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A REVIEW OF THE EFFECTS OF WATER-LEVEL CHANGES ON RESERVOIR FISHERIES AND RECOMMENDATIONS FOR IMPROVED MANAGEMENT

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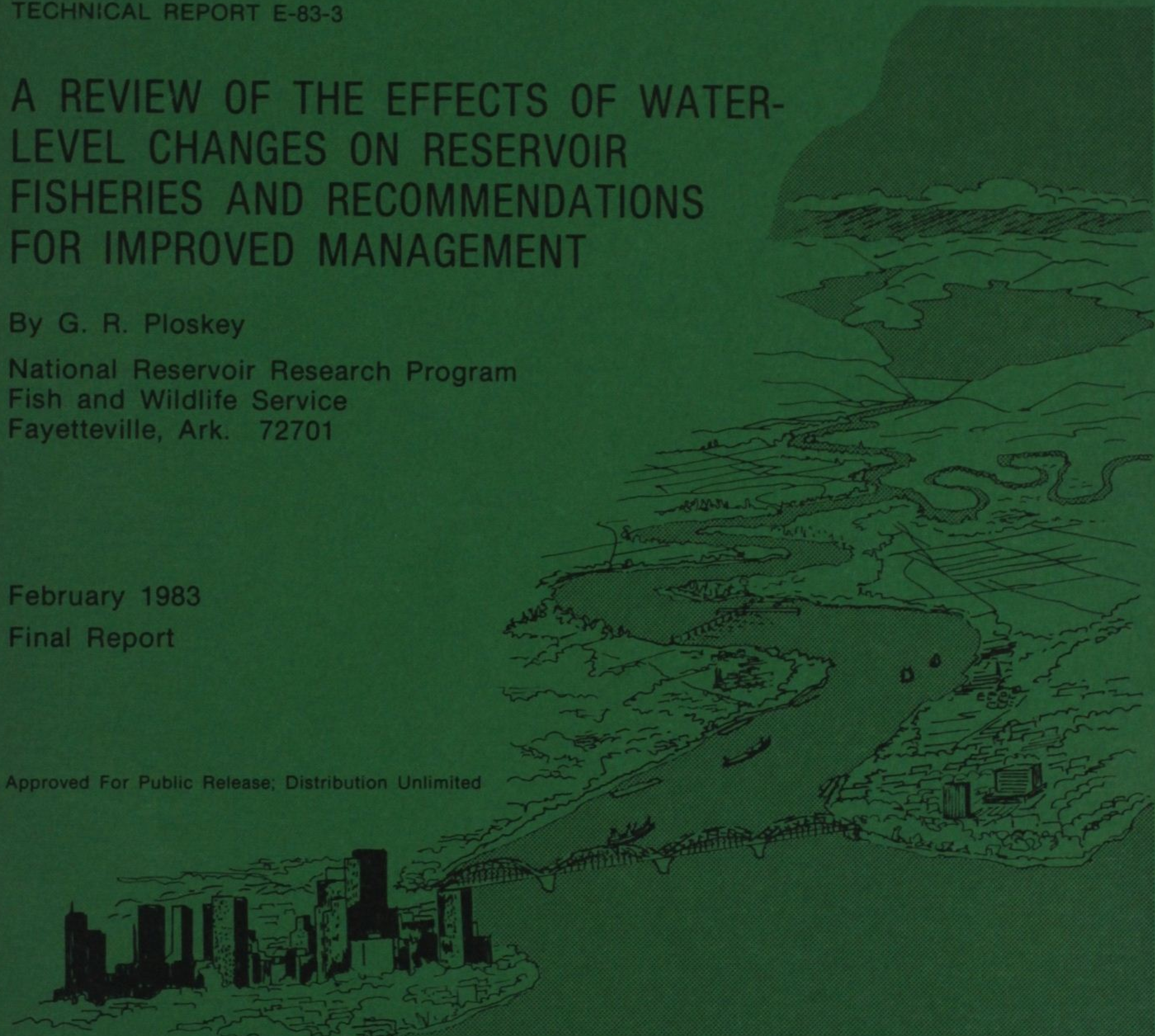

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This report synthesizes and summarizes information gathered from available sources about the physicochemical and biological effects of water-level changes on reservoir ecosystems. It describes how variations in both the physical environment (i.e., basin morphometry, bottom substrates and structures, erosion, turbidity, temperature, and water-retention time) and the chemical

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environment (i.e., nutrients and dissolved oxygen) caused by water-level changes can directly influence a reservoir's production of fish. It also describes the complex ways in which water-level changes affect aquatic plants, zooplankton, and the benthos and how these trophic variations can eventually affect the growth, reproduction, and harvest of fish.

The final part of the report summarizes the effects of drawdown and flooding on reservoir fish populations and recommends ways to manage reservoir fluctuation zones by making controllable variables as favorable as possible for fish survival, spawning, and feeding.

PREFACE

This report was prepared by the National Reservoir Research Program (NRRP), Fish and Wildlife Service, for the U. S. Army Engineer Waterways Experiment Station (WES) under Intra-Army Order WESRF-82-24, dated 6 October 1981. The study forms part of the Environmental and Water Quality Operational Studies (EWQOS), Task II.E, "Environmental Effects of Fluctuating Reservoir Water Levels." The EWQOS Program is sponsored by the Office, Chief of Engineers, U. S. Army, and is assigned to WES under the management of the Environmental Laboratory (EL).

This technical report was prepared by Mr. G. R. Ploskey, Fishery Biologist (Research), for the NRRP, of which Mr. R. M. Jenkins was Director. The work was conducted under the direct supervision of Dr. John Nestler, Water Quality Modeling Group, and the general supervision of Mr. D. L. Robey, Chief, Ecosystem Research and Simulation Division, and Dr. J. Harrison, Chief, EL. Dr. J. L. Mahloch was the Program Manager, EWQOS.

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CONTENTS

A REVIEW OF THE EFFECTS OF WATER-LEVEL CHANGES ON RESERVOIR FISHERIES AND RECOMMENDATIONS FOR IMPROVED MANAGEMENT

PART I: INTRODUCTION

1. Effects of water-level changes on reservoir ecosystems have been of concern since the early 1930's when the Tennessee Valley Authority (TVA) began its first extensive studies of large reservoirs. Wood (1951) reviewed most of the literature published before 1950. The importance attached to the effects of water-level changes by agencies responsible for reservoir operations (e.g., TVA, U. S. Army Corps of Engineers, leasing utilities) and for management of fishery resources in reservoirs (State fish and game agencies, U. S. Fish and Wildlife Service) is emphasized by the large volume of literature on the subject (see the extensive annotated bibliographies by Fraser 1972; Triplett et al. 1980; Ploskey 1982).

2. Water-level changes have attracted widespread interest because they affect, or are affected by, virtually every use of reservoirs (water supply, irrigation, flood control, water quality control, hydroelectric power generation, and fishing and other forms of recreation). Water-level fluctuations concern some conservation groups because they may degrade or destroy valuable fish and wildlife habitat or unique plant communities such as bottomland hardwoods. They also may adversely affect fish, wildlife, or reservoir-based recreation. Availability of water often determines water levels and is the primary concern of most reservoir users. A volume of water with sufficient potential energy to permit efficient and timely generation of electricity is the principal concern of associated utilities. Although flood control and water quality control may complement one another (i.e., releases of water during dry periods supplement the flow of water downstream and simultaneously provide

additional capacity for containment of flood waters), needs for water quality control and hydropower generation often conflict.

3. Scheduling models have been developed to help reservoir operators optimize reservoir use and resolve conflicts among competing users (Shane 1981). These models enable the prediction of variation in pool levels, water releases, and hydropower generation for specific project purposes. Performance measures (generation, flood damage, operating constraint violations, and power production) normally accompany basic scheduling data. In present reservoir scheduling models, environmental variables are best described as simple prescriptions for water release to regulate pool levels for such purposes as mosquito control or fish propagation. As multipurpose demands on reservoirs increase, so does the need to evaluate and assign priorities to different uses. Informed, equitable decisions concerning alternative reservoir operations to benefit fish require extensive data on the effects of water-level changes on reservoir ecosystems and fisheries. Current scheduling models rarely address fishery concerns because useful quantitative data on fish, fisheries, and limnology are scarce.

4. While detailed information required to properly manage reservoir ecosystems and enhance fisheries is slowly being accumulated, the demand for quality fisheries is increasing. The Sport Fishing Institute (1977) estimated that 34.3 million freshwater anglers fished about 638 million angler days in 1975. With the number of anglers increasing about 3.2 percent per year (about twice as fast as the U. S. population), the Institute estimated that by 1985 47 million freshwater anglers would be fishing about 871 million days per year. If reservoir fishing continues to account for 26 percent of all freshwater fishing (U. S. Bureau of Sport Fishing and Wildlife 1962) in 1985 and the cost of an angler day--estimated to be $11.50 in 1975 (U. S. Fish and Wildlife Service 1977)--increases an average of 5 percent per year from 1975 to 1985, there will be about 12.2 million anglers on

reservoirs in 1985 fishing an estimated 226 million angler days per year and spending about $4.2 billion for retail goods, services, and fees.

5. This report is a summary and synthesis of information gathered from available literature about the effects of water-level changes on reservoir ecosystems. Recommendations on reservoir operation were either taken directly or synthesized from these sources.

PART II: PHYSICOCHEMICAL SYSTEMS

Introduction

6. This section presents a discussion of how water-level changes affect several physicochemical variables that, in turn, influence the population dynamics, production, or harvest of fish. Such a discussion is warranted because it is essential to an understanding of the effects of water-level changes on fish. Most water-level effects on fish are indirect, mediated by physicochemical changes that alter essential habitat or trophic conditions. These indirect effects are described under the heading "Biological Systems." Among the most important physical variables affecting fish or fisheries are aesthetics, basin morphometry, bottom substrates and structures, erosion, turbidity, temperature, and water-retention time. Important chemical variables include nutrients (carbon, nitrogen, and phosphorus) and dissolved oxygen.

Physical Variables

7. The flooding and exposure of reservoir bottoms and terrestrial vegetation are the most visually obvious effects of water-level fluctuations. Among other reasons why reduced water levels are unpopular is that exposed mud flats and dead, decaying vegetation are not aesthetically pleasing (Davis 1967). Flooding frequently kills trees and other higher terrestrial plants, which then become recurring eyesores whenever water levels are lowered. The early establishment of herbaceous vegetation for aesthetic purposes and erosion control in summer drawdown zones is important (Benson 1976). Drawdown may interfere with boating and recreation by reducing surface area, exposing previously submerged structures that are hazardous to navigation, and by reducing the number of ramps usable by boaters. Marinas and boat docks must be moved or become stranded, and recreation areas (e.g., beaches, picnic sites) may be left considerable distances from the water.

8. A less immediate effect of water-level changes is shoreline modification due to erosion and redeposition of sediments from bank and bottom areas. Waves driven by the wind distribute sediments vertically

according to particle sizes; gravel-sized and larger rocks remain near shore, whereas slightly smaller particles may be displaced somewhat offshore and still smaller particles may be suspended and removed from the shore zone altogether (Zhivago and Lange 1969). Wind and rain also erode substrates exposed by drawdown.

9. The area modified by erosion is largely determined by the magnitude of water-level fluctuations and the morphometry of the basin (Turner 1981). Rates of shoreline changes depend on characteristics of the fluctuation zone--its slope, degree of exposure, and composition. When steep shores of mountain impoundments of Norway were exposed to 6-m fluctuations in water level, they eroded rapidly, leaving a zone of barren rock interspersed with gravel. Although the area of bottom in the fluctuation zone was small because of the steeply sloped basin, an extensive area below the drawdown limit was covered with eroded materials and adversely affected (Grimås 1961). Lowering of mean lake levels in Llyn Tegid, Great Britain, eliminated most of the shallow littoral zone and left behind a steep-sided basin with a mud bottom (Hunt and Jones 1972b). Steeper shores accelerated fallout of organic matter and sediment to greater depths.

10. In contrast to the relatively permanent rapid changes in steep-sided impoundments, Missouri River reservoirs (Benson 1980) and large shallow reservoirs of the USSR (Zhivago and Lange 1969) required over 25 years of erosion and shoreline modification before a dynamic equilibrium was established between erosion and shore building. Alluvial soils in these exposed, wind-swept reservoirs were easily eroded. However, because of the gradual slope of most shores, erosion was slow and involved large areas, even when vertical changes in water levels were small. Rising turbid waters redeposited sediments at higher elevations, and eroded sediments often collected to form terraces in adjacent areas. Terrestrial vegetation that developed in dewatered areas undoubtedly helped to slow erosion, at least temporarily.

11. Aggus (1971) observed that cleared areas of Beaver Reservoir, Arkansas, were subjected to greater and more rapid erosion than areas with vegetation. Breakup and decomposition of flooded herbaceous vegetation resulted in a conspicuous increase in erosion and redeposition. Erosion also was noticeably slowed in several Kansas reservoirs by flooded herbaceous vegetation established during a drawdown in the previous growing season (Groen and Schroeder 1978).

12. Periodic exposure of sediments by reduced water levels may consolidate flocculent sediments and thereby increase reservoir capacity slightly. In experiments with sediments dredged from Lake Apopka, Florida, Fox et al. (1977) noted that dewatering and drying for various periods of time shrank bottom sediments; and water used to refill the test containers had the same or lower nutrient concentrations, reduced turbidity, and higher dissolved oxygen tensions than water originally drained from the containers. Reduced water levels and concomitant compaction and aerobic decay of organic matter in Lake Tohopekaliga, Florida, reduced the depth of organic sediments by 50 to 80 percent (Wegener and Williams 1974).

13. Sources of colloidal turbidity in reservoirs include inflowing tributaries, erosion of banks (by waves, wind, and rain), and suspension of bottom sediments by waves or currents. Water-level changes affect the gradient and rate of flow through reservoirs, thereby determining rates and sites of sedimentation (Lara 1973). At low water levels, sediments previously deposited near inflow areas may be sluiced farther down the reservoir. Turbidity from shores and shallow areas is largely controlled by the composition of soils or sediments, rates of erosion, and the extent of mixing of water. Other factors being equal, the more extensive the mixing, the greater the turbidity.

