

Longitudinal Gradients along a Reservoir Cascade

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Abstract.—Reservoirs have traditionally been regarded as spatially independent entities rather than as longitudinal segments of a river system that are connected upstream and downstream to the river and other reservoirs. This view has frustrated advancement in reservoir science by impeding adequate organization of available information and by hindering interchanges with allied disciplines that often consider impounded rivers at the basin scale. We analyzed reservoir morphology, water quality, and fish assemblage data collected in 24 reservoirs of the Tennessee River; we wanted to describe longitudinal changes occurring at the scale of the entire reservoir series (i.e., cascade) and to test the hypothesis that fish communities and environmental factors display predictable gradients like those recognized for unimpounded rivers. We used a data set collected over a 7-year period; over 3 million fish representing 94 species were included in the data set. Characteristics such as reservoir mean depth, relative size of the limnetic zone, water retention time, oxygen stratification, thermal stratification, substrate size, and water level fluctuations increased in upstream reservoirs. Conversely, reservoir area, extent of riverine and littoral zones, access to floodplains and associated wetlands, habitat diversity, and nutrient and sediment inputs increased in downstream reservoirs. Upstream reservoirs included few, largely lacustrine, ubiquitous fish taxa that were characteristic of the lentic upper reaches of the basin. Fish species richness increased in a downstream direction from 12 to 67 species/reservoir as riverine species became more common. Considering impoundments at a basin scale by viewing them as sections in a river or links in a chain may generate insight that is not always available when the impoundments are viewed as isolated entities. Basin-scale variables are rarely controllable but constrain the expression of processes at smaller scales and can facilitate the organization of reservoir management efforts.

The river continuum concept (RCC; Vannote et al. 1980) describes spatial gradients within a river, as reflected by gradual changes in abiotic and biotic components. Based on the RCC, rivers have been regarded as longitudinally connected systems with unequivocal linkages between upstream and downstream segments (Ward and Stanford 1983; Naiman et al. 1987). The longitudinal connectivity of the Tennessee, Columbia, Missouri, Paraná, Volga, Dnieper, and Angara rivers and hundreds of other large and small rivers has been severely disrupted by transformation of the rivers into reservoir cascades, which consist of a series of reservoirs aligned in sequence along the main river and its tributaries. Research and management of reservoirs in these impounded systems have emphasized the study of

isolated reservoirs (e.g., Miranda and DeVries 1996) and for the most part have disregarded the longitudinal connectivity described by the RCC. Assessments of correlations among biotic and abiotic characteristics over multiple reservoirs are not lacking (e.g., Godinho et al. 2000; Claramunt and Wahl 2000; Carol et al. 2006), but they normally involve a comparison of reservoirs over multiple basins without consideration of the spatial distribution along a single river basin. Basin-scale studies of reservoir cascades are few, and most have focused on water quality (e.g., Barbosa et al. 1999; Abe et al. 2003) and invertebrates (e.g., Sampaio et al. 2002; Callisto et al. 2005); not many of these studies have focused on fish (e.g., Chick et al. 2006). Without an understanding of basin-scale gradients, differences among individual reservoirs are difficult to interpret.

This void has frustrated advancement in reservoir science by impeding adequate organization of available information and by hindering interchanges with allied disciplines that view the impounded river at the basin scale. We reason that much like rivers show longitudinal organization (Vannote et al. 1980; Belliard et al.

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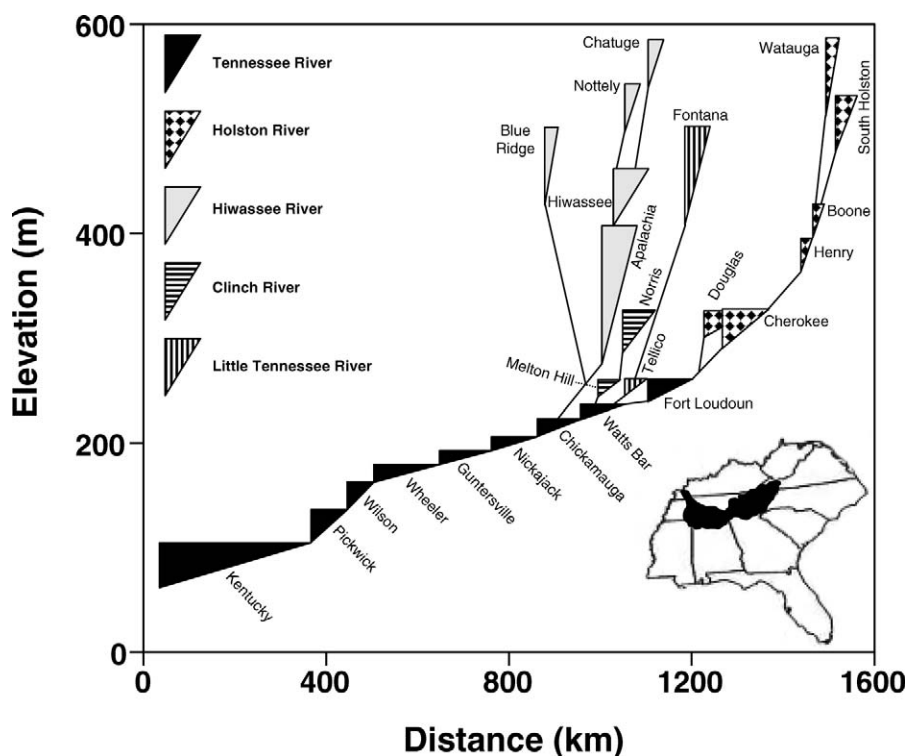


FIGURE 1.—Sketch of the Tennessee River, identifying 24 study reservoirs, major tributaries, elevation, and distance from the river's confluence with the Ohio River. Height and width of each triangle reflect a reservoir's approximate maximum depth and length, respectively. Inset shows the position of the Tennessee River basin within the southeastern United States.

1997; Romanuk et al. 2006), reservoir cascades are likely to show predictable longitudinal gradients in environmental and fish assemblage characteristics. Longitudinal gradients may be anticipated based on basin hydrology and geomorphology that often change in a predictable manner from highlands to lowlands, dictating the broad physical characteristics of reservoirs. An understanding of these gradients might serve to organize existing knowledge about single reservoirs and to develop wide-ranging guiding principles for research and management of reservoir fish. Therefore, we analyzed morphometric, water quality, and fish assemblage data available for reservoirs in the Tennessee River to understand how they change longitudinally at the scale of the entire reservoir cascade and to test the hypothesis that fish communities and environmental factors display predictable gradients along a reservoir cascade.

Methods

Study area.—The Tennessee River originates in the Appalachian mountains of North America and flows westerly 1,045 km through a section of the east-central

United States, draining 106,000 km² over seven states. It is the fifth largest river in the United States, and average discharge is about 1,800 m³/s at the river's confluence with the Ohio River. Precipitation in the basin averages 132 cm annually, of which approximately 50 cm fall during December–March, when vegetative cover is lowest. Impoundment of the river by the Tennessee Valley Authority (TVA) began in 1933. The system currently has 40 reservoirs (36 TVA reservoirs), of which 24 were included in this study (Figure 1). We excluded reservoirs that were not operated by TVA, reservoirs for which no data were available, or reservoirs in tributaries that joined the Tennessee River near its terminus and therefore were a marginal part of the cascade. Ten of the study reservoirs included navigation locks that allowed passage from the Ohio River up to the Melton Hill and Fort Loudoun reservoirs and to Tellico Reservoir that is connected through a canal to Fort Loudoun Reservoir. The other reservoirs were constructed for water storage, flood control, and hydropower (TVA 1990). Elevation of the study reservoirs ranged from 110 to 597 m above mean sea level.

