

4. TRANSFORMED BIOLOGICAL SYSTEMS

The transformation of biological systems occasioned by the creation of a reservoir is profound and extraordinarily intricate. The main theme is obvious: inundation wipes out terrestrial production and replaces it with aquatic production. Solar energy is trapped by rooted aquatic plants and phytoplankton, rather than by grass, shrubs, and trees, and is eventually converted into a potential crop of fish rather than a crop of terrestrial birds and mammals. The detailed steps in the transformation are neither simple nor obvious. A great many kinds of organisms are involved in the machinery of biological production, either on land or in water. A square meter of land may contain more than 1500 kinds of organisms. An equal number of kinds may occur in a square meter on the bottom of a lake, and most of them are different kinds of organisms than occur on land. In both environments the same basic ecosystem functions are performed, but by quite different performers.

Thus the transition from production on land to production in water is a complex of changes comparable to the most profound social upheavals we can imagine. In the first phases of flooding there is mass mortality and migration of land forms, and a virtual explosion of aquatic organisms in the new land enlarging lake. Only after several years or decades is a new stability perhaps established. In the period of transition there are transient bursts in both the quantity and kinds of organisms produced. The transitional steps depend in large part on the character of the particular reservoir and the physical environment it creates.

In brief, the biological impact of a new reservoir is a highly complex metamorphosis from terrestrial to aquatic production. Some of the features of this change are becoming known from experience and are discussed in the section that follows.

Process and Understanding

Understanding of the interlinked processes (Figure 4.1) that lie between physical conditions on the one extreme and final production on the other is a central concern of aquatic ecosystem studies. If we understood fully the mechanics of production of undisturbed natural ecosystems, we would be better able to predict the effect of perturbations caused by man, or the effect of creating an « instant lake » by building a dam. As it is, we have imperfect knowledge of aquatic ecosystem dynamics, and as a consequence we are imperfect in our interpretations of the transient initial conditions in reservoirs and of the relative stability they eventually assume.

There is a growing body of observations that enables us to anticipate some of the biological features of reservoirs. For example, we know qualitatively that flooding of vegetation may contribute to oxygen deficits as the plant material decays under water during the first year or two; that floating aquatic vegetation may cause an array of inconveniences; and that an initial enlargement of productivity may be followed by less luxurious and more stable communities. But the scope of these and other effects is difficult to predict except in the most general way. They are events about which we can have concern on the basis of past experience, rather

