

Fish functional gradients along a reservoir cascade

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Abstract

1. The transformations of fish assemblages caused by reservoir cascades can be severe at the reach scale, but basin-scale effects are less clear. However, prevailing river concepts provide a framework for predicting basin-scale effects.
2. To determine if predictions made by the River Continuum Concept relative to the function of fish assemblages are sustained in a temperate river transformed into a reservoir cascade, we examined longitudinal trends in the distribution of fish functional traits over 23 reservoirs of the Tennessee River, U.S.A.
3. In all, 115 species were recorded representing 62 traits, with trait richness increasing longitudinally in a downstream direction. Trophic, reproductive, and habitat traits showed various increasing and decreasing patterns up and down the reservoir cascade. The observed gradients in trait richness and trait distributions were generally consistent with those expected in unregulated rivers, with few unexpected results.
4. The transformation of lotic systems into lentic ones has changed habitats and sources of food and encouraged the proliferation of certain feeding (e.g., detritivores, planktivores, invertivores, piscivores), reproduction (e.g., nest spawners polyphils, broadcast spawners phytolithophils), and habitat (slow current, lacustrine, large river) traits. In essence, reservoirs have expanded downstream habitats in an upstream direction, and thus allowed upstream expansion of species and traits that would have normally not been well represented in upper reaches of the Tennessee River basin. Nevertheless, the impounded Tennessee River has maintained much of its functional integrity, despite extensive alterations to the riverscape.
5. We suggest that, while reservoirs have been shown to have major local-scale effects on riverine fish assemblages, with access to riverine habitats, and with proactive conservation strategies, fish functional richness can remain remarkably high at the basin scale.

KEYWORDS

canonical correlation analysis, dams, impoundments, life history, river continuum concept, species richness, Tennessee River, traits

1 | INTRODUCTION

The River Continuum Concept (RCC) is a fundamental framework in river ecology that has been supported, refined, and refuted over the past four decades (Doretto et al., 2020; Vannote et al., 1980). The concept is applicable to interpret clinal patterns in lotic geomorphology, hydrology, and ecology. Applications of the concept have been expanded into numerous aspects of stream ecology including trophic ecology (Gaglio et al., 2021; Greathouse & Pringle, 2006), reproductive ecology (Aarts & Nienhuis, 2003; Gaglio et al., 2021), and biodiversity with a heavy focus on macroinvertebrates (Tornwall et al., 2015). The RCC has also been adapted to recognise longitudinal physical gradients and habitat distributions along rivers (Gaglio et al., 2021; Rice et al., 2001; Torgersen et al., 2006). The RCC has encouraged developments of various alternative concepts including: (1) the River Ecosystem Synthesis (Thorp et al., 2006), Hierarchical Patch Dynamics (Poole, 2002), and Process Domains (Montgomery, 1999) to account for the patchy nature of river systems moulded by factors such as local climate, physiography, geomorphic processes, and distribution of tributaries and floodplains; (2) Network Dynamics to account for the dendritic nature of river ecosystems (Altermatt, 2013; Benda et al., 2004; Osborne & Wiley, 1992); (3) the River Wave Concept to account for the temporal characteristics of energy and nutrient storage and transport (Humphries et al., 2014); and (4) the Serial Discontinuity Concept to accommodate the discontinuities created by dams and impoundments (Ward & Stanford, 1983).

Many river systems have been impounded to support a multiplicity of societal needs (Grill et al., 2019). Rivers such as the Columbia (U.S.A.), Mississippi (U.S.A.), Murray-Darling (Australia), Paraná (Argentina, Brazil, Paraguay), Volga (Russia), and Yangtze (China), have been transformed into a series of impoundments, a reservoir cascade, that impounds the mainstem and associated tributaries. Various longitudinal riverine ecological processes can be interrupted and restarted by a cascade of reservoirs. These disruptions are encapsulated by the Serial Discontinuity Concept (Ellis & Jones, 2013; Ward & Stanford, 1983) that provides an essential modification to the RCC and helps account for the longitudinal impacts of impoundments. The influences of a cascade of impoundments on a river include loss of connectivity, reduced environmental and species diversity, and oligotrophication (Agostinho et al., 2004; dos Santos et al., 2018). Connectivity through the river network is interrupted by each dam, by the vast reaches of lentic water impounded behind each dam, and by the changes in physicochemical qualities that occur above and below the dams (Bunn & Arthington, 2002; Poff & Zimmerman, 2010). Reductions in environmental and species diversity are commonly associated with the loss of connectivity and environmental homogenisation produced by expansive reaches of stored water (Dias et al., 2021; Ganassin et al., 2021; Yang et al., 2020). The transformations caused by reservoir cascades can be severe at the reach scale, but overarching basin-scale effects are less clear.

At the basin scale the physical attributes of reservoir cascades may more closely echo the physical attributes of river networks. Dams and impoundments were constructed across river basins to provide water storage, flood control, hydropower, transportation, and recreational opportunities, which have permanently altered river systems leading to far-reaching changes in river characteristics. However, because dams are inserted into river systems, it is reasonable to expect that reservoir characteristics are dictated by their position along the river continuum. The attributes of many reservoir cascades display lengthwise patterns just as different reaches of a river do (Faucheux et al., 2022). For example, in reservoir cascades the feeding traits structure of fish assemblages often changes longitudinally along the cascade (Faucheux et al., 2022), which aligns with patterns observed in river networks (Bowen, 1983; Grenouillet et al., 2004; Schlosser, 1987).