Morphometric variables.—The Tennessee River drains a rather uniform climatic basin considering its somewhat restricted geographical position; the most distinct changes to the landscape are associated with an elevation gradient. Elevation shapes the lay of the land and hence the reservoir basin, reservoir morphometry, and stream discharge. Accordingly, reservoir surface area (area of the reservoir at summer pool level), average depth (mean depth at summer pool level), water retention time (mean time required for all water in the lake to pass through the outflow), relative water level fluctuation (calculated as annual vertical fluctuation/mean depth), and shape (as indicated by the shoreline development index, calculated as $\text{shoreline length}/[2(\text{area} \times \pi)^{0.5}]$) were examined relative to reservoir position in the reservoir cascade. The shoreline development index reflects the degree of irregularity of the shoreline; an index value of 1.0 indicates a perfect circle, and larger values indicate a higher degree of irregularity. These variables were selected because they were readily available for all reservoirs (Turner and Cornelius 1989), have been commonly used to characterize reservoirs (Jenkins 1970), and were expected to be influenced by a reservoir's position in the cascade.

Water quality variables.—Urban and agricultural development within the Tennessee River basin affects nutrients and water quality in the river. Nevertheless, we expected that longitudinal changes in physical characteristics would produce corresponding longitudinal changes in water quality metrics, although the gradients might be strongly influenced by local development. Vertical depth profiles of dissolved oxygen (DO) and temperature were recorded at a station in front of the dam during August, which is generally the warmest and driest time of the year in the southeastern United States, resulting in the strongest potential for vertical stratification. Vertical profiles measured the range in DO and temperature. At the same time and location, water samples representing a composite over the epilimnion were collected to measure concentrations of total phosphorus, total Kjeldahl nitrogen, total organic carbon, and chlorophyll *a*. Nitrogen : phosphorus, carbon : nitrogen, and carbon : phosphorus ratios were computed to assess relative nutrient distributions along the cascade. Visibility through the water column was recorded with a standard Secchi disk. Additional details about collection of water quality data are given by Dycus and Baker (2001). Analyses are based on data averaged over the 1994–1997 study period.

Fish assemblages.—Like morphometry and water quality, fish assemblages were hypothesized to change

longitudinally. Fish assemblages were evaluated through boat electrofishing and gillnetting surveys conducted by TVA in spring 1990–1996 using the methods outlined by Hickman and McDonough (1996). Shoreline boat electrofishing was used to sample nearshore littoral zones, and gillnetting was employed to sample areas away from shore. Fish were collected at randomly selected fixed stations distributed throughout the reservoirs and represented existing habitats relative to their occurrence in the reservoir. Proportional to reservoir area, 10–60 electrofishing transects (mean = 28 transects) were sampled annually in each reservoir; each sample lasted 10 min and covered roughly 300 m of shoreline, although occasionally longer or shorter samples were taken. A boat electrofisher system similar to that described by Reynolds (1996) was used (60-Hz pulsed DC; 4–6 A). Experimental gill nets consisting of five 6.1-m panels (mesh sizes = 2.5, 3.8, 5.1, 6.4, and 7.6 cm) were fished on or near the bottom. Proportional to reservoir area, 10–40 (mean = 22) overnight sets were made in the most common habitat types, alternating mesh sizes toward the shoreline between sets. Captured fish were separated by species and enumerated prior to release.

Species richness and species ordinations were used to describe fish communities for the 1990–1996 collections combined. Richness was defined as total count of species. Ordination was performed with nonmetric multidimensional scaling (NMS) applied to the pooled electrofishing and gill-net catches. Pooling was considered only after electrofishing and gill-net catches were examined separately; it was apparent that while the gear types emphasized different but overlapping species, there was no difference in the outcome relative to our hypothesis that fish communities display predictable gradients along a reservoir cascade. Pooling was performed according to reservoir by adjusting the catch by each gear type to a fixed catch (i.e., $N = 1,000$ fish/gear type) and then adding the two adjusted frequencies so that each gear contributed equally to the pooled catch. The NMS analysis was applied with PRIMER software (Clarke and Gorley 2006) to a Bray–Curtis similarity matrix constructed from adjusted frequencies that were transformed ($\log_e[x + 1]$) to downweight high-abundance species. We subjectively limited the NMS analysis to species that occurred in more than one reservoir; species included in the analyses were recorded as zero rather than missing where they were not collected.

The representation of trophic guilds in the fish assemblage was expected to change along the reservoir cascade as habitats, primary production, and food sources changed. To test for such gradients, individuals

of each species were reclassified into trophic groups that were modified slightly from those proposed by Goldstein and Simon (1999). Trophic groups included herbivores (consumers of plants, including phytoplankton, epilithic algae, or macrophytes), detritivores (consumers of nonliving organic matter and associated microflora accumulated on the bottom), planktivores (consumers of plankton suspended in the water column), invertivores (consumers of invertebrates from midges to mollusks), and carnivores (consumers of the whole bodies of other fish). Several species belong to more than one trophic classification during their life cycle; their food habits were denoted by coupling some of the five major trophic categories to create 11 trophic groups (Table 1).

Spatial organization.—Longitudinal organization along the reservoir cascade was examined by assessing the environmental and fish assemblage descriptors for each reservoir relative to drainage area. Drainage area adequately tracks the longitudinal order of reservoirs along the main stem of the Tennessee River. However, when the main-stem river branches into multiple tributaries, each with their separate reservoir cascade, drainage area no longer tracks order accurately. Despite this limitation, drainage area is a simple indicator of position in a cascade. Relationships with drainage area were examined statistically by use of Spearman's rank correlation coefficient (r_s) but were also examined graphically to detect potential inadequacies of drainage area as a position indicator.

Results

Morphometric Variables

The small number of reservoir physical characteristics included in our study exhibited various gradients relative to position along the cascade (Figure 2). As expected, drainage area and elevation were highly correlated ($r_s = -0.97$, $P < 0.01$), suggesting that either variable indicates position in the cascade. Reservoir area increased exponentially as the cascade descended ($r_s = 0.79$, $P < 0.01$), whereas retention time decreased exponentially ($r_s = -0.97$, $P < 0.01$). Mean depth ($r_s = -0.42$, $P = 0.04$) and relative water level fluctuation ($r_s = -0.52$, $P = 0.01$) decreased in a downstream direction, although these relationships were highly variable due to diversity in local physiography; thus, it was difficult to discern whether the gradients were linear or curvilinear. A wedge pattern was apparent between the shoreline development index and drainage area, suggesting that downstream reservoirs had the propensity to become more elongated and more dendritic, but this propensity was not always realized.