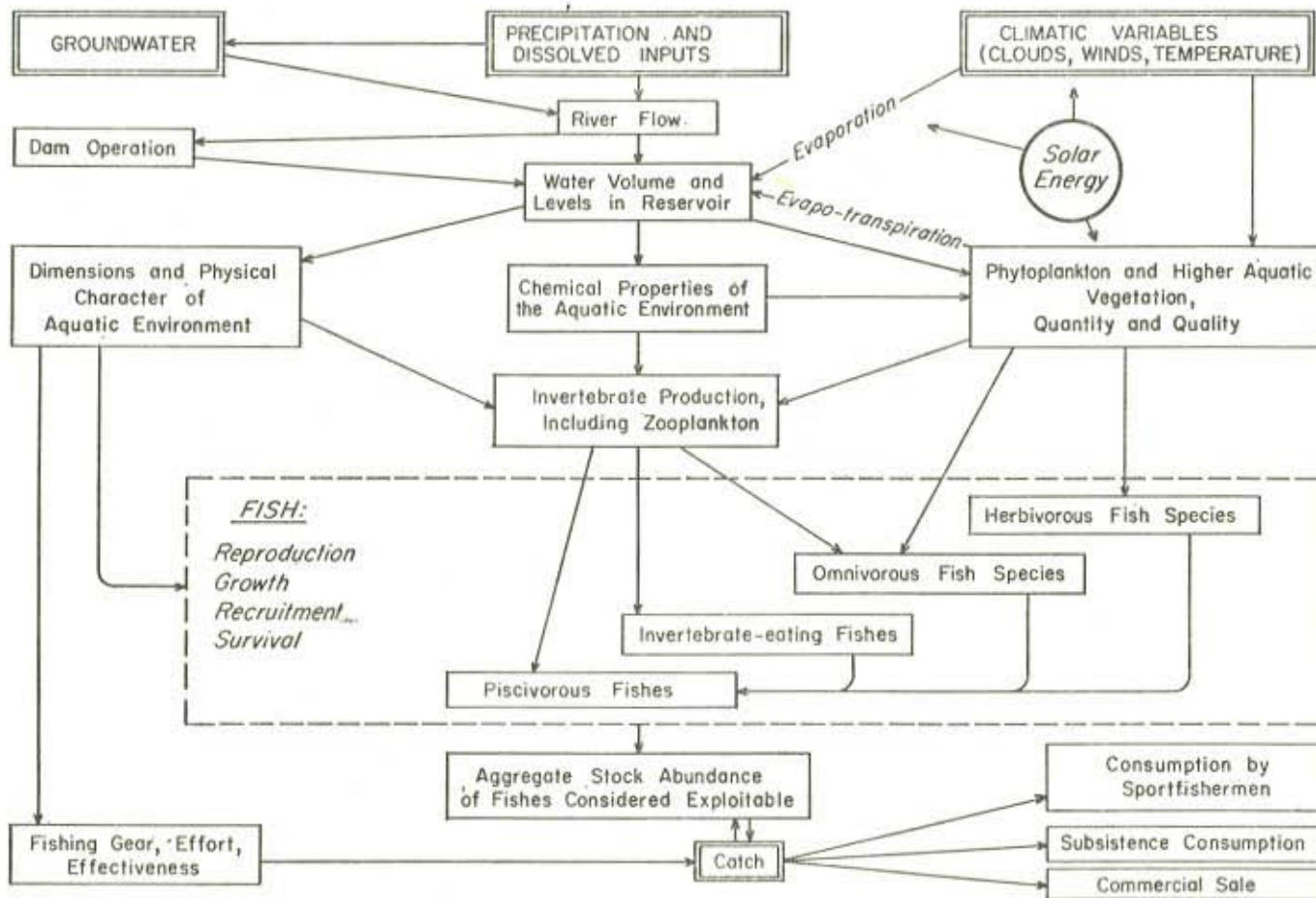


FIG. 4.1 - Reservoir Fish Production and Harvest

than events that we can predict with confidence as consequences of particular projects, or events for which we can prescribe solutions before they occur.

The level of scientific understanding of reservoir biology is relatively primitive because of the numbers of parameters and multidimensional aspects involved. Ecosystem modelling of biological production in reservoir situations may nevertheless be within the grasp of contemporary research. Within the next decade several models will have been constructed for lakes (natural and man-made), streams, portions of the world's oceans, bays, estuaries, grasslands, forests, and tundras.

With regard to fish production in reservoirs, empiricism is even more the prevailing level of the science. For single species populations in virtually any environment, stock assessment techniques of varying degrees of sophistication are readily available, and can be applied to management of the fishery. But in the rapidly changing conditions following filling of a reservoir, recruitment and growth are not stable, nor are the interspecific communities. The catch of fish is accordingly opportunistic and it is potentially misleading before or during the stabilizing process of a man-made lake to suggest the size of sustainable yields. Once conditions are more stable, conventional techniques of stock assessment may be useful, especially if the fish community contains few species or is dominated by few. For tropical and arid reservoirs, these assumptions may be as dubious as they are for large tropical lakes, and the best advice for the management of fisheries is still to document what is going on in hopes of gaining experience that will lead to new model systems on which to base predictions and harvesting practices.

Modern fishery resource management increasingly considers the social and economic factors involved. In many respects the principle *maximum sustained yield* is a myth, because it can be uneconomic. More relevant to human affairs is *maximum economic yield*, and most relevant is some sort of management that optimizes social benefits for specified goals. This, of course, brings in a multitude of considerations that transcend the narrow confines of a reservoir or a watershed. In fact, reservoirs may provide a deceptively tidy focus for analysis of economic and social implications, and more ideally, systems modelling should proceed from perception of social and economic goals through consideration of options to achievement — options among which reservoir schemes are only one of many possible contributors.

The initial biological explosion in some man-made lakes is due both to the spatial expansion of the aquatic environment and to the release of nutrient materials from the bottom soils and submerged plant and animal remains. The lake normally evolves rapidly from artificially high productivity to the expected phase of relatively stable but lower productivity. Unless complicated by changes in water quality as, for example, from pollution, the future evolution will be reasonably predictable and generally slow, with the actual rate depending on climate (latitude). The direction of this long-term evolution is much the same as for natural lakes — ultimate filling and return to terrestrial production.

In downstream reaches, which are excluded from detailed treatment here, the effects of dam construction in changing the regimen of water-level fluctuations may be large. Extensive areas adjacent to or in flood plains, like those in the middle and lower Amazon and Paraná basins, would be likely to proceed from pool and prairie landscape toward swamp conditions.

Evaluation of the effects of a man-made lake on potential production in the land

and water biological systems is based largely on predictions or on comparisons with natural or other man-made lakes. Although techniques for making predictions or comparisons are rough, they are improving. The requisite predictions can be posed as questions:

- 1) What is the actual and potential terrestrial production (crops, forest resources, and livestock production) that is lost by inundation? What are the short-term interactions of the modified production in the biological system with other components, especially with the socio-cultural system?
- 2) What is the actual and potential aquatic production (fish and other useful aquatic animals and plants) that is lost from the river, at the lake site, upstream, downstream, estuarine, and adjacent sea? Gained in the reservoir, upstream, downstream? What are the risks from changes in abundance and distribution of aquatic vectors of disease and nuisance animals and plants that may be favored by quiet waters? What rare or endangered plant and animal species and communities may be lost?
- 3) What are the agricultural and livestock production gains that may be derived in the newly created habitat of the drawdown zone and adjoining lake-influenced land?

Biological System Interactions

For simplicity in presentation and to emphasize the dynamic character of the biological changes we have chosen to divide the life history of a new man-made lake into the four stages presented earlier (Fig. 1.4): Stage I, the determination of the ecological, economic, social, and political feasibility of the project; Stage II, if the project is determined to be feasible, the actual planning of construction and related social moves, and conduct of necessary studies; Stage III, the period during which the reservoir is filling for the first time and extending through the period during which the lake is biologically very unstable; Stage IV, the period during which the lake can be considered stabilized and undergoing its more or less long-term evolution.

