Chapter 17

Large Reservoirs

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17.1 INTRODUCTION

Large impoundments, defined as those with surface area of 200 ha or greater, are relatively new aquatic ecosystems in the global landscape. They represent important economic and environmental resources that provide benefits such as flood control, hydropower generation, navigation, water supply, commercial and recreational fisheries, and various other recreational and esthetic values. Construction of large impoundments was initially driven by economic needs, and ecological consequences received little consideration. However, in recent decades environmental issues have come to the forefront. In the closing decades of the 20th century societal values began to shift, especially in the developed world. Society is no longer willing to accept environmental damage as an inevitable consequence of human development, and it is now recognized that continued environmental degradation is unsustainable. Consequently, construction of large reservoirs has virtually stopped in North America. Nevertheless, in other parts of the world construction of large reservoirs continues.

The emergence of systematic reservoir management in the early 20th century was guided by concepts developed for natural lakes (Miranda 1996). However, we now recognize that reservoirs are different and that reservoirs are not independent aquatic systems inasmuch as they are connected to upstream rivers and streams, the downstream river, other reservoirs in the basin, and the watershed. Reservoir systems exhibit longitudinal patterns both within and among reservoirs. Reservoirs are typically arranged sequentially as elements of an interacting network, filter water collected throughout their watersheds, and form a mosaic of predictable patterns.

Traditional approaches to fisheries management such as stocking, regulating harvest, and in-lake habitat management do not always produce desired effects in reservoirs. As a result, managers may expend resources with little benefit to either fish or fishing. Some locally expressed effects, such as turbidity and water quality, zooplankton density and size composition, or fish growth rates and assemblage composition, are the upshot of large-scale factors operating outside reservoirs and not under the direct control of reservoir managers. Realistically, abiotic and biotic conditions in reservoirs are shaped by factors working inside and outside reservoirs, with the relative importance of external factors differing among reservoirs.

With this perspective, large reservoirs are viewed from a habitat standpoint within the framework of a conceptual model in which individual reservoir characteristics are influenced by both local- and landscape-scale factors (Figure 17.1). In the sections that follow, how

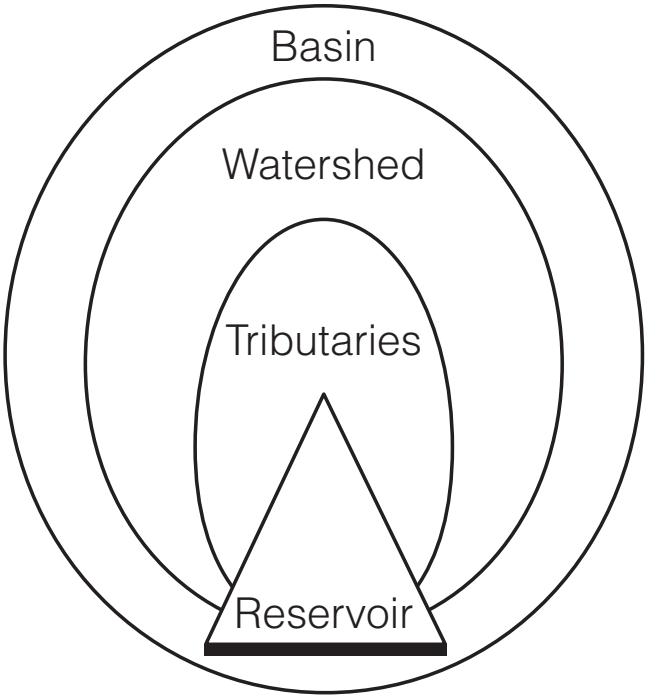

Figure 17.1. Abiotic and biotic conditions in reservoirs are shaped by factors working inside (section 17.3) and outside the reservoir (tributaries, section 17.4; watershed, section 17.5; and basin, section 17.6), with their relative importance differing among reservoirs.

each element of this hierarchical model influences habitat and fish assemblages in reservoirs is considered. Important in-reservoir habitat issues and reservoirs as part of larger systems, where reservoir management requires looking for real solutions outside individual reservoirs are described

17.2 THE DIVERSITY OF RESERVOIRS

The geographic distribution of reservoirs reflects a complex interaction among topography, climate, and economic needs to control water passage through river basins. Some large river systems have been transformed into chains of reservoirs by stacking reservoirs in sequence. Altogether, there are over 2,000 large reservoirs in the USA, and most are described as multipurpose (NID 2008). The uses of these reservoirs include hydropower (26.9%), irrigation (16.4%), water supply (16.3%), recreation (15.7%), flood control (13.0%), navigation (6.3%), or other uses (5.4%). Canada boasts several of the world's largest reservoirs, particularly in the eastern provinces of Quebec (e.g., Manicouagan Reservoir; 195,000 ha), Newfoundland, and Labrador (e.g., Smallwood Reservoir; 652,700 ha). Most (78%) of the large dams built in Canada have been constructed for hydropower (Prowse et al. 2004); dams built to aid navigation or control flooding are far less common in Canada than they are in the USA. The James Bay Project in northwestern Quebec is one of the largest hydroelectric projects in the world. In fact, hydroelectric dams meet nearly all of Quebec's electrical needs, and they often produce electricity to export to the USA. In the United Mexican States (Mexico),

from the arid north to the subtropical south, the Mexican government has built a patchwork of dams, primarily for irrigation and power generation, that supply nearly 30% of the energy flowing on the nation's electric power grid (Robinson 2000).

Marked patterns in the geographic distribution of large reservoirs in North America are evident. In general, hydropower reservoirs are regionalized in mountainous areas (e.g., the western slopes of the Rocky Mountains, Cascade Mountains, and Sierra Nevada) and along the edge of the Laurentian Plateau (i.e., the Canadian Shield). Precipitation and topography in these areas provide ideal inflows and required head conditions to generate hydropower. Irrigation reservoirs in the USA are common in drier areas of the central plains and the western coastal valleys. Irrigation reservoirs in the central plains have low-relief topography and are often shallow and turbid owing to the effects of wind action and inputs from highly-erodible soils. Demands for drinking and industrial water in densely populated areas have led to the development of water supply reservoirs throughout the arid central and populated eastern USA and near urban centers in western coastal regions. Flood control reservoirs have been constructed in areas where strong, short-duration rainfall events and allied runoff are common, especially in the central USA. Maintaining navigable channels for transportation has encouraged the impoundment of low-gradient rivers to retain passage throughout most of the year in the western (e.g., Columbia and Snake rivers) and central USA (e.g., Mississippi, Missouri, and Tennessee rivers). Normally, reservoirs in the USA constructed for navigation and hydropower tend to be very large due to their location on large rivers. Some large hydroelectric reservoirs in Canada have been created not by a single dam on a large river, but by damming the outflow of natural lakes and impounding other lakes in the watershed (e.g., Caniapiscau Reservoir in Quebec). Other large Canadian hydroelectric reservoirs have been created by building dikes to flood numerous lakes in a watershed to create a single, large reservoir (e.g., 88 dikes spanning 64 km created Smallwood Reservoir in Labrador).

A reservoir's purpose has much to do with how its water regime is operated (Kennedy 1999). Hydropower and navigation uses require that reservoirs be maintained near 100% of the storage capacity and no less than about 70%. Hydropower is most efficient at maximum hydraulic head, whereas navigation, which often occurs in shallow channels, requires stable water levels. Water level fluctuations are often minimal and may exhibit diel patterns. Although there is great variability, reservoirs with their main purpose being water supply for agriculture are generally maintained between 40% and 80% of their maximum capacity. Water level often varies on a scale of years, as the reservoir may be used to store water during wet years to compensate for dry years. Conversely, flood control reservoirs experience seasonal drawdowns to 10–30% of capacity due to their requirement to store excessive runoff. Water levels in flood control reservoirs generally follow sharp annual patterns.

Large impoundments may also be classified as tributary storage, main-stem storage, or run-of-river reservoirs (Table 17.1). Tributary storage reservoirs are generally located on low-order, high-gradient streams and are often small to moderate in surface area because they have relatively small watersheds. Main-stem storage reservoirs provide moderate to large storage capacity and are impounded on mid-order rivers. Because they inundate more of the floodplain than do tributary storage reservoirs, main-stem storage reservoirs tend to have more shallow littoral areas. Run-of-river reservoirs often occur in series over hundreds of kilometers and are most common on large rivers; therefore, run-of-river reservoirs are typically shallow with low retention time. These reservoirs tend to be long and narrow, with minimal lateral expansion. Tributary storage reservoirs are generally deep relative to their area, presenting vertical abi-

Table 17.1. Physical and operational characteristics of tributary storage, main-stem storage, and run-of-river reservoirs. Peaking hydropower differs from baseline hydropower in that water is released (and electricity is generated) for short periods of time when demand on the regional power grid peaks, typically in the morning and early evening. Peaking hydropower is also available to supply electricity quickly to a power grid in the event of a problem or emergency shutdown at a baseline power production facility (e.g., a coal-fired plant or nuclear facility).

	Reservoir type		
Attribute	Tributary storage	Main-stem storage	Run-of-river
Primary uses	Peaking hydropower flood control	Navigation, hydropower flood control	Navigation, hydropower flood control
Basin morphology	Steep banks; deep basin; small littoral zone	Expansive overbank (littoral areas); relatively shallow	Long and narrow
Typical water retention time	Months or years	Weeks	Days
Water level fluctuations	Large	Modest	Slight

otic and biotic diversity. In contrast, run-of-river reservoirs can be much larger in surface area (although perhaps not volume), tend to be shallow relative to their area, and show longitudinal diversity. Main-stem storage reservoirs are intermediate in diversity relative to vertical and longitudinal gradients. It is important to know why a particular reservoir was built and how it is operated because fish habitat and primary production are profoundly influenced by reservoir operations. Also, it is important to understand that promoting recreational or commercial fisheries is usually not the reason why large reservoir projects were proposed, funded, and built. This fact implies that reservoir fisheries management usually occurs within constraints imposed by uses that take priority over fisheries.

As much as possible, considering the vagaries of precipitation, reservoir operators follow pre-established guide curves, which dictate what the water level should be on each day of the year (Figure 17.2). Guide curves are formal (often legal) descriptions of where the water level in a given reservoir should be on any given day of the year to meet the reservoir's primary purposes (e.g., flood control, power generation, or navigation) within the constraints posed by droughts, floods, and other unforeseen circumstances. Regional authorities or regulatory bodies such as the U.S. Army Corps of Engineers, U.S. Bureau of Reclamation, and Tennessee Valley Authority (TVA) develop guide curves to optimize water storage benefits among reservoirs in a river basin. For instance, the TVA manages 41 reservoirs on the main-stem Tennessee River and its numerous tributaries, and the operations of each dam affect the operations of other dams in that system.

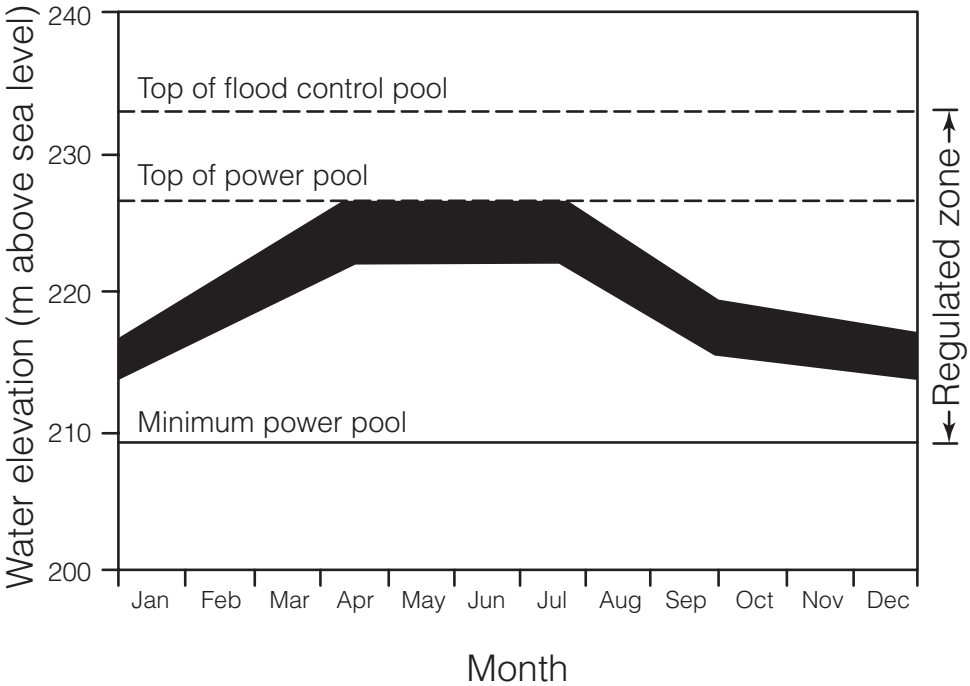

Figure 17.2. Guide curve for a hypothetical tributary storage impoundment. The shaded polygon is the guide curve, and it represents the range of water elevations that are targeted on each day of the year and is established to meet local and regional demands for hydropower, flood control, navigation, and recreation. Extreme floods or droughts can move actual reservoir elevations outside the guide curve.