Water Quality Variables

Position along the reservoir cascade influenced many of the water quality variables considered in our analyses (Figure 3). The temperature range decreased exponentially with drainage area ($r_s = -0.85$, $P < 0.01$), indicating that in late summer the temperature gradient from surface to bottom became wider in an upstream direction. Because of a decrease in DO in the hypolimnion, the DO range was large in reservoirs that were situated high in the cascade; however, the DO range decreased downstream ($r_s = -0.74$, $P < 0.01$) as reservoirs became shallower and retention time lessened. Total phosphorus ($r_s = 0.85$, $P < 0.01$) increased linearly with descent down the cascade, whereas total nitrogen was lower upstream, increased, and then became asymptotic in the main-stem reservoirs ($r_s = 0.66$, $P < 0.01$). These nutrient trends are probably related to a reduction in basin development upstream but could also indicate downstream accrual. Chlorophyll *a* also showed a wedgelike pattern and tended to be higher in downstream reservoirs, although some lowland reservoirs had low concentrations. Secchi depth decreased rapidly with increased drainage area ($r_s = -0.78$, $P < 0.01$), documenting clearer water in upstream reservoirs; however, Secchi depth leveled off in the main-stem reservoirs. Nitrate-nitrogen ($r_s = 0.59$, $P < 0.01$), total organic carbon ($r_s = 0.43$, $P = 0.04$), and total alkalinity ($r_s = 0.42$, $P = 0.05$) exhibited initially rapid increases and then leveled off in the main-stem reservoirs. Nitrogen : phosphorus ($r_s = -0.77$, $P < 0.01$), carbon : phosphorus ($r_s = -0.79$, $P < 0.01$), and carbon : nitrogen ($r_s = -0.70$, $P < 0.01$) ratios all decreased rapidly in the upper parts of the cascade and decreased slowly in the main stem.

Overall, scatter plots (Figure 3) suggested that variability in water quality was smaller among the main-stem reservoirs than among reservoirs within subcascades. This pattern reflected increased homogenization and more uniform conditions in the main-stem reservoirs due to reduced retention time. Also, various trends were restricted to reservoir clusters along the cascade. For example, phosphorus levels decreased in a cluster of consecutive reservoirs but then increased rapidly before the decreasing trend resumed in another cluster of consecutive reservoirs (Figure 3, encircled data points), resulting in an overall increasing trend. This pattern suggests that localized inputs from tributaries, agricultural areas, or major urban areas were absorbed by short series of reservoirs until another major influx occurred. We expect that the patterns observed will change seasonally and will track annual climatic cycles; nevertheless, longitudinal trends along the cascade are likely to occur year-round.

TABLE 1.—List of fish species collected with electrofishing and gillnetting in 24 Tennessee River reservoirs during spring 1990–1996 (N = number of reservoirs from which a species was collected). Major trophic classes include invertivores (I), carnivores (C), planktivores (P), herbivores (H), and detritivores (D). Because several species belonged to more than one trophic classification during the life cycle, their food habits were denoted by the appropriate combination of major trophic classes. Spearman's rank correlation coefficients (r_s) indicate the association between adjusted species density and nonmetric multidimensional scaling (NMS) score (Figure 6); blanks indicate species that were collected from a single reservoir and excluded from NMS analyses. The sample size for each r_s value is 24, because a density of zero was applied to reservoirs where a given species was not collected.

Family	Common name	Scientific name	Trophic class	N	r_s
Petromyzontidae	Chestnut lamprey	<i>Ichthyomyzon castaneus</i>	Parasitic	8	0.54
Anguillidae	American eel	<i>Anguilla rostrata</i>	I/C	2	0.37
Lepisosteidae	Spotted gar	<i>Lepisosteus oculatus</i>	C	9	0.65
	Longnose gar	<i>Lepisosteus osseus</i>	C	15	0.65
	Shortnose gar	<i>Lepisosteus platostomus</i>	C	1	
Amiidae	Bowfin	<i>Amia calva</i>	C	5	0.54
Hiodontidae	Goldeye	<i>Hiodon alosoides</i>	I	3	0.36
	Mooneye	<i>Hiodon tergisus</i>	I	11	0.62
Clupeidae	Skipjack herring	<i>Alosa chrysochloris</i>	P	12	0.73
	Alewife	<i>Alosa pseudoharengus</i>	P	7	0.12
	Gizzard shad	<i>Dorosoma cepedianum</i>	D	24	0.79
Esocidae	Threadfin shad	<i>Dorosoma petenense</i>	P	18	0.85
	Muskellunge	<i>Esox masquinongy</i>	C	5	0.04
	Chain pickerel	<i>Esox niger</i>	C	2	0.46
Salmonidae	Rainbow trout	<i>Oncorhynchus mykiss</i>	I/C	7	−0.07
	Brown trout	<i>Salmo trutta</i>	I/C	2	0.16
Cyprinidae	Common carp	<i>Cyprinus carpio</i>	I/D	24	−0.23
	Bighead carp	<i>Hypophthalmichthys nobilis</i>	I/P	1	
	Grass carp	<i>Ctenopharyngodon idella</i>	H	4	0.49
	Mimic shiner	<i>Notropis volucellus</i>	I	1	
	Ghost shiner	<i>Notropis buchanani</i>	I	1	
	Whitetail shiner	<i>Cyprinella galactura</i>	I	5	−0.35
	Spotfin shiner	<i>Cyprinella spiloptera</i>	I/D	17	0.13
	Steelcolor shiner	<i>Cyprinella whipplei</i>	I	9	0.43
	Striped shiner	<i>Luxilus chrysocephalus</i>	I	4	0.35
	Golden shiner	<i>Notemigonus crysoleucas</i>	I/H	11	0.58
	Emerald shiner	<i>Notropis atherinoides</i>	P	11	0.59
	Silver shiner	<i>Notropis photogenis</i>	I/P	3	−0.06
	Silver chub	<i>Macrhybopsis storeriana</i>	I/P	1	
	Sicklefin chub	<i>Macrhybopsis meeki</i>	I/P	1	
	Pugnose minnow	<i>Opsopoeodus emiliae</i>	D	4	0.48
	Bluntnose minnow	<i>Pimephales notatus</i>	D	12	−0.01
	Bullhead minnow	<i>Pimephales vigilax</i>	I/H	12	0.62
	Longnose dace	<i>Rhinichthys cataractae</i>	I	1	
	Central stoneroller	<i>Camptostoma anomalum</i>	H	6	0.46
Catostomidae	River carpsucker	<i>Carpionodes carpio</i>	P/D	14	0.45
	Highfin carpsucker	<i>Carpionodes velifer</i>	D	2	0.32
	Quillback	<i>Carpionodes cyprinus</i>	I/D	16	0.44
	White sucker	<i>Catostomus commersonii</i>	I/D	2	0.34
	Blue sucker	<i>Cycleptus elongatus</i>	I/D	1	
	Northern hog sucker	<i>Hypentelium nigricans</i>	I/D	21	0.09
	Smallmouth buffalo	<i>Ictiobus bubalus</i>	I/D	14	0.70
	Bigmouth buffalo	<i>Ictiobus cyprinellus</i>	I	10	0.72
	Black buffalo	<i>Ictiobus niger</i>	I/D	11	0.57
	Spotted sucker	<i>Minytrema melanops</i>	I	11	0.74
	Silver redbhorse	<i>Moxostoma anisurum</i>	I	16	0.09
	River redbhorse	<i>Moxostoma carinatum</i>	I	19	−0.42
	Black redbhorse	<i>Moxostoma duquesnei</i>	I	21	0.03
	Golden redbhorse	<i>Moxostoma erythrurum</i>	I	19	0.40
	Shorthead redbhorse	<i>Moxostoma macrolepidotum</i>	I	14	0.30
	Snail bullhead	<i>Ameiurus brunneus</i>	I/D/C	2	−0.37
Ictaluridae	White catfish	<i>Ameiurus catus</i>	I/C	1	
	Black bullhead	<i>Ameiurus melas</i>	I/C	4	0.03
	Yellow bullhead	<i>Ameiurus natalis</i>	I/C	8	0.07
	Brown bullhead	<i>Ameiurus nebulosus</i>	I/D/C	5	−0.20
	Blue catfish	<i>Ictalurus furcatus</i>	I/C	16	0.76
	Channel catfish	<i>Ictalurus punctatus</i>	I/C	24	0.27
	Flathead catfish	<i>Pylodictis olivaris</i>	I/C	24	−0.45
	Blackstripe topminnow	<i>Fundulus notatus</i>	I/H	2	0.30
Cyprinodontidae	Blackspotted topminnow	<i>Fundulus olivaceus</i>	I/H	2	0.43
	Western mosquitofish	<i>Gambusia affinis</i>	I	2	0.03

TABLE 1.—Continued.