14. Turbidity may increase or decrease as water levels change because fluctuating water levels expose areas of different composition or cover to erosion. Reservoir drawdown may increase turbidity by resuspending previously eroded sediments (Neal 1963; Markosyan 1969).

However, low water levels, in Lake Chautaugua, Illinois, reduced turbidity over that in high-water years because pondweed (Sago sp.) became abundant and reduced turbulence (Starrett and Fritz 1965). Increased water levels often reduce turbidity, especially if inundated areas are covered with terrestrial vegetation or are barren of fine sediments. Vegetation decreases erosion by binding soils and precipitating colloidal clay particles (Irwin 1945). Fluctuating water levels may limit the growth of macrophytes that bind soils and dampen waves in the littoral zone, thereby resulting in increased turbidity (Judd and Taub 1973).

15. Water-level changes that significantly alter depth, area, or fetch may change depth of mixing or patterns of stratification. A shift from stable to fluctuating water levels could reduce the tendency for much of a reservoir to stratify (Turner 1981). This possibility is even more likely if changes in water levels result from selective discharge from the hypolimnion (e.g., see Wiebe 1938) or from rapid rates of discharge--i.e., complete water exchange six or more times a year. Temperatures of inflowing waters tend to dominate the thermal regime of reservoirs as the retention time of water in the basin decreases (Carmack et al. 1979). Cooper (1980) found that high water levels and insignificant drawdowns in late summer prolonged thermal stratification in Grenada Reservoir, Mississippi. Serruya and Pollingher (1977) found that lowering of water levels in Lake Kinneret, Israel, reduced the volume-to-area ratio, which accelerated heat transfer by increasing the input of mechanical energy. The volume of mixed water increased while that in the hypolimnion was reduced (i.e., thermocline depth increased).

Chemical Variables

16. Nutrients enter reservoirs in flowing waters or are leached and physically separated from inundated soils, organic debris, terrestrial vegetation, or drowned animals after water levels increase (Ploskey 1981). Significant annual changes in water levels and inflow have more effect on nutrient levels and productivity in older reservoirs

(> 10 years) than in newer ones. Effects of water-level changes in new reservoirs usually are masked by exceptionally high rates of biological productivity and nutrient cycling. However, as reservoirs age and nutrients are lost to inactive sediments, outflow, or fish harvest (Ellis 1937; Kimsey 1958), the effects of yearly variations in inflow and water levels become more apparent, especially if land use in the watershed changes significantly (e.g., see Mitchell 1975).

17. The quantity of nutrients released from soils after they are inundated by rising waters depends on the organic content, state of decay, and amount of soil involved (Sylvester and Seabloom 1965). Rates of release and use depend on temperature and dissolved oxygen concentration. Soils with organic detritus (e.g., leaves and twigs) provide more food for aquatic detritivores (some bacteria, benthos, zooplankton, and fish) and nutrients for algae than do inert soils.

18. Ball et al. (1975) found that vegetation type influenced the rate and quantity of nutrients released from recently inundated areas in the basin of Palmetto Bend Reservoir, Texas. Grasses and herbage released nutrients faster than trees, contained a greater quantity of nutrients per unit of vegetation weight, and were available in greater quantities (weight per unit area). Similar findings were reported by Denisova (1977). Ball et al. (1975) listed the following conclusions:

- a. Effects of inundated terrestrial vegetation on water quality are not necessarily permanent but depend on flushing rates, land use, temperature, and basin morphometry.
- b. Decomposition rates of vegetation are largely a function of tissue type, and leaves decompose and release nutrients more rapidly than do bark and wood.
- c. Phosphorus is rapidly leached from dead hardwood leaves and particularly from leaves that are damaged or broken.
- d. Grasses may be completely decomposed within one year after inundation.

19. Moreover, the type of terrestrial biome (e.g., coniferous forest, grassland, deciduous forest, desert--after Odum 1971) in which a reservoir is located may determine the quality and quantity of nutrients and detritus supplied by changes in water levels. Because herbaceous plants, as in grasslands or deciduous forests, die and decay rapidly after inundation, they are assimilated into the trophic system as high-energy detritus. Though the largest quantities of herbage seldom are as great as the quantity of litter in mature forests, herbaceous plants may be more important per unit of weight than litter, because litter generally contains a greater proportion of indigestible matter--i.e., twigs and wood debris with large amounts of cellulose (Sylvester and Seabloom 1965; Ball et al. 1975). Inundation of a relatively barren fluctuation zone (alpine or desert reservoirs) provides only small quantities of detritus or nutrients.

20. Seasonality of changes in water levels is yet another factor influencing the amount of nutrients and detritus made available. Yount (1975) found nearly constant oven dry weights of needle litter in coniferous forest throughout the year (ca. 1.4×10^4 kg/ha), whereas weights of litter in deciduous forest fluctuated seasonally, with maxima in November and May and minima in September and March. Quantities of phosphorus (P) and nitrogen (N) in coniferous and deciduous forest litter also varied seasonally, generally peaking in winter. More P and N were present when rainfall was below normal because leaching was reduced. Use of nutrients and detritus by aquatic plants and animals is greater if flooding occurs during the growing season than if it occurs in winter.

21. Increased duration of inundation and exposure to waves increases the potential assimilation of nutrients from shoreline areas. Petr (1975) observed that prolonged filling of reservoirs contributes more toward increasing fish production than rapid filling. Short-term fluctuations of water levels (days or weeks) have seldom been related to major changes in water chemistry or biological productivity. By contrast, large seasonal or annual changes have the greatest effect

because low water of sufficient duration provides time for exposed soils to aerate, thereby increasing the availability of nutrients (Birch 1960; Bennett 1962) and time for herbaceous terrestrial plants to colonize exposed sediments (Frey 1967; Groen and Schroeder 1978). When dewatered areas with vegetation are flooded for 3 or more months of the growing season, aquatic animals and plants have enough time to fully colonize the areas and benefit from the nutrients available.

22. In reservoirs with large annual fluctuations in water level, water-exchange rates may vary greatly because of changes in reservoir operation or volume. Water exchange rate and outlet depth influence nutrient retention or "nutrient trap efficiency" (Turner 1981) by determining the amount of nutrient loading and loss, as well as thermal characteristics and mixing of water. If inflow and release of water are constant, a reservoir exchanges water more frequently and retains fewer nutrients when water levels are reduced than when they are high. Nutrient retention and biological production are high as reservoirs fill, because most inflowing nutrients and those from within the basin are retained. By contrast, drawdowns during periods of low inflow flush nutrients downstream. Martin and Arneson (1978) found that a reservoir with a deep outlet released nutrients, whereas a lake with a surface outlet acted as a nutrient trap.

23. The quantity of nutrients retained in a reservoir does not always reflect the amount available for biological production. Jenkins (1973), for example, found that among impoundments with similar concentrations of total dissolved solids (TDS), those with higher rates of water exchange supported larger standing crops of fish, although not necessarily of the desired species. Between TDS concentrations of 100-300 mg ℓ^{-1}, fish crops increased as TDS increased in hydropower mainstream reservoirs; however, total crops remained relatively constant as TDS increased in hydropower storage impoundments. Also, not all nutrients retained in reservoirs are available to biota because many are adsorbed to particulate matter or sediments (Cooper 1967). Fitzgerald (1970) found that aerobic lake muds have a strong affinity for phosphate phosphorus (PO_4) and can sorb as much as 0.125 mg PO_4 per gram of dry

sediment in 30 minutes. Complex interactions among biota and nutrients alter the form and availability of nutrients, as well as major paths of nutrient cycling in reservoirs. Many nutrients occur in several forms (i.e., in different compounds or as living biomass) which are in dynamic equilibrium (Wetzel 1975).

24. Spatial and temporal variations in oxygen concentration may be caused by changes in water levels that inundate areas with varying amounts of organic matter or that alter the amount of surface area exposed to the wind. The greatest oxygen demands result from respiration of microorganisms associated with decay of organic matter in organically rich sediments, herbaceous vegetation, or leaf and grass litter. Inundated inorganic soils and woody vegetation have less effect on biochemical oxygen demand than does readily digestible organic matter (Sylvester and Seabloom 1965; Ball et al. 1975). Vertically, oxygen sources and demands may be separated; demands are greatest in the metalimnion and upper hypolimnion in summer (Lund et al. 1963; Lasenby 1975); whereas primary sources are in the epilimnion, which is reaerated from the atmosphere and by photosynthesis in the euphotic zone. Organic load and water temperature are the major factors controlling oxygen demand at different depths. However, basin morphometry and mixing determine whether the demand for oxygen will exceed the supply.

25. Anoxic conditions may occur throughout the water column if prolonger ice or ice and snow cover prevents diffusion and circulation, or limits light penetration. Such anoxia may cause extensive fish kills (Il'ina and Poddubnyi 1963; Il'ina and Gordeyev 1972). However, without ice cover, concentrations of oxygen are less apt to be low in winter than in summer because temperature is inversely related to the solubility of oxygen in water and directly related to rates of oxygen use by biota.

26. Except in extremely nutrient-rich areas, anoxia is unlikely to occur in shallow water mixed by the wind or in reservoirs where water exchanges rapidly. Stewart (1979) observed that inundated terrestrial vegetation in Rising Sun Lake, New Jersey, lowered oxygen

concentrations (but not below 4 mg ℓ^{-1}) in the epilimnion (areas above a depth of 4.6 m) in summer. In two reservoirs of the Churchill Falls hydroelectric project, Labrador, Canada, no oxygen deficiency was observed in newly flooded areas because of rapid rates of water exchange and mixing of water (Duthie and Ostrofsky 1975).

27. Nutrient loading and oxygen demands in shoreline areas are controlled by the number and characteristics (vegetation and geology) of inundated areas, as influenced by basin slope, height and frequency of water-level fluctuations, and reservoir age (Scully 1972; Denisova 1977). For example, McLachlan (1970b) noted that changes in concentrations of oxygen and nutrients were greater and more rapid over gently sloping shores than over steep rocky ones, because more area was involved and growths of terrestrial vegetation were more dense. As waters rose over gradually shelving areas covered with grasses and animal feces, oxygen concentrations were reduced significantly (McLachlan 1970b, 1974). Anaerobic conditions in sediments can result in release of nutrients. When water levels increased in Lake Apopka, Florida, (a hypereutrophic reservoir) and reflooded nutrient-laden sediments, nutrient concentrations increased and ultimately caused anoxia that killed fish (Fox et al. 1977). By contrast, in nutrient-poor reservoirs or in older impoundments where the upper portion of the fluctuation zone lacks nutrients and vegetation due to years of erosion and water-level fluctuation, increased water levels may have little effect on water chemistry. In Lake Blåsjön, Sweden, Grimås (1961) observed increased crops of zooplankton when 6-m fluctuations were initially implemented; after several years, however, increases in water levels over barren rocky areas did not affect zooplankton populations.

28. Effects of reduced water levels on nutrient concentrations and oxygen demands depend on reservoir age and site-specific characteristics. As aerobic water recedes from shallow areas where a sharp gradient in nutrient concentrations exists across the substrate-water interface, some interstitial water concentrated with nutrients may drain into adjacent surface waters (Turner 1981). Increased nutrient

concentrations and reduced oxygen tensions have been observed in waters receding from marshes (Kadlec 1960; Pazderin 1966; Henson and Potash 1977) or from partly exposed and decaying beds of macrophytes (Geagan 1961). However, in a new African reservoir, McLachlan (1970b) observed no significant changes in the concentrations of nutrients or dissolved oxygen as waters receded from rich, gradually shelving areas. Erosion of exposed beds by rains could increase nutrient levels by washing materials into reservoirs. In older impoundments (> 10 years), where nutrient concentrations at high elevations are lower than at low elevations because of erosion, reduced water levels may increase nutrient concentrations and biochemical oxygen demands by recirculating previously eroded sediments (Markosyan 1969). By contrast, in relatively new reservoirs (< 10 years), where the concentrations of nutrients in sediments usually vary less with elevation than in older reservoirs, reduced water levels probably would not greatly alter the input of nutrients.

PART III: BIOLOGICAL SYSTEMS

Introduction

29. In this report, biological systems are divided into two broad categories: fish-food biota and fish and fisheries. Such a division is useful because it places emphasis on fish and still includes essential information about the effects of water-level changes on plants and invertebrates.

30. Water-level changes affect fish populations most by altering trophic conditions (prey abundance, type, and availability) or habitat. Trophic conditions for fish are affected by changes in the abundance of fish-food biota. Fish respond to altered trophic conditions or habitat by increasing or decreasing growth, reproductive success, and standing crop. Resulting changes in fish populations are ultimately reflected in the annual harvest of fish by anglers.

31. Outstanding in the documented effects of water-level changes on biological systems is the scarcity of quantitative data. This paucity is not surprising, however, given the complexity and variability of biological systems. Although responses of some fish populations to seasonal changes in water levels can be forecasted, actual results may vary because of the effects of unpredictable variables such as temperature, prey availability, or disease. In short, because of multiple variable effects, water-level changes and biological consequences do not have simple cause-effect relations.

Fish-Food Biota

32. Aquatic plants. The three major groups of plants in reservoirs are phytoplankton (microscopic planktonic algae), periphyton (attached microscopic algae), and aquatic macrophytes. The importance of each group as fish food varies among reservoirs because of variations in the productivity of plant communities and in the structure and efficiency of aquatic food webs in different reservoirs. Most of the energy flow from plants to sport fish is indirect, by way of herbivorous zooplankton, benthos, or fish. The net transfer of energy to fish is less efficient in long food chains where energy is transferred several times than in short food chains because about 90 percent of the energy produced at one

level is lost to respiration, egestion, and excretion (Kozlovsky 1968). The species composition and relative abundance of fish may determine the relative use of phytoplankton, periphyton, or macrophytes because of species-specific differences in diets.

33. In addition to serving as food for fish, attached plants often serve other valuable functions in reservoirs. Periphyton and macrophytes provide habitat for invertebrates and fish (e.g., see Cowell and Hudson 1967; Johnson and Stein 1979) and after dying release large quantities of nutrients (Denisova 1977). Macrophytes, like other underwater structures in the littoral zone, may influence productivity and predator-prey relations (Cooper and Crowder 1979). Vegetation of some form (aquatic or terrestrial) is important to the spawning of many species of fish (Lapitskii 1966; Carlander 1969, 1977).

