MODIFYING DAM OPERATIONS TO RESTORE RIVERS: ECOLOGICAL RESPONSES TO TENNESSEE RIVER DAM MITIGATION

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Abstract. The Tennessee Valley Authority (TVA) initiated a Reservoir Releases Improvement Program in 1991 to increase minimum flows and improve water quality by modifying its dam operations. We compiled a comprehensive data set from ecological monitoring below nine dams to evaluate the effects of these modifications on physicochemical conditions and benthic macroinvertebrate assemblages. Abiotic and biotic data were collected in tailwaters by the TVA for three dam operation "treatments" (i.e., before any modifications, following flow modifications, and following both flow and dissolved oxygen [DO] modifications) at three different stations (Upper, Middle, and Lower) located at increasing longitudinal distances below each dam. Analysis of variance was used to test for differences in ecological conditions among treatments and stations.

Dam modifications had significant effects on both abiotic and biotic variables, and macroinvertebrate assemblages exhibited significant longitudinal differences. Yearly mean DO and mean minimum velocity increased following dam modifications. Across all sampling stations, macroinvertebrate family richness increased and the percentage of pollution-tolerant macroinvertebrates (% Tolerant) decreased after dam modifications. Family richness also increased, and % Tolerant decreased, with increasing distance below the dams. Total abundance of macroinvertebrates increased after flow modifications and then decreased following changes in DO. The percentage of individuals belonging to the orders Ephemeroptera, Plecoptera, and Trichoptera (% EPT) increased following flow and DO modifications, but only at the Upper station. EPT family richness was unaffected by increased flow alone but increased following increases in both flow and DO. The design of the reoperation "experiment" made it difficult to ascertain the relative contributions of flow and DO changes to the observed biotic responses, but flow alone appeared to have a smaller beneficial effect than the combined effects of flow and DO.

Key words: benthic macroinvertebrates; dam mitigation; dam modifications; dissolved oxygen; EPT; minimum river flow; river rehabilitation; Tennessee Valley Authority (USA).

INTRODUCTION

Many studies have shown that dams can adversely affect river ecosystems by changing flow patterns, disrupting thermal regimes and sediment transport, disconnecting river corridors, and modifying aquatic and terrestrial habitats (Ward and Stanford 1983, Ligon et al. 1995, Poff et al. 1997). One way to reduce these impacts is by removing dams, and a growing body of research has focused on the effectiveness of dam removal as a method of river restoration (Bednarek 2001, Hart et al. 2002). But dams can also provide valuable socioeconomic goods and services, including hydropower, flood control, and recreation, so there is considerable interest in learning how to balance river re-

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habilitation efforts with the continued use of dams (Palmieri et al. 2001, Poff et al. 2003, Robinson and Uehlinger 2003). For example, some dam managers and owners are trying to reduce the impacts of dams through various structural or operational changes, including increased minimum flows, installation or improvement of fish ladders, and periodic releases of flushing flows (Hueftle and Stevens 2001, Vinson 2001, Scheurer and Molinari 2003).

Attempts to rehabilitate regulated rivers by modifying dam operations are still in their early stages (Hueftle and Stevens 2001). Researchers can list many of the ecological attributes of a "healthy" river (Meyer 1997, Poff et al. 1997), and some conceptual models suggest how rivers might respond to dam influences, including how dam effects may diminish with increasing downstream distance (e.g., Ward and Stanford 1983). But documentation of actual physical and biological responses to dam mitigation is much more limited. Moreover, the few mitigation assessments have usually focused on one dam or river at a time (e.g.,



FIG. 1. Map of Tennessee River watershed and location of the nine dams used in the study.

Weisberg and Burton 1993, Travnicheck et al. 1995, Vinson 2001, Scheurer and Molinari 2003) or have involved short-term studies (Travnicheck et al. 1995). Unfortunately, it can be hard to draw clear inferences about the effectiveness of dam mitigation from studies of single dams, especially when these studies span short time scales (Downes et al. 2002). In addition, many of these dam-mitigation experiments have focused on rivers where altered temperature patterns and modified flows are postulated to be the major factors impairing ecosystem structure and function (Ward 1974, Lieberman et al. 2001). In contrast, few studies thus far have focused on mitigating the effects of low dissolved oxygen, which is a common problem of dammed rivers in the southeastern United States (Isom 1971, Mulholland et al. 1997) and many other regions of the world (Dudgeon 1992, Boon et al. 2000). To promote environmentally and economically efficient management of regulated rivers, scientists and managers need to understand more fully how different types of rivers respond to alternative dam-mitigation practices.