Family	Common name	Scientific name	Trophic class	N	r_s
Atherinidae	Inland silverside	<i>Menidia beryllina</i>	I/P	4	0.53
	Brook silverside	<i>Labidesthes sicculus</i>	I/P	13	0.56
Percichthyidae	White bass	<i>Morone chrysops</i>	I/C	22	-0.40
	Yellow bass	<i>Morone mississippiensis</i>	I/C	12	0.70
	Striped bass	<i>Morone saxatilis</i>	I/C	18	0.40
	White bass × striped bass hybrid	<i>Morone chrysops</i> × <i>M. saxatilis</i>	I/C	18	0.32
Centrarchidae	Rock bass	<i>Ambloplites rupestris</i>	I/C	14	0.12
	Redbreast sunfish	<i>Lepomis auritus</i>	I	20	-0.29
	Green sunfish	<i>Lepomis cyanellus</i>	I/C	23	-0.24
	Warmouth	<i>Lepomis gulosus</i>	I/C	20	-0.09
	Orangespotted sunfish	<i>Lepomis humilis</i>	I	1	
	Pumpkinseed	<i>Lepomis gibbosus</i>	I	1	
	Bluegill	<i>Lepomis macrochirus</i>	I	24	-0.84
	Longear sunfish	<i>Lepomis megalotis</i>	I	14	0.60
	Redear sunfish	<i>Lepomis microlophus</i>	I	16	0.66
	Redeye bass	<i>Micropterus coosae</i>	I/C	1	
	Smallmouth bass	<i>Micropterus dolomieu</i>	I/C	24	-0.71
	Spotted bass	<i>Micropterus punctulatus</i>	I/C	21	-0.23
	Largemouth bass	<i>Micropterus salmoides</i>	I/C	24	-0.47
	White crappie	<i>Pomoxis annularis</i>	I/C	19	0.62
	Black crappie	<i>Pomoxis nigromaculatus</i>	I/C	21	-0.34
Percidae	Snubnose darter	<i>Etheostoma simoterum</i>	I	2	0.37
	Tangerine darter	<i>Percina aurantiaca</i>	I	4	-0.43
	Logperch	<i>Percina caprodes</i>	I	16	0.51
	Slenderhead darter	<i>Percina phoxocephala</i>	I	1	
	Dusky darter	<i>Percina sciera</i>	I	3	0.28
	Olive darter	<i>Percina squamata</i>	I	1	
	Yellow perch	<i>Perca flavescens</i>	I/C	15	0.21
	Sauger	<i>Sander canadensis</i>	I/C	13	0.65
	Walleye	<i>Sander vitreus</i>	I/C	17	-0.70
	Saugeye	<i>Sander canadensis</i> × <i>Sander vitreus</i>	I/C	6	0.32
Cottidae	Banded sculpin	<i>Cottus caroliniae</i>	I	4	0.36
Sciaenidae	Freshwater drum	<i>Aplodinotus grunniens</i>	I/C	15	0.71

Fish Assemblages

Over 3 million fish representing 94 species and 19 families were collected during the 7-year study period (Table 1). In all, 91 species were captured by electrofishing (9–63 species/reservoir) and 64 species were captured by gillnetting (10–47 species/reservoir). Species richness estimates based on combined electrofishing and gill-net catches ranged from 12 to 67 species/reservoir and showed a marked exponential increase in a downstream direction ($r_s = 0.86$, $P < 0.01$; Figure 4). Seven species found in all 24 study reservoirs were the gizzard shad, common carp, channel catfish, flathead catfish, bluegill, smallmouth bass, and largemouth bass. Twenty-eight species were collected only in the lower 11 main-stem reservoirs connected through locks; such species included the skipjack herring, yellow bass, spotted gar, spotted sucker, mooneye, bowfin, emerald shiner, chestnut lamprey, inland silverside, and brook silverside. Conversely, seven species were limited to upper reservoirs that lacked connection through navigation locks; these species were mainly uncommon cyprinids or darters and introduced fishes from neighboring

Atlantic slope basins (e.g., pumpkinseed, white catfish, and snail bullhead).

Catch rates exhibited substantial dissimilarity along the cascade, as suggested by their scatter plots (Figure 4). However, exponential increases in catch were evident as the reservoir cascade descended down the Tennessee River basin (Figure 4). Electrofishing catch rates increased ($r_s = 0.75$, $P < 0.01$) from 200 to 300 fish/h in reservoirs with small drainages to over 1,000 fish/h in reservoirs near the lower end of the cascade; the exception was Apalachia Reservoir, which exhibited catch rates averaging 25 fish/h. Similarly, gill-net catch rates increased ($r_s = 0.75$, $P < 0.01$) from about 100 fish/10 nets in reservoirs with small drainages to over 400 fish/10 nets in reservoirs at the end of the cascade; the exception again was Apalachia Reservoir, where the average catch rate was 27 fish/10 nets.

Percentage composition and richness of trophic groups also changed along the reservoir cascade (Figure 5). The percentage of fish belonging to the detritivore group increased in a downstream direction from under 10% to over 40% ($r_s = 0.64$, $P < 0.01$). In contrast, planktivores increased from 0% or near zero at mid- to upper-level cascade positions to almost 40%