Traits are morphological, physiological, structural, phenological, or behavioural characteristics that define organisms in terms of adaptations to their environment (Frimpong & Angermeier, 2010; Violle et al., 2007) and can reflect aspects such as morphology, physiology, behaviour, and life-history expressions (Frimpong & Angermeier, 2010). Relying on traits to examine fish assemblages can be more informative than taxonomy (e.g., species) because traits can pinpoint function (Culp et al., 2011; Frimpong & Angermeier, 2010; Jung et al., 2010; Lima et al., 2017; Verberk et al., 2013). Traits can also facilitate comparisons over biogeographic regions because a species' response can be predicted based on the functional role the species exhibits (dos Santos et al., 2017; Jung et al., 2010). However, there can be challenges and limitations to using a traits-based approach. These include limited information about species' traits, losing the interspecific variability often defined by more than just the observed traits, and associated reduced discriminatory power (Culp et al., 2011; Hoeinghaus et al., 2007; Lima et al., 2017; Verberk et al., 2013). Nevertheless, traits have been used successfully to study aspects such as effects of reservoir aging (dos Santos et al., 2017), oligotrophication (Ganassin et al., 2021), and responses of fish assemblages to impoundment (de Bem et al., 2021).

Most studies of fish assemblages in reservoir cascades have focused on species composition (Chick et al., 2006; Ganassin et al., 2021; Loures & Pompeu, 2018; Miranda et al., 2008). Considering fish assemblages from a trait-based perspective may enable improved understanding of functional relationships and make results of analyses transferable across biogeographic scales. Our objective was to examine longitudinal changes in trait compositions across a major reservoir cascade in eastern North America. To a large extent guided by the RCC, we predicted that trait richness would increase downstream, that trait representation in fish assemblages would change alongside environmental gradients in the cascade, and that traits would retain vestiges of natural riverine gradients, albeit distorted by the impoundments. To explore these predictions, we estimated reservoir-specific trait richness and trait composition and examined if there were linkages between traits and position of the reservoir along the cascade. Whereas we apply the RCC to guide our predictions, our aim was not

to test the RCC but rather to assess how far the distorted fish assemblages developed in an impounded river basin deviated in their functional characteristics from those expected in the original river.

2 | STUDY BASIN

The Tennessee River and major tributaries flow south-westerly 1,499 km from the Appalachian Mountains in eastern North America to the lower Ohio River (Figure 1). The Tennessee River basin is the most biodiverse in North America including 259 native fish species and the highest number of endemic fish species in the continent (NatureServe, 2022). Elevation in the basin ranges from 95 m at the confluence with the Ohio River to 2,037 m at its headwaters in the Appalachian Mountains (Hampson et al., 2000). It is the biggest tributary of the Ohio River, with a drainage area of 105,000 km² and an average annual discharge of 2,000 m³/s at its mouth (White et al., 2005). Land cover in the basin is dominated by forests (58%) and cultivated lands (23%) (Miranda, Coppola, et al., 2021). The basin was impounded principally during the first half of the 20th century and now has 56 reservoirs >100 ha with a mean age of 70 years as of 2020 (Miranda, Coppola, et al., 2021). The 23 study reservoirs ranged in area from 3 to 647 km², catchment area from 490 to 104,000 km², elevation from 110 to 597 m, and were located 36–1,336 km upstream of the confluence of the

Tennessee and Ohio rivers. The primary uses for these reservoirs are flood control and hydroelectric production, although they support various recreational activities.

3 | METHODS

We examined longitudinal changes in species traits along the reservoir cascade by linking three matrices: (1) a species assemblage by sample unit matrix; (2) a species by trait matrix containing values that represent one or more ecological traits of the species; and (3) a sample unit by position in the cascade matrix. Below we describe compilation of these matrices and the methodology used to connect them.

3.1 | Species matrix

Fish assemblages were evaluated through daytime standardised boat electrofishing by the Tennessee Valley Authority in autumn, 1990–2018, but not all reservoirs were sampled every year. A boat electrofisher system like that described by Miranda and Boxrucker (2009) was used (60-Hz pulsed DC; 8–12 peak A) to collect fish at transects randomly distributed nearshore throughout the reservoirs, including lacustrine, transition, and riverine

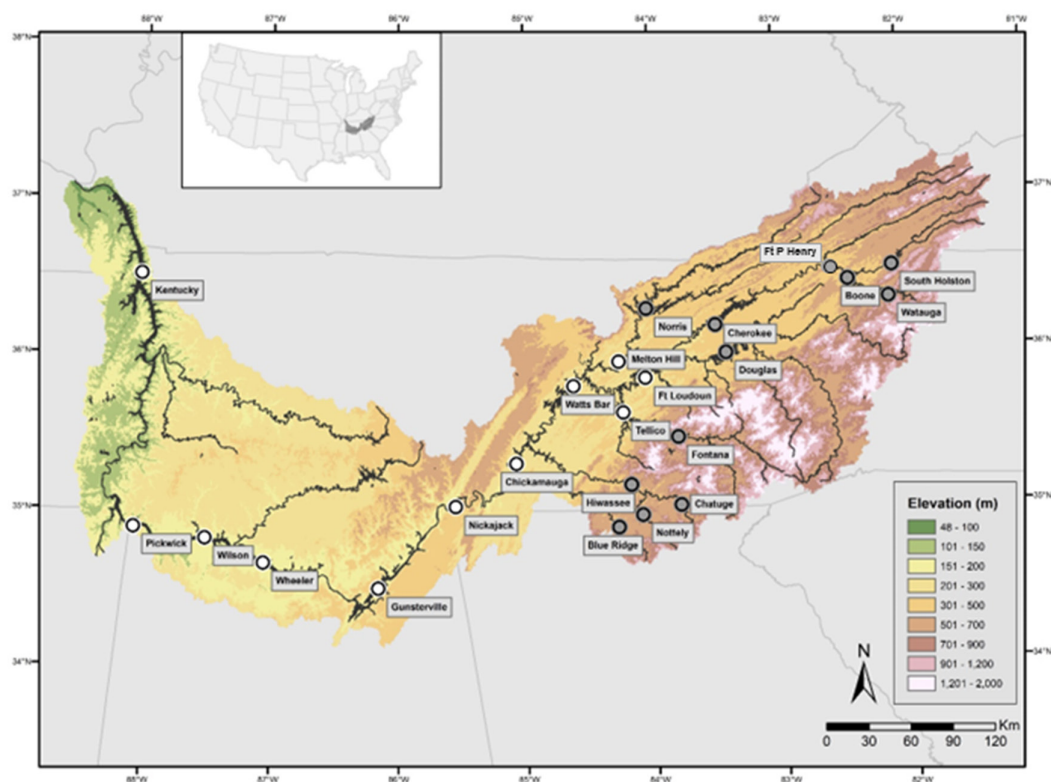


FIGURE 1 Outline of the Tennessee River basin in the south-eastern U.S.A. showing location of the 23 study reservoirs. White markers identify reservoirs connected through locks or a navigation canal (Tellico), and grey markers identify reservoirs not connected through upstream passages.

segments within each reservoir. Transects extended an average 750s ($SD=92$ s) and covered roughly 300m along depths generally <3m.

