced fishes affecting native species to the point of extinction either directly (through predation, competition, hybridization, or introduction of disease or parasites) or indirectly by altering the habitat. Great care is needed to ensure that the most suitable and most productive species is introduced, since once fish are liberated in open waters it may well prove impossible to eradicate them. Tropical faunas present special difficulties here, since the young of so many species live together and look so much alike but may have very different growth potentials. Expert supervision is essential to see that the desired species do in fact get stocked without a whole lot of undesirable accessory species being introduced too. Numerous small cichlids, for example, have been carried around in Africa with *Tilapia* in this way, and, indeed, *Tilapia leucosticta* gained access to Lake Victoria when other larger growing *Tilapia* were introduced.

Either introduced fish may be very aggressive and oust local species, or they may not 'take' (as *Tilapia macrochir* and *T. melanopleura* did not take in Lake Kariba). Russian experience suggests that it is often no good to introduce a fish unless there is a vacant niche for it, since an introduced species will suffer not only from predators but also from competing species, which eat their food, eggs, and so on. When a local species is available, it would seem more likely to do well in a new lake. On the other hand, there is something to be said for using species for which management techniques are already known.

Certain species have been regarded as fish of golden promise because they are very productive in their home areas or where they were first introduced (often by accident), and so they have been moved around a great deal. These include carp (*Cyprinus carpio*) from Eurasia (introduced into the United States in 1872 according to *Miller* [1961]) and *Tilapia*, the mainstay of African lake fisheries. But introductions of even these species often have undesirable side effects. Carp make the water so turbid that they alter the habitat for indigenous species, and therefore they are now banned in parts of Africa and Australia. *Tilapia* too are now unwelcome in certain areas, for they runt badly and they compete with the more desirable milkfish (*Chanos*) in milkfish ponds [*Food and Agriculture Organization*, 1968]. Results may be somewhat unpredictable even for 'well-known' species.

Man-made changes, such as lakes and canals, are allowing fish increasingly free movement from one water system to another, and any introduced species may now spread over a very wide area in most continents. The zoogeographic role of reservoirs was considered by *Dzyuban* [1962], who cited the progress of the smelt *Osmerus eperlanus* from freshwater around the Baltic southward through the Volga reservoirs.

Fish parasites and diseases may spread from introduced fishes to local fishes not resistant to them. The decimation of the Lake Titicaca endemic cyprinodontoid fishes since the introduction of salmonids to Andean streams (already mentioned) is an example.

Sport fishermen are particularly prone to carry fish around. *Miller* [1961] pointed out that in the southwestern United States about 36 exotics have been introduced, mainly from the eastern United States, as intentional plants of game fishes during the construction of major dams between 1930 and 1950. These established aliens have led to the virtual extinction of about 20 species (20% of the indigenous fish fauna). Exotic fishes in Southern Rhodesia, about 17 species, are listed and discussed by *Toots* [1969]. It is very important that reliable records of introductions be kept.

In some cases (the United States, the USSR, and India) the total destruction of the indigenous fauna is advocated, and the lakes are stocked with new fish: trout in cooler waters, centrachids in warmer waters in the United States, and major carps in India. The use of chemicals such as rotenone, toxaphene, or others may have serious consequences for local species, local extinctions being brought about. Some chemicals may affect the fish flesh of the stocked fish [*Konar*, 1970]. Chemical poisoning is not a step to be undertaken lightly. In the USSR it is found really useful only for fry-rearing ponds not for commercial fishponds.

The present fish of golden promise are the Chinese carp; the grass carp or white Amur, *Ctenopharyngodon idella* (a herbivore); the silver carp or white tobilisk, *Hypophthalmichthys molitrix* (primarily a phytoplankton feeder); and the bighead, *Aristichthys nobilis* (primarily a zooplankton feeder). These three have very high growth rates, are tolerant of a wide range of temperature conditions, and make good complementary species producing very high yields. Grass carp can grow to 5 kg in a year [*Hickling*, 1965]. They do not, however, breed in many places in the wild (they come from the Amur

River, bounding the USSR and China), and, until spawning could be induced by pituitary injections, the supply of young fish for stocking limited their use in other water bodies. Grass carp are now known to be breeding in the Kara Kum canal in Turkmenia [*Konradt*, 1968] and in one river in Japan. The grass carp is remarkably effective in clearing weeds. In the USSR their use in coolant reservoirs of power stations is advocated, they are also stocked to keep channels and canals open, and they are now stocked in southern reservoirs and in impoundments as far north as around Leningrad. An enormous amount of research has been carried out with these fishes in the USSR both where they are in their natural habitats and where they have been introduced or used as pond fish.