We can identify within each stage the different analytical, investigational, and operational priorities which should be given to the disciplines involved in decision-making. We apply two approaches at each stage: 1) identifying and defining the components of each of the systems involved, and 2) determining the interrelationships and the mechanisms of all of the components (or at least of the key components) both within each system and between and among all of the systems that make up the lake ecosystem. In the biological system, for example, components to be considered include not only the species and communities of living organisms but also the particular life history stages (ecophases) of each species.

It is beyond the state of our present understanding to discuss the total complex of reasons behind many of the changes that take place in reservoir development. Although investigation of the interlinked processes (Fig. 4.1) is a central theme of aquatic ecosystem studies, there is as yet far from adequate insight into the factors that influence production and numbers of various kinds of organisms even in natural environments. In consequence much of our present basis for prediction of effects in reservoirs is based on experience rather than understanding.

Fortunately, in most ecological systems a large proportion of the energy flow takes place between a relatively small proportion of the total number of species of plants and animals. Moreover, these ecologically dominant forms are grouped into fairly separate communities. Thus, while the complexity of ecosystems is very great, the main features such as productivity and standing crops at different trophic levels can be assessed fairly simply once they are in existence. When augmented by studies of the dynamics of the dominant species, relatively superficial assessments can give a good guide to broad management practice. These techniques, of course, have been best developed for temperate aquatic ecosystems. The great diversity of species in tropical environments and paucity of scientific workers continue to hamper understanding of tropical ecosystems.

Feasibility Studies

At the feasibility analysis stage (I, Fig. 1.4), the challenge is to anticipate the effects of the proposed environmental manipulation on various kind of terrestrial and aquatic organisms: those of short life term and frequent population turnover (e.g., nutrient cycling bacteria and many algae); those of intermediate life span and turnover (e.g., cereal crop plants, some small fishes, and such insects as mosquitos); those of long life span and slow population turnover (e.g., perennial plants such as forest trees, and large wild aquatic or terrestrial animals or domestic livestock); and people.

To predict these effects it is important to know the species and community composition of the terrestrial and aquatic environments affected. The plants and animals can then be analyzed for their uses, actual and potential.

Those organisms which are or may become nuisances or threats to the health of man or his animals and crops can be appraised especially as to whether their numbers or distribution will be altered. Where the lake site includes all or part of the range of a rare or endangered organism or community, costs for offsetting possible loss may enter feasibility decisions.

The foregoing assumes that biologists have prior knowledge of the organisms that are to be influenced by the flooding, but unfortunately this is seldom the case. In general terms, the vertebrates from fish to mammals, and the higher groups of plants, are well known or, if not well known, rather readily surveyed. Microorganisms, whether plants such as algae, soil or mud organisms such as protozoans or nematodes, or plankton organisms such as copepods, are neither as well known nor as easily assigned to species rank. Because these organisms may play important roles in ecosystem dynamics, a better knowledge of their systematics and biology is much needed. Meanwhile, they are treated as large groups that jointly perform ecologically wondrous things which we hope they will continue to perform.

Terrestrial Production Gains and Losses by Inundation

One of the persistent shortcomings in benefit-cost analysis commonly applied to development schemes resulting in ecosystem modification is the actual and potential benefit of *not* undertaking the scheme. This involves assessment of the elements of biological production that are lost if the scheme *is* undertaken.

The elimination of terrestrial production from inundated land has often been overlooked. This production may be natural, culminating in wild plants and animals (some of them deemed useful), or it may be managed production, yielding agricultural, livestock, or forest crops. Values for current production may be estimated, with relative precision. More difficult to obtain are current and potential values of the unmanaged natural production, which may be used for nature study, tourism, and recreation, and as raw materials for subsistence, construction of dwellings, or manufactured articles. Even more difficult, and perhaps less precise when obtained, may be potential production derivable from application of known techniques or from theoretical application of possible technologies.

The potential area for a different kind of agriculture than practiced in the former river bottom land is highest in the drawdown zone and in the immediately adjacent land. For most tropical man-made lakes to date the evaluation of this potential has been inadequate (see Chapter 2).

Gains Versus Losses in Aquatic Production

Like considerations apply to aquatic production. Elimination of actual and potential riverine production can be compared with anticipated gains from production in the new lake. Aquatic production is most evidently fish but it also includes aquatic plants, shellfish (crustaceans and molluscs), amphibians, reptiles (alligators, crocodiles), birds (resident and migratory waterfowl and shore birds), and mammals (beaver, otter, manatee). While man has learned to use some of each of the foregoing kinds of organisms, many remain unexploited. It is desirable that surveys of potential effects should consider the full spectrum of human use of aquatic biological resources.

Governmental statistics often provide a good measure of the current worth of a stream fishery prior to inundation by the reservoir. Where statistics are not available, a substantial survey should be part of feasibility studies. A survey is also useful in providing data that has value for broad approximation of fishery yields in the eventual reservoir.

Although the actual and potential values for production may be estimated with relative ease for many rivers, techniques for prediction of yield from large stabilized reservoirs are far from perfect. As previously indicated, predictions are being made with practical success in some areas by two methods: a) comparison with known catch in existing bodies of water judged to be similar to the one that may be created; b) application of morphoedaphic indices and multiple regression techniques based on combinations of selected physical and chemical characteristics of the lake and its basin, and preliminary estimates of primary and secondary production and biomass. The second of these two methods (b) holds the greatest hope for the precision required if economic and social values of the fishery are to be assessed properly.