34. Effects of water-level changes on phytoplankton have received little attention (Mitchell 1975), and quantitative data are sparse. Accurate estimates of primary production are difficult to obtain because phytoplankters are highly responsive to changes in their immediate environment and crops turn over rapidly. As suspended algae, phytoplankton production probably is affected more by changes in nutrients, light, temperature, grazing pressure, etc., that result from water-level fluctuations than from the fluctuations directly. An exception is the physical removal of phytoplankton by release of water from the euphotic zone in stratified reservoirs (e.g., see Sreenivasan 1966) or rapid release of water from unstratified mainstream impoundments (Benson and Cowell 1967).

35. Productivity of reservoirs varies greatly seasonally and yearly due to variations in runoff from the drainage basin. High turbidity in inflowing water may limit productivity by reducing light, or if the retention time of water in the euphotic zone is low, phytoplankton populations may not have sufficient time to develop productive densities before being discharged through the dam. According to Wetzel (1975), as the concentrations of phytoplankton increase, the integral photosynthetic efficiencies generally increase until the maximum levels are restricted by self-shading of light.

36. Observations of changes in the abundance, biomass, or production of phytoplankton concomitant with, or after, changes in water levels can almost always be explained by changes in nutrient levels or light, as modified by factors such as temperature, turbidity, or basin morphometry. Guseva (1958) observed that the greatest abundance of littoral phytoplankton in Rybinsk Reservoir, USSR, was associated with high water levels that flooded large areas of terrestrial litter and detritus. Populations in the pelagic zone were less well developed and not influenced by water levels. Similarly, in Lake Mikolajskie, Poland, Pieczyn'ska (1972) found that the biomass of algae was 6 times greater and primary production 11.5 times greater in the fluctuation zone than in the pelagic zone. Pieczyn'ska concluded that the rich fluctuation zone affected total lake productivity and that the extent of the effects depended on the configuration of the shoreline terrace, shoreline development, and water-level fluctuations. Lowering of water levels 10 m in Lake Sevan, USSR, exposed 85 km^2 of bottom area and resuspended previously eroded sediments and nutrients. Although turbidity increased, certain bacteria and phytoplankton populations, which may have been nutrient limited before drawdown, increased exponentially. In Lake Laurel, Georgia, reduced phosphorus concentrations, measured after the lake was drawn down for 6 months and then refilled, helped to explain a post-drawdown decrease in phytoplankton biomass (Barman and Baarda 1978), though flooding of terrestrial plants in the drained zone suggested that phytoplankton biomass would increase.

37. Observations in new reservoirs also suggest that productivity is directly related to nutrient availability and light, as influenced by water levels. Primary production during the first 2 or 3 years of impoundment is high in shallow reservoirs where slight increases in water levels inundate large areas of terrestrial vegetation (Baranov 1961), unless high turbidity limits it (e.g., see Duthie and Ostrofsky 1975). In new deep reservoirs, where nutrients can be limiting, trophic upsurge is uncommon (Baranov 1961), though two- to three-fold increases in phytoplankton crops and production were observed temporarily in

in Lake Ransaren, Sweden, after water levels inundated rich terrestrial areas (Axelson 1961; Rodhe 1964).

38. Increased nutrient availability, resulting from high inflows or changes in water level, has little positive effect on primary productivity during cool months of the year because production is regulated by solar radiation and temperature in temperate waters (Wetzel 1975). In tropical impoundments, nutrients usually are more limiting than temperature, and seasonal changes in primary production are often related to mixing of water or rainy seasons.

39. Mitchell (1971, 1975) conducted the most quantitative study of the effects of water-level changes on phytoplankton productivity. Primary productivity was estimated bimonthly by the uptake of radioactively labeled (^{14}C) bicarbonate during 2-hour incubations taken before and after 1230 hours on sampling days in Lake Mahinerangi, New Zealand. Results of multiple-regression analyses on seasonal productivity trends for 1964-66 suggested that water level and temperature were major factors influencing productivity at near optimal light intensities. Mitchell (1971) explained 78.3 percent of the variability in light-saturated photosynthesis (Y_{est} in mg $C \cdot m^{-3} \cdot hour^{-1}$) in 1964-66 by the following equation:

$$\underline{Y}_{est} = 3.3326 \log_e \underline{X}_1 + 0.1635\, \underline{X}_2 - 0.1381\, \underline{X}_3 - 13.6933$$

where $\underline{X}_1$ is water-level elevation at the dam (ft), $\underline{X}_2$ is temperature (°C), and $\underline{X}_3$ is hours of daylight. Partial regressions of photosynthesis on temperature and water level were significant; day length apparently was the least significant of the three factors. Water levels were more or less continuously rising in 1964-66 when productivity data were used to develop Mitchell's predictive equation, whereas they were higher and more stable in 1968-70 (Mitchell 1975). Productivity in 1968-70 was higher than predicted by Mitchell's (1971) equation, probably because of continuous delayed releases of nutrients from inundated pastures. Other possible responses of phytoplankton were (a) to water level (linear responses as predicted by Mitchell's equation, where nutrients are released from inundated areas at a constant rate and are mineralized and used completely or not at all) or (b) to changes in water levels (where nutrients are released and used rapidly, relative to the time of fluctuations). Mitchell concluded that whatever the response, it is probably modified by variations in the ratio of reservoir volume to the area of land inundated. In stratified reservoirs, the ratio of the epilimnial volume to the area inundated may be more important than the ratio of total volume to that area.

40. Periphyton is affected more directly than phytoplankton by changes in water levels because it is usually attached to fixed substrates (e.g., trees, sediments, rocks, or sand) in the euphotic zone. When water levels decline and expose substrates to the air for more than a few days, attached algae desiccate and die. In Lewis and Clark Lake, South Dakota-Nebraska, where water levels fluctuate little, submerged trees were important substrates for periphyton development. Dense growths (6×10^6 cells cm^{-2}) developed in May, whereas the maximum density on trees in Lake Francis Case--a reservoir upstream where water levels fluctuated 9-11 m annually--was only 6.6×10^3 cells cm^{-2}, about 0.11 percent of that on trees in Lewis and Clark Lake (Benson and Cowell 1967). Winter drawdown in Lake Francis Case apparently destroyed the full development of periphyton communities (Cowell and Hudson 1967; Claflin 1968). Claflin (1968) observed that periphyton growths were heaviest between 3 and 7 m, being limited by wave action in the upper 3 m and by light availability at depths exceeding 7 m. Barman and Baarda (1978) found that periphyton biomass was significantly reduced for almost a year after substrates of Lake Laurel, Georgia, were exposed for 178 days and reflooded. Accrual rates also were below normal in the first summer after treatment. By the second summer, accrual rates were near those observed before the lake was drained.

41. Growth of periphyton is determined by the content and availability of nutrients, required elements (e.g., silica, calcium), and light intensity which attenuates with depth. "Shock events" (Round 1971), such as the breakdown of thermal stratification, intense shading (by turbidity), or water-level changes, may act to regulate species composition and production.

42. The importance of periphyton production to total primary production should not be overlooked, especially in relatively shallow reservoirs or ones with extensive shoreline and littoral development. For example, Pieczyn'ska (1972) showed that periphyton production in the fluctuation zone of Lake Mikolajskie, Poland, amounted to over 40% of the total for that area, whereas phytoplankton production made up only about 10%. Ultimately, the size of the fluctuation zone compared with that of the pelagic zone will determine the relative contribution of algae in each zone to total primary production.

43. From a fisheries standpoint, the presence of some macrophytes is desirable because they increase productivity and diversity of littoral areas. However, at high densities, macrophytes may cause fish kills at night due to oxygen depletion, or limit the surface area available for fishing or boating. Control of overabundant aquatic vegetation often is of more concern to fisheries managers than the absence or scarcity of macrophytes in widely fluctuating reservoirs.

44. Success in regulating densities of macrophytes by manipulating water levels has been inconsistent (Kadlec 1960; Bennett 1962; Holcomb and Wegener 1971; Judd and Taub 1973; Lantz 1974; Lantz et al. 1964). Manipulation effectively controls some species (Hulsey 1958; Nichols 1972, 1974), and it offers a viable alternative to chemical controls that are expensive or detrimental to aquatic animals (Davis 1967). Dunst et al. (1974) listed many accounts of macrophyte control by drawdown. Apparently desiccation, freezing, and soil compaction during drawdowns act to reduce densities of aquatic macrophytes, but drawdown also facilitates mechanical removal. Nichols (1972, 1974), who studied the effects of prolonged winter drawdowns on aquatic macrophytes in Chippewa Flowage, Wisconsin, categorized many species of plants according to their preferences for fluctuating or stable water levels.

45. Increased water levels also may eliminate or reduce the abundance of some species (e.g., Runnström 1951, 1955; Stube 1958; Posey 1962). Merna (1964) found that the construction of a dam on Big Portage Lake, Michigan, which raised lake levels 1 m, reduced the number of species present from 20 (10 of which were common) to two.

46. Aside from species-specific responses, effects of water-level changes on aquatic macrophytes depend on magnitude, duration, and timing. In general, aquatic macrophytes seldom become established in widely fluctuating reservoirs, whereas they commonly are found in reservoirs that fluctuate little (Eschmeyer 1949; Kimsey 1958; Wajdowicz 1964; Grimås 1965; Grimås and Nilsson 1965). Short-term fluctuations (< 3 months) have little effect unless they dry littoral areas and allow them to freeze, or flood them to a depth where plants are limited by light or their ability to reach the atmosphere. Winter drawdowns at below-zero temperatures are more effective than warm-weather drawdowns for controlling aquatic plants. Also, chances of oxygen depletion and fish kills are reduced.

47. Zooplankton. Zooplankton, like phytoplankton, is rarely directly affected by changes in water level because it is suspended in the water column. Direct effects are limited to displacement of zooplankters within reservoirs due to changes in water retention time. Production of zooplankton may be more limited than that of phytoplankton by high rates of water renewal because zooplankton turnover rates are slower (Rodhe 1964). Also, zooplankters with rapid turnover rates such as rotifers, probably are less affected than those with slow rates of turnover (e.g., crustacean zooplankters). Effects are most apparent in mainstream reservoirs where water-retention times are short (< 60 days). Losses of crustacean zooplankton from Lewis and Clark Lake (a mainstream Missouri River reservoir) amounted to 12,619 metric tons (wet weight) in 1963-64 and 29,752 metric tons in 1964-65 (Benson and Cowell 1967). Benson (1973) noted that zooplankton abundance in Lake Sharpe, South Dakota, was higher in 1966-68, when water exchange rates ranged from 26 to 50 days, than it was in 1969, when exchange rates were 18-22 days.

48. Because zooplankton concentrations (numbers and biomass) are highest during the growing season and lowest in winter, the rapid discharge of water is more detrimental during summer than during winter. Increased abundance of zooplankton in Lake Ransaren, Sweden (an impounded natural lake), was the result of low discharge of lake water in summer (Axelson 1961). Rodhe (1964) observed that seasonal regulation of

water levels that resulted in damming from spring to late autumn and discharge during winter favored zooplankton production more than natural regimes of water replacement where highest flushing rates are in spring and summer. Using multivariate analyses, June (1974) found that zooplankton densities in areas near the dam of Lake Oahe, North and South Dakota, were inversely related to discharge rates in summer. Water temperatures and turbidity also were major factors controlling abundance, but both were occasionally influenced by the retention time of water. Similarly, Mayhew (1977) found that flushing rate explained 94 percent of the variation in copepod density in Lake Rathbun, Iowa; temperature explained 74 percent.

49. Outlet depth may determine the amount of zooplankton discharged from a reservoir, because the vertical distribution of plankters varies seasonally and diurnally. Because zooplankton usually is most abundant above a thermocline in summer, discharge from the epilimnion probably would eliminate more biomass than would discharge from greater depths. Rodhe (1964) found that rapid discharge of water from Lake Ransaren removed one third of the epilimnial volume monthly and significantly reduced the volume of zooplankton present in 1958. In 1959, when discharge was reduced, zooplankton volumes were higher than in 1958.

50. Long-term changes in the species composition of zooplankton in old bodies of water have been examined by identifying subfossil remnants of animals in sediments and relating findings to historical oscillations in water levels (Alhonen 1970; Mikulski 1978). Seemingly, high waters favor the development of pelagic plankters such as Bosminidae and Daphnidae, whereas low or receding waters favor littoral plankters such as Chydoridae (Mikulski 1978). The index ILL = Bosminidae + Daphnidae/Chydoridae was directly related to historical water-level changes in Goplo Lake, Poland. Many littoral species were especially abundant when macrophytes were present. Pelagic plankters undoubtedly were favored by the relatively long retention time of water, when water levels were high.

51. With unlimited food and adequate oxygen tensions, temperature regulates zooplankton production by controlling rates of consumption, respiration, growth, and reproduction. Biomass in DeGray Lake, Arkansas, was highest in spring, declined through summer, and was lowest in winter from 1976 to 1981 (unpublished data, Multioutlet Reservoir Study Group, U. S. Fish and Wildlife Service). Changes in water levels have their greatest impact on zooplankton during the growing season primarily because the potential for production is low in winter due to low water temperatures.

52. During the growing season, production of zooplankton probably is most regulated by food availability and quality, both of which can be influenced by water levels or changes therein. Zooplankters eat phytoplankton, bacteria, protozoa, other zooplankton, and suspended detritus. Preferences for different foods vary among species, but increased concentrations of any foods are likely to increase the production of some species. Increased numbers, biomass, or production after impoundment of natural lakes or reservoirs often has been associated with increased food availability after water inundated terrestrial areas. Dahl (1933) observed an increase in the standing crop of Eurycercus lamellatus and other cladocerans after water storage in a Norwegian hydroelectric impoundment. Similar observations of increased abundance after impoundment of natural lakes in Norway or Sweden have been made (Aass 1960; Axelson 1961; Grimås 1961; Lötmarker 1964; Rodhe 1964; Nilsson 1964). Newly impounded lakes probably had higher densities of zooplankton than natural lakes or old reservoirs because the levels of detritus and phytoplankton production were temporarily high (Lötmarker 1964). Increased zooplankton abundance lasted only a few years (Grimås 1961; Nilsson 1964). Rodhe (1964) believed that the two- to three-fold increase in zooplankton volume in Lake Ransaran resulted from increased nutrient and detrital inputs from flooded terrestrial areas. Benson (1968) attributed the increased abundance of rotifers in two Missouri River reservoirs to rising water levels that continually inundated grassy areas. Duthie and Ostrofsky

(1975) noted that zooplankton populations in shallow water increased greatly and changed qualitatively after impoundment of two reservoirs in Labrador, Canada.