Electrofishing adequately represents density of littoral species in lentic water bodies (Bonar et al., 2009), although it is biased towards larger individuals and species inhabiting nearshore shallow waters (Dolan & Miranda, 2003; Reynolds & Kolz, 2012). In reservoirs of the Tennessee River, standardised electrofishing represented different aspects of the fish assemblages than captured by standardised gillnetting (Miranda, Fauchaux, et al., 2021). Nevertheless, the assemblages documented by these gears were correlated with the spatial location of the reservoirs in the river basin. Thus, even as the two gear types reflected different aspects of fish assemblages, they tracked spatial differences, suggesting that electrofishing, and gillnetting, reflected standing fish assemblages.

All species of fish captured were counted before release. These counts were pooled over samples and years by reservoir to create a species-count-by-reservoir matrix. All species collected were represented in the matrix except the invasive silver carp (*Hypophthalmichthys molitrix*), which were removed from the matrix because this species has just started to invade the Tennessee River basin and has neither saturated their environments nor expanded beyond some of the most downstream reservoirs.

3.2 | Trait matrix

We assembled a trait-by-species matrix relying on the FishTraits database created by Frimpong and Angermeier (2009). We focused on three types of traits in the database: feeding, reproductive, and habitat (Table 1). We partitioned the reproductive traits into three sets: guarders, non-guarders, and life history traits. Habitat traits were partitioned into substrates and macrohabitat preferences assigned to each species. Because of missing values, we inserted reproductive traits for the slabrock darter (*Etheostoma smithi*) and saddleback darter (*Percina vigil*) from FishBase (Froese & Pauly, 2010). Also, one feeding trait (i.e., non-feeding adults) and two reproductive traits (i.e., psammophils open-substratum spawners and lithophils rock-gravel nest spawners) were each recorded in single reservoirs, so these traits had to be removed from analyses that required presence in at least two reservoirs.

3.3 | Network position matrix

The basic question in the analysis was whether fish functional trait composition in the reservoir cascade exhibits a longitudinal gradient as predicted by the RCC in unpounded rivers. We quantified longitudinal position with three metrics for each reservoir: elevation of a reservoir above mean sea level, cumulative drainage area above the dam (\log_{10} transformed to remove right skewness), and distance between the dam and the confluence of the Ohio River (square-root

transformed to remove left skewness). All three of these indicators are highly correlated but provide different estimates of position within the river network. Thus, a third matrix included the reservoir-by-network-position matrix as indexed by these three metrics.

3.4 | Analysis

Assessing traits associations with position in a reservoir network requires analysis of the three matrices previously described (Dray et al., 2014): the reservoir-by-network-position matrix (R), the species-abundance-by-reservoir matrix (L), and the trait-by-species matrix (Q). Several different approaches generally known as RLQ or fourth-corner analyses have been used to examine relationships among these three matrices (Dray et al., 2014; Kleyer et al., 2012; McCune, 2015). In our analysis we followed McCune (2015) and multiplied L and Q using the MMULT function in Excel software (Microsoft Corporation, 2018) to create a trait-by-reservoir matrix (LQ). Then following Kleyer et al. (2012) we applied the community-weighted mean approach that standardises counts by dividing the total counts for each trait by the total count of fish of all species, which is equivalent to weighting traits by species abundances (McCune, 2015). Rather than applying the redundancy analysis method suggested as one of many alternatives by Kleyer et al. (2012), we applied canonical correlation analysis (CCA; Sherry & Henson, 2005) to estimate the correlation between the R matrix and the LQ matrix (i.e., the association between longitudinal position in the cascade and traits composition). Redundancy analysis assumes that one of the two matrices can be considered the *independent variable*, and the other matrix the *dependent variable* (Muller, 1981), an assumption that affects the outcome of the analysis. In contrast, CCA makes no such assumptions and puts both matrices on equal footing, which is consistent with our stated objective.

4 | RESULTS

In all, 7,651 boat electrofishing samples were completed in the 23 study reservoirs over 1990–2018. Each reservoir was sampled an average of 10.3 years (range, 2–26 years). Total effort per reservoir averaged 333 boat electrofishing transects (16–938 transects). Effort relative to reservoir area averaged 6.1 samples per square kilometre. Whereas more sampling effort was allocated to larger reservoirs, the amount of effort allocated was directly correlated to reservoir surface area (Spearman rank correlation, $\rho=0.84$). This effort produced 1.36 million fish representing 115 species (excluding silver carp) and 20 families.

The 115 species retained for analyses represented 62 traits (Table 1). The CCA indicated that the canonical correlation between trait richness and the reservoir position matrix was 0.92 ($p<0.05$). A plot of elevation versus trait richness illustrated the strong canonical correlation between trait richness and position along the cascade

TABLE 1 Representation of functional traits along the reservoir cascade in the Tennessee River basin, U.S.A. Trait codes are those used by Frimpong and Angermeier (2009).