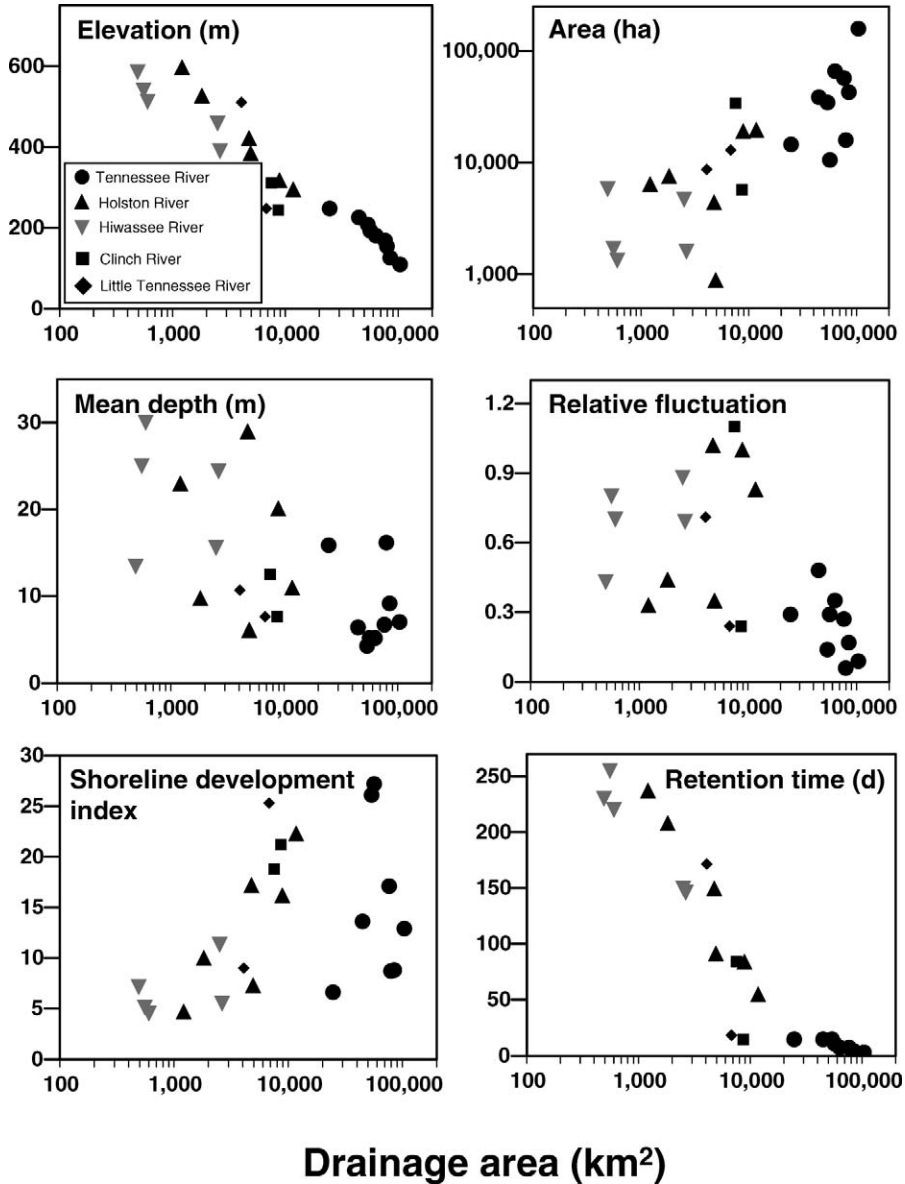


FIGURE 2.—Selected physical characteristics of 24 study reservoirs relative to their positions (indexed by drainage area) in the reservoir cascade of the Tennessee River and associated subcascades (Holston, Hiwassee, Clinch, and Little Tennessee rivers). Relative water level fluctuation was calculated as annual vertical fluctuation divided by mean depth; shoreline development index was calculated as shoreline length/[2(area \times π)^{0.5}]. Retention time was the mean time required for all water to pass through the reservoir outflow.

in downstream reservoirs ($r_s = 0.91$, $P < 0.01$). Invertivores decreased in a downstream direction from near 40% to less than 10% ($r_s = -0.62$, $P < 0.01$), and invertivores/carnivores decreased from over 50% to less than 20% ($r_s = -0.77$, $P < 0.01$). Invertivores/detritivores generally decreased in a downstream direction, ranging from over 30% to near 0%; however,

the Hiwassee River cascade did not conform to this pattern, and therefore the overall relationship was only marginally significant ($r_s = -0.36$, $P = 0.09$).

Representation of a trophic class often varied among subcascades, yet general trends relative to reservoir position in the subcascade persisted (Figure 5). This pattern was particularly obvious for herbivores but was

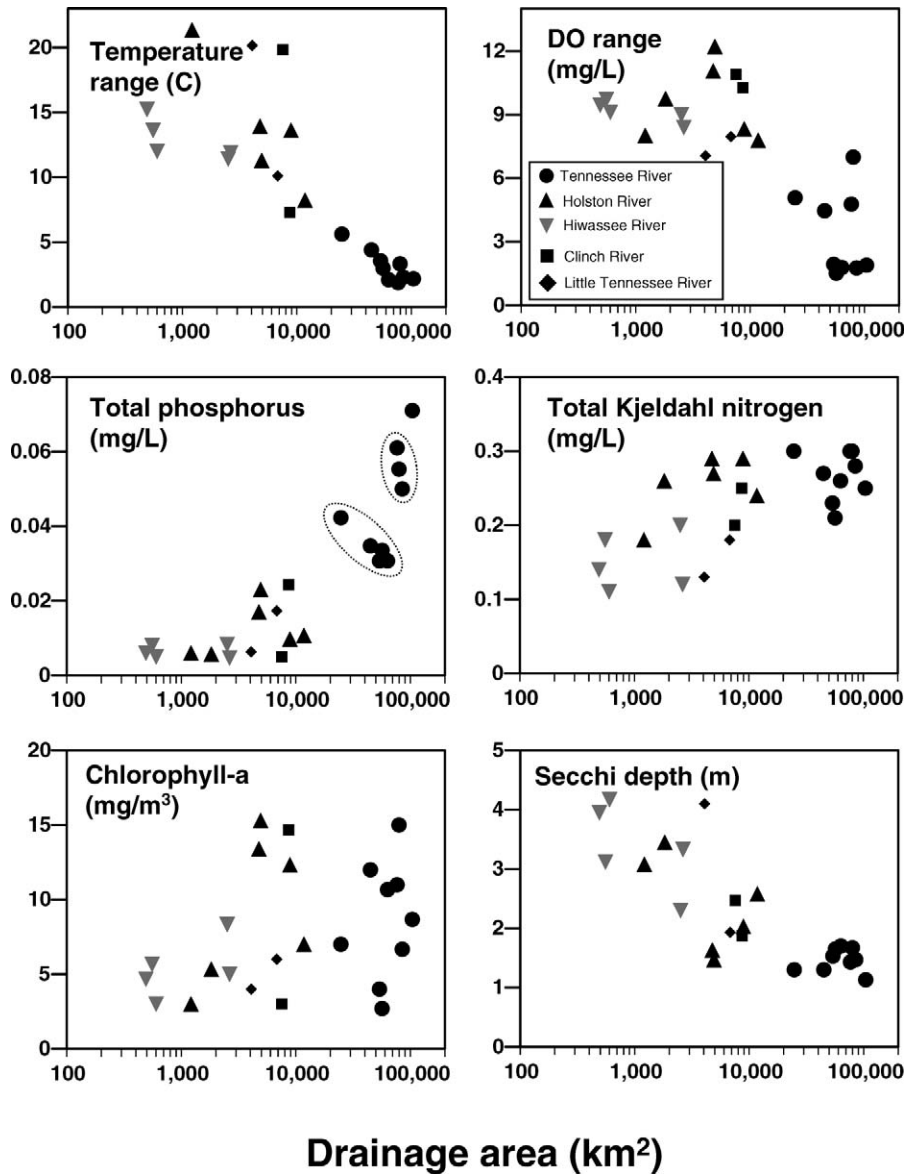


FIGURE 3.—Selected water quality characteristics of 24 study reservoirs relative to their positions (indexed by drainage area) in the reservoir cascade of the Tennessee River and associated subcascades (Holston, Hiwassee, Clinch, and Little Tennessee rivers). Symbols surrounded by ovals identify reservoirs for which phosphorus levels decreased uninterruptedly. In order of increasing drainage area, the lower oval includes Fort Loudoun, Watts Bar, Chickamauga, Nickajack, and Guntersville reservoirs; the upper oval includes Wheeler, Wilson, and Pickwick reservoirs.

also apparent for invertivores and invertivores/carnivores. Richness of trophic guilds ranged from 4 to 10 groups/reservoir. Trophic group richness exhibited a great deal of variability in relation to drainage area, but a direct relation between the two factors was still apparent ($r_s = 0.69$, $P < 0.01$).