53. Observations of zooplankton responding to large-magnitude changes in water levels in old reservoirs parallel those made of zooplankton in new impoundments. Wright (1950 and 1954) observed that production of animals in all trophic levels was low before the draining of Atwood Lake, Ohio. After draining and refilling of the lake in 1947, zooplankton crops increased greatly in response to the inundation of large amounts of organic matter. Standing crops remained high in 1948 but declined in 1949, apparently due to decay and depletion of terrestrial foods. From 1964 to 1966, water levels in Lake Mahinerangi, New Zealand, increased almost linearly, as did phytoplankton production (Mitchell 1975). Although the densities of the three most abundant species of zooplankton did not increase with increased primary productivity, densities of two large-sized but less abundant taxa (*Daphnia carinata* and cyclopoid copepods) increased significantly.

54. Even falling water levels may increase zooplankton numbers or biomass if they increase food concentrations. For example, Gras and Lucien (1978) observed that the juvenile periods of *Moina* sp. and *Diaphanosoma* sp. were shortened by accelerated development and a decrease in the number of instars between 1968 (a high-water year) and 1973 (a low water year). Improved nutritional conditions after the high-water year apparently accelerated development. Zooplankton biomass in July in Lake Sevan, USSR, increased from 0.77 g m^{-3} to 1.36 g m^{-3} between 1947 and 1956 (Markosyan 1969). As water levels declined, primary production increased in response to recirculation of nutrients in sediments.

55. Because zooplankton productivity is mostly related to changes in trophic conditions (primary production and input of detrital foods), it probably is affected little by water-level changes that are small, rapid, or frequent. Zooplankton production should increase when water levels are periodically (every 2-3 years) manipulated to temporarily increase detrital inputs and primary production, while discharge rates

are simultaneously reduced during the growing season. Zooplankton production may be increased substantially by increasing water levels during most of a single growing season and inundating terrestrial vegetation, especially in reservoirs with large fluctuation zones that develop extensive growths of terrestrial vegetation seasonally or every 2 or 3 years.

56. Benthos. Benthic invertebrates are directly and indirectly affected by changes in water levels. Direct effects include (1) exposure and mortality of species that have poor mobility or that lack a diapause or resting mechanism (Aass 1960) and (2) entrainment and loss of benthos from reservoirs during periods of rapid water exchange. Indirect effects result from changes in habitat, food resources, or the chemical environment.

57. Of the direct effects of water-level changes, discharge of benthic invertebrates has been studied the least, though it can be significant in reservoirs with periodically or continuously high flushing rates (Benson 1973). For example, in Lewis and Clark Lake, a Missouri River reservoir with a rapid rate of water exchange, 24 metric tons (wet weight) of Hexagenia nymphs and 20 metric tons of diptera larvae were passed through the turbines of the dam in the spring of 1965 (Swanson 1967; Cowell and Hudson 1967). Most of the discharge occurred at night when insects were most active in the water column. Although densities of benthos in the water column were low (0.5 to 8 m^{-3}), the high rate of discharge of water (about 7.08 m^3 $second^{-1}$ from April to June) resulted in significant numerical losses--e.g., 1.7 x 10^9 Hexagenia nymphs from April to July.

58. The most visually obvious effect of water-level changes on benthos is the exposure and mortality of organisms when water levels are reduced. In Lake Francis Case, a 4-m drawdown in August 1966 stranded up to 6,146 chironomids m^{-2} (Cowell and Hudson 1967). Kaster and Jacobi (1978) observed that annual fluctuations of 7.7 m in a central Wisconsin reservoir exposed 1.8 g m^{-2} (dry weight) of benthos. McLachlan (1974) observed that drawdown in Lake Kariba, Africa, stranded up to 200 mg of benthos m^{-2} and that shorelines receded up to 2 km. Winter

drawdown of Laurel Creek Reservoir, Canada, exposed and killed much of the benthic fauna. Substrates frozen to depths > 20 cm also eliminated burrowing organisms (e.g., oligochaetes, nematodes, chironomids, and mites) that might have survived drawdown if ice or snow had provided a protective cover or if drawdown had occurred during warm weather (Paterson and Fernando 1969). Similar observations were made by Ioffe (1966).

59. Mortality of organisms, due to exposure, undoubtedly reduces populations within the fluctuation zone and may partly explain observations of inverted vertical distributions of benthos in widely fluctuating reservoirs. In bays protected from water-level fluctuations in impounded lakes in Southern Norway, Grimås (1964) noted that the vertical distribution of animals was similar to that in nonfluctuating lakes (i.e., abundance was greater in the littoral zone than at greater depths). Similarly, when water levels of Lake Kariba, Africa, were stable, benthos densities were greatest in shallow areas and decreased rapidly with increasing depth (McLachlan 1970a). However, distributions of benthos were inverted in fluctuating Lake Blåsjön, Sweden (Grimås 1961); densities were greatest just below the drawdown limit. Similar observations have been made in Katta-Kurgan Reservoir, USSR (Stepanova 1966), Barrier Reservoir and Upper and Lower Kananaskis reservoirs, Alberta (Fillion 1967), and in Big Eau Pleine Lake, Wisconsin (Kaster and Jacobi 1978).

60. In addition to losses of organisms in the fluctuation zone due to exposure, the migration of mobile species during drawdown also may concentrate them at or just below the drawdown limit. Engelhardt (1958) observed that many littoral organisms in Lake Walchensee, Germany, descended as waters receded and were concentrated in sublittoral areas. Cowell and Hudson (1967) noted that active migrations by some Hexagenia sp. and chironomids in Lake Francis Case resulted in enormous densities (e.g., 60,620 m^{-2}) at the waters edge, after waters reached minimum levels. Davis and Hughes (1965) observed that increased concentrations of benthos after drawdown caused crowding in Bayou D'Arbonne, Louisiana. Movements to avoid exposure may force

invertebrates into areas where they are more susceptible to predation or expose them to lethal oxygen concentrations.

61. Whatever the cause (mortality, migration, or both) inverted vertical distributions of benthos tend to reduce benthos populations that are available as fish food (see the next section "Fish and Fisheries: Trophic relations and growth"). When benthic organisms are forced to concentrate in deep waters to avoid exposure, they are spatially removed from most fish that feed in the littoral zone and also are confined to cool waters (at least in stratified reservoirs) where rates of production are low.

62. Large seasonal changes in water levels are undoubtedly harmful to benthic populations in the fluctuation zone. Littoral benthic communities (crustaceans, mayflies, caddisflies, stoneflies) in impounded natural lakes of Norway and Sweden were destroyed by large water-level fluctuations of 13 m. Grimås (1962) reported that densities were reduced 50% during 10 years of 6-m fluctuations and then another 40% during 2 years of 13-m fluctuations. Findings of Benson and Hudson (1975) reinforce those of Grimås. Water levels of Lake Francis Case were customarily drawn down 10-12 m each fall from 1953 to 1970 to increase the reservoir's water capacity. In 1971-73, drawdowns were reduced to 6-7 m. Benthos samples collected from 1966 to 1973 showed that average total densities in May were five times greater in years of reduced drawdown (May 1972 and 1973) than in years of extreme drawdown. Abundance of benthic organisms in September was similar under both drawdown regimes, suggesting that extensive winter drawdown reduces the production of benthos below its potential in the fluctuation zone in winter, spring, and perhaps early summer.

63. The impact of changes in water levels is modified by basin morphometry and the frequency, timing, and duration of fluctuations. Water-level changes in shallow, gently sloping reservoirs affect more benthic habitat per unit of change than they do in steep-sided deep reservoirs because of the relation of area to depth. Frequency and duration of changes determine the potential for recovery of benthos, the annual loss of production, and the impact on littoral habitats and

faunas. Grimås (1964) concluded that the shore fauna in Lake Rödungen was diverse because the slow rhythm and restricted amplitude of fluctuations reduced the impact on littoral habitat and insects. Seasonal timing of water-level changes also is important in determining effects. Winter drawdowns can adversely affect survival of burrowing species that remain in drained areas if substrates freeze and do little to improve trophic conditions for fish because predation is reduced in cold water. Flooding terrestrial vegetation in winter does not increase benthos production as much as flooding during the growing season.

64. In addition to effects on numbers and biomass, water-level fluctuations often alter the species composition and reduce the diversity of benthos. Cowell and Hudson (1967) found that chironomids were three times more abundant in fluctuating Lake Francis Case than in Lewis and Clark Lake, which fluctuated little. The dewatered zones of three reservoirs in Alberta, Canada, were dominated by chironomids that survived in drained areas for up to 85 days (Fillion 1967). In Llyn Tegid, North Wales, a dam was constructed in the outlet in 1955, and annual water-level fluctuations increased from 2 to about 5 m. Although total density of bottom organisms increased along shores, many littoral species (e.g., freshwater sponges, flatworms, snails, stoneflies, caddisflies, and amphipods) that were very important as fish foods were reduced in number or completely eliminated. A 42% increase in total density after fluctuations increased resulted almost exclusively from increases in chironomids and oligochaetes (Hynes 1961; Hunt and Jones 1972a). In 1967-69, annual fluctuations in water levels of Llyn Tegid were reduced to 2 m. Hunt and Jones (1972a) found that all major groups of animals recorded before 1955 were present in 1968-69, and most were fully reestablished. Similar observations of shifts in the species composition of benthos have been made in other impounded natural lakes in Norway and Sweden (see, e.g., Dahl 1933; Aass 1960; Grimas 1961, 1962, 1965).

65. Shifts in species composition and abundance result from changes in environmental conditions and habitat, as a result of water-level fluctuations. Many chironomids and oligochaetes are more tolerant of low oxygen than other aquatic invertebrates, and they also are favored by water-level changes that enhance the deposition of sediments. Hunt and Jones (1972b) observed that reduced water levels increased the fallout of rich organic matter to the profundal zone of Llyn Tegid and increased the abundance of profundal chironomids and oligochaetes. Benson and Hudson (1975) attributed increased abundance of burrowing benthos to reduced water-level fluctuations which caused sediment to be deposited at higher elevations. In impounded lakes in southern Norway, Grimås (1964) noted that the littoral fauna was maintained in areas protected from erosion and that more individuals were present in moss and submerged vegetation than in eroded sediments. He concluded that retention of original forest vegetation helped preserve littoral organisms important to fish.

66. Density of benthos is usually greater in areas with dense vegetation (aquatic or inundated terrestrial) than in other habitats (mud, gravel, rock, or sand), and diversity often varies directly with the diversity of habitat. Areas with vegetation support more benthos (numbers and species) because they provide food as well as structure. The positive influence of vegetation on littoral benthos is exemplified by the high numbers and diversity of benthos in beds of aquatic macrophytes. In Lake Francis Case, for example, invertebrates were twice as abundant in smartweed than in adjacent bottom areas (Cowell and Hudson 1967). During the winter of 1971-72, the density (number m^{-2}) of benthic macroinvertebrates in Lake Tohopekaliga, Florida, was higher in beds of macrophytes (3,272-14,682) than in limnetic areas (1,055-2,626) or in barren areas of the littoral zone (1,658-2,619) during the winter of 1971-72 (Wegener et al. 1974). Diversity also was greater in beds of macrophytes than in littoral or profundal areas. As might be expected, when water levels were high, densities of benthos in the littoral zone and in beds of macrophytes were higher than

densities in deep-water areas. However, when water levels were lowest, benthos was more abundant in profundal areas than in littoral areas with or without vegetation.

67. Periphyton on submerged trees also serves as habitat and food for many benthic invertebrates (Cowell and Hudson 1967; Clafin 1968; Benson 1973). Clafin (1968) found a significant positive correlation between the density of chironomid larvae and the standing crop of periphyton on submerged timber in Lewis and Clark Lake. Cowell and Hudson (1967) observed densities of benthos on tree-based periphyton that were 11 times greater than densities on adjacent bottom areas. In Lake Francis Case, where annual fluctuations of 6 to 13 m exposed the periphyton and tree substrates for 4 to 5 months each year, densities of benthos were only four times greater than on adjacent bottom areas.

68. The importance of habitat that produces food for benthos also is demonstrated by the high density and biomass of benthos that develop in areas of recently submerged herbaceous terrestrial vegetation. During filling of Beaver Lake, Arkansas, Aggus (1971) observed that areas of recently flooded herbaceous plants contained far greater numbers and biomass of benthos than cleared areas or those with woody vegetation only. Presumably, food, substrate, and refuge were provided by the plants. After shrub covered areas of Tsimlyanshoe Reservoir, USSR, were flooded for 2 months, Ioffe (1966) observed densities of benthos as high as 18,000 m^{-2} (wet weight biomass = 315 g m^{-2}). Ioffe also mentioned that biomass on tree substrates in the Rybinsk Reservoir, USSR, was 123 g m^{-2}. In Lake Oahe, North and South Dakota, the densities of benthos were higher in areas where large amounts of terrestrial vegetation had been recently inundated than in barren areas (Jones and Selgeby 1974).

69. McLachlan (1977) divided benthos development in new reservoirs into two phases that also may be used to describe the effects of large seasonal changes in water levels in older impoundments. "Flooding" is a short, productive phase during which water levels rise to cover terrestrial vegetation and when most benthos depends on terrestrial organic matter for food. "Post flooding" is a less productive phase

during which diets of benthic animals shift to include more autochthonous foods (primary production and detritus) after inundated terrestrial foods have been consumed. Biomass of benthos in Lake Chilwa, Africa, for example, declined from 2,967 to 1,051 mg dry weight m^{-2} after the flooding phase had passed. Concomitantly, the percent of allochthonous organic matter in diets of chironomids decreased from 93 to 64. McLachlan (1977) also mentioned similar observations for benthos in Ladyburn Lough, Great Britain, and Lake Kariba, Africa.