Trait code	Trait definition	<i>n</i>	Min	Mean	Max	<i>r</i>
	Trophic ($R_c=0.93$; $p<0.01$)					
NONFEED ^a	Adults do not feed	1	<0.01	<0.01	<0.01	NA
ALGPHYTO	Algae or phytoplankton, including filamentous algae	45	31.91	73.79	95.26	-0.62
MACVASCU	Any part of macrophytes and vascular plants	40	28.81	63.81	92.77	0.26
DETRITUS	Detritus or unidentifiable vegetative matter	41	0.64	51.60	96.06	-0.73
INVLVFSH	Aquatic and terrestrial invertebrates including zooplankton, insects, microcrustaceans, annelids, molluscs, and larval fishes	112	99.97	99.99	100.00	0.63
FSHCRCRB	Larger fishes, crayfishes, crabs, frogs, and others	53	2.58	52.66	99.92	0.84
BLOOD	Parasitic lampreys that feed mainly on blood	1	0.00	0.01	0.03	-0.60
EGGS	Eggs of fishes, frogs, and others	23	1.71	31.11	72.80	0.64
	Reproduction: non-guarders ($R_c=0.94$; $p<0.01$)					
A_1_1	Open substratum spawners; pelagophils (a pelagic spawner with numerous buoyant eggs)	4	0.00	1.76	6.06	-0.86
A_1_2	Open substratum spawners; lithopelagophils (eggs initially deposited on rocks/gravel but eggs or embryos are carried away from spawning substrates)	6	0.00	0.12	1.13	0.24
A_1_3A	Open substratum spawners; lithophils (rock-gravel)	11	0.06	0.63	1.87	-0.60
A_1_3B	Open substratum spawners; lithophils (gravel-sand)	4	0.00	0.20	0.83	-0.18
A_1_3C	Open substratum spawners; lithophils (silt-mud)	-	-	-	-	NA
A_1_4	Open substratum spawners; phytolithophils (deposit eggs in clear water on submerged plants or logs, gravel and rocks)	26	0.04	43.66	97.15	-0.62
A_1_5	Open substratum spawners; phytophils (scatter eggs with an adhesive membrane that sticks to submerged, live or dead, aquatic plants, or to recently flooded terrestrial plants)	7	0.00	0.31	1.57	-0.77
A_1_6 ^a	Open substratum spawners; psammophils (eggs scattered directly on sand or near fine roots of plants that hang over the sandy bottom. Eggs adhesive)	1	<0.01	<0.01	<0.01	NA
A_2_3A	Brood hiders; lithophils (rock-gravel)	6	0.00	0.04	0.26	-0.67
A_2_3B	Brood hiders; lithophils (gravel-sand)	6	0.00	0.52	2.21	-0.56
A_2_3C	Brood hiders; lithophils (mud)	-	-	-	-	NA
A_2_4A	Brood hiders; speleophils (rock cavity)	-	-	-	-	NA
A_2_4C	Brood hiders; speleophils (cavity generalist rock crevices, under log bark, openings in vegetation, metal cans, and others)	4	0.00	5.04	29.20	0.44
	Reproduction: guardians ($R_c=0.91$; $p<0.01$)					
B_1_3A	Substratum choosers; lithophils (eggs deposited in single layer or multilayer clutches on cleaned rocks in pits dug in gravel)	3	0.00	0.01	0.03	-0.40
B_1_4	Substratum choosers; phytophils (eggs are scattered onto submerged plants. Male guards and fans eggs)	4	0.00	0.01	0.02	-0.11
B_2_2	Nest spawners; polyphils (circular nests with sticks and roots left in place)	13	1.80	43.68	94.48	0.77
B_2_3A ^a	Nest spawners; lithophils (rock-gravel)	1	<0.01	<0.01	<0.01	NA
B_2_3B	Nest spawners; lithophils (gravel-sand)	2	0.00	0.91	4.79	0.41
B_2_4	Nest spawners; ariadnophils (skilled nest building and parental care remarkably well developed. Nest materials are bound together by a viscid thread secreted by male)	-	-	-	-	NA
B_2_5	Nest spawners; phytophils (nests built on a soft, muddy bottom usually amid algae, plant roots, leaves)	1	0.00	0.05	0.29	-0.45
B_2_6	Nest spawners; psammophils (the eggs are deposited on the sand)	-	-	-	-	NA
B_2_7A	Nest spawners; speleophils (rock cavity/roof)	4	0.00	0.01	0.20	-0.22
B_2_7B	Nest spawners; speleophils (bottom burrows or natural holes associated with structure or bank)	6	0.01	0.83	2.63	-0.24

(Continues)

TABLE 1 (Continued)