Our study examined ecological responses to a multidam mitigation program initiated by a public utility, the Tennessee Valley Authority (TVA), Tennessee, USA. The TVA's Reservoir Releases Improvement (RRI) Plan, implemented in 1991, was part of an attempt to redress deteriorating ecological integrity within the Tennessee River watershed. During the 1970s and 1980s, environmental conditions downstream of many TVA dams were often poor. Hydropower demands meant that water releases through dams were timed to meet power production needs. As a consequence, water depths and velocities in the tailwaters (i.e., the length of river below a dam before it flows into another reservoir) during periods of non-generation declined to extremely low levels (Higgins and Brock 1999). Furthermore, reservoir conditions and dam structure (i.e., hypolimnetic releases) produced low dissolved oxygen (DO) concentrations. Low minimum flows often exacerbated the low DO because of decreased atmospheric mixing in the tailwaters. Through the RRI program, the TVA spent US \$44 million over five years to implement modifications to their dams to improve DO and minimum flow in tailwaters.

We used data from a long-term TVA monitoring program to evaluate the effects of dam modifications on ecological conditions below nine different dams. Although the TVA performed some preliminary analyses (Scott et al. 1996) to examine relationships between biological assemblages and two abiotic factors (i.e., DO and flow), these analyses were based on limited data and did not explicitly test whether the biota changed in response to different dam-operation "treatments." We used analysis of variance (ANOVA) to test hypotheses about responses of physical, chemical, and biological characteristics of tailwaters to structural and operational changes to nine dams. The TVA monitoring program included data on ecological conditions at three sampling stations located different distances downstream from the dams. Because the impact of dams on tailwater conditions is likely to vary with downstream distance, we also examined ecological differences among these stations.

Methods

Study site

Nine TVA dams were used in this study: Blue Ridge, Chatuge, Cherokee, Douglas, Norris, Nottely, South Holston, Tims Ford, and Wilbur/Watauga (Fig. 1). TABLE 1. Characteristics of tailwaters, modification methods, and year of implementation for dissolved oxygen (DO) and reservoir discharge flows for nine TVA dams used in this study.

Dam (River)	Reser- voir area (km ²)	Mean discharge (m ³ /s)†	Stream length impacted by low flow (km)	Mean minimum DO (mg/L)†	Stream length impacted by low DO (km)	Minimum flow method	Year of implementa- tion	DO method	Year of imple- menta- tion
Blue Ridge (Toccoa)	13	17	21	3.4	24	small turbine	1995	line diffusers	1994
Chatuge (Hiwassee)	29	13	29	1.3	11	infuser weir	1992	infuser weir	1992
Cherokee (Holston)	123	130	76	0.2	80	pulsing	1991	pumps, line diffusers, turbine venting	1994 1994 1995
Douglas (French Broa	123 ad)	197	40	0.9	129	pulsing	1991	pumps, line diffusers, turbine venting	1993 1995 1996
Norris (Clinch)	138	119	21	1.0	21	weir	1984	auto-venting turbine	1995
Nottely (Nottely)	17	12	23	1.0	5	small turbine	1993	air blowers, compressor	1993 1993
South Holston (South Fork)	31	28	23	0.8	10	labyrinth weir	1991	labyrinth weir	1991
Tims Ford (Elk)	43	27	69	0.4	64	small turbine	1987	penstock hoses, forced air	1992 1993
Watauga (Watauga)	26	20	13	3.8	3	none	none	turbine venting	1994

† Mean discharge and DO values are based on daily flow and weekly DO data 1960–1996 before Reservoir Releases Improvement (RRI) modifications for each dam (data and format modified from Higgins and Brock [1999]).

These 9 projects were chosen from 16 dams involved in the RRI program due to the availability of benthic macroinvertebrate data for these particular dams and because all share a similar hypolimnetic release structure. Although the tailwaters used in this study varied by \geq 10-fold in mean minimum discharge (cubic meters per second) and mean minimum DO concentration (milligrams per liter), more than 350 km of the study tailwaters had experienced low DO (i.e., ≤4 mg/L) and intermittent low flow (Table 1). Variations in the size, use, and physical features of each tailwater and dam in this study led to the use of several different techniques for increasing minimum flow and DO; moreover, these changes were implemented in different years for different dams (Table 1, see Higgins and Brock [1999] for details). Changes to flow were made by increasing the mean minimum flow and decreasing the length of time that peak flows were released, although the peak discharge magnitude was not altered (Higgins and Brock 1999). Thus, the TVA continued to generate hydropower while increasing minimum flows during the periods before and after flow peaks for power production. DO concentrations were increased by adding oxygen to the water released through the dam (e.g., by turbine venting) or in the tailwater itself (e.g., via an aeration weir).

Data set structure

The TVA designed the monitoring plan and collected the data used in our analyses. The monitoring design involved three sampling stations (i.e., Upper, Middle, and Lower) located along a longitudinal gradient below each dam. The mean (± 1 SE) distance between a dam and the Upper, Middle, and Lower stations was 3.0 (± 0.5), 11.7 (± 1.1), and 21.0 (± 1.9) km, respectively. Not all abiotic and biotic variables were measured at all stations.