A tidy, straightforward index advanced by Ryder (1965) for use in estimating fish yields from certain North American natural lakes has been shown to be applicable to prediction of U.S.A. reservoir fish crops and angler harvests (Jenkins, 1970). The index, total dissolved solids divided by mean depth, explained 62 % of the variability in standing crop in 37 hydropower storage reservoirs and 28 % of the var-

iability in sport fish harvest in 103 reservoirs. Regier et al., have recently applied such morphoedaphic indices in estimating potential commercial fish harvests in African lakes and reservoirs (unpublished working papers, FAO Department of Fisheries).

Altered land use in the drainage area inevitably accompanies creation of a man-made lake. In addition to gross elimination of terrestrial production from the flooded area, a number of biological interactions between uses of the land and water may develop. Hydrologically, a reservoir is a sink both for the sediments transported by, and, to a smaller degree, the nutrients dissolved in tributary waters. Forestry and agricultural practices in the watershed thus affect aquatic production. Conversely, if chemicals are used to manage parts of the aquatic production, for example to control aquatic vectors of disease or nuisance aquatic plants, there may be impacts not only on fish but on domestic consumption of the water and on the plants receiving downstream irrigation. Careless land management in the lake basin can accelerate erosion and thereby hasten filling of the lake and otherwise interfere with aquatic production through both siltation and turbidity. These kinds of effects should be anticipated by attempts to predict patterns of land and water use before the dam is constructed, and should be monitored thereafter.

The Biological System During Planning and Construction

In the planning and construction stage (II) the study and resource management activities center on action best taken before inundation of the substrate. Thus, they concentrate on favoring species and communities considered useful or rare or endangered, and on suppressing species and communities not so considered, including ones that may become obnoxious or nuisances in the modified ecosystem. The activities involve manipulation of species populations, multispecies communities, and the environment, and thus constitute a beginning of production management in the biological system. At this stage, land in and adjacent to the drawdown zone can be prepared for agriculture, and, if necessary, experiments may be conducted on new agricultural uses and practices.

While the dam is under construction is the time to prepare the future lake bottom for aquatic production and its harvest, for safety and convenience in navigation, and for reduction of health hazards by disease vectors. Installation of cover, shelter, or spawning beds for fishes may be provided. Similarly, where tree and bush clearance is judged to favor fishing and boating, it is best done in advance of flooding. At Lake Kainji, 40 km² (some 10,000 acres) were cleared at high cost but early experience in fishing suggests that fishing yields are highest per unit of effort in the shallows that were not cleared (El-Zarka, AGU, in press). Experience at Lake Kariba was similar. For both lakes the tentative conclusion is that lanes for fishing and boating are the most efficient forms of clearing. Clearance may also be required to suppress the buildup of weedbeds or calmwaters areas that encourage multiplication of disease vectors such as mosquitoes and snails.

Marking the future shoreline prior to filling is advantageous for environmental manipulations for aquatic production. It is also required for shoreline clearance and site preparation for foreshore agriculture, construction of port, dock, and other shore facilities, and siting of towns and intersecting roads.

Construction operations can be ecologically devastating at and in the vicinity of a dam site. Blocking anadromous fish migration during construction frequently has an effect that persists for many years.

Hypothetically, even a fine fishway would be to no avail if obstruction during the construction period prevented spawning by a sufficient number of year classes. For example, the tigerfish (*Hidrocynus*) of the Pongola River in South Africa did not move upstream into the Pongola Reservoir. The Pacific salmon are particularly vulnerable to construction effects because their spawning populations so frequently comprise one or two age groups. There are many instances in the Pacific Northwest of North America of longlasting effect from short-term stream obstruction. Although disruption of flow during construction may be only temporary, denudation of the landscape, creation of erosion sores, and local destruction of wildlife can also require lengthy periods for recovery.

The Biological System During Filling and Stabilization

When the reservoir begins to fill for the first time (early part of Stage III) the terrestrial and riverine (lotic) environments progressively disappear and the lacustrine (lenitic) environment originates and expands.

In the lake basin, there is a sequential shift from dominance by flowing water species and communities to those of more quiet water. Soil moisture and microclimatic conditions are modified around the outward moving and lengthening shoreline. Stream conditions below the dam are drastically modified, particularly because of the reduction in flow during reservoir filling.

This is the time when it is advantageous to begin verification and adjustment of predictions made during the feasibility stage (I) and of the substrate and other preparations made during the planning and construction stage (II) in order to offset unwanted effects. In so doing, unanticipated responses of the organisms are discerned and possibly redirected.

It is at this stage that the advice of biologists and ecologists has commonly, and often belatedly, been sought. In one instance, diversion of water to enable dam construction so increased the hazard of river blindness by creation of an improved stream habitat for the blackfly (*Simulium*) vector, that costly and environmentally problematic control was required. This is representative of the kind of error of omission in feasibility study or planning that results in a salvage operation. In another instance (the Peace River, Canada), it was not anticipated that reduction of flows would influence waterfowl and muskrat marshes several hundred miles downstream.

If selection of the time of closure of the dam is based solely on hydrological considerations (usually when the river is lowest just before a seasonal rise), chances are against the choice being biologically advantageous. Unfortunately, there is only sketchy experience with this overall problem of timing.