Trait code	Trait definition	n	Min	Mean	Max	r
B_2_7C	Nest spawners; speleophils (guard spawn in natural holes and cavities or in specially constructed burrows)	5	0.00	0.36	2.29	-0.07
C1_3_4_C24	A lumping of all bearers. May also be regarded as substrate indifferent	1	0.00	0.01	0.01	-0.48
	Reproduction: life history ($R_c=0.95$; $p<0.01$)					
MATUAGE	Average age at maturity (years)	115	1.33	1.71	2.17	0.72
SEASON	Average spawning season period (months)	115	3.06	3.73	4.41	0.80
MEANMONTH	Average month of the year when spawning occurs (month)	115	5.16	5.53	6.04	0.81
SERIAL	Serial or batch spawner (spawning in seasonal bursts or pulses more than once in a spawning season in response to an environment stimulus)	40	31.91	72.4	96.25	0.29
POTANADR	Potamodromous or anadromous species that exhibit significant movement related to spawning within river systems	5	0.00	0.66	2.07	-0.72
	Habitat: substrates ($R_c=0.88$; $p<0.01$)					
MUCK	Muck substrate (sediment with >60% silt + clay, >75% water by weight and >10% organic matter)	33	2.81	15.41	46.94	0.07
CLAYSILT	Clay or silt substrate	45	3.35	19.14	50.20	0.03
SAND	Sand substrate (0.06–4 mm diameter)	66	4.08	27.86	55.92	-0.06
GRAVEL	Gravel substrate (small rocks or pebbles, 4 mm–6 cm diameter)	81	4.25	32.05	68.42	0.14
COBBLE	Cobble substrate (rocks >6 cm and <25 cm diameter)	66	4.19	22.70	37.16	0.12
BOULDER	Boulder substrate (rocks >25 cm diameter)	35	0.55	3.45	10.08	-0.10
BEDROCK	Bedrock substrate (soft sandstone to conglomerate to hard igneous and metamorphic types. classify an area as bedrock if it has at least 50% cover of bedrock)	32	0.19	3.11	8.84	-0.61
VEGETAT	Aquatic vegetation substrate	51	4.50	45.10	98.47	0.73
DEBRDETR	Organic debris or detrital substrate	35	28.45	56.09	93.90	0.58
LWD	Large woody debris (at least 10 cm diameter and 1.8 m long that protrudes into a stream's bank-full channel, LWD is also known as logjams, snags, or debris dams)	19	0.38	7.53	33.29	0.61
	Habitat: macrohabitat ($R_c=0.92$; $p<0.01$)					
PELAGIC	Open water	11	0.00	36.67	94.38	0.01
PREFLOT	Lotic and lentic systems but more often in lotic	74	1.37	23.72	61.75	-0.25
PREFLEN	Lotic and lentic systems but more often in lentic	20	4.11	37.27	81.25	0.26
LARGERIV	Medium to large river	100	98.76	99.72	100.00	-0.71
SMALLRIV	Creek to small river	104	97.01	99.21	100.00	0.57
CREEK	Creek (smallest of streams, may not be perennial)	62	4.67	49.56	99.58	0.16
LACUSTRINE	Lentic systems	67	70.10	88.49	99.11	0.09
LOWLAND	Lowland elevation	98	82.80	95.96	99.92	-0.51
UPLAND	Highland elevation	106	97.66	99.42	100.00	0.87
MONTANE	Mountainous physiography (river that runs in mountains, in narrow, deep valley with steep banks, rocky stream bed, and accumulated rock debris)	27	0.40	5.33	14.10	0.00
SLOWCURR	Slow current	86	70.54	90.39	99.08	-0.37
MODCURR	Moderate current	54	1.26	13.94	30.10	0.04
FASTCURR	Fast current	24	0.08	0.94	2.51	-0.21
SPRGSUBT	Spring or subterranean water	4	0.00	0.01	0.20	-0.04

Note: n is the number of species representing a trait (total species = 115). The minimum, mean, and maximum represent percentage composition by counts except for four of the reproduction life history traits that represent the units listed. R_c is the adjusted canonical correlation between the first canonical axis for the set of traits and the first canonical axis for the set of reservoir locations (i.e., elevation, drainage area, distance from mouth of the Tennessee River). Statistically significant ($p<0.05$) correlations (r) between each trait and the location factor are bolded; a negative correlation indicates the trait decreased in representation in an upstream direction, and a positive correlation indicates the trait increased in representation in an upstream direction.

Abbreviations: NA = not applicable; dash = not collected.

^aTrait was not included in the canonical correlation analysis because it was reported in a single reservoir.

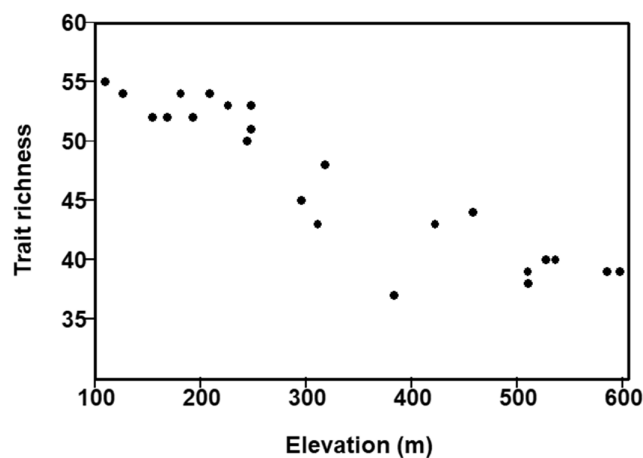


FIGURE 2 Richness of fish traits documented relative to elevation of the 23 reservoirs in the Tennessee River basin, U.S.A.

(Figure 2). Additionally, all sets of traits, though not every individual trait, showed statistically significant canonical correlations ($p < 0.01$) with longitudinal position of reservoirs in the cascade (Table 1), suggesting fish functional gradients along the reservoir cascade.

Eight feeding traits were documented, and species were often classified into multiple feeding traits. The most common trait was feeding on invertebrates and larval fish (INVLFVFSH) assigned to nearly all species, whereas other feeding traits were represented in less than half of species (Table 1). The least common feeding traits were non-feeding adults (NONFEED), egg feeders (EGGs), and blood feeders (BLOOD) identified for one, 23, and one species, respectively. Nevertheless, some feeding traits, while less common among species, accounted for a large percentage of the fish collected. For example, algae or phytoplankton feeders (ALGPHYTO) represented 39% of the species and 74% of the fish counts. Three traits increased in representation in an upstream direction (INVLFVFSH; feed on larger fishes, crayfishes, crabs, and frogs, FSHCRCRB; EGGs), three decreased in an upstream direction (ALGPHYTO; feed on detritus or unidentifiable vegetative matter, DETRITUS; BLOOD), and one trait showed no significant longitudinal gradient along the basin (feed on macrophytes and vascular plants, MACVASCU).

Whereas most species exhibited multiple feeding traits, each species was represented by a single reproductive trait (Table 1). Overall, non-guarders represented 64.3% of the species while guarders represented 35.7% (Table 1). Non-guarders were dominated by phytolithophils open substratum spawners (A_1_4), which accounted for 22.6% of the species and 44% of the fish counts, and guarders by polyphils nest spawners (B_2_2), which accounted for 11.3% of species and 44% of the fish counts. The rest of the traits contributed less than 5% of the counts. Notably five traits (lithophils open substratum spawners, A_1_3C; lithophils brood hid-ers, A_2_3C; speleophils brood hid-ers, A_2_4A; ariadnophils nest spawners, B_2_4; psammophils nest spawners, B_2_6) did not occur in the reservoirs and two (psammophils open substratum spawners, A_1_6; lithophils nest spawners, B_2_3A) occurred in only one reservoir each and were thus left out of the CCA analysis. Over half of

the reproductive traits exhibited longitudinal gradients with eight increasing downstream and two increasing upstream.