The geographical, hydrological, and morphological diversity of reservoirs has created a diversity of fish assemblages and fisheries. Most fishes that flourish in reservoirs are generalists and have wide native distributions. Salmon, important to western reservoirs (mainly coho salmon, sockeye salmon, and Chinook salmon), are native to the western states. Trout are also important to western reservoirs and have been introduced into selected deep eastern U.S. reservoirs. Native trout in western reservoirs include mainly cutthroat trout and rainbow trout; introduced trout include brook trout (native to the central and eastern USA), lake trout (native to northern North America), and brown trout (native to Europe). Other major fishes in reservoirs are native to the central and eastern parts of North America but have been introduced into many western reservoirs. In fact, reservoir fisheries in the southwest are maintained mainly or entirely by species introduced from east of the Rocky Mountains. Two species, northern pike and muskellunge, and their hybrid (tiger muskellunge) support most of the esocid fisheries in reservoirs, but these species are mostly absent from southern U.S. reservoirs. Percids, which include walleye and sauger, that are native to the central states west of the Appalachian Mountains and their hybrid, the saugeye, have been introduced into many Midwest reservoirs. Another percid is the yellow perch, which is native to the northern portions of North America, although native populations can also be found east of the Appalachian Mountains and in some southern reservoirs. Catfishes include the *Ameiurus* species that are native east of the Rocky Mountains, and the *Ictalurus* and *Pylodictis* catfishes that are native to central North America west of the Appalachian Mountains and east of the Rocky

Mountains, although they have been introduced elsewhere. Of four *Morone* species, in general two are limited to central drainages (white bass and yellow bass), one to Atlantic drainages (white perch), and one to Atlantic drainages and Gulf of Mexico drainages east of the Mississippi River (striped bass), although striped bass and white bass have been introduced in the west coast. Both hybrid crosses between the striped bass and white bass (palmetto bass and sunshine bass) are commonly introduced into southern reservoirs. Of the centrarchids, several species of sunfishes, three species of black basses, and both species of crappies contribute to reservoir fisheries in North America. Distributions of centrarchid species appear to be influenced largely by latitude, the Rocky Mountains, and the Appalachian Mountains. Representation of these major groups of fishes in reservoir fisheries vary geographically as well as within geographical regions due to peculiarities associated with the different types of reservoirs (Miranda 1999).

Considering reservoir fish assemblages from a trophic perspective, fishes in North American reservoirs are often organized into herbivore, detritivore, planktivore, invertivore, and carnivore guilds. Many species operate in multiple trophic guilds as their niche shifts over life history stages or their diets shift due to changes in prey availability. Representation by these groups varies greatly among reservoirs depending on abiotic characters of reservoirs (Miranda et al. 2008). In warmwater reservoirs the most abundant species in term of biomass are usually filter-feeding herbivores–detritivores (e.g., gizzard shad) and planktivores (e.g., threadfin shad). Other guilds common to warmwater reservoirs include invertivores–carnivores (e.g., black basses, crappies, and catfishes), invertivores (e.g., sunfishes and minnows), invertivores–detritivores (e.g., common carp), invertivores–herbivores (e.g., buffaloes), planktivores, carnivores (e.g., gars), and detritivores–planktivores (e.g., carpsuckers).

17.3 THE RESERVOIR

In-lake characteristics of reservoirs exert major influences on fish assemblages and fisheries. Many chemical, physical, and biological factors characterize reservoirs, and their relative importance varies geographically. Some of the most universal influences include suspended sediments and sedimentation, nutrients and water quality, water retention and fluctuation, and submerged structure and vegetation. Moreover, many of these factors show marked longitudinal variation along the length of a reservoir.

17.3.1 Suspended Sediments and Sedimentation

Suspended sediments enter reservoirs principally through tributaries but also through overland runoff from their watersheds. Sedimentation typically occurs in natural lakes on a geologic time scale, but it occurs much faster (i.e., over several decades) in reservoirs. This effect is due to differences in incoming volumes of water caused by differences in watershed sizes—given a lake and a reservoir of similar size, the watershed for the reservoir will almost always be larger. That is, the ratio of watershed area to water surface area will usually be higher (sometimes several times higher) for reservoirs because reservoirs are designed to capture as much water as possible by means of the smallest possible dams.

Reservoirs are efficient sediment traps. As sediments settle, they alter the surface of coarse rock substrates into a homogenous surface of fine silt and clay particles. In fact, depending on the geology of the watershed and basin morphology, the useful lifespan of tributary storage

reservoirs (where retention times are high) may be measured in decades or a few centuries because of sediment accumulation. Extreme examples of sedimentation problems in reservoirs can be found in Africa, Australia, and Puerto Rico, where humid tropical environments and highly erodible soils promote high sedimentation rates and storage capacity losses exceeding 1% per year. Sedimentation is a major concern of reservoir fisheries managers because lithophilic fishes (i.e., those that prefer rock substrates for spawning or feeding) will eventually decline in abundance and be replaced by species with broader habitat requirements. The "carpeting" of reservoir substrates by layers of fine sediment eliminates substrates for invertebrates and periphyton, both of which are important biotic components of reservoir food webs. Of all the processes regulating reservoir aging, sedimentation is perhaps the most dominant.

As reservoirs age, sedimentation and shoreline erosion produce a loss of littoral habitat. Within a few years after impoundment, aging is apparent in the littoral zones (Agostinho et al. 1999). Reservoir aging received scant attention from fisheries managers before the 1970s, perhaps because the construction of new reservoirs proceeded at a rapid pace between the 1920s and 1960s, and new reservoirs, along with "boom" fisheries, were constantly coming on line. The 1950s and 1960s were considered the "golden age of dam building" in the USA (Doyle et al. 2003). Robert Jenkins, an early pioneer of reservoir ecology, was one of the first to note that sport fish harvest was inversely related to reservoir age (Jenkins 1967). In many parts of North America it was easy for anglers dissatisfied with the fishing in an "old" reservoir experiencing trophic depression to travel to a new nearby reservoir to exploit fisheries in the boom phase associated with trophic upsurge (see section 17.3.2). However, construction of large reservoirs in the USA declined precipitously in the 1970s because dams had been constructed at most prime reservoir construction sites. Although new, large reservoir projects in the USA are now relatively rare, construction of large reservoirs in other parts of the world is proceeding at a rapid pace, particularly in developing countries such as China and Turkey (World Wildlife Fund 2004), as well as in remote regions of Canada (e.g., northern Quebec, Manitoba, and Northwest Territories), which may be experiencing a golden age of large reservoir projects (Prowse et al. 2004). Mexico began building dams in the late 1930s and continued at a fast pace until the 1980s, but large dams are still being constructed in that country. Given the current prevalence of aging reservoirs in the USA (and in the future in Canada and Mexico), fisheries managers can no longer rely on new reservoirs to satisfy the demand for quality fishing. Instead, managers will have to rely on innovative ways to manage the habitat, the fish assemblage, and the fisheries in aging reservoirs.

Sediments and suspended fine materials can have a major influence on fish assemblages that develop in reservoirs or individual embayments of reservoirs. Suspended fine materials can limit light penetration and photosynthesis, diminish plant biomass, alter zooplankton assemblages, reduce visibility, reduce fish growth, decrease fish size at sexual maturity, limit maximum fish size, and produce a shift in habitat use by fishes (Bruton 1985). The influence of suspended fine materials entering reservoirs is exacerbated by loss of depth from sedimentation. Loss of depth encourages resuspension of sediments through wave action (Hamilton and Lewis 1990) as well as through stirring action by benthivorous fishes searching for food (Scheffer 2001). Decreases in water clarity driven by suspended fine materials interfere with the feeding of large zooplankton but not of smaller zooplankton such as rotifers (Kirk and Gilbert 1990), favoring dominance by small zooplankton and fish that feed on small zooplankton. Excessive sedimentation and suspended fine materials also reduce benthic production, which is reflected by diminished representation of fishes that depend on benthic plants or invertebrates.

Foraging by visual piscivores is limited in turbid reservoirs, such that their representation in fish assemblages declines. However, tactile, nonvisual species that forage by ingesting sediment often thrive, including common carp, adult gizzard shad, some catfishes, and buffaloes. Turbid environments may also allow prey fishes to expand because turbidity decreases vulnerability to predation. In advanced stages of sedimentation, fish assemblages in reservoirs generally include few predators and many species that thrive in turbid, shallow systems.

17.3.2 Nutrients and Water Quality

Another major factor influencing reservoir function is nutrient loading (i.e., the amount of nutrients entering the water body). Kimmel and Groeger (1986) were among the first to describe in limnological terms what fisheries managers had long known, namely, that the quality of sport fisheries and overall fish production are initially high after dams are closed but decline after a decade or so. Part of the decline can be attributed to loss of high-quality habitats due to sedimentation, but much of the decline can be attributed to changes in internal nutrient loading. Internal nutrient loading refers to organic detritus and inorganic nutrients liberated following inundation of soils and terrestrial vegetation. Conversely, external nutrient loading refers to input of nutrients into reservoirs that originated from outside reservoirs; that is, externally loaded nutrients are carried downstream into reservoirs by tributary streams or overland from surrounding watersheds. Both forms of nutrient loading are important, but it is the internal nutrient loading flux that drives the characteristic boom–bust fisheries among new reservoirs. As depicted in Figure 17.3, rates of external nutrient loading remain essentially unchanged in the absence of human-induced changes in watersheds. Changes in the rates of internal nutrient loading assume overarching significance to fisheries managers because of the tight linkage between nutrient concentrations (principally nitrogen and phosphorous), fish biomass, and production.

The limnology of reservoirs is greatly affected by trophic state, which ultimately refers to the amount of primary production in a reservoir during a particular time, usually summer. Primary production can be represented by rooted or floating macrophytes or, more commonly, microscopic algae in the water column (i.e., phytoplankton). Reservoirs fall along a trophic state continuum ranging from unproductive (oligotrophic) to moderately productive (mesotrophic) to extremely productive (eutrophic or hypereutrophic). Trophic state refers to primary production but also provides insight into how productive a particular water body will be in terms of fish. Classifications of reservoir trophic state diverge from lake-based classification schemes that rely on the presence or absence of oxygen in the hypolimnion. For instance, it is not uncommon for oligotrophic reservoirs to have depleted concentrations of dissolved oxygen in the hypolimnion (which indicates eutrophy in natural lakes) because they experience high rates of nutrient and sediment loading.

Several indices of trophic state based on readily obtainable water quality data are used to describe the trophic state of reservoirs. Two of the most widely used are those by Carlson (1977) and Forsberg and Ryding (1980). Both indices assign trophic states according to the algal biomass present during summer (indexed by chlorophyll-*a* biomass), the concentrations of key nutrients (phosphorous and nitrogen), and water transparency as measured with a Secchi disk (Table 17.2). Chlorophyll *a* is a photosynthetic pigment common to all photosynthetic organisms in freshwater (e.g., green algae, diatoms, and cyanobacteria); thus, high levels of chlorophyll *a* (the most common form of chlorophyll) in a filtered water sample generally equates to high standing crops of algae.

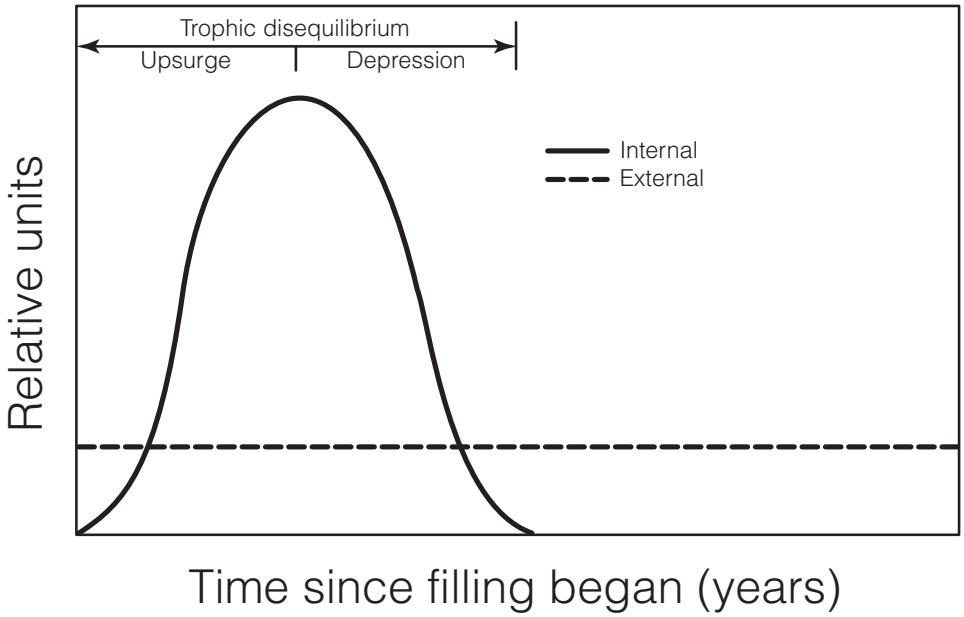

Figure 17.3. The "boom-and-bust" aspect of most reservoir fisheries is driven in large measure by fluxes in nutrient loading; specifically, internal nutrient loading. Rates of primary production and fish production will lag slightly behind the pulse in internal nutrient loading. External nutrient loading rates will remain unchanged in the absence of any cultural eutrophication activities (Adapted from Kimmel and Groeger 1986).