While the lake fills there are opportunities to encourage or suppress species or communities deemed either desirable or unwanted, and to implement measures for the protection of rare or endangered species, especially in the aquatic habitat. In some instances, this is when «rescue» operations have been conducted for organisms threatened by drowning. Such activities are biologically unwarranted re-

ardless of however else they may appear to be justified — with the possible exception of non-mobile rare species.

Costly rescue and translocation of animals threatened by flooding at Lake Kariba were judged to be a failure from a biological point of view (Crowcroft, 1960) but may have had social benefits in focusing attention on a problem of land-use conflict. The same is true of the experience at Lake Afobaka (Brokopondo), Surinam (Walsh and Gordon, 1970; Bardach and Dussart, AGU, in press). Little is known about the impact of the outward movement of land animals as the water rises, of their competition with resident populations, or of their eventual fate (except for those that went to zoos).

Most striking in first filling is the sudden beginning and rapid development of the lacustrine system. The cycle of biological production is fueled initially, at least, by a microbiological population explosion in the new standing-water habitat. This explosion releases nutrients from the submerged organic matter which is quickly cycled (in days) into primary production — the initial harnessing of solar energy by planktonic algae. With differential rapidity, depending, among other things, on latitude and on the food web involved, this upsurge in primary production is typically transferred through the food chains to a rapid (in months) rise in fish production, often with a consequential convergence of fishermen. In deep reservoirs, this accelerated and differential biological production may be accompanied by seasonal density and chemical stratification of the water (see Chapter 3), characterized by stagnation and deficiency of dissolved oxygen in the deeps. As a result, recycling of bottom nutrients may be slower, and there may be a corresponding decrease in production. In addition, the deeper parts of the lake may become uninhabitable for fish and other organisms. In some instances the deeper water areas become so laden with hydrogen sulfide as to become toxic to organisms and corrosive to engineering installations (for example, Lake Ayame, Ivory Coast, and Lake Volta). Stagnation can be overcome by artificially inducing circulation, as with aeration pumps, although this technique is not yet feasible for large reservoirs.

Because of imperfect understanding of the dynamics of production in reservoirs, especially in the tropics, there is still substantial need for studies of the processes and interrelationships during first filling.

Studies of successive dominance and evolution extend from phytoplankton at one extreme, through intermediate food webs, to fishes at the other. A major requirement here is elementary knowledge of the biology of the dominant species and of the factors regulating their abundance.

Most of the rapid ecological changes started by filling continue while the new lake is stabilizing. During the stabilization process, lake evolution is irregular in speed and direction with wide fluctuations in numbers of various organisms. Progressively, a new and more stable community is established.

In the stabilizing period, the permanent pattern of benefits in fisheries and agriculture begins to emerge. Fixation of the highwater shoreline and the extent and timing of the drawdown zone enable new agricultural and aquacultural developments. Establishment of favorable and predictable soil moisture and microclimatic conditions adjacent to the foreshore, also enables more stable agricultural development.

It is in the early part of the process, leading to stabilization, that greatest production per unit area occurs in terms of useful aquatic organisms, especially fish. For example, fish catch, as a partial indicator of production, in the section of the Volta River later covered by Lake Volta, changed within 5 years from 4,000 to some 60,000 metric tons per year in the new lake. Also, in Nam Pong reservoir of the Mekong basin, the fish catch soared in the third year after filling to some 1,200 metric tons to constitute a revenue of \$ 500,000 which was two-thirds of the annual income from the production of hydroelectricity (Bardach and Dussart, AGU, in press).

At this time, explosive development of nuisance weeds has also occurred which, in the tropics, include the water hyacinth, water fern, and water chestnut. One of the more striking characteristics of a lake in the process of stabilizing is the change in the area covered by emergent aquatic weeds and occurrence of dense phytoplankton blooms. In Lake Afobaka, three years of spread of emergent aquatics covered some 53 per cent of the surface area of the lake (Leentvaar, AGU, in press).

To the present, there have been no valid predictions of the rate of increase and peak of early aquatic production in reservoirs. This has made it difficult to manage fisheries in the early stages of exploitation, and difficult to control entries into the fishery, the kind of gear to be used, and investment in gear. The common response to the early upsurge in fishing is like a goldrush with all of its entrained social and economic problems.

During the stabilizing period, selection of environmental and population parameters for measurement over the long term is critical if eventual understanding and management is to be sophisticated. A central problem of monitoring is that the sampling processes be representative and reliable. Water composition measured at only one station in a lake is usually not representative of the whole lake. Reservoirs, like some natural lakes, show depression and basin individuality as well as local influences from tributary streams. This is particularly the case for reservoirs in long narrow valleys in which circulation may be a series of eddies with complex mechanisms of interchange. Depression individuality is evident at lakes Kariba and Volta, and has been carefully described for several reservoirs in the United States. The consequence of these patterns of circulation is that there are differences in water quality that are reflected in differences in species composition and growth rates, differences in the depth range of various species, and, in effect, differences within parts of a reservoir as great as differences between reservoirs.

While stabilization occurs, the effects upon biological production of the typical regime of water level fluctuation become evident. On the basis of that new experience, the system of regulating water outflow may then be revised and integrated for optimal returns, giving full consideration to the multiple-use aspects of the reservoir.