Grass carp and silver carp do escape. They are now turning up in rivers in east and central Europe [*Holčik*, 1970*b*; *Holčik and Par*, 1970]. Grass carp have been imported into several hatcheries in the United States, but the policy is, very wisely, to wait and see what side effects there may be before liberating them into open water [*Lachner et al.*, 1970]. It is being found in England that their copious feces cause water blooms unless they are stocked with other species. There is already considerable literature about this species [*Nair*, 1968].

Fish passes, locks, and screens. Although gravity pool fish passes have long been used alongside dams, particularly in areas where salmonids are important, the scientific design of more ambitious fish passes and fish locks has only come to be studied since about the 1950's. This study is of increasing importance in view of the increasing number of river barrages. Most of the work has been and is being done in the United States and the USSR by biologists in cooperation with engineers.

The types of fish passes, locks, and other devices for lifting fish over dams in the United States are well summarized by *Eicher* [1970]. The Bonneville Fishway Laboratory of the U.S. Bureau of Commercial Fisheries, funded by the U.S. Army Corps of Engineers, has since 1956 been looking at the economics of various constructions (such as shorter pools, smaller flows, and less costly entrances). The Bonneville Dam fishway, built on the Columbia River in 1938, was 12 meters wide with 0.3-meter rises between 5-meter pools and flow velocities kept down to 0.6 m/sec in the channels. Other types of fish pass described by Eicher include Denil fishways, which were developed in the late 1950's and have vanes set in straight chutes to reverse the flow (aluminum sections 55 cm wide and 62 cm high based on this principle are being flown into Alaska to aid fishes over natural obstacles), and vertical slot fishways, in which a vertical opening of constant width from the top to the bottom of a pool directs the water through a constriction to release its full energy away from the next slot. These operate very well at varying water levels. They have been used so successfully at Hell's Gate on the Columbia River that it is estimated that they have increased the salmon runs so much that the initial cost of installation is recovered many times over every year.

Locks, either at atmospheric pressure or pressurized, have been tried in the United States but are not used much (in contrast with the USSR). Many fish, of course, must slip through locks that are opened for navigation. Many other devices have been tried, such as tramways and trolleys and other forms of trapping and hauling fish around dams.

However, getting downstream migrants safely downstream is proving much more difficult than getting upstream migrants past dams, and getting juvenile downstream migrants through impoundments (with their very different oxygen, temperature, and flow conditions) is just as important as moving them through turbines, over spillways, and around dams. Devices used in the United States are discussed by *Eicher* [1970]. These include louvers, mechanical screens (a drum or screen panels on a belt, success varying depending on the ability of the screen to clean itself), and devices known as 'skimmers,' 'gulpers,' and gate wells. If the young fish go through the turbines, mortalities can amount to 5–100% depending on factors such as cavitation in the back of the turbine blades, and, as a result of study, turbines can be operated with least injury during migration periods. Mortalities over a spillway are reduced if a ski jump type of free fall is arranged. Trapping and transportation from the head of a lake are used sometimes.

The passage of fishes up or down fishways presents opportunities for them to be counted. Visual techniques have long been used, sometimes in underwater observation chambers, and various photographic or photocell techniques have been developed.

Fish passage facility studies in the USSR are summarized by *Nusenbaum* [1968]. Again, there is a special laboratory to study fish passage facilities and screens staffed by biologists and engineers. Fishways provide facilities for the independent passage of fish from a lower to an upper level, but, on the very high dams on the Don and Volta, special fish locks have been constructed. Fish are attracted and accumulated in fish collectors (80 meters long) for 2 hours; then they are impelled by a moving lattice into a square lock chamber (8.5 m^2). A horizontal impellent screen then lifts the fish into the outlet chute (95 meters long and 12 meters wide). The passage time from tail water to headwater is about 40 min.