Species composition showed strong organization relative to position in the reservoir cascade. Eighty

species occurred in more than one reservoir and were included in the NMS ordination. Three ordination axes were identified by NMS and the stress value was 0.07 (scale = 0–1, where 0 represents an absolute fit and values < 0.1 represent a good fit), but only the axis 1 scores were correlated with drainage area ($r_s = 0.85$, $P < 0.01$; Figure 6). Notably, upstream reservoirs were characterized by a greater representation of bluegills,

smallmouth bass, and walleyes (i.e., the correlation between the percentage contribution of each species and NMS score was -0.6 or better; Table 1). At the low end of the basin, reservoir fish assemblages included greater percentages of shads, blue catfish, buffalos, freshwater drum, gars, yellow bass, redear sunfish, white crappies, and other species listed in Figure 6 (i.e., the correlation with NMS score was 0.6 or better; Table 1). A three-dimensional projection of ordination scores (cube in Figure 6) suggested that fish assemblages differed over subcascades. A one-way analysis of similarities conducted in PRIMER software (Clarke and Gorley 2006) indicated that fish assemblages in the subcascades differed significantly (global coefficient of determination $[R] = 0.79$, $P < 0.01$). Pairwise tests provided by the analysis of similarities clarified that fish assemblages of the Holston, Clinch, and Little Tennessee River subcascades were similar ($P \geq 0.36$) but differed from the assemblages of the Hiwassee River subcascade ($P \leq 0.04$) and the Tennessee River subcascade ($P \leq 0.02$); the Hiwassee and Tennessee River subcascade assemblages also differed from each other ($P < 0.01$).

Discussion

The RCC offered a clinal view of rivers (Vannote et al. 1980). According to the RCC, the physical character of a river shows a gradient of conditions from headwaters to downstream, and upstream processes affect downstream processes. The RCC does not apply directly to reservoir cascades; in fact, reservoirs are artificial structures that alter the river continuum (Ward and Stanford 1983). However, the notion of clinal change along a basin does apply to a reservoir cascade, as seen in the Tennessee River. Clinal trends in reservoir attributes are probably basin specific. The Arkansas River, for example, is initially charged by runoff from the Rocky Mountains and then flows southeast through arid regions of eastern Colorado and western Kansas before it picks up substantial runoff in eastern Oklahoma and Arkansas. In such a diverse river basin, longitudinal gradients among reservoirs may arise, and restart multiple times as the river travels through different climatic zones. Thus, the exact patterns we describe here may not apply directly to other systems. Nevertheless, predictable gradients are likely to be observable in all reservoir cascades. In the Upper Mississippi River, fish communities exhibited substantial spatial structure across pools, but pools positioned closer together exhibited greater similarities than pools located farther apart (Chick et al. 2006), suggesting that longitudinal structuring gradients existed.

Physical differences across basins are expected. Nevertheless, some basic similarities do exist, and

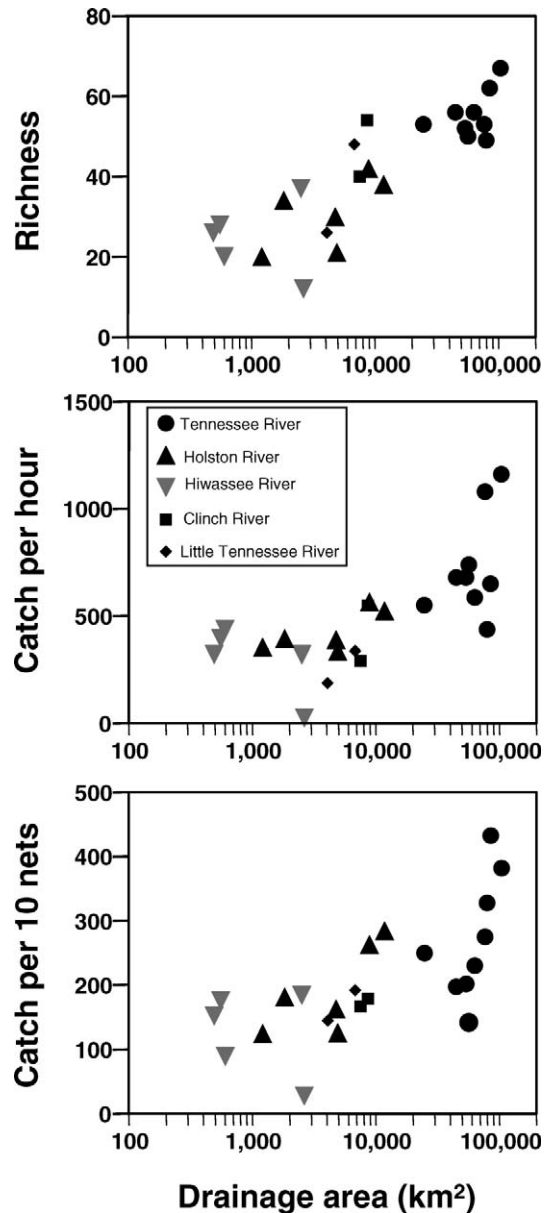


FIGURE 4.—Species richness, electrofishing catch rate (fish/h), and overnight gill-net catch (fish/10 gill nets) in 24 study reservoirs of the Tennessee River reservoir cascade and associated subcascades (Holston, Hiwassee, Clinch, and Little Tennessee rivers), 1990–1996.

these can lead to commonality in gradients of fish assemblages. Basins tend to be more forested in the upper reaches because of the higher elevations and slopes that dissuade agriculture and other human activities. Ordinarily, the lower reaches of basins receive various levels of modification to accommodate