70. To date, management of water levels to benefit benthos has dealt mainly with reducing fluctuations (e.g., see Benson and Hudson 1975), or with introducing species (e.g., _Mysis_ sp., _Pallasea_ sp., or _Gammaracanthus_ sp.) capable of surviving extensive fluctuations (Fuerst 1970). Extensive drawdowns, planting of vegetation, and reflooding probably is successful in increasing benthic production for a year or two, inasmuch as the biomass of benthophagous fish usually increases for several years after such a treatment.

Fish and Fisheries

71. _Trophic relations and growth._ Water-level changes alter trophic relations and growth of fish by regulating the input of allochthonous foods, the productivity or species composition of fish-food biota, or the availability and vulnerability of prey. Changes in water levels that significantly affect fish communities have three characteristics: they are of large magnitude and of long duration and occur during at least part of the growing season. As mentioned in earlier sections on nutrients and fish-food biota, small short-term fluctuation in water level have little effect on nutrients, plants, or invertebrates, and winter fluctuations generally do not increase productivity because low temperatures retard or stop the growth of plants (terrestrial or aquatic) and cold-blooded animals. If areas of the fluctuation zone are barren, even large changes in water level usually have little effect on productivity.

72. Effects of frequent (daily or monthly) fluctuations in water levels on feeding and growth of fish are more subtle than effects related to long-term (1-3 year) cycles of water levels. Although

Hassler (1955) could not correlate changes in water levels to first year growth of sauger (Stizostedion canadense), he did notice a relation between first year growth and a longer cycle of water-level changes. Estes (1971) observed that growth of black basses (Micropterus spp.) and bluegills (Lepomis macrochirus) in Smith Mountain Lake, a pumped storage reservoir in Virginia, was not directly affected by weekly fluctuations of 6 to 8 feet, though reduced reproductive success of gizzard shad (Dorosoma cepedianum) may have reduced growth potential of the basses. In Lake Oahe, North and South Dakota, water-level fluctuations during the growing season had no discernible effect on fish growth unless areas with terrestrial vegetation were flooded (Nelson 1974).

73. Rapidly rising waters that inundate terrestrial areas--especially areas supporting extensive growths of vegetation--temporarily increase supplies of food for opportunistic fish. Areas of flooded herbaceous plants probably provide more food (drowned terrestrial animals, plants, or detritus) than do barren or wooded areas (Dale and Sullivan 1978). Many fish take advantage of temporary increases in food availability during and after increases in water levels. For example, Goodson (1965) observed that white catfish (Ictalurus catus) ate terrestrial plants as waters rose in Pine Flat Lake, California. Diets of black bullheads (Ictalurus melas) in Beaver Lake, Arkansas, changed during flooding to include terrestrial animals, such as earthworms and insects, which made up 56 percent of the volume of stomach contents. When water levels were stable, terrestrial animals composed less than 6 percent of total food volume (Applegate and Mullan 1966). Stomachs of young 4- to 8-inch centrarchids also contained high percentages of terrestrial foods--68 (bluegills), 61 (green sunfish, Lepomis megalotis), 58 (largemouth bass, Micropterus salmoides), and 40 (spotted bass, Micropterus punctulatus--during flooding (Mullan and Applegate 1967).

74. Changes in trophic conditions after waters have flooded areas of vegetation may be inferred from growth rates as well as from changes in diet. Although the changes were only temporary (1 year or less),

consumption of terrestrial animals and growth by brown trout (Salmo trutta) and Arctic char (Salvelinus alpinus) increased after water levels were increased in natural lakes of Norway, Sweden, and England (Huitfeldt-Kaas 1935; Runnström 1951, 1955; Frost 1956; Stube 1958; Aass 1960; Nilsson 1961, 1964). In virtually all studies, growth declined below preimpoundment levels after a year when no additional terrestrial areas were inundated and the staple diet of brown trout (benthic amphipods) was replaced by less desirable chironomids. In Lake Oahe, Nelson (1978) associated the inundation of areas with terrestrial vegetation with increased growth of 13 species of fish (goldeye, Hiodon alosoides; northern pike, Esox lucius; common carp, Cyprinus carpio; river carpsucker, Carpiodes carpio; smallmouth buffalo, Ictiobus cyprinellus; white bass, Morone crysops; white crappie, Pomoxis annularis; black crappie, Pomoxis nigromaculatus; yellow perch, Perca flavescens; sauger; walleye, Stizostedion vitreum; and freshwater drum, Aplodinotus grunniens). Similar observations have been made for spotted bass (Schultz 1966); largemouth bass (Wright 1950; Jackson 1957; Schultz 1966; Aggus and Elliott 1975; Shirley and Andrews 1977); blue sucker, Cycleptus elongatus, and shorthead redhorse, Moxostoma macrolepidotum (Elrod and Hassler 1971); gizzard shad and spotted sucker, Minytrema melanops (Jackson 1957); white crappie (Jackson 1957; Schultz 1966); and for bluegills, yellow perch, and channel catfish, Ictalurus punctatus (Wright 1950).

75. In addition to the terrestrial foods made available by flooding, production of fish-food biota also is increased in newly inundated areas. However, the terrestrial areas must be inundated long enough to enable fish to benefit from this increased production. According to Benson (1973), 25 days of inundation were required for periphyton development on plant stems in Missouri River reservoirs and 40 days for the colonization of epiphyton by aquatic insects.

76. Declining water levels may concentrate prey fish and thereby increase predator foraging and growth (Aggus 1979). Intense predation during periods of low water may selectively cull smaller fishes, provided the drawdown is large enough and occurs when water temperatures are

above 13° C (Bennett 1954, 1962). Jenkins (1970) observed that short drawdowns (2-3 months) seldom produce measurable changes in species composition or abundance of prey fishes. Some authors have observed increased feeding activity or growth by piscivores during or immediately after drawdown--e.g., northern pike (Beard and Snow 1970); smallmouth bass, Micropterus dolomieui (Heisey et al. 1980); and largemouth bass (Heman et al. 1969). However, after prolonged drawdown, growth of fish often decreases as concentrations of prey are diminished and the productivity of most invertebrates and small fish is reduced. Growth of large crappies (Pomoxis spp.) and flathead catfish (Pylodictis olivaris) was inversely correlated with mean annual water levels in Lake Carl Blackwell, Oklahoma (Johnson and Andrews 1973), perhaps because water levels declined progressively for 5 years and continually concentrated prey.

77. Prolonged loss of benthos production from the littoral zone may reduce the production of benthos-feeding fishes or young sport fish. Johnson and Andrews (1973) and Johnson (1974) reported reduced growth of white crappie (age I), channel catfish (ages I, II, and VI), and common carp (ages I and III) as water levels declined in Lake Carl Blackwell, Oklahoma, from 1962 to 1967. Eschmeyer (1949) suggested that food limitations experienced by benthophagous fishes in widely fluctuating reservoirs may account for their low abundance in storage impoundments and that relatively stable water levels may account for their high densities in mainstream reservoirs. Also, low water during or after a spawning period, when food demands by young-of-the-year (YOY) fish are high, may severely reduce survival and annual production of an entire year class of fish (e.g., see Houser and Rainwater 1975). Schultz (1966) noted that growth of white crappies, spotted bass, and largemouth bass in three Mississippi reservoirs was lowest in 1959 and 1963, when water levels were lower than normal in spring. Reduced allochthonous input of nutrients and reduced spawning success in spring by prey fishes probably account for reduced growth.

78. In contrast to spring drawdown, fall drawdown may significantly increase forage for young predators (Benson 1973) and simultaneously reduce populations of small fish (Bennett 1962). Decisions to employ fall drawdown are best made after examining total standing crop and assessing the ratio of available prey to predators--e.g., as determined by the predator-prey model of Jenkins and Morais (1976) or the YOY/Standing Crop (Y/C) ratio of Swingle (1950).

79. Another aspect of predator-prey relations involves changes in the structural complexity of habitat as water levels change. Not only are prey physically concentrated by large drawdowns, but they are often forced to abandon refuge (i.e., aquatic or terrestrial vegetation, artificial structure, or rocks) in the littoral zone. Consequently, prey become more vulnerable to predators (Bennett 1962; Keith 1975). Complex structure not only provides refuge for prey but also reduces the foraging efficiency of predators (Murdock and Oaten 1975). Heman (1965) observed increased growth of largemouth bass (except for YOY) after drawdown of Little Dixie Lake, Missouri, and noted an inverse relation between the amount of inundated vegetation and feeding. Cooper and Crowder (1979) and Crowder and Cooper (1979) concluded that densely structured habitats decrease productivity of predators by reducing their feeding effectiveness and that in barren habitats prey biomass is low due to predation. Water-level manipulation can provide fishery managers with a crude means of regulating structural complexity, and therefore the predator-prey relations of littoral fish in reservoirs, by providing a more complex habitat at high than at low elevations.

80. Changes in the species composition and abundance of prey available to predators as a result of years of water-level fluctuations may alter consumption and growth. Lewis (1967) suggested that food consumption and production of sport fish is limited to a maintenance level by the availability of highly vulnerable foods. Part of the success of drawdowns in improving sport-fish production is a result of an increase in the vulnerability of forage. Aside from increased vulnerability due to concentrating effects or changes in the amount of refuge available, vulnerability and quality of forage vary among species

of prey. Conceivably, water-level changes might be designed to benefit highly vulnerable prey such as threadfin shad (Dorosoma petenense), while adversely affecting species such as bluegills, which presumably are less vulnerable to predation. Evidence collected to date does not corroborate or refute such a hypothesis. It does show that certain assemblages of fish are more productive of sport fish than others, though apparently for other reasons. Drawdown of Ridge Lake, Illinois, in 1951 and 1952 significantly reduced populations of small sunfish (Bennett 1954). Bass reproduction and recruitment were much greater in years after sunfish populations were reduced, suggesting that bass production was previously limited by predation on bass eggs and fry by sunfish. Early introductions of threadfin shad in fluctuating California reservoirs were successful in increasing forage of yearling and older black basses, but survival of YOY bass apparently was limited by competition for zooplankton with YOY threadfin shad (von Geldern and Mitchell 1975).

81. Reservoirs with widely fluctuating water levels favor euryphagous fish (i.e., those that eat a wide variety of food). Nilsson (1964) observed that littoral benthos is typically scarce in impounded natural lakes as a result of water-level fluctuations and that brown trout production in these lakes declined significantly when the fish were forced to feed on zooplankton, profundal benthos, or fish. Arctic char were less affected by fluctuating water levels because they fed more on zooplankton than on benthos. Miller and Paetz (1959) noted that increases in weight of lake trout (Salvelinus namaycush) usually ceased at about 0.45 kg in three Canadian reservoirs in which littoral benthos was poorly developed. Apparently the fish were prevented from switching from a diet of zooplankton and benthos to one of fish. Grimås (1962) observed that chironomids, which dominated the benthos after water levels fluctuated in impounded natural lakes and inhabited deep waters, were less available as food for brown trout than were the pre-fluctuation species of littoral benthos.

82. Reproduction. Reproduction of fish that spawn in the fluctuation zone of reservoirs is influenced by water levels and by changes in water levels. Adverse effects on reproduction of near-shore spawning fishes are related to (1) a loss of habitat by drawdown or shoreline modification or (2) mortality of eggs or YOY fish by exposure or suffocation with eroded sediments (Hassler 1970). Mortality of eggs or YOY fishes stranded by drawdown has been documented for many species--e.g., salmonids (Aass 1964; Runnström 1951, 1964); sunfishes, Lepomis spp. (Heman 1965); walleyes (Priegel 1970); common carp (Shields 1958a; Aronin and Mikheev 1963; Yakovleva 1971); and black basses (Estes 1971). Species of fish that spawn in tributaries (e.g., white bass) or in open-water areas (e.g., goldeye and freshwater drum) generally are not adversely affected (Benson 1973; Gabel 1974). Walburg (1976) observed that the spawning success of channel catfish in Lewis and Clark Lake was unaffected by water levels because they spawned at depths below the drawdown limit. Also, walleyes and saugers that spawned in the Missouri River were unaffected by fluctuations in the lake except indirectly because of adverse effects of water levels on reproduction of forage fish.

83. Control of water levels during spawning is the most practical and inexpensive method of producing fish. Methods to alleviate problems associated with dewatered spawning sites in fluctuation zones have included (1) provision of artificial spawning sites (Ellis 1937, 1942; Martin 1955), (2) construction of nonfluctuating "inlet impoundments" adjoining reservoirs (Ellis 1937; Grimås 1965), (3) artificial propagation of important fish in hatcheries (Il'ina and Gordeyev 1972), and (4) control of water levels during the spawning period. Artificial spawning sites are expensive and impractical for large reservoirs, and inlet impoundments do not make up for the loss of littoral areas, at least in steep-sided, deep reservoirs (Grimås 1965). Although important sport and forage fish are stocked extensively in many reservoirs by State fishery agencies, most of the fish stocks in large reservoirs are produced by natural reproduction.

84. Drawdown has been used to control spawning of rough fish such as squawfish, Ptychocheilus sp. (Jeppson 1957), and common carp (Shields 1958a, 1958b). Although enormous numbers of eggs may be exposed and killed, success in controlling populations varies. Attempts to control common carp spawning in Lake Francis Case in 1956 were not successful; though millions of eggs were destroyed, the 1956 year class made up 78% of the commercial catch of fish in 1959 (Gasaway 1970). Short-term manipulation of water levels to destroy eggs was of limited value because common carp spawned over an extended period of time. Drawdowns combined with selective culling of small fish (e.g., bluegills) has been more consistently effective, at least in small lakes (Bennett 1954).

85. In addition to stranding eggs or young fish, rapidly receding waters may result in desertion of nests, failure of nests, disrupted spawning, or atresia (intraovarian mortality of eggs) in species that build nests along shorelines (black basses, Lepomis sunfishes, and crappies) or spawn in shallow water (yellow perch, northern pike, common carp, buffaloes, and gizzard shad). Walburg (1976) noted that low and variable spring water levels adversely affected spawning success of gizzard shad, emerald shiners (Notropis atherinoides), white bass, white crappies, and yellow perch in Lewis and Clark Lake. June (1970) concluded that a sudden lowering of water levels prevented female northern pike from entering previously used spawning areas and increased the incidence of atresia. Nest desertion (Buck and Cross 1951; Webster 1954) permits sunfish to prey intensively on eggs (Vogele 1975). Poor spawning success of largemouth bass, carpsuckers (Carpiodes sp.), and channel catfish in Lake Carl Blackwell, Oklahoma, was attributed to declining water levels (Johnson 1974). Decreasing or fluctuating water levels can result in the failure or weakening of a year class. For example, year classes of largemouth bass failed when water levels of Lake Nacimiento, California, were lowered excessively (von Geldern 1971).