Five other traits were used to characterise reproductive life history along the reservoir cascade. The average age at maturity was 1.7 years, length of spawning season 3.7 months, and on average spawning occurred in mid-May (Table 1). The serial or batch spawners (SERIAL) represented 35% of the species and 72% of the fish counts. The potamodromous species trait (POTANADR) represented 4% of the species and <1% of the fish counts. The incidence of these traits increased in an upstream direction, except SERIAL, which showed no statistically significant pattern ($p > 0.05$), and POTANADR, which decreased upstream.

Substrates and macrohabitat traits were often common among many species. Relative to substrate traits, gravel substrate (GRAVEL), cobble substrate (COBBLE), and sand substrate (SAND) were shared by over 50% of the species. Relative to macrohabitat traits, preferences for lotic systems (PREFLOT), medium to large rivers (LARGERIV), creeks to small rivers (SMALLRIV), smallest of streams (CREEK), lentic systems (LACUSTRINE), lowland elevation (LOWLAND), highland elevations (UPLAND), and slow currents (SLOWCURR) were also shared by over 50% of the species. Only 21% of the species and <1% of the fish counts represented the fast currents trait (FASTCURR). One third of the substrate and macrohabitat traits exhibited longitudinal basin gradients (Table 1). Taxa with affinities towards bedrock substrates (BEDROCK), medium to large rivers, and lowlands increased in representation downstream, whereas taxa attracted to aquatic vegetation substrate (VEGETAT), debris and detrital substrate (DEBRDETR), large woody debris (LWD), small streams, or uplands increased in representation upstream.

5 | DISCUSSION

The Tennessee River basin has the highest species richness of all the sub-basins in the Mississippi River basin (NatureServe, 2022), and nearly one-half ($n = 129$; Miranda, Fauchaux, et al., 2021) of these species have been recorded in reservoirs of the Tennessee River. Species known to the Tennessee River basin that were not included in the 115 species analysed were mostly pelagic and benthic species (e.g., alewife *Alosa pseudoharengus*, paddlefish *Polyodon spathula*, river carpsucker *Carpionodes carpio*), various small lotic darters and minnows occasionally collected at the mouth of tributary creeks, and silver carp removed from the analyses. The 115 species analysed represent the highest of any reservoir system in North America, which makes the Tennessee River an ideal location to assess trends in trait richness and composition. The 62 traits identified included most of the trophic, habitat, and reproduction traits listed by Frimpong and Angermeier (2009) except for five reproductive traits that include species requiring certain sand and silt substrates, rock cavities, or build nests from plant materials. The richness of traits in the study reservoirs is likely to be supplemented by species that occupy the upper riverine sections of each reservoir (Buckmeier et al., 2014; Miranda & Dembkowski, 2016; Pennock et al., 2021) and

by species that occupy tributaries part time (Dunn & Paukert, 2021; Marques et al., 2018; Pracheil et al., 2009). The extraordinary trait richness in the Tennessee River assisted in exposing the observed longitudinal gradients.

Species and trait richness in unimpounded or lightly regulated rivers have been reported to increase in a gradient from upstream to downstream (e.g., Bhat, 2004; Ibanez et al., 2007; Miranda & Killgore, 2020; Pease et al., 2012). Downstream river reaches can support more species as they are larger, more hydrologically stable, and include more habitat types (Dias et al., 2021; Muneeppeerakul et al., 2008; Schlosser, 1987), all of which may facilitate colonisation rates (Gotelli & Taylor, 1999). Similarly, in the Tennessee River reservoirs farther downstream tend to be more riverine (i.e., more closely resemble the original river because of more elongated morphology, shorter hydrologic retention time, upper reaches with minimal water velocity), have less flashy water levels, and have increased habitat diversity and stability. All these characteristics may facilitate retention of more traits and a larger fraction of the original fish assemblages. Nevertheless, this pattern is not universal and probably varies across impounded basins depending on the characteristics of the reservoir cascade and the ecological regions crisscrossed by the river system. Faucheux et al. (2022) investigated longitudinal patterns in species richness across 16 reservoir cascades in North America and reported that various patterns existed including some that increased in an upstream direction in some basins and decreased in others, and some that simply remained constant throughout the basin. In South America, various authors (dos Santos et al., 2018; Loures & Pompeu, 2018; de Bem et al., 2021; Ganassin et al., 2021) have also reported gradients in species and trait richness that increased or decreased over reservoir cascades, depending on the basin. Factors that influence these apparently contradictory trends include regional climates and physical geography, distribution of tributaries and unimpounded reaches, and reservoir morphometry along the cascade. This variability creates diverse longitudinal patterns caused by local and regional physical peculiarities or induced by the arrangement of reservoirs in the river system.

Feeding traits in reservoir fish assemblages showed marked upstream and downstream gradients along the reservoir cascade that generally conformed with predictions of the RCC. Although formulation of the RCC was focused on changes in the macroinvertebrate community, fish assemblages are also expected to follow predictable longitudinal patterns influenced by physical gradients and resource availability. Invertivores predominate in headwater streams (McGarvey & Hughes, 2008; Oberdorff et al., 1993; Oberdorff & Porcher, 1992). A transition to detritivore- and herbivore-dominated communities follows the increase in autochthonous resources in middle and lower riverine reaches (Bhat, 2004; Dias et al., 2021; Ibanez et al., 2007); and piscivores reportedly increase in proportion and richness downstream, as vertical, and horizontal foraging space in larger rivers increases (Dias et al., 2021; Ibanez et al., 2007; McGarvey & Hughes, 2008; Oberdorff et al., 1993). Furthermore, representation of planktivores is expected to increase with stream order, reflecting the semi-lentic nature of these environments