Table 17.2. Trophic state classification scheme proposed by Forsberg and Ryding (1980). Nitrogen (N), phosphorous (P), and chlorophyll-*a* concentrations are expressed in mg/m^3; water transparency is expressed as Secchi disk depth in m. To account for chlorophyll and nutrients sequestered in aquatic macrophytes, see Canfield et al. (1983).

Trophic state	Total N	Total P	Chlorophyll *a*	Transparency
Oligotrophic	<400	<15	<3	> 4.0
Mesotrophic	400–600	15–25	3–7	2.5–4.0
Eutrophic	600–1,500	25–100	7–40	1.0–2.5

Hypolimnetic oxygen concentrations are not used to assign reservoirs to a particular trophic state; nevertheless, the depiction of dissolved oxygen (DO) and water temperature in a vertical profile tells a great deal about a reservoir's trophic state. In particular, DO–temperature profiles show what habitat (especially offshore) is available to fishes with differing DO and thermal preferences and tolerances. Clinograde DO profiles (Figure 17.4, panel A) are common in eutrophic reservoirs and result from high DO consumption in the hypolimnion due to excessive biological oxygen demand (e.g., algal respiration and decomposition of organic matter), chemical oxygen demand (e.g., anoxic groundwater containing reduced chemicals such as Fe+2 will lower DO concentrations), or both processes. Heterograde curves can be either positive or negative depending on whether or not the metalimnion, with its higher phytoplankton concentration, is in or out of the photic zone. The metalimnion (also known as the thermocline) serves as a barrier to mixing between the warm epilimnion and colder hypolimnion; differences in density of water at different temperatures slow the settling of phytoplankton and leads to their accumulation in the metalimnion. The photic zone refers to the layer of water where photosynthesis can occur; it extends from the surface down to a depth where light intensity is approximately 1% of that at the water's surface. In Dale Hollow Reservoir (Figure 17.4, panel B) water clarity is sufficient to allow photosynthesis as deep as 10 m (and oxygen is generated by photosynthetic activity in the metalimnion). However, in Center Hill Reservoir (Figure 17.4, panel C) phytoplankton accumulated in the metalimnion cannot photosynthesize because too little light reaches that depth; thus, oxygen is consumed via bacterial decomposition and algal respiration. It is common in mesotrophic reservoirs for zones of hypoxia to extend up from the bottom and merge with hypoxic metalimnetic waters in late summer and early fall (before fall overturn), resulting in clinograde DO profiles. In riverine reservoirs with short retention times turbulent flows prevent strong stratification. The water column remains mixed throughout the year, so water temperatures are nearly isothermal and DO concentrations usually vary little from top to bottom.

The amount of DO available in the water column does not fully describe how much (or where) habitat is available to reservoir fishes. Being poikilothermic, all fishes exhibit preferences for a particular range of water temperatures that is mediated by numerous factors such as fish size, genetics, and acclimation state. The thermal acclimation state of a fish refers to the physiological status it assumes in response to the thermal environment it inhabits. The environment (e.g., presence of structure) also mediates temperature selection (Bevelhimer 1996). Eurythermic species such as centrarchids are capable of occupying waters with broad ranges of temperatures and DO concentrations relative to stenothermic species such as salmonids. Nevertheless, all fish species will perform best bioenergetically at particular temperatures and with some minimum DO. When habitats with optimal combinations of temperatures and DO are not present or availability is limited, fish will experience a "temperature–DO squeeze," a long-recognized concept in reservoir fisheries management (Coutant 1985). To visualize how much habitat is available to coolwater fishes such as striped bass, a profile of temperatures in summer (when habitat is most limited) can be overlain onto a DO profile (Figure 17.5). For example, Zale et al. (1990) noted that striped bass in an Oklahoma reservoir selected the coolest water where DO concentrations were at least 2 mg/L; if the temperature in that layer was 27–28°C for more than 1 month, fish would die (at warmer temperatures they would die sooner).

The temperature–DO squeeze phenomenon is not limited to coldwater or coolwater species. Hale (1999) observed the occurrence of late-summer growth depression of crappies that

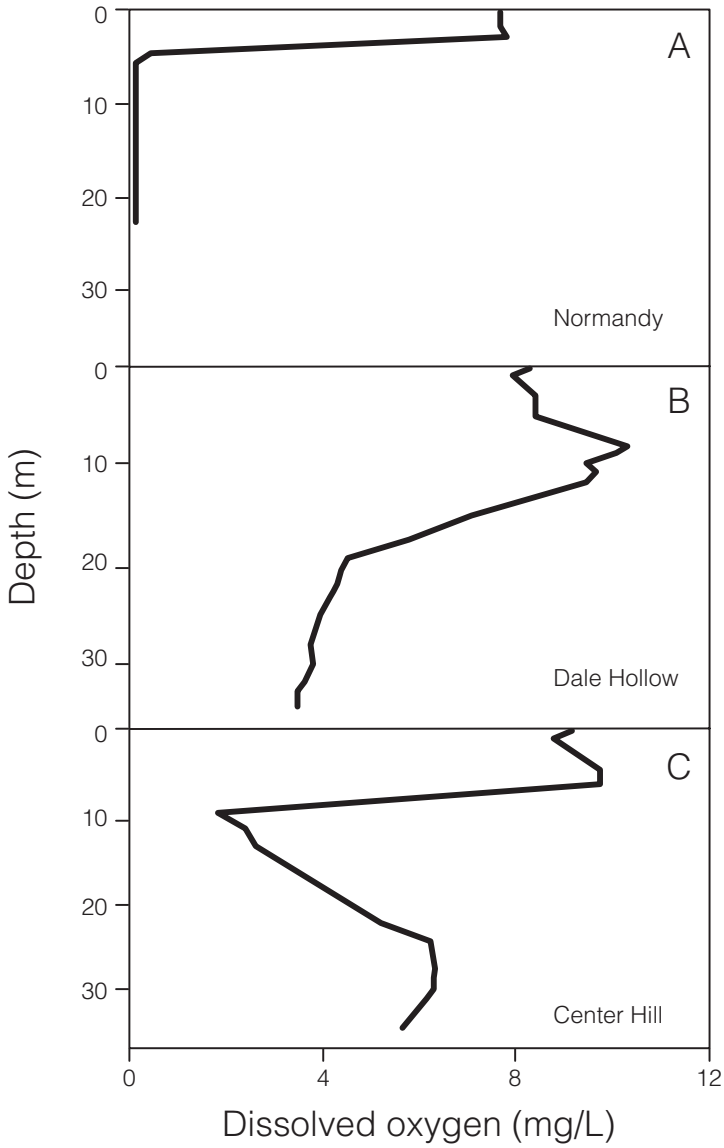

Figure 17.4. Midsummer dissolved oxygen profiles for three middle Tennessee reservoirs exhibiting **(A)** a clinograde curve, **(B)** a positive heterograde curve, and **(C)** a negative heterograde curve. Note that panels (B) and (C) also reveal the presence of oxygen-consuming processes in the hypolimnion.

were forced by low DO concentrations to inhabit water too warm for growth in a Kentucky reservoir. The problems experienced by crappies and other species forced to inhabit waters that are either too warm or too cold can be explained with bioenergetics principles (e.g., Hayward and Arnold 1996). The thermal preferences and tolerances of most freshwater fish species that occur in reservoirs have been described. Conversely, the specific DO requirements of fishes are not understood nearly as well as their temperature requirements; however, U.S. Environmental Protection Agency and state or provincial water quality standards for DO are typically around 5 or 6 mg/L. All fish species can tolerate low DO concentrations for short

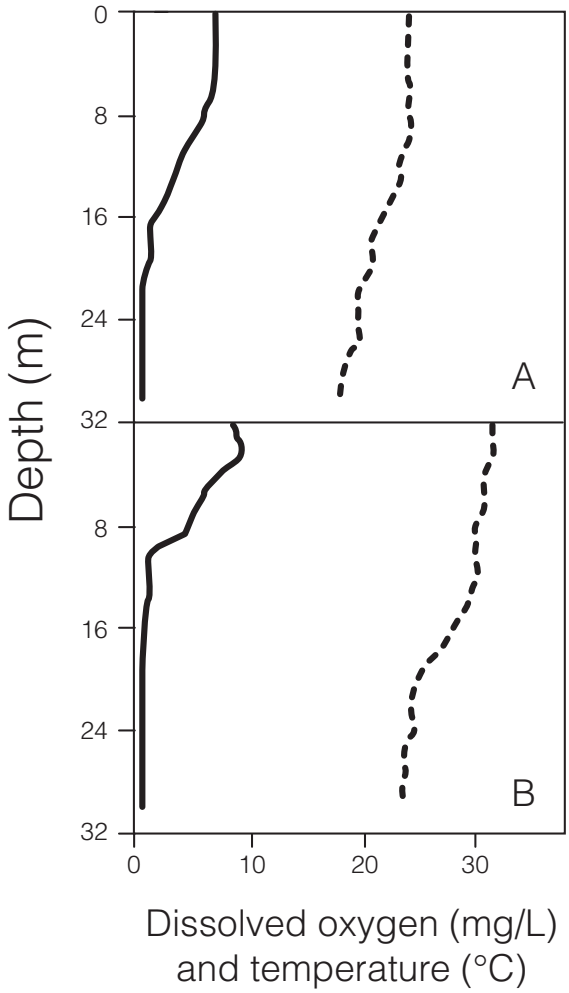

Figure 17.5. Dissolved oxygen (solid line) and temperature (dashed line) profiles in the forebay of Lake Texoma, Oklahoma–Texas, 2003, a eutrophic reservoir with a naturally-reproducing population of striped bass. Good habitat for large (>5 kg) striped bass (defined as water cooler than 25°C with at least 2 mg DO/L) is restricted to the upper 15 m of the water column in June **(A)**. By August **(B)**, the coolest water with at least 2 mg DO/L is 27.8°C; thus, there is no good habitat for large striped bass in the reservoir forebay by midsummer. Reservoirs with similar water quality can support exceptional fisheries for small striped bass because they tolerate warmer temperatures, but the lack of cool, well-oxygenated water will limit the abundance of large adults. (Data courtesy of Matt Mauck, Oklahoma Department of Wildlife Conservation).

periods of time (coldwater species less so than warmwater species), but the physiology and health of a fish will be compromised if it is forced to inhabit waters with less DO than it requires to meet minimum metabolic needs, which will vary among species.

If well-oxygenated, cold (<20°C) water is present in a reservoir, the ability to develop and maintain a "two-story" fishery is available to fisheries managers, especially in deep storage impoundments in the lower latitudes of North America. A classic two-story reservoir fishery consists of warmwater species (e.g., centrarchids and ictalurids) inhabiting the warm epilim-

nion and coldwater species (salmonids) inhabiting the cold hypolimnion. Spawning habitat for salmonids is often lacking in reservoir environments and many salmonid fisheries are supported wholly by stocking programs. Black bass, crappie, and sunfish populations are usually self-sustaining in two-story fisheries. In practice, two-story fisheries are often managed as three-story fisheries because the thermal and oxygen requirements of coolwater species such as walleyes, muskellunge, and striped bass are usually present in two-story reservoirs. As with salmonids, such coolwater species may not be able to reproduce and may have to be maintained through stocking (see Chapter 9). The advent and popularity of two-story fisheries beginning in the 1950s and 1960s served to justify the indiscriminate stocking of coldwater prey fishes to satisfy new predator demands, often with unexpected consequences. For instance, the introduction of alewives into many eastern U.S. water bodies (as prey for percids and salmonids) invariably led to the collapse of some native fisheries via mechanisms that are still being debated, such as competition with, or predation on, early life history stages of sport fishes (Brooking et al. 1998) and dietary deficiencies when alewives are the primary forage (Honeyfield et al. 2005). Introductions of rainbow smelt to serve as a coldwater prey species have caused similar problems; for instance, their introduction into a Colorado reservoir to boost growth rates of walleyes and smallmouth bass ultimately led to recruitment failure by walleyes (Johnson and Goettl 1999). Fisheries managers at the present time are unlikely to stock coldwater prey species to improve growth rates by sport fishes when the specter of such negative consequences exists; unfortunately, many prey species that *could* be stocked *were* stocked through the 1990s, and managers now have little control over the species assemblage present in a particular reservoir.