The fish lock on the Volga hydroelectric station has since 1961 taken up very large numbers of migrating sturgeon, herrings, and other species (including sheatfish, *Silurus glanis*; bream; carp and other cyprinids; and perch), which accumulate temporarily in a dam zone. Up to 600 sturgeon and 12,000–15,000 herring have passed during one locking (the period of attraction being 2 hours). Every year, 25,000 sturgeon and 1 million herring and other fishes were said to pass at this site. A great deal has been learned about the migrating behavior of these fishes. The intensity of the fish run varies within the season, and different species run at different times of day, sturgeon mainly in the dark and herrings by day. In the River Ob, which flows to the Arctic Ocean, it was found that many 'resident' (i.e., non-anadromous) fish spread over a wide area during feeding and spawning migrations, the ide (*Leuciscus idus*), pike (*Esox lucius*), and *Acipenser ruthenus* migrating over 400–600 km.

A great deal of work on fish screens to keep fish out of turbines and the wrong channels has been carried out in the USSR. Electrical and mechanical screens give the best results, though the use of lights, sounds, chemicals, and so on have been tested. Electrical screens are, of course, only useful to stop or steer upstream moving fishes. Details are given by *Nusenbaum* [1968].

In South America, *de Godoy* [1959] has shown by marking experiments that the commercially important *Prochilodus scrofa* migrate very long distances (>400 km) up the rivers of southern Brazil and return to their original river at comparable times each year. The valuable *Salminus* migrate upriver in Argentina and Brazil [*Ringuelet et al.*, 1967], and many other species make spawning runs upstream (references given by *Lowe-McConnell* [1969]). In Africa, *Bell-Cross* [1960] has shown that indigenous freshwater fishes, even *Tilapia* and nonbreeding fishes, move upstream and downstream more than was formerly believed. In India, some major carps run upriver to their spawning grounds. Some very large Mekong species are reputed to move long distances upstream and downstream [*Smith*, 1945].

The question of the need for fish passes on tropical rivers has perhaps been too easily dismissed in the past. However, where there is a whole series of impoundments, fish passes may become obsolete for some species. They appear to have become obsolete to some extent on the Volga, where the sturgeon can no longer find spawning grounds above the Volgograd Dam and so induced spawning and hatchery rearing is needed [*Vovk*, 1968].

Effects of impoundments on fisheries in other parts of the river system and in the estuaries and neighboring sea. From the case histories and papers in this section we have already seen examples of effects from impoundments downstream of a dam. Thus, below the Kainji Dam, catches have fallen to about half their former value in the River Niger and its associated swamps for a considerable distance. The change from annual flooding to short-term irregular water level fluctuations seems to be the potent factor here.

In the River Niger in areas upstream of the dam (the French-speaking territories of Dahomey and Niger), catches have also declined (R. L. Welcomme, verbal communication, 1971), but the decline seems to be a reflection of the fishing effort. Fishermen no longer migrate north as they used to do from March to October to tap these stretches while water was receding from the floodplain. Some of these fishermen are perhaps fishing in the new lake, but the imposition of controls on fish imported from the French-speaking territories into Nigeria and Ghana has apparently affected fish sales and lessened the incentive to fish further upriver. There seems to be a case here for treating fishery development on a regional basis.

Petr [1969] noted that migratory species disappeared from Volta Lake in later years. These presumably went upstream and did not return, but we know little about the changes in fish populations above the dam. Controls on fish imports from the north may also have obscured the situation here. Downstream of Volta Lake the oyster fishery has apparently diminished.

Jackson [1961] suggested that Lake Kariba might improve the fisheries below the lake by turning this stretch of the Zambezi into a 'reservoir' type of river with regulated flow rather than a 'sandbank' type of river with greatly reduced flow in the dry season. The effects of the discharges from Lake Kariba, which are 'ecologically speaking wrongly timed,' on the wildlife below the dam have been considered, but there appears to be no published information about the effects on the fish.

The effects of dams on the fisheries downstream of them are considered for the Mekong and mentioned for Lake Nasser in this section. We need a great deal more information on the effects of dams on other fisheries in the river systems and neighboring seas.