86. Reproductive success is determined by spawning success and post-spawning survival, as regulated by many factors: temperature, wind, and turbulence (Summerfelt 1975); predatory mortality of eggs, embryos, or larvae (Bennett 1962, 1974); and the amount of food available for

young fish (Hassler 1970; Eipper 1975). Provision of ideal spawning conditions does not always insure a strong year class. Fourt (1978), for example, reported success in producing large numbers of YOY black basses and crappies by flooding terrestrial vegetation on about 7,000 acres of fluctuation zone in Beaver Lake, Arkansas. However, the poor survival of YOY fish after August that resulted from inadequate prey abundance, prevented the development of a strong year class.

87. Although good spawning success may not insure a strong year class, it does increase the chances of producing one, given environmental conditions favorable for survival of the YOY. Good spawning success has often been related to rising waters that flooded terrestrial areas and provided appropriate spawning substrates--e.g., flooding of gravel areas used by walleye (Johnson et al. 1966) or areas of terrestrial vegetation used by yellow perch (Beckman and Elrod 1971), northern pike (Benson 1968; Hassler 1970), buffaloes (Moen 1974), or common carp (Gabel 1974). The importance of spawning habitat cannot be overlooked. Hassler (1970) concluded that rising waters contribute little to the reproductive success of northern pike, unless herbaceous grasses are available. Johnson (1961) found that survival of walleye eggs to the "eyed stage" was high (25%) on gravel but low (0.6%) on mud. Smallmouth bass typically require rock or gravel areas for nesting (Vogele 1981), but other black basses have less specific requirements for nesting habitat.

88. Strong year classes of many freshwater fish have been correlated with rising or high water during and for several months after the spawning season (see LeCren 1965). Other examples include largemouth bass (von Geldern 1971; Summerfelt and Shirley 1978); black basses (Rainwater and Houser 1975); northern pike (Hassler 1970); saugers (Walburg 1972); and common carp, river carpsuckers, smallmouth buffaloes, and bigmouth buffaloes (Gasaway 1970; Elrod and Hassler 1971). Spring water levels and the amount of terrestrial vegetation inundated during spawning explained 79 percent of the variation in year-class strength of yellow perch (Nelson and Walburg 1977). Rainwater and Houser (1975) found that the reproductive success of black basses in Bull Shoals Lake

from 1966 to 1973 was negatively correlated ($\underline{P} < 0.01$) with fluctuation of water levels during the 3-month spawning season.

89. Rapid exchange rates can affect the survival of young fish (Walburg 1976). In Lewis and Clark Lake, the abundance of YOY fishes was directly related to water-exchange time ($\underline{P} < 0.02$, $\underline{r} = 0.73$), as was the catch of young fish in trawls ($\underline{P} < 0.05$; $\underline{r} = 0.68$). A reduction in water retention time from 10 days to 4 or 5 days increased the discharge of larval fish through the dam. Year-class strengths of freshwater drum (a pelagic spawner) and channel catfish were correlated with the mean rate of water exchange in July and August (Walburg 1976).

90. The reproductive success of fish that spawn near shores in reservoirs is influenced by the time and duration of flooding and the type of substrate inundated (Aggus 1979). Holčík and Bastl (1976) observed that fish stocks were higher in rivers with flood plains than in rivers without them. Water levels determine available refuge (nursery areas) for young fish by inundating vegetation or receding from it. Survival of YOY fish is enhanced greatly when cover is abundant. Aggus and Elliott (1975) found that the number of YOY largemouth bass in August in Bull Shoals Lake, Arkansas, was directly related to the acre-days of flooding of terrestrial vegetation. Nelson and Walburg (1977) found the abundance of young walleyes to be directly correlated with water levels ($r = 0.62$; $\underline{P} < 0.01$). Decreasing water levels reduced cover and refuge for larval and juvenile stages of spotted bass (Vogele 1975), and consequently exposes YOY fish (e.g., black basses--Hogue 1972; Aggus and Elliott 1975) to increased predation.

91. Year-class strength of most fishes in reservoirs varies greatly among years (Aggus and Elliott 1975), depending on environmental conditions and predator-prey relations. Strong year classes of one species may suppress future year classes of its own or of other species for several years (1-4) by competing for food (von Geldern 1971) or by preying on eggs, embryos, or larvae (Bennett 1962), or on other YOY fish (Aggus and Elliott 1975). Jenkins (1975) concluded that cannibalism (mostly by yearlings feeding on YOY) and a scarcity of submerged vegetation in some years made it virtually impossible to produce strong

year classes of largemouth bass every year. Swingle and Swingle (1967) noted that weak year classes of crappies occurred when a strong year class of largemouth bass had developed in the previous year.

92. Provision of suitable spawning and nursery areas every year may not be necessary to maintain fish populations because of natural yearly variation in recruitment. Basin-wide management of water levels, where levels of selected reservoirs in a series are manipulated in different years, seems to be the most efficient approach (Neel 1963). Yearly sampling of fish populations to assess species composition, age-class structure, and ratios of prey to predator biomass is necessary to determine which reservoir in a series would benefit most from management.

93. The abundance and species composition of fish changes primarily in response to changes in the quality and quantity of spawning and nursery habitats, as influenced by the long-term effects of water-level changes and waves on the shore zone of reservoirs. The species composition of fish present before shorelines stabilized in Missouri River reservoirs was substantially different from that which finally developed (Benson 1980). The abundance of species that spawned in tributaries or along rocky shores that developed after years of erosion (walleye, sauger, channel catfish, white bass, and river carpsuckers) either remained unchanged or increased as shorelines were modified. Populations of other species that required vegetation or suitable substrates for nest building declined. Walleye reproduction in Ohio reservoirs (Erickson and Stevenson 1972) improved after years of water-level fluctuations had cleaned gravel bars and riprap. Il'ina and Gordeyev (1972) noted that terrestrial vegetation required for reproduction of many fish would not grow in much of the fluctuation zone of the Rybinsk Reservoir, USSR, because years of erosion had removed soils and left a bed of sand.

94. Knowledge of spawning and nursery requirements of fishes is essential for the development of effective strategies for water-level manipulation. Benson (1976) listed spawning and nursery habitats for 16 species of fish. Carlander (1969, 1977) listed temperature and

habitat required for spawning of many sport and commercial fishes. Because time of spawning varies directly with temperature, temperature is more reliable than time of year as an index to spawning, given variations in water temperature with latitude. In reservoirs dominated by warm-water species (black bass, Lepomis sunfishes, catfish, and crappies), virtually all important forage, sport, and commercial fish spawn when temperatures are between 11 and 22°C. In reservoirs dominated by coolwater species (northern pike, walleyes, saugers, and yellow perch), the temperature range for spawning is about 5 to 17°C.

95. Some fishes such as salmonids in cold-water reservoirs spawn in fall. Winter drawdowns in these reservoirs are extremely harmful to reproductive success because spawning and nursery periods are prolonged in cold waters. Aass (1964) found that recruitment of char in Pålsbufjord Lake, Norway, was limited by extreme drawdowns that exposed 75 percent of the bottom area and killed eggs and alevins. In years when the magnitude of drawdown was reduced and water levels were lowered slowly, strong year classes were produced. In Tunhovdfjord Lake, Norway, drawdown occurred in late winter, and although spawning areas were drained, most eggs had hatched and alevins were able to move with the receding waters. Consequently, annual recruitment was less variable in Tunhovdfjord Lake than in Pålsbufjord Lake.

96. Standing Crop and Harvest. The effects of changes in water levels or rates of water exchange on trophic relations, growth, reproduction, and survival of fish are ultimately reflected in fish standing crop. Jenkins (1967) found a significant ($P < 0.005$) negative correlation between the total standing crop of fish and the vertical extent of annual fluctuations in water levels in 70 reservoirs of carbonate-bicarbonate chemical types. Jenkins (1970) found positive correlations between annual water-level fluctuations and standing crops of spotted gar (Lepisosteus osseus), flathead catfish, black bass, and white crappies. Water-level fluctuations were negatively correlated with the biomass of gizzard shad, northern pike, pickerel (Esox spp.), carpsuckers, and sunfish. Aggus and Lewis (1976) found that total standing crop and crops of sunfishes, clupeids, and small fishes

were larger in reservoirs with rapid water exchange (storage ratios < 0.165, as in most mainstream reservoirs) than in those with slow exchanges. Standing crops of fish were more variable in reservoirs with large seasonal changes in inflow and water levels (e.g., storage reservoirs) than in stable mainstream impoundments.

97. Although fish-carrying capacity may be reduced by seasonally fluctuating water levels, large changes that occur every 2 to 4 years can be beneficial. Productivity and carrying capacity can be significantly increased by large water-level changes that are infrequent enough to permit the growth of terrestrial vegetation in dewatered areas. Controlled annual drawdown and reflooding of three Louisiana lakes resulted in a gradual increase in fish standing crop and rapid increases in the biomass of harvestable-size fish in the first 2 or 3 consecutive years of treatment; however, the beneficial effect of annual drawdowns apparently diminished after 4 or 5 consecutive years (Lantz 1974). In Council Grove Reservoir, Kansas, the percent of harvestable-size fish increased from 30.3 to 44.1 percent of the total standing crop, after water levels were managed (Groen and Schroeder 1978). Wegener and Williams (1977) observed a large increase in the total standing crop of fish (from 214 to 510 kg ha^{-1}) within 3 years after water levels of Lake Tohopekaliga, Florida, were manipulated. Drawdown of the lake exposed 50 percent of the bottom for 6 months, and refilling to normal pool required another 6 months. Afterward, high inflows caused water levels to rise and remain above normal pool for the next year. The biomass of black basses alone increased from 39 to 67 kg ha^{-1}.

98. Harvest of fish is affected by many factors, some of which are influenced by water-level changes. Direct effects of water-level fluctuations on angler harvest are rarely documented because of difficulties associated with quantifying short-term responses that are frequently determined by fish behavior. For example, Heman et al. (1969) observed that the harvest of bluegills increased immediately after a midsummer drawdown of Little Dixie Lake, Missouri, and then declined for 2 months. One may speculate that the benthos, the primary food of bluegills, was reduced by drawdown and that this shortage of food

temporarily made bluegills more susceptible to harvest by anglers; however, no conclusive data are available. Harvest of largemouth bass was reduced immediately after the drawdown in August but increased significantly in September and October. Increased predation that the authors concluded reduced the abundance of fry and intermediate-size bluegills also may have increased the vulnerability of bass to anglers. However, other factors probably were involved. Because of the complexity of relations, observed changes in harvest often cannot be readily explained by changes in water level alone. Some other factors that affect harvest are the standing crop; length, frequency distribution, and production of harvestable-size fish (as determined by reproductive success, growth, and recruitment); the local distribution of fish relative to anglers; and environmental conditions such as season and turbidity.

99. Jenkins (1967), who examined relations between nine descriptive variables and the sport and commercial harvest of fish in 127 reservoirs, found that sport-fish harvest per unit area was directly related to total dissolved solids, storage ratio, and shoreline development (shoreline length/ $2\sqrt{\pi \cdot \text{area}}$) and inversely related to reservoir age, area, and mean depth. Consequently, sport-fish harvest should be highest in nutrient-rich, productive reservoirs that entrain water for a year or more and that have a large littoral area relative to the area overlying deep water. Harvest of commercial fishes was inversely related to storage ratio, mean depth, shoreline development, and water-level fluctuation; it was directly related to reservoir age. High commercial harvests are more common from old mainstream reservoirs that are not dendritic, but that are linear and shallow and exchange water rapidly. These reservoirs are generally more productive and easier to fish than deep, dentritic impoundments.

100. Changes in the reproductive success and standing crop of fish ultimately affects harvest. After several natural lakes in Norway were impounded and seasonal water levels began to fluctuate greatly, Aass (1960) observed that catches of brown trout declined while those of Arctic char increased. Trends in harvest of both species paralleled

relative abundance. Abundance was determined by variations in year-class strength that caused single year classes of fish to dominate the creel for several years. Chevalier (1977) correlated the commercial catch of walleyes from Rainy Lake, Minnesota, with water level and its effect on reproductive success 4, 5, and 6 years earlier. Low water during spawning apparently limited year-class strength, which in turn reduced the harvest 4 to 6 years later. Similar observations were made by Johnson et al. (1966) and Derksen (1967). Manipulation of water levels in Lake Tohopekaliga, Florida, nearly quadrupled the harvest of black basses (Wegener and Williams 1974). In Ridge Lake, Illinois, recruitment of largemouth bass was limited by bluegills preying on bass eggs and fry in years of stable water levels. Harvest in these years averaged 19 kg ha^{-1} and the mean weight of bass caught was 0.15 kg (Bennett 1974). Draining of the lake and culling of egg and fry predators such as bluegills allowed the production of strong year classes of bass. Drawdown improved the growth of bass. In years following the years of draining and culling operations, harvest averaged 23 kg ha^{-1}, and the mean weight of bass harvested was 0.35 kg.

101. Drawdown of water levels allows fishery managers to improve the submerged structures in littoral areas or to alter the amount of structure available to fish if structural complexity varies with elevation. Harvest of fish may be significantly increased if fish are concentrated in specific areas that fishermen are aware of or to which they can be directed. Attraction of many sport fishes to structure, because of increased prey availability, refuge, or spawning habitat, improves harvest. Davis and Hughes (1971) found that the presence of submerged trees greatly increased the local abundance of catchable-size largemouth bass and black crappies. Other species--e.g., gars (Lepisosteus spp.), buffaloes, and bullheads--were more abundant in open water. In Barkley Lake, Kentucky, Pierce and Hooper (1979) found total standing crops of 2,418 kg ha^{-1} in brush shelters, 998 kg ha^{-1} in tire attractors, and 773 kg ha^{-1} in control areas that lacked structure. It was clear that attracting structures concentrated four species of sport fishes. The ratios of mean standing crop in brush structures to that in control

areas were 10:1 for channel catfish, 61:1 for bluegill, 35:1 for largemouth bass, and 44:1 for white crappie. Structures made from tires concentrated 3.9 times more channel catfish than did control areas without submerged structures and 15, 20, and 14.2 times more bluegills, largemouth bass, and white crappie, respectively.