The discussion of trophic states in reservoirs is important to fisheries managers because the amount of fish biomass a system can support is linked to its primary productivity (i.e., trophic state). Researchers have investigated the relationship between surrogate measures of trophic state (e.g., phosphorous or chlorophyll-*a* concentrations) and fish biomass in and harvest from reservoirs. Some of the earliest work focused on the relationship between Canadian fisheries and the morphoedaphic index (MEI), which incorporated a measure of a system's nutrient availability and its ability to process those nutrients (Ryder 1965). Specifically, the MEI was the ratio of total dissolved solids (mg/L) over mean depth (m). Despite many field investigations and published papers, the MEI eventually fell out of favor because of statistical concerns over the spurious correlations between ratios and their denominators (Jackson et al. 1990). Nevertheless, early work on MEI spurred research into the statistical relationship between indices of primary production and fish biomass and harvest. For instance, Jones and Hoyer (1982) explained more than 80% of the variability in biomass of sport fish harvest in midwestern U.S. lakes and reservoirs as a simple linear function of chlorophyll-*a* concentrations. Yurk and Ney (1989) explained 75% of the variation in fish community standing crops in southeastern reservoirs as a function of the concentration of phosphorous. The 1980s was a period when the paradigm of fisheries management (especially in reservoirs) shifted (Rigler 1982), and fish populations were no longer viewed or managed as separate entities in aquatic ecosystems but as components of complex systems; such research is now commonplace around the world (e.g., Gomes et al. 2002). Reservoir fisheries biologists need to be aware of the relationships between limnology, trophic state, and fisheries because it is likely that reservoirs they manage will undergo shifts in trophic state through time on a human scale. A solid working knowledge of these relationships allows biologists to communicate with environmental engineers and others tasked with maintaining quantity and quality of water to meet societal needs.

The fear that all freshwater systems were in danger of undergoing cultural eutrophication (i.e., the addition of nutrients into a water body due to direct human action) was one of many catalysts to the U.S. Clean Water Act of 1972. Although early stages of eutrophication may enhance fish growth and biomass and seem to be desirable from a fisheries perspective (i.e., more nutrients = more fish), water quality changes associated with higher trophic states (e.g., hypoxia, denser algal blooms, reduced water clarity, and altered fish fauna) usually argue against promoting higher trophic states because of changes in fish food habits, spatial distribution, and community composition. In fact, extreme cases of hypereutrophication promote dense, noxious algal blooms that can cause fish kills. Moreover, phytoplankton communities in eutrophic reservoirs can shift from domination by green algae to potentially noxious cyanobacteria (i.e., blue–green algae, which are actually bacteria that photosynthesize). While this dominance may shift seasonally in many reservoirs, cyanobacteria tend to dominate for an increasingly longer segment of the year in eutrophic and hypereutrophic reservoirs (Smith 1998) and are considered "sentinels" of eutrophication (Stockner et al. 2000). In turn, zooplankton composition is affected by phytoplankton availability because macrofiltrators (usually large-bodied zooplankton) that are more abundant in oligotrophic reservoirs give way to low-efficiency, small-bodied, algal and bacterial feeders as nutrients increase (Taylor and Carter 1998). In hypereutrophic reservoirs, the food supply for zooplankton may actually decrease because of the dominance by cyanobacteria. Eutrophication is particularly relevant in reservoirs because of their large watersheds relative to their surface areas and corresponding high sediment and nutrient inputs. As a result of the U.S. Clean Water Act, sweeping changes in infrastructure have been undertaken to reduce nutrient inputs and prevent eutrophication in aquatic systems. In 1970, Canada passed the Canada Water Act. One of its key provisions was to regulate nutrients in cleansing products (to combat cultural eutrophication). Although still on the books, the Canada Water Act has been supplanted by provincial laws aimed at protecting water quality in rivers, lakes, and reservoirs (e.g., 2005 Water Protection Act of Manitoba and 2006 Clean Water Act of Ontario). A similar program in Mexico, the *Programa Agua Limpia* instituted by the *Comisión Nacional del Agua* in 1991, aims to assure that water resources are of adequate quality for a variety of uses by society.

Concerted efforts by government agencies and private citizens to reverse cultural eutrophication (e.g., promoting or mandating the use of phosphorous-free laundry detergents and building new wastewater treatment plants) led to unexpected consequences. Specifically, nutrient loading rates into reservoirs were reduced at a time when many reservoirs were experiencing (or were about to experience) reduced internal nutrient loading rates and trophic depression. Rates of nutrient loading and trophic states were changing so abruptly in some systems that a new word entered the lexicon of reservoir and lake managers: *oligotrophication*. Moving from eutrophy to mesotrophy or from mesotrophy to oligotrophy usually resulted in clearer water because of reduced phytoplankton biomass, which most citizens equated to "cleaner" water. However, the costs to fisheries were largely ignored for decades until the trade-offs between "clean water" and productive fisheries began to be discussed by fisheries biologists (e.g., Ney 1996; Stockner et al. 2000), and those discussions have continued to the present (Anders and Ashley 2007). The tight linkage between algal standing crops or phosphorous concentrations and fish biomass and sport fish harvest meant that fisheries could suffer in reservoirs that shifted to a lower trophic state. Such shifts in trophic state are particularly important in southern and western U.S. reservoirs. Oligotrophication also receives considerable attention in Canada, where reservoir trophic states often are low (i.e., oligotrophic), even during the period of trophic upsurge and can drop even

lower into ultra-oligotrophy as reservoirs age (Stockner et al. 2000). The trade-offs between cleaner water and popular sport fisheries were subsequently investigated; for instance, Maceina et al. (1996) showed that modest shifts in trophic state could achieve cleaner (i.e., clearer) water while still maintaining good black bass fisheries.

In the mid-1990s, the TVA sought to improve releases from its 41 reservoirs. Discharging water with low DO was a chronic, widespread problem, and various approaches were investigated including aerating the forebay (i.e., immediately upstream of the dam) by pumping liquid oxygen through submersed, porous, diffuser lines. In Cherokee Lake, a 11,000-ha reservoir in east Tennessee, nearly 15 km of porous line were suspended just off the bottom in the reservoir's forebay in 1995, and as predicted, DO in discharges improved. In some systems it makes more sense from an engineering perspective to pump compressed air into the hoses. The oxygen (or air) bubbles aerated the cool, anoxic waters in the turbine withdrawal layer above the diffuser lines, but they did not destratify the forebay. This approach to aerating Cherokee Dam's discharge provided summer refuges for fishes such as striped bass, a species that historically suffered from a temperature–DO squeeze every summer. The forebay refuge was used so extensively by striped bass (and anglers that pursued them) that emergency legislation was enacted to prohibit fishing in the forebay during summer to prevent overfishing and excessive catch-and-release mortality (Bettoli and Osborne 1998). The success of this approach to aerating downstream discharges led to the installation of similar systems in eight other TVA reservoirs with an unintended benefit, pelagic reservoir habitat was created in those reservoirs.

17.3.3 Water Retention and Water Level Fluctuations

Hydraulic retention time influences the trophic state of reservoirs. Phytoplankton communities reach their full production potential in reservoirs with high retention times that behave more like lakes and less like rivers. In a study of lakes and reservoirs across the USA, Soballe and Kimmel (1987) noted that algal communities needed about 60–100 d of retention time to realize their full potential at any given level of nutrients. In Alabama reservoirs, the relationship between retention time and algal production (and trophic state) was confirmed, but the threshold retention time was thought to be closer to 35 d (Maceina and Bayne 2003). The retention time in any reservoir is driven by the amount of rain falling in the watershed, and the amount of rainfall in region varies seasonally and annually. Thus, a reservoir's trophic state could vary within and between years.

Although the amount of precipitation falling into a reservoir's watershed cannot be controlled, hydraulic retention times and water levels are under the direct control of reservoir operators, and both of these aspects of reservoir hydrology are known to influence reservoir fisheries. Whereas relationships between retention times and fisheries can be subtle or complex, the impact of water levels on fish populations can be direct and dramatic. For instance, rapid changes in water levels can disrupt or eliminate spawning by some species (e.g., littoral nesting species), and statistical relations are regularly observed between water levels and recruitment by many species (e.g., gizzard shad, Michaletz 1997; largemouth bass, Sammons et al. 1999; white bass, DiCenzo and Duval 2002; crappies, Maceina 2003). The ecological mechanisms are not well understood, but responses of many fish species to hydrologic factors are well established. Unfortunately, it is difficult to alter the manner in which reservoirs are operated (i.e., change the guide curve), even when clear relationships between fish production and hydrology are identified.

Water level fluctuations within the regulated zone (i.e., between the minimum pool and top of the flood control pool) may partially or fully encompass the original floodplain near inlets or may occur entirely within bands occupied by upland vegetation in regions toward the dam. Substitution of a naturally variable flooding pattern with a standardized one, and loss of wet–dry cycles, has lasting ecological effects. Biotic communities in littoral areas of reservoirs become dominated by species adapted to lakes and standing water and may be less diverse or abundant than those in floodplain backwaters. Floodplain vegetation often dies with prolonged flooding, removing a major component of floodplain ecosystems. Flooding upland terrestrial vegetation in the regulated zone also creates habitat diversity, shelter, and a favorable environment for littoral fishes. Nevertheless, uniform fluctuations over time controlled by an engineered hydrograph (i.e., guide curve) will limit vegetation growth and produce barren slopes and mudflats, except perhaps near inlets where the regulated zone straddles the original floodplain. Guide curves are often justified and maintained by the misperception that a fixed guide curve will benefit all sport fish species (Miranda and Lowery 2007).

Managed floods within the regulated zone are often used to simulate a flood pulse and maintain ecological processes associated with random floods. During high water in free-flowing rivers, nutrients are exchanged between rivers and their floodplain, generally resulting in a net nutrient gain in floodplains. In reservoirs, nutrients normally dissolved in the incoming water may have already settled in upstream reservoirs, or may settle soon after entering reservoirs, resulting in reduced particulate organic matter and nutrient deposition in regulated zones. In fact, a net reduction in nutrients may occur, as these are extracted from regulated zones by nutrient-impoverished water (Thomaz et al. 2004).

Enhancement of regulated zones to recreate floodplains is central to reservoir habitat management. Unvarying, standardized guide curves produce regulated zones devoid of vegetation and of limited ecological value to floodplain species and do not provide a diversity of floods needed to maintain a diverse fish assemblage (Miranda and Lowery 2007). Some year-to-year variation in the flood pattern is necessary to maintain a full complement of species, periodically enhance nearly all species, and produce extreme events that have a rejuvenating function by connecting the basin to distant backwaters. Operational flexibility can often be found to produce floods artificially of suitable extent and duration, but institutionalizing a realistic level of flood-regime randomness into highly engineered systems is challenging. In developing water management plans, regulatory agencies could consider incorporating managed randomness into guide curves.

Many hydropower reservoirs in the USA operate under licenses issued by the Federal Energy Regulatory Commission, and those licenses periodically come up for renewal (see Box 4.5). Dams in the USA can be relicensed for up to 50 years; therefore, agencies tasked with managing reservoir fisheries devote substantial resources to providing input into the relicensing process when those opportunities arise to ensure that fishery resources are given consideration along with hydropower, flood control, and navigation needs. The relicensing process is complex and time consuming but provides a rare opportunity to influence reservoir operations for decades because a consideration in relicensing is mitigation of environmental damage. Under the auspices of the U.S. Environmental Protection Act, an environmental impact statement is required for any major federal action that may have a significant impact on the environment. Such mitigation can take many forms, including altering guide curves to promote spawning in a reservoir, improving the quality and (or) quantity of water discharged

through a dam, and developing management plans to protect littoral habitats and riparian zones. The Canadian Environmental Assessment Agency, which administers the Canadian Environmental Assessment Act of 1995, does not permit dam operations per se. However, upgrades to hydroelectric facilities in Canada or changes in how reservoirs are operated will trigger mandated federal assessment of environmental impacts, and fisheries managers have ample opportunity to participate in that process.

17.3.4 Submerged Structure and Vegetation

The lack of submerged woody or vegetative structure in reservoirs, particularly old reservoirs and those that experience substantial winter drawdowns, has prompted collaboration among many agencies and citizens groups to add structure. According to a recent survey (Tugend et al. 2002), most fish and game agencies in the USA devote money and personnel to adding structure and evaluating its impact in otherwise barren littoral zones. The response of fish assemblages to artificial structures placed in littoral zones is also being investigated in neotropical reservoirs such as Lajes Reservoir, Brazil, an oligotrophic reservoir built for hydropower production (Santos et al. 2008). Enhancement structures are typically made of either natural materials (e.g., brush or discarded trees) or manufactured products such as automobile tires (Figure 17.6). Structures made of artificial materials are not as effective as those constructed of logs or brush in providing refuge areas or serving as fish attractors (Roni et al. 2005). Stake beds (i.e., lengths of slender lumber driven into soft substrates to create a matrix of vertical structure) are common in reservoirs supporting crappie fisheries. Such management efforts fall under the category of habitat enhancement, and the primary objective is usually to attract fish to improve angler catch rates, not to boost population density. In some locales, the placement of half-log structures (Hoff 1991) to attract spawning black bass species, especially smallmouth bass, is commonplace (Figure 17.6). In most instances, only demersal or structure-oriented species (e.g., centrarchids and cichlids) will use structures placed in barren littoral zones; there should be no expectations that open-water, pelagic species will benefit (Santos et al. 2008).