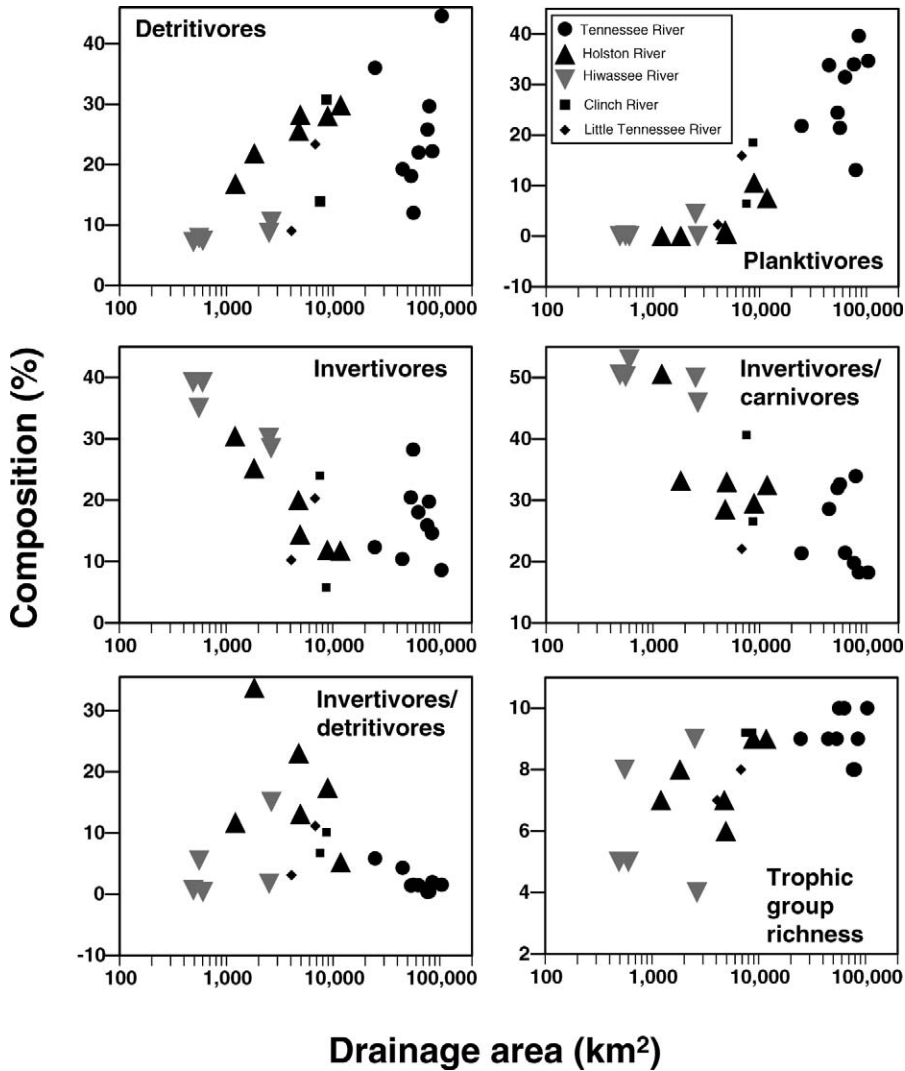


FIGURE 5.—Contribution (%) of various fish trophic groups to electrofishing and gill-net catch (1990–1996) and trophic group richness (number of groups; maximum = 11) in 24 study reservoirs relative to their positions (indexed by drainage area) in the reservoir cascade of the Tennessee River and associated subcascades (Holston, Hiwassee, Clinch, and Little Tennessee rivers).

agriculture and other human activities, which often extend into reservoir floodplains. Characteristics like depth, relative size of the limnetic zone, water retention time, DO and thermal stratification, substrate size, and water level fluctuations have a propensity to be greater 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 be greater in downstream reservoirs. Many of these patterns are dictated by landscape characteristics and are also evident in chains of natural lakes (Kratz et al. 1997;

Riera et al. 2000), but exceptions are common due to the diversity of landscapes.

Nutrient trapping by reservoirs along a basin reportedly reduces productivity down the cascade, but in reservoirs with low retention time nutrients and productivity may actually increase downstream. Lake Mead experienced a drastic drop in productivity after the impoundment of Lake Powell upstream in the Colorado River (Vaux et al. 1995). In the Tietê River, Brazil, the uppermost reservoir in a series of nine impoundments captured most of the nutrients released from São Paulo, the largest city in South America

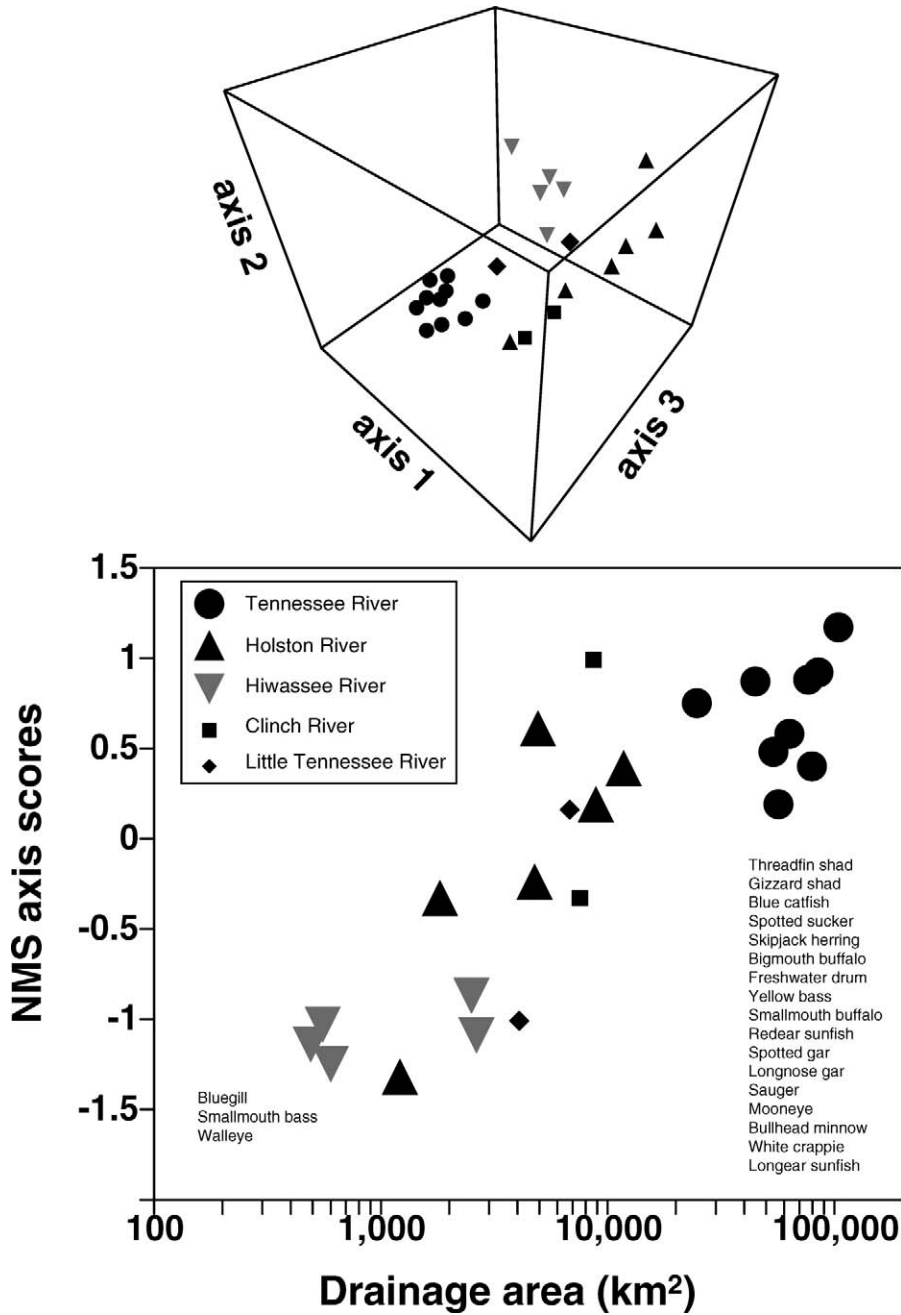


FIGURE 6.—Fish assemblage characteristics (nonmetric multidimensional scaling [NMS] axis scores) based on electrofishing and gill-net catch (1990–1996) in 24 study reservoirs of the Tennessee River reservoir cascade and associated subcascades (Holston, Hiwassee, Clinch, and Little Tennessee rivers). Upper panel identifies reservoir positions relative to the three NMS ordination axes (stress value = 0.07). Lower panel shows the relationship between drainage area and axis 1 (the only axis correlated with a reservoir's position in the cascade). Listed fish species had significant ($P \leq 0.05$) negative (lefthand list) or positive (righthand list) correlations with drainage area (Spearman's rank correlation coefficients, Table 1).

(Barbosa et al. 1999). In reservoirs that are impounded on large rivers with low retention, multiple influential tributaries, or both, the effects of an upstream location may not be as pronounced as in the two preceding examples (Bruns et al. 1984; Agostinho et al. 2004a). In the Tennessee River, upstream reservoirs retain a greater proportion of inflowing nutrients because of high water retention. Nevertheless, net loads are lower in these upstream reservoirs than in reservoirs downstream because of the smaller size of upper drainages and because of differences in geomorphology and land cover (Voigtlander and Poppe 1989). Thus, we observed that dissolved nutrients generally increased in a downstream direction but nutrient ratios changed, reflecting nutrient-specific gradients along the reservoir cascade. Nutrients and associated primary productivity variables therefore show spatial gradients within the basin such that conditions in a given reservoir are to some extent predictable based on the reservoir's position in the basin.