102. The concentrating effects of natural timber also have been documented. The standing crop of fishes in a cove with standing timber in Tuttle Creek Reservoir, Kansas, was significantly higher than that in a cleared cove (data collected by the Kansas Fish and Game Commission). The biomass of largemouth bass, crappies, buffalofishes, common carp, river carpsuckers, and minnows was significantly less in the cleared than in the wooded cove ($P < 0.05$). The biomass of lepomid sunfishes also was greater in the wooded cove, but not significantly ($P < 0.10$). Mean weights of largemouth bass, crappies, and flathead catfish were generally higher in the wooded than in the cleared cove, suggesting that larger sport fish may be concentrated more than smaller ones. Davis and Hughes (1971), who conducted a 3-year creel survey of anglers in timbered and open-water areas of Bussy Brake Lake, Louisiana, found that trees had no significant effect on the catch (kg $hour^{-1}$) of black basses, crappies, sunfishes, or catfishes. However, fishing success (the chance of catching at least one fish per trip) was consistently higher in timbered than in cleared areas--90 versus 79 percent in 1960-61, 87 versus 74 percent in 1961-62, and 86 versus 66 percent in 1962-63.

103. In new impoundments where structural habitat in the form of submerged timber, brush, or boulders is present in the fluctuation zone, the construction of artificial structures probably is unjustified. Jensen and Aass (1958) observed that timber in the seasonally drained zone of fluctuating Norwegian lakes was still present after 36 (birch forest) and 51 (fir and juniper forest) years. As reservoirs age, terrestrial vegetation in littoral areas eventually deteriorates, and the use of artificial shelters may become an economically viable management measure for concentrating certain fish and improving harvest.

104. Although artificial structures are valuable in bringing structure-oriented fish (e.g., black basses, crappies, and sunfishes) and anglers together, problems with placement of structures to avoid exposure during drawdown and periodic maintenance costs have inhibited their use (Jenkins 1973). As Calhoun (1966) stated, "California experience with brush shelters has been generally unsatisfactory... An experimental program at Millerton Lake, a large fluctuating warm-water reservoir, proved expensive and unprofitable."

105. Several authors who have reviewed and contributed to the existing information on the effectiveness of artificial structures in improving sport fisheries have developed valuable references for further information (see, e.g., Brouha and Prince 1973; Wilbur 1974; Prince et al. 1975; and Wilbur 1978). Prince et al. (1975) discussed research on species abundance, biological productivity, spawning, fish movement, and fishing success at artificial reefs. The effectiveness and economics of artificial reefs were examined by Prince and Maughan (1978), and Prince et al. (1979) discussed periphyton production, predator-prey relations, and condition and growth of fish in relation to reef structures. Recent research on fish responses to structure (principally artificial) was presented in a symposium by the North Central Division of the American Fisheries Society (see Johnson and Stein 1979).

106. Seasonal changes in harvest probably result from seasonal changes in the vulnerability of fish to anglers and in the fishing pressure exerted by anglers. It is well established that species spawning along shores are particularly vulnerable to anglers because they are concentrated in particular areas. Parsons (1957) noted that fishing pressure on reservoirs in the southeastern United States was highest in spring as was the harvest of sport fishes. Sixteen years of creel-survey data from Beaver Lake, Arkansas, corroborate Parsons' observations (unpublished data, National Reservoir Research Program). Fluctuating or reduced water levels in spring or early summer may not only be harmful to the reproductive success of fish but also could seriously reduce annual harvest by disrupting concentrations of fish or perhaps by limiting access of anglers to the lake. If drawdowns affect angler

pressure at all, they would have more impact during the growing season (spring, summer, and fall) than in winter, because most anglers fish during the growing season. Seasonal changes in harvest may also result from changes in water levels if turbidity increases greatly. For example, some sport fishes (such as black basses) are primarily sight feeders. Sight impairment may explain why black basses are seldom abundant in turbid impoundments. Kirkland (1963) observed that turbid floodwaters in mid-April greatly reduced the catch of spotted bass in Allatoona Reservoir, Georgia.

PART IV: SUMMARY AND RECOMMENDATIONS

Introduction

107. Increasing demands on reservoirs for water supply, irrigation, flood control, hydroelectric power generation, water quality control, and recreation require that priorities be assigned to these often conflicting uses. Demands for quality fisheries are increasing; fishing pressure on reservoirs is expected to increase 60 million angler days (a total of 36 percent) during the interval 1975-85. The present review was prepared to document the known effects of water-level changes on reservoir ecosystems and biota and to provide recommendations for water-level management to benefit reservoir fish and fisheries.

State-of-the-Art Perspective

108. The findings of this review corroborate the conclusions of a panel of experts who attended a workshop on research needs to have ecological issues considered in basin-level hydropower planning (Hildebrand and Goss 1981). The panel concluded that the capability to quantitatively predict the physical extent of water-level changes was adequate but that the capability to predict biological consequences was not. They also concluded that (1) the theory of bank and bed stability was poorly understood, (2) the capability to predict the effects of water-level changes on aquatic biota in lower trophic levels was poor, and (3) ecologists have not quantified the effects of water-level changes on fish, except to determine optimum or minimum requirements for spawning. The consensus of the panelists was that the ability to address ecosystem-level effects was qualitative at best.

109. After 50 years of studying reservoir biology, biologists have accumulated many observations of physicochemical and biological changes resulting from fluctuations in water levels. Although the observations are sometimes disjunct or contradictory and exceptions to accepted hypotheses are common, enough qualitative information is available so that preliminary recommendations for management of water levels to enhance fisheries can be formulated. However, rigorous quantitative analyses and the development of improved predictive capability must await the

acquisition of appropriate quantitative data and a better understanding of aquatic biology in general. Available information suggests that many of the responses of aquatic biota to water-level changes and their effects are generally predictable. However, almost all reservoir ecosystems have distinct physicochemical and biological characteristics that may cause them to respond differently to similar water-level regimes. Consequently, the guidance presented here is not intended as a broad-brush prescription for enhancing fisheries in all reservoirs. Rather, it is designed as an outline of potentially desirable ingredients for water-level management plans and presents a flexible scheme that can be modified to meet the specific needs of biota in different reservoirs. After all, general management plans are seldom applicable to all reservoirs because operational requirements vary greatly. Water-level regimes required to benefit fishery resources may be completely incompatible with the required operations of some reservoirs (e.g., some hydropower impoundments). By contrast, operational flexibility is possible for many other reservoirs, and water levels can be manipulated to enhance fish production or at least to substantially reduce major adverse effects on fish-food biota and fish communities.

Summary of Effects

110. Drawdown. Drawdown that exposes mudflats, dead and decaying vegetation, benthos, or fish is the most visually obvious type of water-level change. Drawdowns may interfere with fishing and navigation by reducing surface area and exposing previously submerged navigational hazards. It may limit the number of access points available to anglers and other boaters, force marinas and boat docks to be moved, and leave recreational areas such as swimming beaches far from the water. Limitations on access often cause fishing pressure and harvest of fish to decline, especially if drawdown occurs during the spring when harvest is usually highest.

111. Periphyton and benthos which are important sources of food for many littoral fishes, including YOY sport fishes, are adversely affected by drawdowns. Generally, the annual loss of periphyton production is directly related to the magnitude, frequency, and duration

of exposure. Drawdowns in winter presumably have less effect on periphyton than drawdowns during the growing season because of the direct relation between production and water temperature. Benthos associated with periphyton may be more important as food for many fishes than the periphyton itself. The full establishment of benthos associated with periphyton requires about 40 days of inundation and periphyton growth in some reservoirs. Consequently, exposure of these communities during the growing season results in a loss of standing crop throughout the period of exposure and lower biomass for about 40 days thereafter. Winter exposure of the littoral zone reduces the standing crop of benthic insects until late spring or early summer or until the insects have had time to reproduce and recolonize the substrates. During drawdown, standing crops of benthos are generally reduced by exposure or nonpredatory and predatory mortality while animals move to avoid exposure. Many forms survive in the drained zone by burrowing into substrates and entering resting stages. The net result of periodic drawdowns often is an inverted distribution of benthos. Maximum crops occur below the drawdown limit where littoral fish feed infrequently. Also, production of benthos is usually lower in deep water than in shallow water if water temperature diminishes greatly with increasing depth. The species composition of benthos in stable reservoirs usually differs significantly from that in fluctuating reservoirs. Diverse littoral communities of crustaceans and insects (e.g., mayflies, caddisflies, hemipterans, and crustaceans), which are extremely important as food for littoral fishes, are eliminated and replaced by organisms better equipped to survive drawdowns (e.g., chironomids and oligochaetes).

112. As suspended biota, phytoplankton and zooplankton probably are affected less by drawdown than by other changes in the environment, unless flushing rates are high. During the growing season, primary production by phytoplankton generally increases in response to increased nutrients and light until one or both of these factors become limiting. Zooplankton also increases production in response to increased levels

of food, regardless of the cause of the improved trophic conditions, providing other factors are not adverse.

113. Rapid release of water during growing-season drawdowns may adversely affect phytoplankton, zooplankton, some benthos, and larval fishes. Suspended algae, animals, nutrients and detritus in the water column may be flushed downstream. High runoff from the drainage basin may increase turbidity and limit light required for primary production. Concentrations of phytoplankton may not reach sufficient concentrations to fully use available nutrients before being eliminated by discharge. The standing crop of zooplankton also is inversely related to the rates of flow through reservoirs and may be reduced significantly when water retention time is short (e.g., < 30 days). Consequently, in reservoirs where flushing rates are not consistently high, standing crops of phytoplankton, zooplankton, and larval fish may be increased significantly by reducing rates of flushing during warm weather.

114. Most reservoirs that experience large drawdowns seasonally or more frequently do not support extensive growths of aquatic macrophytes. To increase fish production in littoral areas of these reservoirs, man can provide structure by planting and seasonally flooding terrestrial plants, by retaining timber, or by constructing artificial structures.

115. Drawdowns during or within 3 months after the spawning season may limit the reproductive success of fish by reducing survival of eggs, larvae, or fingerlings. Survival is reduced by stranding of eggs or young fish, predation on eggs and YOY fish, or a shortage of food. Reduced standing crops of benthos after drawdown eventually may limit the production and survival of YOY fishes and benthophagous fishes. Severe drawdowns may force fish into anoxic waters in summer, thereby causing mortality by suffocation.

116. Some effects of drawdowns are beneficial. For example, drawdowns have been successfully used to consolidate and aerate sediments. Aeration remineralizes nutrients such as nitrogen and phosphorus and reduces the organic load of sediments by aerobic decay. Consolidation of sediments may reduce turbidity after sediments are reflooded. Inflow

of water when lake elevations are low may move some sediments accumulated in headwater areas downstream, thereby reducing the formation of deltas in upstream areas. Drawdown may disrupt thermal stratification and increase the rate of oxidation and decay of organic matter in sediments at low elevations in the basin by providing oxygen for aerobic metabolism.

117. Drawdowns have also provided the benefit of controlling overabundant aquatic macrophytes that often become established in shallow impoundments with relatively stable water levels. Congested areas have been opened to boats and fishermen. Because the effects of drawdowns on macrophytes are species specific, a review of case-history studies (e.g., see Hulsey 1958; Holcomb and Wegener 1971; Beard 1973; Lantz 1974; Nichols 1972, 1974) is recommended to determine the applicability of drawdown as a control measure. The greatest control by drawdown is usually achieved by winter dewatering in areas where substrates freeze. Short-term drawdowns (< 3 months) during the growing season generally have little effect on macrophytes.

118. Herbaceous terrestrial plants that become established on suitable substrates after drawdown are beneficial. These plants provide excellent spawning and nursery sites for many species of fish when inundated at the appropriate times. They also provide food and refuge for bacteria, zooplankton, benthos, and fish; substrates for attached algae; and nutrients for all aquatic plants.

119. Drawdown provides a chance for fishery managers to plant desirable vegetation, construct or refurbish artificial structures for fish, or to mechanically remove overabundant aquatic macrophytes. Large drawdowns may be used to increase the availability of prey fish for piscivores by concentrating prey and predators or by reducing the amount of refuge available for prey. Benthic invertebrates also may be concentrated by drawdown, and growth rates of many piscivores and benthophagous fishes commonly increase immediately after drawdown. Increased predation may eliminate many egg and fry predators that can limit the reproductive success of some sport fish such as largemouth bass.

120. Drawdowns may help limit the reproductive success of undesirable fishes such as common carp, but few applications have yet been clearly successful in exclusively controlling the abundance of undesirable fishes.

121. Flooding. Flooding of terrestrial areas (especially those with vegetation) often has been associated with increased nutrient and detrital inputs, reduced turbidity, and increased primary and secondary production during the growing season. Flooding may have adverse effects on attached plants such as macrophytes and periphyton if turbidity or depth increase to the point that light becomes limiting. When light is available, phytoplankton production increases if flooding increases nutrient levels. Zooplankton abundance and biomass usually increase if detritus and phytoplankton concentrations increase. Flooding may deposit sediments at higher elevations and thereby enhance the potential of the upper portion of the fluctuation zone to support terrestrial or aquatic plants or burrowing species of benthos. After flooding, many species of benthos and fish rapidly colonize new areas, and fish growth may increase briefly in response to the temporary abundance of drowned terrestrial animals as food. The number and quality of sites available for spawning for many species of fish may change depending on the type of substrate inundated. Benson (1976) listed the spawning requirements of many important sport and commercial fishes, and similar information was provided by Carlander (1969, 1977). Survival of eggs and nests of sport fish such as black bass and crappies may be improved if cover is inundated; nests then are more sheltered from waves, and their defense is facilitated. Increased structural complexity made available by flooding has been associated with improved survival of young littoral fishes. Additional refuge and food account for positive correlations of year-class strength and growth of many fishes with extensive flooding of terrestrial areas.