Brown (1986) stated that few evaluations of the effects of fish attractors or other habitat enhancements on fisheries production had been published, and that is still true over two decades later (Roni et al. 2005). Similarly, few publications documenting the positive influences of such habitat enhancements on angler catch rates are available, despite the ubiquity of this management activity. Wills et al. (2004) provided a review of the rationale behind reservoir habitat enhancement techniques and noted the pervasive role that habitat variables (e.g., substrate) play in determining whether fish use artificial structures. For instance, the proximity of complex physical structures to habitat enhancement structures affects the use of enhancement structures by spawning largemouth bass (Hunt et al. 2002).

Although the efficacy of habitat enhancement techniques is weakly established and additional studies are needed to determine population level responses to habitat enhancements (Roni et al. 2005), there is little doubt that reservoir managers will promote such activities because they are embraced by the angling public, regardless of the public's species preferences. For example, in Norris Lake, Tennessee, collaborating anglers and biologists have placed more than 21,000 structures along the shoreline of the reservoir since 1992 to enhance fish habitat. It took decades for anglers to accept that the hatchery truck could not solve all fishing woes and that the key, invariably, to healthy fish populations and good fishing was

Figure 17.6. Barren littoral zones often prompt agency biologists and anglers to add natural and artificial structures to increase habitat complexity. Christmas trees and wooden pallets (upper photo) attract various species. Spawning benches (also known as half-logs, lower photo) placed along an exposed shoreline provide spawning habitat for black bass, particularly smallmouth bass. Stake beds (particularly attractive to crappies) and downed trees are visible in the background of the lower photo.

good habitat (e.g., Quinn 1992). As with planting vegetation or seeding shorelines, habitat enhancement projects provide opportunity to forge relationships and establish lines of communication among stakeholders and biologists, which promote mutual trust and help resolve conflicts (Box 17.1; see also Box 5.2). If the ecological impact of collaborative, in-reservoir habitat enhancement techniques is subsequently shown to be modest (or absent), the credibility of biologists is not lost if they acknowledged early in the process that the science is not well established and that such enhancements may not result in improved fisheries.

If soil substrate exists and water level fluctuations are not too severe, aquatic plants will inevitably colonize the littoral zone of reservoirs. Aquatic vegetation management has been debated for decades, and the responses of reservoir ecosystems to vegetation colonization and vegetation control are broadly understood (e.g., Bettoli et al. 1993). Most biologists would agree that some aquatic vegetation is desirable because studies have demonstrated that sport fish production is maximized at intermediate levels of vegetation (e.g., Wiley et al. 1984; Miranda and Pugh 1997). Nevertheless, controversies over vegetation management routinely besiege fisheries professionals because different stakeholders have different opinions regarding what constitutes desirable levels of vegetation (Wilde et al. 1992; Henderson 1996). When reservoir shorelines are urbanized and shoreline homeowners and developers enter the arena, the potential for conflict escalates. The likelihood for conflict rises even further when reservoirs are colonized by exotic species such as hydrilla or water hyacinth. In the absence of natural pathogens or grazers, these and other exotic species are much more likely to reach nuisance levels. In our experience, if vegetation coverage reaches 40–50% of the surface area of a reservoir, the ability to manage the vegetation is compromised and vegetation eradication may become the only option, even in large reservoirs. Ideally, the decision to manage vegetation will be made early when more options are available.

Four approaches are often used to manage nuisance aquatic vegetation: chemical, biological, mechanical, or water level manipulation. Reservoir managers often find themselves weighing the pros and cons of chemical and biological control. With few exceptions, biological control of aquatic vegetation is synonymous with stocking grass carp (either diploid or sterile triploid fish). The use of grass carp to control aquatic vegetation has been well studied for more than 30 years. Grass carp are long-lived, obligate herbivores capable of consuming all submersed and floating vegetation if stocked at a large-enough size (>300 mm total length) and at high-enough rates (20–70 fish/ha of vegetation; Martyn et al. 1986; Bonar et al. 2002). The ability of grass carp to control a wide array of plant species is not debated, nor is their inability to reproduce in reservoirs and small impoundments questioned; rather, the challenge is to devise strategies to control, rather than eliminate, vegetation with grass carp. It was once thought that incremental grass carp stockings combined with close monitoring of vegetation might achieve desirable, intermediate plant densities (e.g., Bain 1993); however, the responses of individual ecosystems to grass carp stocking vary widely. A consensus has been reached that grass carp should be stocked only in water bodies where most stakeholders can tolerate the complete elimination of submersed plants (Bonar et al. 2002).

Whereas the amount of plant biomass consumed by grass carp cannot be controlled once the fish are stocked, herbicides have long been used to control vegetation in reservoir ecosystems. A voluminous literature exists on chemical control of nuisance aquatic vegetation, and information on herbicide use is readily available on the Internet. In most locales, herbicides and pesticides can be dispensed only by certified applicators. Although chemical treatment of aquatic vegetation can be much more expensive than introducing grass carp, the ability of

Box 17.1. The Costs of Ignoring Human Dimensions in Reservoir Fisheries Management: The Norris Lake Story[1]

The abundance of nutrients released from the flooded reservoir basin (i.e., trophic upsurge), combined with the creation of expansive and unoccupied lacustrine habitat allowed sauger, walleye, smallmouth bass, and other native species to flourish in Norris Lake, Tennessee, in the two decades after its impoundment in 1936. In fact, at one time reservoir biologists advocated letting private citizens use gill nets to catch fish that would otherwise go to waste! The boom fishery did not last, as the trophic upsurge phase was followed by trophic depression (i.e., a decline in the rate of internal nutrient loading) and by loss of high-quality habitats. In the 1960s, biologists introduced striped bass and a popular fishery quickly developed—but not among those anglers who grew up learning to fish for species native to the river system. Those "native-species" anglers soon voiced their concern that striped bass were being promoted and managed to the exclusion of native species (walleye, black basses, and crappies), most of which were less abundant in the late 1960s than during the two decades following impoundment. The response of the state fisheries management agency to such angler concerns through the 1970s was to continue and eventually to expand the striped bass stocking program. The agency also conducted field studies to "prove" that striped bass did not compete with, or prey upon, native sport fishes to any appreciable degree. The response of biologists to growing complaints was to do what they had been trained to do—establish new fisheries to take advantage of pelagic habitats and abundant prey resources in reservoirs and collect biological data to defend their management activities.

A state-agency-sponsored task force was created in 1992 to address the concerns of organized, increasingly vocal opposition to striped bass management in Norris Lake. Unfortunately, no amount of persuasion or data could convince opponents to abide by the findings and recommendations of the task force; instead, they sought redress through legislative mandates. Five bills were introduced by state legislators on behalf of these constituents, but none passed and became law. Anglers on each side of the striped bass issue assumed hardened positions that made resolution of the problem difficult.

Thousands of dollars were spent on research (e.g., Raborn et al. 2002) and an advisory committee was created in 1998 to move opposing factions toward common ground regarding management of the reservoir's diverse fisheries. The balancing role of a diverse group of stakeholders on the Norris Lake Advisory Committee played an important part in achieving compromises and resolving most of the major issues regarding stocking of various species, including native species such as crappies and walleye. Ten years later in 2008, anglers from diverse backgrounds and with different attitudes toward fishing on Norris Lake regularly interact with state biologists and collaborate on projects beneficial to all parties (Figure 17.6).

Failure to consider the importance of human dimensions, a much more common component of fisheries education in the 21st century, led to the creation and prolonging of the Norris Lake controversy, and at one time or another threatened the entire structure and existence of the Tennessee Wildlife Resources Agency. As populations grow and public pressure for water and quality fishing increase in this century, reservoir biologists will find more and more opportunities and needs to consider human dimensions in their regular management activities.

[1] Adapted from Churchill et al. 2002.

herbicides to kill plants only where and when desired justifies their use in many situations. Advances in herbicide formulations and delivery systems have made large-scale plant control using chemicals more cost-effective in recent years. For example, a drip-delivery system of Sonar™ (a fluridone herbicide that inhibits carotenoid photosynthesis) in the headwaters of an embayment in Lake Seminole, Georgia, eliminated 1,200 ha of hydrilla (Sammons et al. 2003). Fluridone was considered an excellent herbicide to treat hydrilla for nearly two decades because the dose that killed hydrilla had minimal impacts on native emergent and submersed plant species such as *Vallisneria* spp., *Potamogeton* spp., and *Scirpus* spp. (Hoyer et al. 2005). However, fluridone-resistant hydrilla was discovered in Florida in 2000, and the higher doses and longer exposure times necessary to control resistant hydrilla negatively affect native plant species. Efforts are underway to develop and license new herbicides to control hydrilla (and other noxious plants) economically and safely and to determine whether hydrilla biotypes maintain resistance to fluridone in the absence of fluridone-selective pressure (Puri et al. 2007). Reservoir managers concerned with maintaining ecological function and habitat diversity face significant challenges if and when fluridone-resistant hydrilla spreads into new reservoirs.

The topic of native vegetation establishment has received far less attention than has vegetation control, but interest has increased in recent years. Field studies have usually entailed planting native vegetation (e.g., American pondweed and wild celery) in exclosures to serve as founder colonies (Smart et al. 1996). Exclosures are critical because small patches of transplanted plants or propagules growing along a barren shoreline will quickly be grazed by terrestrial, aquatic, amphibian, and avian herbivores (Smart et al. 1998). Although the prospect of establishing native plants is appealing to stakeholders, the efficacy of such programs has not been well demonstrated. Exclosures are prone to failure when they are forcibly entered by turtles and other grazers (Bettoli and Gordon 1990), and plants that expand outside the exclosures are often cropped by herbivores. Nevertheless, successful establishment of aquatic macrophytes in selected reservoirs may be possible (Smart et al. 1996).

There are many obstacles to establishing aquatic plants (with or without exclosures) in reservoirs that lack suitable substrate or experience large water level fluctuations. This fact prompted biologists to investigate the efficacy of seeding exposed shorelines with annual terrestrial grasses (e.g., winter wheat, millet, and ryegrass) at reservoirs that experience winter drawdowns. After numerous investigations, the general consensus is that any benefits to fisheries resulting from seeding shorelines are modest and transitory (Strange et al. 1982). Annual grasses will grow readily on exposed shorelines with little or no preparation of the soil, and lush stands of vegetation can grow in lower latitudes through fall and winter. However, the vegetation often does not persist once inundated in spring; thus, no vegetation is available to serve as nursery habitat for juvenile fishes later in spring and early summer. A benefit of shoreline seeding projects is that lush grass growing along dewatered shorelines will prevent erosion when the soil is exposed to rainfall.

American water willow, an emergent plant species, has been extensively planted along reservoir shorelines throughout North America for decades, with mixed success. This species has a semirigid, fibrous stem, and it is capable of rapidly colonizing new habitats via rhizomatous growth. Although American water willow is not readily grazed by herbivores (e.g., Dick et al. 2004), transplanted shoots and established plants will not survive if they experience extensive periods of inundation or desiccation, although they tolerate the latter more than the former (Strakosh et al. 2005). Ongoing research seeks to define reservoirs, habitats,

and water-level-fluctuation regimes for which American water willow and other transplanted species might have a good chance of colonizing reservoir shorelines.

The importance of woody vegetation to reservoir ecosystems has prompted many investigations into the feasibility of establishing pioneer riparian tree species such as willows and cottonwoods, and water-tolerant trees such as baldcypress, in the drawdown zone of reservoirs. The same environmental hurdles limiting herbaceous vegetation re-establishment (e.g., herbivores and periods of desiccation and freezing followed by periods of inundation) can be present when saplings or seedlings are planted along reservoir shorelines. A general consensus is being reached that woody species (as well as herbaceous species) are more likely to become established if the pattern of water level fluctuations is altered (i.e., change the guide curves) to promote plant survival in the drawdown zone. However, altering guide curves of hydropower reservoirs to favor plants along shorelines will likely incur steep costs in lost power generation (BC Hydro 2007).

Caveats not withstanding, shoreline seeding and efforts to establish aquatic vegetation or riparian trees invariably garner instant and enthusiastic public support. Such projects serve to inform stakeholders that their fisheries are regulated in large part by the quality of the habitat. The following excerpt from an article that appeared in *BASS Times* (December 2004), a popular sportfishing magazine, illustrates the point that planting vegetation is enthusiastically received by the fishing public—even when it is not successful.

> "The grass plantings also served to strengthen the relationship between the West Virginia BASS Federation and the DNR [West Virginia Department of Natural Resources], in addition to helping to generate interest in this ongoing project. While setbacks are inevitable, the establishment of a successful aquatic vegetation program in West Virginia will take both time and effort. But the DNR has made a solid commitment to its anglers that quality fish habitat remains a priority in the Mountain State."