(Vannote et al., 1980). All these riverine patterns were reflected in the study reservoirs, except that the trend was reversed for predator traits (i.e., fishes that prey on other fishes, crayfishes, amphibians, and eggs). This inconsistency may be caused by various factors, including turbidity and fisheries management practices. The clearer water associated with upstream reservoirs encourages prey and predator interactions and promotes predator abundance in reservoirs (dos Santos et al., 2017; Gardner, 1981; Montaña et al., 2014; Pyron et al., 2019). Interestingly, the pattern was inverted in some Brazilian reservoir cascades where water clarity was reduced in downstream reservoirs by sediment and nutrient retention and by local environmental particularities (dos Santos et al., 2017; Ganassin et al., 2021). Moreover, fisheries management agencies often stock and introduce piscivorous game species, focusing on upstream reservoirs where stocking benefits fish assemblages with fewer traits the most, possibly influencing the reverse longitudinal gradient in predator traits observed.

Reproductive strategies in the reservoir cascade also exhibited longitudinal gradients with the representation of non-guarders increasing downstream and guards increasing upstream. This same pattern has been reported in unregulated rivers (Dias et al., 2021; Goldstein & Meador, 2004). Non-guarders in the cascade were dominated by open substratum spawning phytolithophils that in streams deposit eggs in clear water over submerged plants or logs, gravel, and rocks. Similarly, phytolithophils have been reported to increase downstream in lightly regulated streams (Aarts & Nienhuis, 2003; Przybylski, 1993). Guards were dominated by nest-spawning polyphils that build circular nests. Lithophilic and psammophilic spawners, guards and non-guarders, are reportedly dominant in the upper reaches of rivers (Aarts & Nienhuis, 2003), but lithophilic spawners were numerically not well represented in the study reservoirs and psammophilic spawners were absent. Overall, phytolithophils open substratum spawners and polyphils nest spawners accounted for 35% of the species and an average 87% of the fish counts, possibly reflecting reduced diversity of reproductive traits fostered by impoundments (e.g., Stewart et al., 2016). Representation of potamodromous species decreased in an upstream direction as expected; nevertheless, potamodromous fishes were overall uncommon (5 species). It is not clear if this group does not occupy the reservoirs during autumn sampling, is not adequately sampled by electrofishing, or has been greatly reduced by impoundments as reported elsewhere (e.g., Agostinho et al., 2004; Dias et al., 2021).

Notably, fishes occupying reservoirs farther upstream exhibited a progressively higher age at maturity, mean month of spawning, and length of spawning season. Longitudinal trends in fast to slow life histories and associated effects on maturation age and body size have been reported in stream fishes, but infrequently (e.g., Keck et al., 2014; Parra et al., 2014; Torres Dowdall et al., 2012). Clinal variation in life-history traits along a river system could be fish assemblage adaptations to heterogeneity and stability of environments. In the study system, the increased hydrological stability downstream shaped by reservoir operations and the discharge averaging effect of a large river, along with enhanced increased primary productivity,

could facilitate establishment of early-spawning species. Upstream, interannual variability in water availability and reservoir water levels would select for species that have a long spawning season, which artificially produces a later mean month of spawning. Life-history gradients driven by differences in habitat quality occurring at the landscape-scale have been reported for egg size–fecundity relationships (Jones et al., 2017). Thus, organisation of life history traits in the reservoir cascade may be closely linked to the level of disturbance created by an impoundment. Nevertheless, it is unclear if the trait patterns observed in our study reflect cosmopolitan gradients in impounded rivers, or a pattern specific to the study basin induced by factors such as colder water in upstream reservoirs because of more groundwater influence, or by cold water sluicing designed to control stratification in the reservoir or cool power plants downstream. Moreover, the Tennessee River flows east to west but with a strong latitudinal curvature (Figure 1), an idiosyncrasy that coincides with earlier warming at lower elevations and latitudes, which may allow downstream establishment of species adapted to spawning earlier in the season.

Reservoirs have profoundly shifted the availability of substrates and macrohabitats available in the Tennessee River. River substrates have become submerged in deep water where they are often blanketed by sediment, and surface only in the upper riverine reaches of the reservoir. Nearshore earthy substrates in shallow littoral zones are generally not of river origin as they represent flooded uplands, but organic substrates such as woody debris and aquatic or terrestrial plants remain. At the same time, large spans of open water have been created, typically lentic. Consequently, the fishes retained by the reservoirs are mostly generalists with no strong trait affinity towards inorganic substrates or are fishes that occupy the reservoir only part time and access habitats in tributaries to complete their life history. Whereas the canonical correlation between the substrate traits was high, most of the correlations with inorganic traits (e.g., clay, sand, gravel) were not statistically significant, but those associated with organic materials (e.g., aquatic vegetation, organic and woody debris) were significant. Moreover, a solid majority of the fishes retained in most reservoirs represent still or sluggish water traits (e.g., slow current, lacustrine, large river traits) and traits representing moving water were less well represented. Nevertheless, reservoirs upstream retained progressively higher representations of upland fishes, and those downstream retained progressively more lowland fishes. Thus, although reservoirs tend to notably alter fish assemblages at local scales, at the cascade scale, fish assemblages may retain trait gradients that conform with riverine expectations.