Water-Level Changes--Effects and Management

122. Management of the fluctuation zone. Intensive management of the fluctuation zone is highly desirable for increasing biological productivity and enhancing fisheries. Because substrates exposed by

drawdown are vulnerable to erosion that may eventually create a barren nutrient-limited fluctuation zone, the early establishment of herbaceous terrestrial vegetation after drawdown is important for erosion control, aesthetic purposes, and nutrient retention. Herbaceous terrestrial plants established during drawdowns increase the availability of nutrients by removing them from sediments to form biomass. Inundated terrestrial plants significantly benefit aquatic plants by providing nutrients or substrates. They provide substrates, refuge, and food for many animals and spawning sites for many species of fish. Herbaceous vegetation also provides nursery habitat that can be expected to increase the survival of YOY sport fishes. When reflooded, vegetation-covered areas also are less apt to contribute to turbidity which is detrimental to spawning and foraging of some fish.

123. Drawdown must occur during the growing season for successful seeding of herbaceous terrestrial plants in fluctuation zones of reservoirs. The time of drawdown should allow for full development of vegetation before winter. Hulsey (1958) recommended drawdown by 15 September in Arkansas for plantings of rye. Groen and Schroeder (1978) also discussed planting of rapidly growing plants such as annual ryegrass, wheat, or rye during September or October after fall drawdowns in Kansas. Ryegrass was usually seeded at 11 kg ha^{-1} and wheat and rye at 34 to 68 kg ha^{-1}. For early drawdowns before August, Japanese millet and hybrid sudan-sorghum were also seeded successfully in fluctuation zones of Arkansas and Kansas reservoirs. Other herbaceous plants may be equally beneficial but have not been used extensively. Species of plants best equipped to grow in fluctuation zones vary with the region of the country, edaphic factors, and climate. In general, plants that grow rapidly and produce lush stands of vegetation within 1 to 3 months are most desirable.

124. Submerged structures (e.g., timber or artificial reefs) have been shown to provide substrates for periphyton and benthos communities and shelter that significantly concentrates fish, thereby increasing angler harvest. The productivity of periphyton-benthos communities on submerged structures increases the availability of food for fish. Structure may modify predator-prey relations of fish by providing refuge

or by decreasing the effectiveness of predator foraging. By manipulating water levels, managers may be able to decrease the structural complexity of shallow-water habitats (by dewatering areas with structure) and thereby increase the use of forage by predators. Conversely, they may be able to increase structural complexity and the survival of YOY sport fishes by inundating upper sections of the fluctuation zone.

125. In new reservoirs, timber should be retained in the fluctuation zone to provide habitat for littoral fish. Stands of timber perpendicular to shorelines and extending vertically through the entire fluctuation zone provide submerged structure at all water levels. Inverted triangular stands of timber or other structures that extend through the fluctuation zone provide more structure at high than at low elevations.

126. In older reservoirs where standing timber has deteriorated, artificial structures or fish attractors should be constructed in the fluctuation zone. Structures can be built or refurbished during drawdowns. They may consist of no more than three or four trees chained together and to the bottom, or they may be more elaborate, such as those described by Brouha and Prince (1973), Wilbur (1974), Prince et al. (1975), Wilbur (1978), Johnson and Stein (1979), and Pierce and Hooper (1979).

127. In large reservoirs where other essential uses prohibit the manipulation of water levels to benefit fishery resources, a potentially valuable alternative is the construction of inlet or subimpoundments of 40 to 200 ha. The idea is not new; subimpoundments were discussed by Ellis (1937) and inlet impoundments were studied by Grimås (1965) in Norway. Subimpoundments can be formed by building flood-control structures across large coves, embayments, or arms of reservoirs. Early views of subimpoundments held that they provided areas of stable water for fish reproduction or feeding. Small subimpoundments preserved some littoral areas but were insufficient mitigation for extensive water-level fluctuations. Subimpoundments do have potential for providing highly productive fisheries in parts of large fluctuating reservoirs where fisheries are limited by extensive fluctuations in water level. Water

levels in subimpoundments could be intensively managed by biologists to benefit fish or waterfowl.

128. Magnitude and frequency of water-level changes. The amount of bottom area affected by changes in water levels is determined by the vertical magnitude of changes and the shape of the reservoir basin. Direct effects of drawdowns on sediments, periphyton, macrophytes, benthos, and littoral fishes are largely a function of the amount of bottom exposed, and consequently, methods to estimate exposed area are valuable. For example, the amount of area exposed annually may be valuable as an independent variable in regression analysis because it can be directly related to changes in elevation or volume, which are important variables in current models for scheduling operations. Hildebrand et al. (1980) developed two methods to estimate the amount of area affected by water-level changes from (1) data on shore slope, (2) the vertical change in water levels, and (3) the length of shore of a given slope. A third method involved a simple geometric model and can be used when no detailed topographic data are available.

129. A simple index to the amount of littoral area affected by water-level changes is the change in surface area ($\pm$ dA). The index is positive when waters rise and negative when they decline. The index is easy to calculate from readily available data (standard area-capacity curves) and accounts for the effect of basin slope on the productivity of the littoral zone. Littoral areas generally are less well developed and less productive in steep-sided, deep reservoirs than in gently sloping, shallow reservoirs. The effect of a given change in water level on the littoral zone should be directly proportional to the amount of littoral area exposed. In steep-sided, deep reservoirs, the area of bottom exposed by a 2-m drawdown would be small, as would the change in surface area (probably $<$ 5 percent). The littoral zone may be completely eliminated, but the amount of littoral habitat and productivity lost should be low because of the steeply sloped shore areas. A 2-m drawdown in a shallow plains reservoir could reduce surface area by 20-30 percent.

The dA index would be negative and large, reflecting significant losses of productive littoral area. The effect of reflooding these areas should also be related to the index.

130. As discussed above, effects on littoral areas may be related to the amount of bottom area exposed if they result directly from water-level changes. However, if the impacts result indirectly from changes in habitat that accompany water-level changes, factors such as frequency, duration, and timing of water-level changes, as well as edaphic factors, must be considered.

131. Frequent (weekly or monthly) fluctuations in water levels should be avoided because they adversely effect periphyton, benthos, fish reproduction, and the survival of YOY fishes. The fluctuation zone of reservoirs with frequent fluctuations in water levels often become infertile because of erosion. Even long-term (1- to 3-year) changes in water levels would have a little positive effect on nutrients or trophic conditions if the fluctuation zone is infertile or devoid of vegetation. Rapid drawdowns are generally more harmful than slower ones because the time available for benthos or young fish to avoid exposure is shorter. Frequent fluctuations in water levels usually have little beneficial effect on nutrients or trophic conditions, because sediments are not significantly aerated and herbaceous plants do not have time to grow in the fluctuation zone. Flooding of rich stands of herbaceous vegetation can only increase productivity if the duration of flooding extends for 3 or more months of the growing season. Full use of vegetation as food requires time for colonization by bacteria, algae, and invertebrates. Although colonization of newly flooded areas is rapid during the growing season; it is far from immediate in reservoirs with frequent fluctuations, and the full development of algae, zooplankton, and benthos communities would not be complete by the time drawdown would eliminate them. Long periods of flooding (> 3 months) should provide more food and habitat for fish and insure that spawning success is not limited.

132. Drawdowns should last 2 or more months of the growing season (frost-free period) and reduce surface area sufficiently (about 50 percent in reservoirs < 200 ha and at least 20 percent in reservoirs > 200 ha) to improve the growth and condition of sport fishes by concentrating prey. Also, 2 months of low water probably is the minimum time required for predators to have a significant impact on populations of prey fishes (e.g., bluegills), or for lush stands of herbaceous vegetation to become established on suitable substrates in the fluctuation zone. Generally, large drawdowns are more effective than small ones in altering predator-prey interactions and eventually the species composition of fish, but only onsite sampling of fish communities can reveal the optimum magnitude and duration of a drawdown for a specific reservoir.

133. Timing of water-level changes. Drawdowns should be scheduled so that they do not adversely affect the reproductive success of fishes that spawn in littoral areas. In general, provision of high stable water levels during and for a month after the spawning season will not impair reproductive success. Furthermore, water levels should be steady or rising during spring and early summer (April-June) to benefit spring-spawning fishes or in fall (October-January) to benefit fall-spawning salmonids.

134. Evidence from warmwater impoundments suggests that year-class strength is influenced more by survival after spawning than by spawning success. Survival of YOY fishes usually can be improved greatly by maintaining high water levels for as long as possible after spawning is complete, especially if vegetation is present in the fluctuation zone. Because the provision of high water during summer is often restricted by peak demands for water for irrigation, consumptive uses (especially in arid regions), or for generation in hydropower reservoirs, the chances for enhancing the survival of YOY fishes by maintaining high water in summer is remote. However, annual recruitment of many sport fishes in reservoirs is sporadic, suggesting that high water maintained until late summer or fall every 3 to 5 years may be sufficient to produce strong year classes and to maintain quality sport fisheries.

135. Operational flexibility increases where a chain of reservoirs exists. Flexibility generally is directly related to the number of reservoirs in the system, at least for the lower reservoirs in a series. Every 2 years one reservoir in a series could be selected and managed for 1 or 2 years to significantly increase fish production and enhance fisheries. With appropriate scheduling, power and water demands could be made up by releases from other reservoirs. Age structure of fish populations and relations between prey and predator biomass (see methods of Swingle 1950; Jenkins and Morais 1976) should be examined to determine which reservoir would benefit most by intensive management. Impoundments with small populations of mostly older sport fish and few surplus prey would be prime candidates for treatment.

136. A general 2-year plan to manage water levels of non-salmonid reservoirs should include four essential elements:

(1) Drawdown in summer or fall.

(2) Establishment of herbaceous terrestrial vegetation (naturally or by planting) during periods of low water.

(3) Flooding of the drained zone and vegetation in spring.

(4) Maintenance of high water for as much of the growing season as possible.

Variations of this basic plan with regard to magnitude, duration, and time of water-level changes should be adequate to meet the specific needs of most conservation agencies. The Kansas Game and Fish Commission, for example, often limits the extent of drawdown to 10-20 percent of the original area, seeds vegetation extensively, and raises water levels slightly in fall to flood vegetation for waterfowl (Groen and Schroeder 1978). Management of flood-control reservoirs in Arkansas (Hulsey 1958) incorporated extensive drawdowns that reduced surface area by about 80 percent. Drawdowns in most reservoirs are best scheduled for late summer or fall because water temperatures are above 13° C and piscivores are still feeding intensively. Earlier drawdowns are not favorable to the reproductive success of fish that spawn in spring, and drawdown in winter does not permit the establishment of terrestrial vegetation in the drawdown zone.

137. Winter changes in water level have little impact on nutrient levels, oxygen concentrations, or planktonic biota. In winter, low water temperatures reduce rates of nutrient cycling, consumption, respiration, and production of organisms in all trophic levels. Because production is low in winter, rapid releases of water in winter probably would have a negligible effect on phytoplankton or zooplankton production. Inasmuch as feeding by warmwater fish is reduced in water less than about 13° C, significant use of prey by predators is unlikely.

138. Adverse effects of winter changes in water level may occur during that winter or be delayed until the next growing season. Impacts of winter drawdowns probably are most severe on aquatic macrophytes that are exposed and frozen, or on benthos, because the loss of early instars reduces the potential for high production in the next spring and early summer. Winter flooding of terrestrial areas may result in physical separation of detritus and leaching of nutrients, but the use of detritus and nutrients by biota will be low. Vegetation inundated in winter probably will be of less value as spawning and nursery habitat or as food in spring because of physical separation and leaching. Warmwater fish are more susceptible to entrainment and discharge from impoundments in winter than in other seasons because they are less active. In reservoirs with extensive and rapid drawdowns in winter, mortality of fish can be reduced by limiting the rate and extent of drawdown. Survival of eggs or YOY of salmonids spawned in fall may be significantly reduced by drawdown, as a result of stranding or loss of habitat. Development of eggs and fry is slow in cool water; consequently, their vulnerability to potentially adverse conditions is prolonged. The maintenance of stable water levels until YOY fish are able to migrate is essential to the production of strong year classes. If water levels must be lowered, they should be lowered slowly in late winter.

139. There are three primary reasons for intensively managing reservoirs for 1 or 2 years at 3- to 5-year intervals. First, intensive management for 1 or 2 years should do more to increase the primary and secondary production as well as the recruitment of fish than provision of moderately beneficial water levels every year; most reservoir fishes

have evolved boom-and-bust patterns of recruitment, developing strongly during periods of extensive flooding and weakly during periods of drought. Second, by managing water levels every 3-5 years, the necessity of providing water levels suitable for spawning every year is eliminated. Third, improved trophic conditions for invertebrates and fish that result from high inflows and flooding of terrestrial vegetation generally are short-lived because sources of readily available nutrients and detritus are exhausted within 1-2 years. Consequently, even with the most favorable management regime, managers cannot expect to increase fish standing crops for more than 1-2 years.

140. Major perturbations of reservoirs every 3-5 years can be beneficial to sport fish. In unperturbed reservoirs, the biomass of many forage fish is in the form of large fish that are available as food only for large predators. Although high densities of large forage fish require enormous amounts of energy annually, they contribute little to sport-fish production. By perturbing reservoirs with large drawdowns for 3 or more months and then flooding terrestrial areas for 3-5 months of the next growing season, the efficiency of the trophic system can be increased. Populations of larger forage fish should be reduced, and the reproductive success of all fish should be enhanced. Fall drawdowns may force small forage fish from cover and increase the availability of food for YOY and yearling predators at a time when many of the available forage fish have grown too large for them to swallow. Flooding should enhance reproductive success, thereby providing more young fish of a forageable size. Although data are sparse, some evidence suggests that multiple spawnings of gizzard shad (the primary forage fish of most reservoirs) may be produced by brief periodic increases in water levels between June and September (Domermuth and Dowlin 1975; Groen and Schroeder 1978). More research is needed to confirm this phenomenon in other reservoirs, but there is no question that multiple spawns of gizzard shad would be desirable to increase the availability of small forage for young predators late in the growing season.

141. Management plans occasionally are unsuccessful in improving fishery resources because unforeseen factors complicate management of water levels (e.g., excessive drought or flooding). They may fail because the recruitment of fish is poor as a result of stormy weather or low water temperatures during most of the spawning period. The abundance of prey may be low, or large populations of predators may overrun their prey base. Variables such as storms and adverse temperatures are obviously beyond man's control, but provisions of desirable conditions for fish feeding, spawning, and survival should greatly increase the chances of improving fisheries when the uncontrollable variables are favorable.

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