Although the ecological merits, cost-effectiveness, and procedures for shoreline seeding and native aquatic plant establishment projects are still being debated, the public relations impact of such programs is substantial and cannot be dismissed. Thus, managers should view favorably any activity that does no harm to the resource, fosters interactions among fishery biologists and stakeholder groups, and may, through future breakthroughs, potentially reap important benefits. As mentioned earlier, biologists should clearly establish realistic expectations for any such habitat projects in order to maintain their subsequent credibility, in the event that enhancement activities provide no tangible results.

17.3.5 Longitudinal Patterns along the Reservoir

Spatial patterns occur in reservoirs due to longitudinal changes in reservoir morphology, flow velocity, suspended solids, light penetration, and nutrient dynamics (Kimmel et al. 1990). The upper sections of a reservoir and major bays are often characterized by a lotic-like environment that is generally shallower and narrower than are downstream sections and is influenced by the original river's geomorphology and basin contour (Figure 17.7). This lotic region exhibits higher flows, shorter water retention times, higher nutrient levels, lower light penetration, and greater sedimentation relative to downstream regions. Like the upstream river, the water is well mixed and oxygenated and is often turbid. Primary production is lim-

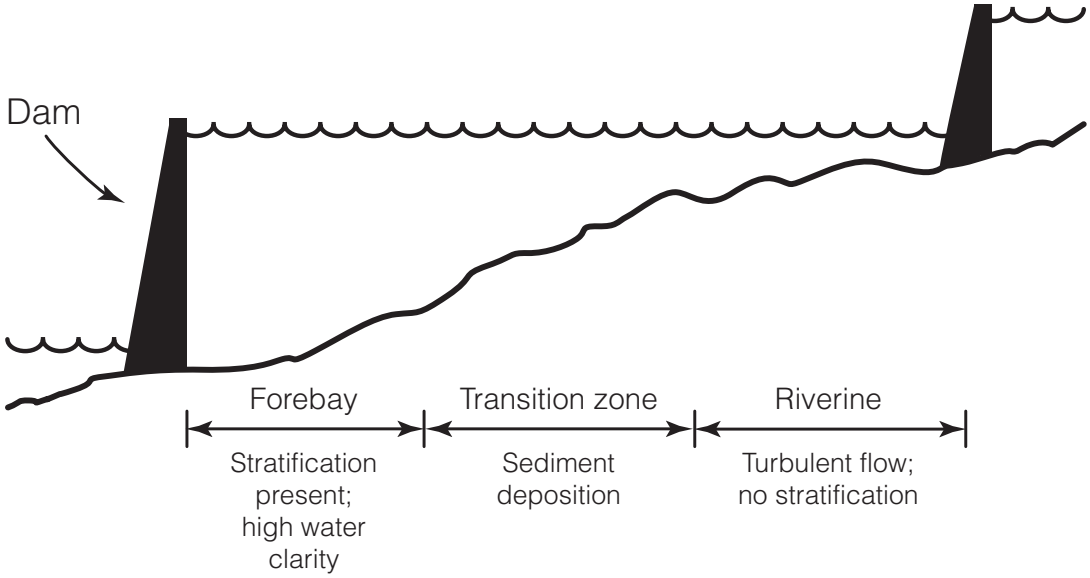

Figure 17.7. Reservoirs of all types and sizes typically display longitudinal gradients in terms of the physical habitat and water clarity. The relative lengths of each of the three zones distinguish one reservoir from another. For instance, the transition zone can be quite short in large tributary storage impoundments; whereas, the forebay can be short (or nearly nonexistent) in main-stem, run-of-river reservoirs. If there is a reservoir upstream, the water clarity in the riverine reach can be high; otherwise, the riverine reach is usually the most turbid zone of the reservoir. Sediment deposition is highest at the upper end of the transition zone, where water velocity drops and suspended particles settle to the bottom.

ited despite high levels of nutrients due to low transparency and low water residence time (Bernot et al. 2004). Further downstream, the reservoir becomes wider and deeper, showing signs of reduced flow, suspended fine materials, and turbidity but augmented light availability. In this transitional zone nutrient levels are lower than those upstream, but because more light is available due to settling of fine sediments, algal photosynthesis increases and might be the highest in the reservoir. In the transitional zone, more of a reservoir's production originates from autochthonous inputs rather than allochthonous inputs from the river. Near the dam, a reservoir is broadest and deepest, flow is generally unnoticeable unless large volumes of waters are being discharged, and water is the clearest. Nutrient concentrations in this lacustrine-like section are low relative to upstream, reducing volumetric primary production but perhaps not total production given a deeper photic zone. It is not uncommon for these three sections to be classified at different trophic states due to differences in nutrient concentrations, sediment loads, and depth. For instance, Center Hill Lake, a 7,400-ha tributary storage impoundment in Tennessee, is classified as eutrophic in the transition zone and embayments but mesotrophic in the lacustrine zone near the dam. Nevertheless, the intensity of the longitudinal gradient observed in reservoirs depends on factors such as size and layout of tributary streams, reservoir basin morphology, and position of the reservoir along the river basin.

Fish assemblages and fisheries may also change in a longitudinal manner. For example, in Itaipu Reservoir, Brazil–Paraguay, fish species richness decreased toward the dam (De Oliveira et al. 2005). Abundances of shads and other major species common to reservoirs in the southeastern USA tend to be lowest near the dam and increase upstream in more riverine en-

vironments (Michaletz and Gale 1999). In John Day Reservoir, Oregon, introduced walleyes were largely restricted to the upper third of the reservoir, whereas the number of introduced smallmouth bass increased progressively down lake (Beamesderfer and Rieman 1991). In Lake Texoma, Texas–Oklahoma, Gido et al. (2002) found the littoral fish assemblage to be highly predictable along the length of the reservoir and along the length of tributary arms. The basis for this predictability was shaped largely by differential responses of individual species to physical and chemical gradients in the reservoir. In general, many species associated with the upper reservoir require flowing water during at least a portion of their life history, are species that orient toward the banks or bottom, or require sand or gravel substrates. These are frequently migratory (i.e., potamodromous) species whose spawning habitat lies in tributaries or upstream floodplains. In contrast, near the dam pelagic species adapted to lake environments are most common, although periodically the deeper layers may not be occupied by fishes because of thermal and chemical stratification. Lentic and lotic species may coexist in transitional segments between the upper and lower reservoir, and thus species richness and diversity may be highest in these segments (Agostinho et al. 1999).

Strong longitudinal patterns observed in many reservoirs can influence management within a single reservoir. For instance, the concept of a cline provided the foundation required to ask what factors affect longitudinal microbial community composition, production, metabolism, and biomass accumulation, facts needed to gain insights into eutrophication processes (Lind 2002). The longitudinal patterns framework has also been used to guide sampling programs to evaluate water quality (Davis and Reeder 2001), sedimentation (Pagioro and Thomaz 2002), total maximum daily loads, and fish populations. For example, longitudinal patterns along Itaipu Reservoir showed dominances by different fish species and disparate fishery yields requiring recognition in fishery management plans (Okada et al. 2005). In Cave Run Lake (a Kentucky reservoir), the intra-lake distributional gradients of three black bass species linked to clinal changes in habitat and nutrients indicated the need to stratify sampling and assess population characteristics separately according to zones (Buynak et al. 1989). In long reservoirs with strong longitudinal patterns, fishery management may be divided according to zones, with different habitat enhancement, harvest regulations, and infrastructure development strategies in each zone. Management alternatives that are appropriate for a particular zone of a reservoir may not be the best choice in other zones with different environmental conditions.

17.4 TRIBUTARIES

Tributary streams are elements of all reservoirs and include the main-stem river impounded by the reservoir and inlets associated with reservoir coves and arms. The discharge, width, and length of tributaries vary greatly, ranging from small creeks to major rivers. Thus, the influence of tributaries over reservoir fish assemblages varies from a minimal effect on reservoirs with small watersheds to a sizeable effect on reservoirs with large tributaries. This range of tributary conditions results in fish assemblages varying between those that are dominated by pool and backwater fish species to those dominated by riverine species.

17.4.1 Tributary Size and the Reservoir Fish Community

Reservoir fishes are mostly of riverine origin (Fernando and Holčík 1982) and many are obligatory tributary spawners. However, many species are generalists able to spawn in

tributaries as well as in a reservoir, although their abundance in a reservoir is often enhanced by access to tributaries. Warmwater species such as longnose gar, paddlefish, white bass, and various catostomids migrate from reservoirs to spawn in tributary rivers and creeks (Colvin 1993; Johnson and Noltie 1996; Hoxmeier and DeVries 1997). Moreover, most salmonids use tributaries for reproduction due to the availability of suitable substrates, current velocities, and temperatures (Parsons and Hubert 1988; Crisp et al. 1990; Stables et al. 1990). In most cases, preferred spawning sites are large gravel bars, but pre-spawn staging occurs in adjacent pools. Gravel bars are used by multiple species, concurrently and segregated spatially and temporally. After hatching, juveniles may migrate immediately back into a reservoir (e.g., kokanee) or rear for months to years in the streams (e.g., trout) and backwaters (e.g., gars, paddlefish, and catostomids) before returning to a reservoir.

In reservoirs with long riverine stretches upstream, large lateral tributaries, or extensive floodplains upriver, a large fraction of the fish assemblages will be composed of potamodromous species. For example, upriver from Itaipu Reservoir, a long stretch of the free-flowing Paraná River connects to an extensive floodplain providing spawning and rearing habitats for many species in ephemeral floodplain lagoons (Agostinho et al. 2001). In fact, 6 out of the 10 species that sustain Itaipu's subsistence and commercial fisheries develop in the floodplains upstream (Okada et al. 2005). At the urging of conservationists and fishers, this section of the river above the reservoir was set aside as a national park by the Brazilian government to prevent impoundment and degradation and maintain fisheries in the reservoir downstream. Among several flood control reservoirs in Mississippi that provide quality crappie fisheries, juvenile crappie densities were one to two orders of magnitude higher in sloughs, backwaters, and oxbow lakes immediately upstream of the reservoirs than in the reservoirs (Meals and Miranda 1991). Those backwaters flooded annually or semiannually, simulating river floodplains, and crappie populations that developed there probably supplemented or even sustained populations in the reservoirs. Backwaters serve as nursery areas for juveniles of many species that spawn in rivers and have larval development in lentic lateral pools. In reservoirs with riverine floodplain habitats upstream, restoration and conservation of such habitats should be a reservoir management priority.

Whereas many short-distance migrators persist in impounded rivers by using the reservoir and associated tributaries, long-distance migrators may be gravely affected by the barrier presented by the dam and the reservoir (Larinier 2001). Elimination or reduction of spawning grounds or delayed access to spawning areas have been significant effects of reservoirs. Dams and reservoirs can affect fish by blocking upstream and downstream passage. These movements are most important to anadromous and catadromous fishes such as salmon and eels, which spend part of their life cycles in rivers and part in oceans or other large water bodies, but also to potamodromous species that, during a certain phase of their life cycle, depend on longitudinal movements in river systems (e.g., paddlefish and sauger). For adult fish trying to move upstream, a dam and associated reservoir can pose an impassable barrier unless passage is provided, and juvenile and adult fish moving downstream are at high risk of being entrained in a turbine or preyed upon in the relatively still waters of a reservoir (Lucas and Baras 2001). The deleterious impact of dams and reservoirs on migrating fishes is clearly illustrated by the plight of many imperiled stocks of Pacific salmon in the Columbia and Snake river watersheds, where 18 large main-stem dams (and many smaller tributary dams) impede upstream migrations of adults and the downstream out-migrations of juveniles. Fish passage facilities have been provided in many impounded rivers (particularly in the Pacific Northwest) where

migratory species are major components of fish assemblages; fish passage facilities are lacking at many other dams, most notably in eastern North America.

17.4.2 Management of Tributaries to Benefit Reservoir Fish

The need to manage tributaries to enhance reservoir species depends on a reservoir's fish assemblage but, in general, includes protecting gravel bars, maintaining bank stability, manipulating access to adjoining sloughs and oxbow lakes, developing artificial backwaters, or providing proper flows and water levels during key periods. A first step in the management process is to inventory tributary habitats and rate their quality relative to reservoir species that use them. There is a large body of literature relevant to stream habitat maintenance and restoration (e.g., FISRWG 1998; also see Chapter 10). This literature has concentrated on river restoration to benefit riverine species rather than to benefit reservoir species that use rivers during part of their life cycle, although these two aims overlap. Depending on a reservoir's position along a river basin (section 17.6), management of fish assemblages requires attention to tributary protection and restoration.

17.5 THE WATERSHED

We define a watershed as an area that drains into a reservoir and its tributaries. Land cover in a watershed is a major determinant of water quality and consequent fish assemblage composition. As described earlier, watersheds contribute nutrients that influence primary production in reservoirs. Nutrients flow to reservoirs from their watersheds by way of streams, groundwater, and runoff, often embedded in organic and inorganic particles. Watersheds typically experience various levels of deforestation, agricultural development, industrial growth, urban expansion, surface and subsurface mining activities, water diversion, and road construction. These changes destabilize runoff, change annual amplitudes and spatial distributions of flow, and enhance downstream movements of nutrients, sediments, and detritus that are ultimately trapped by reservoirs and regulate primary productivity, species composition, and food web interactions.