The observed longitudinal gradients in trait richness and trait distributions were generally consistent with those expected in unregulated rivers, with a few unexpected results. Feeding, reproduction, and habitat traits generally conformed to predictions made by the RCC and reported in river surveys (e.g., Aarts et al., 2004; Aarts & Nienhuis, 2003; Angermeier & Karr, 1983; Goldstein & Meador, 2004; Oberdorff et al., 1993). No pre-impoundment surveys of the Tennessee River are available to confirm this generalisation, and a recent analysis by Keck et al. (2014) in tributaries to

the upper Tennessee River represented mostly small catchments. The species and trait richness observed in the reservoir cascade reflect the riverine origin of the fish assemblages. However, the transformation of lotic into lentic systems has changed habitats and sources of food (Thornton et al., 1990) and encouraged the proliferation of certain feeding (e.g., detritivores, planktivores, invertivores, piscivores), reproduction (e.g., nest spawners polyphils, broadcast spawners phytolithophils), and habitat (slow current, lacustrine, large river) traits. These traits would have otherwise been represented largely in river reaches with deep pools or wide, deep, and slow downstream reaches and would have represented smaller proportions of the overall fish assemblages. Our results concur with many of the streams versus reservoirs trait contrasts reported by Gido et al. (2009). In essence, reservoirs have expanded downstream habitats in an upstream direction, and thus allowed upstream expansion of species and traits that would have normally not been well represented in upper reaches of the Tennessee River basin. The upstream increases in piscivores and age at maturity were unexpected and possibly caused by the growing environmental dissimilarity between the original stream and the present impoundment.

6 | IMPLICATIONS TO CONSERVATION

Our results have various implications to fish conservation. First, the trait gradients detected over the length of the reservoir cascade followed several familiar longitudinal gradients reported in unregulated rivers. The observed patterns indicate that the impounded Tennessee River maintains much of the functional diversity in its native fish assemblages, despite extensive alterations to the riverscape, which are likely to be exacerbated by landscape changes (Zhou et al., 2012). Second, many of the traits reviewed conformed to the predictions of the RCC (Figure 3). These observations imply that this reservoir system retains riverine features, and therefore, the RCC and affiliated riverine concepts could apply to the impounded Tennessee River, and possibly other reservoir cascades. This finding is particularly important for river conservation given river impounding in industrialised nations often preceded standardised monitoring, and therefore the present-day overall rarity of unimpounded reference rivers. Third, richness of traits increased downstream, a pattern reported in unregulated rivers (Pease et al., 2012; Santoul et al., 2005). However, the pattern may be accentuated by the extent of hydrological and environmental alterations and overall reduction in ecological integrity caused by dams, all of which intensify lengthwise as reservoirs downstream retain more riverine attributes than their counterparts upstream. To an undetermined extent, connectivity may influence a decrease in trait richness as the lower reaches connected by locks retain some two-way movement, but the upper reaches mostly confine movement to stretches sandwiched by dams and to adjoining tributaries, which may lead to local extinctions of traits (McManamay et al., 2013). Two fish species have become extinct in the Tennessee River basin, both before damming began

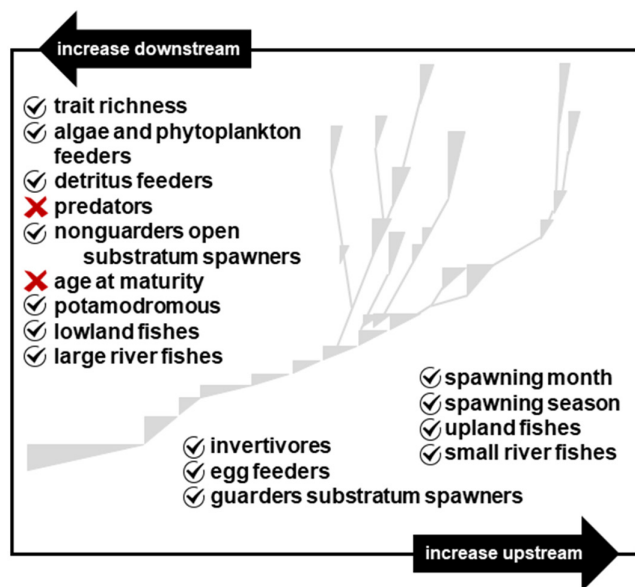


FIGURE 3 Profile of the Tennessee River reservoir cascade. Reservoirs farther downstream tend to resemble the original river more closely with elongated morphology, shorter hydrologic retention, and upper reaches with seasonal flow. Downstream reservoirs have more stable water levels and greater habitat diversity, which may facilitate packing more traits and retention of a larger fraction of the original fish assemblages. Upstream reservoirs tend to be clearer, relatively deeper, and provide extensive areas of lentic habitats not previously available high in the basin. These environmental gradients cause representation of fish assemblage traits to decrease or increase directionally along the cascade. Our directional expectations about various fish functional gradients were derived based on the framework provided by the River Continuum Concept (RCC). Checkmarks indicate that expectations based on RCC matched empirical observations in the reservoir cascade; crosses indicate that they did not. For example, the RCC predicts age at maturity and representation of predators increase downstream, but these traits increased upstream in this reservoir cascade. Additional details in Table 1.

(Etnier, 1997; Etnier & Starnes, 1993); however, there are many more jeopardised species, and most of these favour medium-sized rivers (Etnier, 1997).

Given that many of the traits we documented require some access to lotic environments, our findings indicate that a key to maintaining trait diversity is maintaining access to functional riverine habitats throughout the reservoir cascade. Suitable habitat could be provided downstream in the cascade through conservation that emphasises riverine reaches of reservoirs. River-like reaches become progressively longer down the cascade and seasonally may provide access to some flows, and access to backwaters and tributaries (Miranda & Dembkowski, 2016). Moreover, unimpounded reaches between successive dams tend to be more common higher in the cascade where greater landscape slopes may create longer riverine stretches between dams. Throughout the cascade, tailwaters and tributaries can serve as surrogates to unimpounded reaches to further provide the habitat needed to preserve functional traits (da Silva et al., 2019; Marques et al., 2018; Pracheil et al., 2009).

We suggest that while reservoirs have been shown to have major local-scale effects on riverine fish assemblages, and intensely restructure fish assemblages and their distribution along river basins, with access to riverine habitats, and with proactive conservation strategies, fish functional richness can remain remarkably high at the basin scale.

AUTHOR CONTRIBUTIONS

This paper was a class project. As such, all authors contributed to conceptualisation, developing methods, conducting the research, data analysis, data interpretation, preparation of figures and tables, and writing.

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DATA AVAILABILITY STATEMENT

The data used in these analyses are available from the Tennessee Valley Authority upon reasonable request.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

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