With establishment of the reservoir shoreline, human settlement along it soon takes place — planned or haphazard — and many new kinds of problems may be created. The human population now is exposed to different hazards than formerly from waterborne or aquatic-animal-vector-borne diseases. As suggested in Chapter 2, suppression of disease vectors through biological, physical, or chemical means and intensified education in public health is frequently necessary. Although the best

health-hazard suppression means is obviously that which is most ecologically compatible, the history of man-made lakes shows conspicuous failures in this regard.

Early stages of settlement may also include schemes for artificial culture of aquatic plants or animals. Experience indicates that it is ecologically wise that such action not involve exotic species and that the initial experiments be made with indigenous form, be they plant or fish or other animal. Exotic forms frequently prove to be nuisances rather than assets. Escapes of introduced species from cages or small adjacent ponds into the reservoir are to be expected. Usually the extermination of unwanted introductions is impossible. Accordingly, every precaution should be taken to avoid the early introduction of exotics, the safest policy being not to bring them into the vicinity. This precaution pertains most strongly to the aquatic environment since species-selective and ecologically compatible means of control of introduced plants or animals are so little developed. In this connection, man's ignorance of the cultivability of most aquatic organisms is a barrier to progress. For example, of the some 20,000 species of fishes in the world, only a very few have been explored for their aquacultural suitability. Similarly, opportunities to develop strains by selective breeding are largely unexplored.

The effects of a dam on migratory fish stocks first become evident early while the new lake is stabilizing. The effects are in part generated by the purely physical barrier which the dam creates, and in part by the effect of the storage reservoir on the pattern of discharge and water quality downstream.

For most species of migratory fishes it is convenient to consider the effects of dams and reservoirs as comprising a set of effects on adults going upstream and a set of effects on young migrants going downstream. In some instances, a reservoir may inundate a spawning ground for migratory fishes (for example, sturgeon on the Volga and some salmon streams) but, in general, the problems of movement of mature adults and downstream juveniles are much more serious.

For adults, the central problem is the disturbance of the timing and energy budget for their upstream migration. Changed patterns of seasonal discharge may modify the speed of passage, in some cases creating obstructions to migration and in other instances rendering migration upstream easier. Modified temperature regimes may also have either beneficial or detrimental effects. Where a dam may be provided with orifices that will discharge water from different depths, there are opportunities for manipulating temperature regimes to enhance the ease of migration. A particular problem, however, may be created by discharge of water from great depths in a reservoir. Concentrations of dissolved gases may reach supersaturation levels and cause gas embolisms and death of fish for several miles downstream.

Assuming that the adult fish can adequately negotiate the river up to the dam-site, they are then confronted with the problem of finding the entrance to a fish pass, if one has been provided. The most common mistake in the design of fishways, fishladders, or other such devices, is to assume that the fish will know that a device has been put there for their benefit. In fact, it is a rather simple matter to arrange for the mechanical transport of migratory fish over a dam. The major problem is to get the fish into the devices without delay. These problems increase with the size of the discharge, the variability in discharge, and with the number of fish to be passed. In general, if a dam is over 100 feet in height, it is usually not

possible to construct facilities that will move the adults upstream past the dam without delaying their migration substantially (say by a week or ten days).

The consequence of this kind of delay in migration is that fish may reach the spawning grounds at an inappropriate time and that they may have exhausted their energy reserves and die without spawning. This problem may be a very great concern if the size and the physical structure of the reservoir also cause delays in passage. It is commonly observed that adult fish do not move upstream through reservoirs as quickly as they would through a natural river system. There are many recorded instances in which migratory fish, having passed upstream over a dam are subsequently swept downstream over the spillway so that the whole passage must be renegotiated.

For the young fish in their seaward migration a reservoir may create short-term delays in passage downstream and, for some species, may act as a trap in which downstream migrants remain throughout their lifespan as « residuals ». It has also been the experience that reservoir conditions favor the development of populations of predators. Natural losses to predators are thus increased because of the changed conditions.

At the dam, the effects on downstream migrants depend upon the route. If they go over the dam, there are mechanical injuries from abrasion on the spillway, and at the impact of the spill with the water below the dam. These losses may be ameliorated by special design of the spillway and the tailrace but, in general, they are difficult to avoid, especially on dams over 100 feet high. If the migrants pass through underwater orifices and through turbines, they are subject to injury from cavitation effects at the turbines and sudden pressure changes as they are released into the tailwater. Mortalities of 20 to 30 per cent are common. As a rough approximation, loss is about 10 per cent per hundred feet of head. These losses are also difficult to avoid and, in consequence, for most large dams it is desirable to design facilities that will divert downstream migrants into a safe bypass channel. This usually involves very substantial expenditure because the techniques of guiding downstream migrants by light, sound, and so on, are imperfect and mechanical screening or use of louvre systems is often of prohibitive expense and only partial effectiveness.

If the downstream migrants have successfully passed the dam, they may still be affected by gaseous supersaturation in the tailwater and a variety of downstream changes in water quality.

Because of the many effects on migratory fishes at damsites and in reservoirs, large-scale collection and transportation facilities may be suggested as devices for moving adults and/or juveniles around the dam and/or reservoir. For small populations of migratory fishes confronted by high dams, these transportation schemes may be feasible, but for large populations and large reservoirs, there are many technical problems and a prohibitive price tag.

Special problems are created when a river system is developed with a series of dams. The effects of delays on both adults and juveniles are accumulated. Additionally, as the fish pass either upstream or downstream, there is a progressive deterioration of their ability to cope with additional stresses. Many of these effects are as yet not well understood, but there is substantial evidence that the total effects of a series of dams is more than the sum of their individual effects.