Sediments are a major watershed export into reservoirs and produce suspended fine material and sedimentation discussed earlier. Mean total suspended solids varying from 1.2 to 47 mg/L in 135 Missouri reservoirs were directly related to the proportion of cropland and inversely related to the proportion of forest cover in the watershed (Jones and Knowlton 2005). Sedimentation rates in reservoirs are higher in agricultural watersheds and are affected by agricultural land management. Sedimentation not only affects backwaters of reservoirs, but as backwaters fill, sedimentation extends upwards beyond reservoir into tributaries.

Watershed practices are directly linked to eutrophication (Carpenter et al. 1998). Row-crop agriculture with frequent tillage and fertilizer application is a major disturbance in watersheds (Novotny 2003). Nutrient exports from croplands are several times higher than from grasslands and forestlands (Beaulac and Reckhow 1982). In Missouri reservoirs, phosphorus and nitrogen levels were high in reservoirs surrounded by croplands and lower in reservoirs surrounded by forests, resulting in a sevenfold minimum difference in nutrients between reservoirs with watersheds dominated by forests and ones with watersheds dominated by croplands (Jones et al. 2004). Similar relations have been reported for lakes

and reservoirs in Connecticut (Field et al. 1996), Iowa (Arbuckle and Downing 2001), and Ohio (Knoll et al. 2003). Nutrient input per unit of land area from urban watersheds often equals or exceeds that from agriculture as impervious surfaces enhance runoff (Beaulac and Reckhow 1982).

Critical portions of watersheds are the strips of land immediately adjacent to reservoirs, termed riparian zones, that begin at the shorelines and move inland a loosely defined distance. In tributaries, riparian zones have been defined as encompassing the terrestrial landscape from the high-water marks upland to where vegetation may be influenced by elevated water tables and flooding (Naiman and Decamps 1997). In reservoirs, riparian zones resemble those of tributaries only near the entrance of tributaries. Reservoirs lack true riparian zones in their lower reaches (toward the dam) because original river channels have been submerged and the shoreline contours consist of upland vegetation that provides buffer zones, although not true riparian zones.

Riparian zones are key ecotones for regulating aquatic–terrestrial interactions (Correll 1997). In tributaries, major roles of riparian zones include thermal buffering, shading, contribution of woody debris, bank stability, and sediment and nutrient interception (Pusey and Arthington 2003). These roles remain relevant in reservoirs, but protection from strong winds also becomes an important feature. Furthermore, riparian buffers present esthetic visual barriers that help maintain quality of recreational fishing experiences.

17.5.1 Links between Watersheds and Reservoir Fisheries

The effects on reservoirs of sediment and nutrients imported from watersheds have been described, but in addition to nitrogen and phosphorus, watersheds can contribute large quantities of particulate organic matter to reservoirs. The fish assemblages of many reservoirs in North America are dominated by gizzard shad, a clupeid that depends on small zooplankton at larval stages (Miranda and Gu 1998) but is capable of consuming large amounts of organic detritus during postlarval stages (Mundahl and Wissing 1987). According to Vanni et al. (2005), gizzard shad represent a key link between reservoir fish assemblages and watersheds. Agricultural watersheds tend to export greater quantities of particulate organic matter than do forested watersheds and reservoirs in agricultural watersheds support higher abundances of gizzard shad, probably through mechanisms operating on larval and adult stages. Thus, reliance on watershed exports gives species such as gizzard shad and buffaloes a large advantage over other reservoir fishes because they can utilize this exogenous food resource.

Riparian zones have multiple effects on fish. Without suitable riparian buffers, fine sediments are transferred from watersheds to shallow reservoir environments where they can affect littoral fish species. Increased turbidity and sedimentation alter food availability (e.g., benthic invertebrates and algae; Berkman and Rabeni 1987), affect fish foraging behavior and efficiency (Bruton 1985), and alter intraspecific interactions. Other effects include reductions in habitat suitability for spawning (Walser and Bart 1999) and increased egg mortality, as well as reductions in rates of larval development and survival (Jeric et al. 1995). As banks and associated littoral habitats degrade, densities of fish that rely on littoral zones during all or part of their life history are likely to decrease. Fish assemblages may shift toward dominance by species that depend less on substrate-based resources and can exploit pelagic resources.

With few exceptions, research on the influence of riparian zones to lake and reservoir ecosystems has focused on filtration and its positive effects on water quality; direct influences

on fish assemblages are rarely inferred. In reservoirs of the southern USA, species richness and centrarchid abundance are generally higher in coarse woody habitat (Barwick 2004) provided by forests surrounding reservoirs. In a lake in Wisconsin, experimental removal of coarse woody habitat originating from riparian zones resulted in largemouth bass consuming less fish and more terrestrial prey and growing more slowly (Sass et al. 2006). Moreover, yellow perch declined to extremely low densities as a consequence of predation with little or no recruitment.

17.5.2 Watershed Management

The goal of watershed management is to facilitate self-sustaining natural processes and linkages among terrestrial, riparian, and reservoir environments. Watershed management involves controlling the quantity, makeup, and timing of runoff flowing into reservoirs or tributaries from the surrounding terrain (Box 17.2). The first and most critical step must be halting or eliminating anthropogenic practices causing degradation of reservoirs. Such approaches can involve a wide range of adjustments to human activities. For example, they may involve increasing widths of buffer strips around fields, altering livestock grazing strategies to minimize impacts, moving tillage operations in fields farther away from riparian systems and water, changing tillage methods and timing, or stopping the release of industrial wastes that cause water pollution. To this end, various protocols dubbed best management practices have been developed to target and minimize impacts from nonpoint sources in watersheds. Best management practices are usually applied as systems of practices because one practice rarely solves all problems and one practice will not work everywhere. Reservoir managers should be acquainted with the large body of literature on watershed management; however, watershed management is generally not the direct responsibility of fisheries managers (section 17.7).

Buffer strips with multiple vegetation types may protect water bodies against the negative effects of agriculture. This concept uses three interactive zones that are in a consecutive upslope order from shore: a strip of permanent forest, a strip of shrubs and trees, and a strip of herbaceous vegetation (Schultz et al. 1995). Width and composition of the strips are adapted to the geographical variability of terrestrial plant communities and riparian conditions. The first strip influences the aquatic environment directly (e.g., temperature, shading, bank stability, wind break, and source of coarse woody habitat). The second strip controls pollutants in subsurface flow and surface runoff and is where biological and chemical transformations, storage in woody vegetation, infiltration, and sediment deposits are maximized. The first two strips contribute to nitrogen, phosphorus, and sediment removal. Grasses in the third strip spread the overland flow, thus facilitating deposition of coarse sediments. Grassy riparian areas trapped more than 50% of sediments from uplands when overland water flows were less than 5 cm deep (Magette et al. 1989). In North Carolina, riparian areas removed 80–90% of the sediments leaving agricultural fields (Daniels and Gilliam 1997). Riparian buffer zones accumulate nutrients and absorb them into plant biomass, serving as nutrient filters. In Vermont, reductions of approximately 20% in mean total phosphorus concentrations and 20–50% in mean total phosphorus loads were observed (Meals and Hopkins 2002). In Lake Rotorua, New Zealand, riparian management reduced fine sediment loads by 85%, particulate phosphorus and soluble phosphorus by about 25%, particulate nitrogen by 40%, and soluble nitrogen by 26% (Williamson et al. 1996). These reductions reduced the chlorophyll-*a* concentrations in the lake and helped shift the lake's trophic state from eutrophic to mesotrophic.

Box 17.2. Iowa's Comprehensive Lake and Watershed Management Program[1]

Iowa leads the nation in the proportion of its land area converted to cropland: 72%. An additional 10% of its land is pastureland and 5% is urbanized. Consequently, 87% of Iowa's land area is directly disturbed by humans. As a result, many natural and constructed lakes in Iowa are impaired with poor water quality, fisheries, and recreational value. Over the years, fish assemblages in many lakes were renovated, some multiple times, resulting in improved fisheries that were eventually degraded because the underlying problems of sedimentation, excessive nutrients, and poor water quality were not addressed.

A lake classification system was developed by the Iowa Department of Natural Resources (IDNR) based on systematic assessment of both lake water quality and watersheds. This classification, combined with socioeconomic factors, resulted in a priority ranking of lakes and watersheds for restoration. Once local commitments are demonstrated and feasibility verified, comprehensive restoration is initiated to address both watershed and in-lake issues. Watershed models are used to simulate hydrologic processes and pinpoint the major sources of sediment and nutrient loading. These loads are reduced to acceptable levels through land-use changes and application of best management practices (BMPs).

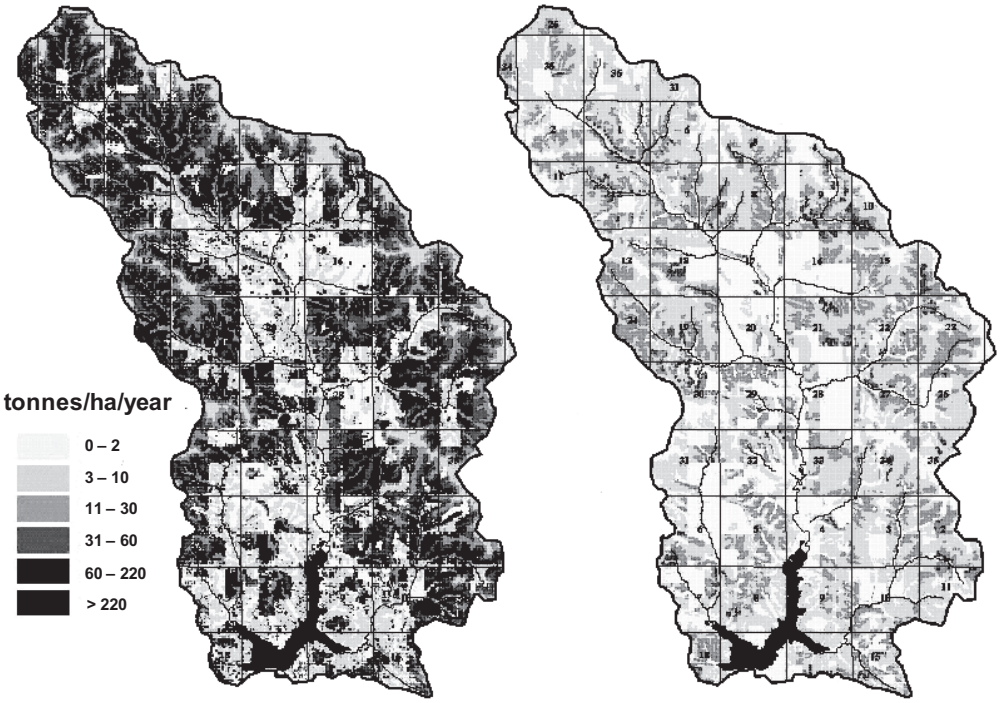

Figure. Geographical information system representation of the Rock Creek Lake, a reservoir in central Iowa. The left plate shows soil erosion estimated by the revised universal soil loss equation assuming no conservation efforts (32.3 metric tons/ha/year) and the right plate shows soil erosion assuming various BMPs (6.5 metric tons/ha/year). Shades of gray identify an array of erosion rates (as per the accompanying scale). (Plates courtesy of IDNR)

[1] Most of the information used in developing this box was contributed by Don Bonneau, Iowa Department of Natural Resources.

(Box continues)

Box 17.2. Continued.

Fisheries managers work in partnerships comprising government agencies, landowners, and nongovernment organizations and invest 25–30% of their time on watershed work associated with lake and stream projects. Fisheries managers work in various capacities within partnerships, often as leaders in providing technical details for specific projects. Although the approach may be intimidating to managers at first, it works by producing success stories that get the public support necessary to obtain funding needed to work at a watershed scale. Restorations are expensive and require years to complete but are also an investment in the local economy, fishing quality, and natural resources as a whole. Consequently, the Iowa legislature approved a state lakes program and allocated US$8.5 million in 2007 and similar amounts from 2008 to 2010. This lake protection and improvement program is administered by the IDNR with local and other matching funds expanding the program by over $5.5 million each year.

First and foremost, vegetation in riparian zones surrounding reservoirs serves to stabilize shorelines and reduce erosion and the flow of sediments into reservoirs. As sedimentation is considered the most important factor contributing to reservoir aging and habitat degradation, anything that can be done to protect riparian zones is desirable. Some reservoir management agencies, such as the TVA, have been active in establishing programs to protect and enhance riparian zones on private lands bordering their reservoirs, especially on main-stem reservoirs where water level fluctuations are less dramatic compared with tributary impoundments. It is generally accepted that retaining walls (i.e., bulkheads) are the worst form of shoreline stabilization because they result in impoverished littoral habitat and fish assemblages (Trial et al. 2001). From a fisheries perspective, the placement of riprap (with native plant establishment above the riprap zone) is a better way to stabilize shorelines subject to severe erosion. Regardless of what form bank stabilization takes, it will reduce the positive effects of the riparian forest (if present) on the distribution and abundance of large woody debris known to benefit freshwater fisheries (Angradi et al. 2004).