STATE OF THE ART CONCLUSIONS

1. The development of a fishery in a new reservoir has in most instances been regarded as an 'optional extra.' The world demands for increased protein and also for increased sport fishing mean that the potential of a reservoir for fishery development now needs to be taken seriously. Furthermore, recent experience in Thailand has shown that sometimes the value of a reservoir fishery can almost equal that of the hydroelectric power produced.

2. It is therefore essential to learn how to manage reservoir fisheries to give maximum sustained yields of desired species and to ensure that damming the river does not affect already existing fisheries in the river system, both upstream and downstream of the new lake, and in the estuaries and neighboring sea.

3. To achieve these ends, fishery biologists need to be included in planning teams from an early stage and to work closely with the engineers and others concerned with the project. Biological problems involve so many variables that getting answers to them generally takes longer than finding answers to engineering questions does, and so biological surveys must be started in good time if they are to provide reliable indications of fish production. Two years of planning followed by 3 years for a feasibility survey are now considered advisable in the United States [*Stroud*, 1966]. Cooperation between biologists and engineers is needed for fish pass design, for practical points such as the advisability of constructing the lake outlet below the future thermocline to draw off hypolimnion water, and for determining the amount of bush clearing that is desirable.

4. After the completion of the dam, continued monitoring of fish populations is essential for sound management, and fishery biologists must continue to work in close cooperation with those responsible for water levels because water level adjustment can be a powerful management tool. Computer studies can now speed up prediction processes.

5. The yield of fish also depends on planning the fishery well in advance, including biological measures to build up populations of desirable fish species, clearing the bottom for use of suitable gear to catch them, and well-organized transport and marketing, which are vital to commercial fishery development in remote areas.

6. The papers in this section have shown that each new impoundment needs a preimpoundment and postimpoundment survey and continued monitoring. Basic research into fish biology at all stages of life history is needed. Information should be collected and made available as soon as possible to allow more accurate predictions for other new impoundments. Information banks are particularly important for tropical reservoirs, where relatively little information is as yet available. Management techniques worked out for temperate lakes may have to be altered considerably for application to tropical waters, since changes occur so much faster there. The complex communities and the difficulty of determining the ages and growth rates of the fishes call for new methods of stock assessment to be developed in tropical waters.

7. Where suitable fish are lacking in the fauna, introductions can make a big contribution to fishery development. It is, however, first necessary to determine the capabilities of local species. It is essential to make very thorough studies of the limnological conditions and to know the biology of the proposed fish very well before attempting an introduction. Introductions often lead to extinctions of local species. Also, it is very important to introduce the best possible fish. Once fish are introduced, they generally prove impossible to eradicate and may spread through a wide area with the aid of man-made canals and lakes. The young of many tropical species live together and may be very difficult to distinguish. Expert care is needed to ensure that only the desired species is in fact in-

troduced. It is very important that reliable records be kept of all introductions.

8. We need more information about the upstream and downstream migrations of tropical species and the economics of the fisheries and potential fisheries for them. When large rivers with rich faunas, such as the Mekong and South American rivers, come to be dammed, fish passes may be advisable. In temperate waters (where salmonids are important), fish passes can pay for their construction very quickly. We also need to know the reproductive biology of such fishes to enable induced spawning and hatchery rearing to be used, if they become necessary.

9. Fishes do change their food spectra in impoundments, whether it be salmonids in Wales or fishes changing to a new food source in *Povilla* in Volta Lake. Foods used are affected both by foods available and by other fish species present.

10. Water level fluctuations affect both food resources and reproductive biology by direct effects on fish physiology and by indirect effects on the habitat. Tropical fishes are likely to be even more sensitive to water level fluctuations than temperate fishes are. Fishes with buoyant eggs will be less affected than littoral zone spawners will be.

11. Eutrophication is an increasing problem. Game fish, such as salmonids, give way to rough (coarse) fish, such as pike or perch, unless preventive steps are taken. The use of waste waters at South Lake Tahoe shows what can be done provided that there is a will to do it and expense is not spared.

In brief, a great deal of basic information about fish ecology is still needed, especially in the tropics where fish populations are as yet hardly monitored. Experience already gained could be used more fully to help plans for new lakes.

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