It is thus apparent that where a very large dam is to be built, or where a series of small dams is constructed, one cannot be optimistic about the economic conservation of migratory fishes. In consequence, it is common practice to examine the possibilities of mitigating losses by the use of hatcheries, artificial spawning channels, or other fish cultural devices.

In some circumstances, fish cultural practices have been notably successful in increasing production of migratory fishes. In large measure, however, these successes have been arrived at empirically — at the expense of a much larger number of failures. For most species of migratory fishes there is far from adequate experience with artificial methods of culture to encourage the belief that they could satisfactorily substitute for natural production. For this reason, where migratory fishes are concerned, it is more likely to be a question of reservoir *or* migratory fish, rather than reservoir *and* migratory fish. Substantial literature on these problems is available for Pacific salmon on the West Coast of the United States and Canada, and this literature is strongly indicative of the complexities of reconciling migratory fish conservation with damming for major power development and flood control on large river systems.

The Stabilized Biological System

The stabilized stage (IV, Fig. 1.4) in the life history of a man-made lake is reached when fluctuations in its biological parameters of production exceed only little, if at all, those in a natural lake of similar physical characteristic and like latitude and elevation. As an example, stabilization is characterized by seasonally cyclic balance in the oxygen budget of the lake. Stabilization is also shown by emergent aquatic plants when either their rapid initial spread has ceased, attained an extent from which there is little annual change, or even retreated from an initial maximum extent, as at Lake Kariba. With more stable fish production, the population of commercial fishermen may also decline or level off, although the number of sport fishing visits may continue to rise.

In an idealized system, biological stabilization may be thought to occur when equilibrium is reached between mortality and natality of the organisms of the system and when the species and community composition of the system becomes relatively fixed. However, natural lake systems may show wide fluctuations in abundance of organisms from year to year, even though productivity characteristics of the lake remain fairly constant. The same is true of reservoirs even when they have small and annually similar patterns of fluctuation. Where fluctuations are large and different from year to year, it is to be expected that conditions for biological production will also be variable. « Stability » is thus a relative matter. Full stabilization never is assured. As already noted, changes in water use can cause a complete revision in the scheduling of water fluctuations and render the biosystem very unstable again.

The concept of the stabilized condition is one of a mean of variable short-term fluctuations. The amplitude of the fluctuations may be exaggerated by unusual events in the hydrological regime (an extremely dry or hot year), in the biological system (an epidemic), or from human interference (over-fishing or drastic pollution).

With stabilization of a reservoir ecosystem there are improved opportunities for fishery stock assessment and for fishery management. These opportunities have not often been firmly grasped, even though they enable rational harvesting policies on a year to year basis without comprehensive understanding of the complex web of circumstances that underlie production. Simply stated, production is the excess of reproduction, growth, and recruitment over natural mortality. A number of model systems are available that combine estimates of these parameters and indicate the rate of harvesting that is consistent with maximum yield for any stated size of first capture, or conversely, a size of first capture consistent with a rate of fishing. The various model systems available differ in their data requirements and their accuracy, and in general it is necessary first to approximate the properties of a fishery by simple model systems before proceeding to the use of more sophisticated, more precise but more data-hungry models. There is certainly no lack of research or experience on which to base dynamic programs of fishery management.

For all fisheries, whether riverine, estuarine, marine or freshwater it is the *usual* practice to manage species singly. This may seem unrealistic because of the many interrelationships among species. Nevertheless, it seems to work well, at least as a first and short-term approach, perhaps because of the dominance of a relatively few species in most aquatic systems. The absence of a theory of harvest for complex associations of species that occur in many tropical lakes and reservoirs is thus often bemoaned unnecessarily. Nevertheless this is an area that is in need of much further study.

Whatever model system is used as a basis for management of fish stocks, it is essential to have a good statistical network to provide data on quantity of catch, composition of catch by species and size, and amount of fishing effort (kinds and quantities of gear used and measures of their efficiency). With this basic information, assessments of the state of fish stocks and their likely fluctuations coupled with knowledge of rates of production can direct fishery management practices, as well as contribute further to our accumulating experience of reservoir biology.

Fish production is of course geared to human consumption and sport, and it is notable that the potential for food production in a reservoir may not be realized because of inadequacy of the mechanisms for catching, handling, distributing and marketing fish. The anticipation of these phases of fish utilization should substantially precede reservoir filling.

Also the routine of statistical assessment after establishment of fisheries should perforce include data on the fate of the fish after they are caught¹.

The management of «stable» species complexes, as in large lakes or in the world's oceans, is still largely a matter of conjecture and it seems likely to remain so for some time. It is nevertheless characteristic, that when one or a few species are as acceptable to human consumers. Humans, though, are notoriously conservative remains relatively constant. This implies that if fishery management fails in its objectives, it may be of little consequence provided that «other species» of fish are overharvested, their places are taken by other species and total production

¹ It is an interesting aside that unreliable statistics plague fishery evaluations. The lack of reliability seems to stem from the desires of data gatherers to please «rather than to be honest». This is understandable, but it is notable that for all of our advice to people in high places, our schemes may stumble on lack of understanding at the grass roots levels of the need for reliable information.

tive in their feeding (or angling) habits. Rather arbitrarily, they characteristically assign to certain species names such as «trash fish», even though these fish may have equal nutritive values to «preferred fish», or perhaps equal sporting value. It must therefore be underlined that social customs are a major factor influencing potential use of the aquatic production from reservoirs. Where complete flexibility of the consumers exists, a «laissez faire» attitude to the fisheries would seem appropriate until rates of harvest on all species are higher than permissible for maximum sustained or maximum economic yield. Where consumer habits are less flexible or not easily manipulated, a more circumspect management is appropriate.