17.6 THE RIVER BASIN

A river basin is the portion of land drained by a river and its tributaries and includes multiple watersheds both upstream and downstream from a reservoir. Broad patterns of reservoir characteristics are evident at the river basin scale. In large river basins, variability in climate and physical characteristics among geographical sections of the basin influence diversity of hydrology. Patterns are also evident within river basins in relation to longitudinal gradients along chains of reservoirs. Basin scale variables are rarely controllable, but they constrain the expression of processes at smaller scales. Thus, an appreciation of basin patterns helps set limits for smaller-scale determinants and thereby helps managers understand the potentials and limits of reservoir management.

17.6.1 Longitudinal Gradients among Reservoirs in River Basins

The river continuum concept (RCC; Vannote et al. 1980) proposed a clinal view of rivers. According to the RCC, the physical character of a river has a gradient of conditions

from headwaters to mouth, with upstream processes affecting downstream processes (see Chapters 18–21). The RCC does not apply directly to a reservoir chain in a basin. However, the notion of clinal change along a basin does apply to a reservoir chain. Clinal trends in reservoir attributes are basin specific yet exhibit broad common patterns. In general, the upper reaches of most basins tend to be forested, whereas the lower reaches tend to have higher levels of modifications due to agriculture. Characteristics such as mean depth, relative size of the limnetic zone, water retention time, oxygen and thermal stratification, substrate size, and water level fluctuations tend to increase in upstream reservoirs. Conversely, reservoir area, extent of the riverine and littoral zones, access to floodplains and associated wetlands, habitat diversity, and nutrient and sediment inputs tend to increase in downstream reservoirs. Many of these patterns are dictated by landscape characteristics and are also evident in chains of natural lakes (Martin and Soranno 2006), but exceptions are common given the diversity of landscapes.

Nutrient trapping by reservoirs along a basin reduces productivity down a series of reservoirs, although in reservoirs with large tributaries, nutrients and productivity may actually increase downstream. Lake Mead experienced a drastic drop in productivity after the impoundment of Lake Powell upstream on the Colorado River (Vaux et al. 1995). Similarly, in the Tietê River, Brazil, the uppermost reservoir in a chain of nine impoundments captured most of the nutrients released from São Paulo, the largest city in South America (Barbosa et al. 1999). In reservoirs on large rivers with low retention and (or) multiple influential tributaries, the effects of upstream reservoirs may not be as pronounced as in the above examples (Bruns et al. 1984; Agostinho et al. 2004). In the Tennessee River, upstream reservoirs retain a greater portion of inflowing nutrients owing to greater water retention, although their net loads are lower owing to smaller watersheds with different geomorphology and land cover (Voigtlander and Poppe 1989). Thus, nutrients and associated primary productivity, and likely many water quality variables, show spatial gradients among reservoirs within basins so that conditions in a given reservoir are predictable based on its position in the basin.

The RCC postulates that fish assemblages change along lotic systems in response to physical and nutrient gradients. Analogously, in impounded basins, reservoirs higher in a chain of reservoirs tend to have largely lacustrine, generalist fishes characteristic of sluggish upper reaches of basins (McDonough and Barr 1979). The reduction of riverine species is particularly evident for large migratory fishes stopped by dams that lack passage or interrupted by multiple dams with passages (Agostinho et al. 1999). Depending on latitude, upstream reservoirs in high elevations may include coolwater and coldwater species assemblages, and reservoirs lower in the series may transition into warmwater species assemblages. Riverine species become more common in downstream reservoirs, an effect that is especially evident in reservoirs below long, unimpounded stretches, with unimpounded tributaries or with extensive upstream floodplains.

In reservoirs of the Tennessee River, fish species richness, composition, and biomass changed longitudinally along the basin. Number of species increased from a low of less than 20 in high-elevation impoundments to nearly 70 in the lowermost reservoir (Miranda et al. 2008). Similarly, fish abundance increased in reservoirs further downstream. Additionally, species composition showed strong organization relative to position in the chain. Reservoirs high in the basin were characterized by a greater composition of bluegill, smallmouth bass, walleye, largemouth bass, river redhorse, and white bass. On the lower end of the basin, reservoir fish assemblages included greater representation by shads, blue catfish, buffaloes,

gars, yellow bass, and redear sunfish. A relatively linear cline existed in between the two extremes. Trophic guild composition also tends to change along reservoir chains, with percentage composition by number of detritivores and planktivores increasing down basins and that of invertivores, invertivores–carnivores, and invertivores–detritivores increasing up basins (Miranda et al. 2008).

17.6.2 The Basin Perspective

Considering impoundments at a basin scale and viewing them as reaches in a river or links in a chain may generate management insight not available when considering them as isolated entities. An obvious feature of reservoir chains is a predictable spectrum of fish assemblages that can provide a diversity of recreational and commercial fisheries. Traditional management approaches may be organized relative to features of the reservoir series. For example, the effectiveness with which typical management efforts influence fish assemblages is likely to decrease downstream because reservoir size, species richness, and fish assemblage stability increase. Correspondingly, stocking, harvest regulations, and habitat manipulation programs are likely to be increasingly more effective in upstream reservoirs. Efforts to foster diverse commercial, subsistence, or recreational fisheries, and to provide multispecies fish-passage facilities to increase connectivity among impounded reaches separated by dams, are likely to be more effective in downstream reservoirs because those reservoirs tend to have more diversity of habitats and water regimes. These principles apply whether a basin has one or many reservoirs. Thus, a basin perspective professed by the RCC can serve as a template for considering reservoirs because they generally show longitudinal gradients at the scale of a single reservoir as well as at the scale of a chain of reservoirs constructed along a river.

17.7 CONCLUSIONS

Management of large reservoirs has emphasized solving reservoir-level problems. Expanding this view of reservoirs to include tributaries, watersheds, and river basin enhances a manager's abilities to influence reservoir fish populations and fish assemblages and can increase the effectiveness of in-reservoir management measures such as stocking (Box 17.3). Given a potentially overwhelming expansion in management problems, there is a need for reservoir biologists to expand the level of human resources involved in management through partnering among state, provincial, and federal agencies, local governments, universities, nongovernment organizations, corporations, and the public. Within this environment, the traditional control exerted by fisheries managers over a resource is diminished, but the potential to bring big, long-lasting changes to reservoir environments and biota is increased.

The importance of looking for solutions to reservoir fisheries problems beyond a reservoir itself is likely to increase with the level of human disturbance in a watershed. Reservoirs in relatively undisturbed watersheds with high-quality tributaries and riparian zones are likely to require mainly watershed protection and traditional in-reservoir management approaches. In contrast, reservoirs in highly-disturbed watersheds with highly engineered tributaries may require considerable out-of-reservoir attention before in-reservoir efforts become effective. In this latter class of reservoirs, a focus on traditional management activities such as regulations, stocking, and littoral zone improvement may be shortsighted and represent only short-term fixes to complicated landscape issues that are the underlying problems to maladies afflicting

Box 17.3. Introductions to Create New Fisheries and Stocking to Augment Native Fisheries

There is no such thing as a "reservoir species," and biologists have leeway when manipulating reservoir fish assemblages. The need to introduce species can arise because of the lack of pre-adapted species to colonize habitats such as the pelagic zone. Stocking existing species is often necessary because aging reservoirs lose their ability to sustain robust, exploitable fish populations. For all of these reasons, reservoir biologists routinely stock fish. A thorough discussion of when these activities are called for and how to determine which species (and how many) to use is presented in Chapter 9, but some comments specific to reservoir programs are appropriate.

Reservoir construction in the 20th century created millions of hectares of lacustrine habitat where aquatic resources were scarce. With the creation of vast expanses of offshore, deep-water habitats, new species were introduced to occupy those habitats. Nonnative lake trout were stocked into many western U.S. reservoirs to create trophy fisheries where none would otherwise have existed. Similarly, nonnative smallmouth bass and walleyes were stocked in impoundments in the Columbia River watershed to provide sport fisheries in new lacustrine habitats that were created when that major river system was regulated by more than two dozen dams (and the wisdom of stocking potential predators of juvenile salmon, some of which are endangered species, has been roundly questioned). One of the most successful reservoir stocking programs in the 20th century involved striped bass, an anadromous species native to the Atlantic and Gulf coasts of North America. Striped bass are stocked widely in the USA and are prized because of the large sizes they can achieve (20+ kg) and their pelagic habits. Their large size and preference for clupeid prey such as gizzard shad that often dominate the fish biomass in reservoirs render them particularly suitable in large reservoirs. Other species that are widely introduced and stocked in reservoirs to create offshore fisheries include hybrid striped bass (the usual cross is the palmetto bass), blue catfish, and several species of trout and salmon.

Whereas introductions of striped bass and other species have created sport fisheries where none previously existed, other reservoir stocking programs seek to replace declining recruitment by species native to impounded watersheds that have declined as reservoirs aged. Some examples include stocking crappies and walleyes in Tennessee tributary storage reservoirs (Isermann et al. 2002; Vandergoot and Bettoli 2003), walleyes in large main-stem Missouri River impoundments (Fielder 1992), and muskellunge in Ohio reservoirs (Bevelhimer et al. 1985). Conservation biologists stock various subspecies of native cutthroat trout (e.g., Bonneville and Rio Grande) into western U.S. reservoirs to preserve those native fishes and their unique genomes. Stocking the nonnative Florida subspecies of largemouth bass into reservoirs containing only native northern subspecies to promote introgression is still common, particularly in Texas (Buckmeier et al. 2003).

The introduction of new prey species into reservoirs was once widespread but has slowed because most candidate species have already been introduced in most reservoirs. The realization that the ecological costs of stocking nonnative prey species sometimes outweigh possible benefits also halted many planned introductions. For instance, nonnative alewives are readily preyed upon by pelagic predators, but alewives have caused the collapse of resident

(Box continues)

Box 17.3. Continued.

fish populations through various mechanisms (e.g., preying on larval sport fish and causing a vitamin deficiency in sport fish). One of the most widely stocked prey species in southern and western U.S. reservoirs is the threadfin shad because it assumes a pelagic existence in reservoirs (unlike many native forage fish species) and has many attributes of the ideal prey species (e.g., small maximum size). Another widely-introduced prey species is the emerald shiner, which has been stocked in reservoirs in Canada and the western and midwestern USA to provide forage for pelagic predators.

reservoir fish assemblages. The science of reservoir management is relatively new, and it is unclear how watershed improvements might improve fisheries (or reverse declines) in old reservoirs that have sustained decades of sedimentation, loss of woody debris, and general habitat degradation. Nevertheless, protecting watersheds is important even for old reservoirs to prevent further habitat degradation and unwanted shifts in fish assemblage structure.

Reservoir managers wishing to engage in out-of-reservoir activities to protect and enhance water quality, physical habitat, and fish assemblages may lack jurisdiction or expertise to operate beyond reservoir shores. Thus, landscape level partnerships must be forged. Partnerships provide the organization needed to plan, fund, and complete restoration work and give reservoir managers the political clout they may not have outside the reservoir basin. As partnership members, managers must be prepared to show linkages between a reservoir and a watershed and to be advocates for change that benefits fish in a reservoir. Managers should be equipped to contribute information suitable for developing restoration and protection plans, particularly relevant to how specific actions may affect reservoir water quality and biotic communities. To this end, river basin and watershed inventories documenting features important to reservoir condition are essential, focusing on critical areas representing major sources of problems likely to have large effects on the reservoir. Such problems might include large stretches of channelized tributaries that discharge excessive sediment loads and lack adequate habitat for reservoir species that spawn in tributaries, mistimed discharges from upstream impoundments, major tracts of wetlands disconnected from adjacent tributaries or the reservoir, agricultural ventures stretching down to the banks, and forest clear-cutting operations.

Considering that reservoir managers have traditionally focused on in-lake processes, links between reservoir fish assemblages and watersheds have not received sufficient attention and are likely to require research emphasis to build the capacity of managers to participate in landscape level partnerships. Fisheries researchers have established links between eutrophication and fish assemblage composition, concluded that oligotrophication can reduce fishery yields, and developed target ranges for optimum nutrient levels in some watersheds. However, the associations between watershed imports and reservoir fish assemblages are tenuous at best and are only beginning to be ascertained. The importance of riparian and buffer zones as filters has been studied in streams, but their contribution to littoral habitats in reservoirs has largely been ignored. Although reservoir managers know that some reservoir fishes use tributaries, the relationships between tributaries, their backwaters, river discharges, and fish assemblages that develop in reservoirs have received little or no attention. Furthermore, the natural gradient in abiotic and biotic features of reservoirs along a river basin deserves greater consideration when developing local or large-scale reservoir management plans.

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