Like nutrients, other water quality characteristics are affected by impoundments and exhibit gradients along reservoir cascades. In the Tennessee River, summer temperature and DO displayed prominent gradients in which vertical differences were large in upstream reservoirs but became smaller downstream. Stratification can negatively affect the ability of reservoirs to support various fish species. However, stratification in Tennessee River reservoirs has been advantageously used by fishery managers to produce two-story fisheries, defined as those that support coldwater species by retaining cool ($\leq 21^{\circ}\text{C}$), oxygenated (> 3.0 mg/L) water throughout the year. The incidence of reservoirs capable of supporting two-story fisheries increases in an upstream direction in the Tennessee River, as the necessary environmental conditions are created by the concurrent reduction in nutrients, increase in depth, and increase in retention time with movement up the cascade. We predict that most limnological characteristics will show longitudinal gradients along the reservoir cascade. Nevertheless, the amount of information available in the literature is limited because limnologists, like fish biologists, have paid much more attention to longitudinal patterns within reservoirs (e.g., Kimmel et al. 1990) than among reservoirs.

The RCC postulates that fish assemblages change continuously along lotic systems in response to physical and nutrient gradients. From upstream to downstream, the species composition of the fish community changes (Huet 1959; Angermeier and Karr 1983; Balon and Stewart 1983; Przybylski 1993) and local species richness increases (Fausch et al. 1984; Beecher et al. 1988; Morin and Naiman 1990). With

few exceptions, species present in upstream reservoirs of the Tennessee River were retained in downstream reservoirs, while new species were added in downstream reservoirs. Ecological modes of fish species (e.g., life history traits, diet) are also expected to change along this gradient (Balon et al. 1986; Penczak and Mann 1990). Such changes were evident in the Tennessee River reservoir cascade. The upstream reservoirs tended to include few, largely lacustrine, ubiquitous taxa that were characteristic of the upper lentic reaches of the unimpounded river (McDonough and Barr 1979). The reduction in riverine species in upstream reservoirs was particularly evident for large, migratory taxa, which are often stopped by dams that lack passage or are hindered by the necessity of traversing multiple dams and multiple passage facilities (Agostinho et al. 1999). Riverine species became more common in downstream reservoirs; this effect is especially evident in reservoirs below long, unimpounded stretches or unimpounded tributaries or in reservoirs with extensive upstream floodplains that can serve as refugia for riverine species in impounded rivers (Agostinho et al. 2004b).

The Tennessee River reservoir cascade has several subcascades that discharge into the main stem. Position of a reservoir relative to a subcascade affected the fish community and trophic guild composition. The Holston and Hiwassee River subcascades were particularly informative because representation of trophic guilds differed, yet gradients persisted. The Holston River originates in the Appalachian Mountains of Virginia and flows southwest, and the Hiwassee River originates in the Appalachian Mountains of North Carolina and Georgia and flows northwest. These two subcascades experience different microclimates mediated by the Appalachian Mountains. They also differ in vegetative cover, as the Holston River drainage has been affected by agriculture and urbanization, whereas the Hiwassee River drainage has retained more of its forests. Thus, longitudinal basin gradients do occur, but patterns may differ over subcascades and conceivably may differ even more across basins.

In addition to species assemblage and trophic guild composition, we predict that variables of interest to fishery managers (e.g., growth rate) are likely to exhibit gradients that are discernable at the scale of the river basin. Because nutrient levels, prey availability, and prey diversity increase downstream along the basin, fish growth rates and biomass are likely to be higher, contributing to greater fish production and standing crop. Moreover, the relatively shallow reservoirs situated lower in the basin have proportionally larger littoral areas that may increase the amount of foraging habitat for species that depend primarily on littoral

detritus, invertebrates, and fish prey. A basin fishery management perspective suggests the need to liberalize harvest in downstream reservoirs given their higher standing crops and productivity, while restraining harvest in upstream reservoirs and focusing on promoting efficiency in fish production.

Reservoir managers have traditionally considered reservoirs as stand-alone systems that are separate from their tributaries, the surrounding watersheds, and the rest of the river basin. Traditional management approaches have focused on in-lake practices, such as controlling selected fish populations, restraining and promoting fish harvest, and enhancing habitat conditions (Hall and Van Den Avyle 1986). By focusing exclusively on the reservoir scale, reservoir scientists have foregone the potential benefits of managing at broader scales. Basin-scale assessment has the advantages of lesser temporal variability and the potential integration of many abiotic, biotic, and socioeconomic characteristics that are active across the basin (Bohn and Kershner 2002). Our analyses of pooled fish collections and a limited number of physicochemical variables identified obvious longitudinal gradients among reservoirs of the Tennessee River. Gradients were evident within the entire cascade as well as within subcascades. We speculate that gradients will be reflected in most of the variables that are relevant to fisheries managers, suggesting the need to research and manage reservoirs at both the single-reservoir scale and the basin scale.

Considering impoundments at a basin scale by viewing them as sections in a river or links in a chain may generate insight that is not always available when considering them as isolated entities. Basin-scale variables are rarely controllable but constrain the expression of processes at smaller scales. An appreciation of basin gradients helps to establish limits for smaller-scale determinants and thereby allows for an understanding of reservoir management potentials and limits. An obvious feature of reservoir cascades is a predictable spectrum of fish assemblages that can provide a diversity of commercial and recreational fisheries. Traditional fisheries management approaches could be organized relative to features in the reservoir cascade. For example, the efficacy with which traditional management influences fish assemblages probably decreases downstream because of increases in reservoir size, species richness, and fish assemblage complexity. Correspondingly, stocking, harvest regulations, and habitat manipulation programs are likely to be increasingly more effective in upstream reservoirs. Efforts to diversify fisheries; overlay commercial, subsistence, and recreational fisheries; and provide multispecies fish passage facilities that increase the

longitudinal connectivity of sections separated by the dams are likely to be more effective in downstream reservoirs because they tend to have more habitat diversity, water regime diversity, species richness, and riverine species than do upstream reservoirs.

Our analyses were restricted to a limited number of ecological properties derived from selected water quality data and species catch rate data recorded in the most comprehensive data sets available to us. We speculate that most ecological properties exhibit longitudinal gradients along reservoir cascades. For example, at the individual level of organization, such properties as optimal ranges, limiting factors, habitat selection, niche partitioning, fecundity, and growth rate will exhibit longitudinal gradients along a reservoir cascade, and knowing the patterns can facilitate reservoir management. Similarly, at the population level of organization, properties like recruitment, mortality, carrying capacity, density dependence, age structure, and genetic variability will probably change along a reservoir cascade; knowledge of how they change would be extremely relevant to reservoir fisheries management, particularly because fishery science has traditionally focused on population-level concepts. At higher levels of organization, such as the community and ecosystem levels, basin-scale questions might focus on properties like gradients in species interactions, trophic dynamics, nutrient cycling, and energy transfer. However, data sets with which to conduct these inquiries are not readily available because most collections have emphasized assessment of single reservoirs in isolation rather than longitudinal gradients in reservoir series. This shortcoming is the consequence of a paradigm in which reservoirs are viewed as spatially independent entities rather than as systems that are longitudinally connected and related by gradients of basin hydrology and geomorphology. We hope that our study will help shift the prevailing paradigm in reservoir fisheries management and encourage a view of reservoirs as segments of an impounded basin, thereby supporting inquiries about longitudinal gradients.

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