The immediate consideration for terrestrial production is the landward limit of soil moisture and microclimate directly influenced by the lake. This set of lake influences is largely unexplored. The critical questions are: to what extent is the habitat modified? and what are the new advantages that may be extracted from the modified habitat by various forms of investment and technology? Little can be done on a rational basis to take advantage of improved soil moisture and microclimatic conditions in many parts of the world without further study and experimentation followed by extension and institutionalization of the necessary monitoring systems.

Interest in some terrestrial potential may have to be subservient to other needs. For example, since the lake may be attractive to many people, there is every likelihood that its immediate surroundings may be in demand for parks, marinas, and other touristic uses, for roads, docks, and other communication facilities, for settlements, villages, and industrial sites, and for possible access to new resources. The principal objective is to assure that multiple use conflicts on the shoreland as well as between land and water uses may be minimized, or be reconciled on reasoned grounds.

In an even wider context and in the longer term it is necessary to consider the whole pattern of basin development, including the impacts of upstream land use on the reservoir and of the reservoir on downstream land use. It has not been common to view a reservoir in the broadscale perspective of watershed management and regional ecology, though this should be the aim in the future.

With the terrestrial part of the biological system as with the aquatic part, study, experimentation, monitoring, harvest statistics, and modelling are required as a basis for rational action.

Requisites for Modelling

The advent of computers particularly has made possible the large-scale numerical simulation of complex entities such as reservoirs and the regional systems of which they are a part. More traditional mathematical treatment poses intractable analytical problems and massive problems of calculation. In essence, the technique requires a conceptualization of quantities and the processes which transform them in a dynamic system. Given such conceptualization, various projections can be made of likely consequences of particular courses of action. For natural biological systems, there are characteristically a large number of quantities and the processes which link them are imperfectly known. As a result, the art of modelling ecosystems for predictive purposes is presently in an early stage of development. Nevertheless,

there is promise of rapid scientific advance, particularly because of the impetus that has been given to such studies by various major projects (for example, some of those conducted under the aegis of the International Biological Programme).

Serious attempts to model stable reservoir ecosystems, with inputs of nearly 100 physicochemical and biological parameters, are now underway. Among the efforts in this direction are those of Czechoslovakian scientists. A three-dimensional model is being developed for Walnut Creek, California, and the U. S. Department of Interior, in cooperation with the University of South Dakota, is attempting to model biological production in 11,400-hectare Lewis and Clark Lake.

In a model of aquatic biological production in a reservoir, a number of *initial* components can be visualized. Values for some of these components are to be taken from the data of related physical systems, others may be obtained from continued monitoring of physical and biotic factors (automated where possible), and still others require particular studies. When operational, even with extrapolated or assumed values where empirical data do not yet exist, such a model can become not only the basis for rational exploitation and management of the living aquatic resources of the reservoir in question, but can also be of predictive value in the feasibility and planning efforts for man-made lakes yet to come.

The following are suggested for minimal automated monitoring with special attention to use of physical data in modelling of aquatic biological production on man-made lakes: water temperature; solar radiation and light penetration; dissolved oxygen; conductivity and dissolved solids; redox potential; and density currents. All of the foregoing need to be measured and registered at appropriate depths and times and at different stations corresponding to areas of morphometric and water quality individuality.

Where not otherwise similarly obtained and adequate, the following may be added for the atmospheric system just above the surface of the water: wind direction and force; relative humidity; and precipitation. Selected instruments to obtain data on other factors dealing with aquatic biological production, or on water characteristics related to other water uses, may be added to the instrumentation column at each station as specific needs and costs warrant.

The technical and economic feasibility of an automated monitoring program of this type remains to be established. A pilot experiment would be desirable.

It will always be important to backstop such monitoring with calibration by classical methods and with selected qualitative measurements of interpretative value (e.g., the amount of turbidity that is due to plankton, and qualitative composition of crops of phytoplankton, zooplankton, and benthos). Automated sampling of plankton for both quantitative and qualitative purposes is beginning to prove both feasible and valuable.

In spite of the thousands of published studies on aspects of terrestrial and aquatic production in new lake systems, both the scientific understanding of the processes and their management leave much to be desired. The overriding need is for comprehensive international review — far more penetrating than has been possible in this report — of existing knowledge: to disclose what is known adequately for predictive purposes; and to indicate what studies should be pressed forward with greatest vigor, and which theories are ripe for testing. Such a review would be prerequisite to intensified efforts at modelling of the processes involved and could

be part of interdisciplinary reviews of the other related systems. It should include diagnoses of the differences and similarities in the mechanics of biological production in artificial lakes and in natural lakes, and between tropical and temperate reservoirs. The result would be welcomed by scholars and resource managers, and great gains in investigational and managerial efficiency could be anticipated. Short of the foregoing, measures to increase information flow and retrieval would serve to encourage investigators to undertake relevant studies.