The TVA provided measurements of four abiotic variables (i.e., DO, temperature, minimum velocity, and discharge) in each of the nine tailwaters. Values for DO (in milligrams per liter) and temperature (degrees Celsius) were obtained via grab samples at monthly intervals for the Upper stations only, and these were collected at a distance close to the dams but far enough away to allow for mixing of the turbine discharges. These monthly values, from April to July, were averaged to provide yearly measurements of DO and temperature, although the years in which these data were available varied among tailwaters. These months were chosen because they spanned the May-June period when benthic macroinvertebrates were sampled. Yearly flow measurements (including discharge and minimum velocity) were not available for the tailwaters due to the absence of gauging stations, so predicted values were obtained from a TVA one-dimensional, hydrodynamic model (Hauser and Walters 1995). The TVA used this model to estimate discharge and minimum velocity before and after the implementation of the Reservoir Releases Improvement (RRI) program for each of the nine tailwaters. Thus, a single minimum velocity and discharge value before and after the RRI modifications was available for each dam. Discharge esti-

Variable	Repli- cates ANOVA		Statistical model	Planned comparisons		
DO (mg/gL), tem- perature (°C)	years	one way	$X_{ij} = \mu + A_i + e_{ij}$	B vs. BDO; BDO vs. A		
Velocity (m/s)	dams	two way	$X_{ikl} = \mu + B_i + C_k + BC_{ik} + e_{ikl}$	none		
Discharge (m ³ /s)	dams	one way	$X_{kl} = \mu + C_k + e_{kl}$	none		
Macroinvertebrate metrics	years	two way	$X_{ijk} = \mu + A_i + B_j + AB_{ij} + e_{ijk}$	 B vs. BDO; BDO vs. A; Upper vs. Middle; Middle vs. Lower. Upper: B vs. BDO; BDO vs. A. Middle: B vs. BDO; BDO vs. A. Lower: B vs. BDO; BDO vs. A. B: Upper vs. Middle; Middle vs. Lower. BDO: Upper vs. Middle; Middle vs. Lower. A: Upper vs. Middle: Middle vs. Lower 		

TABLE 2. Summary of ANOVA models used in analyses.

Notes: DO = dissolved oxygen; B = before any modifications in DO or minimum flow, BDO = after minimum-flow modifications but before DO modifications, and A = after both DO and minimum-flow modifications.

[†] Here μ = the mean of all sampled populations; all factors are fixed. A = yearly replicates for each dam, treatment, and station, including B, BDO, and A (e.g., replicate year at a single sampling station in which tailwater was sampled before DO and flow were modified); B = sampling stations: Upper, Middle, and Lower, located along a longitudinal gradient below each dam; C = dam replicates for two treatments (B, A) and each station (e.g., model value for a single sampling station before DO and flow were modified).

mates were available for the Upper stations and minimum velocity estimates were available at all three stations.

Benthic macroinvertebrates were sampled by the TVA once per year at the three sampling stations in each of the nine tailwaters (Higgins and Brock 1999). Four Surber samples (area = 0.093 m^2 ; mesh size = 908 µm) were usually collected at each of these stations from 1981 through 1992 in May-June. In some years for some dams, however, Hess samples (area = 0.086 m^2 ; mesh size = 1000 μ m) were used instead. Beginning in 1993-2000, three Surber samples and three Hess samples were collected at each of the three stations. TVA personnel sorted and identified all samples. Because neither sampling method spanned all years and dams, we used data collected via both methods to maximize the available years of data, which included years before and after RRI changes. The wide span of years used, coupled with changes in macroinvertebrate identification over this time period, led to variable taxonomic resolution in the data set (e.g., before 1991, Chironomidae genera were not differentiated). Thus, the data were lumped at the family level to maximize the taxonomic consistency of the analyses.

We used common metrics of benthic macroinvertebrate assemblages (Lenat 1993, Resh et al. 1996, Scott et al. 1996) in our assessment of biological responses to the RRI program. These metrics were: (1) total number or abundance of macroinvertebrates [Total Abundance]; (2) family richness (i.e., number of families) [Family Richness]; (3) number of EPT (Ephemeroptera, Plecoptera, Trichoptera) families, which are generally considered to be less tolerant of low water quality than other invertebrate groups [EPT Richness]; (4) percentage of Total Abundance made up by EPT individuals [% EPT]; and (5) percentage of Total Abundance comprised by invertebrates considered tolerant of low water quality (i.e., Chironomidae, Simuliidae, Oligo-chaeta, Isopoda, Amphipoda, and Planariidae) [% Tol-erant].

These five metrics ("biotic") are commonly used by the TVA or by others for biomonitoring purposes (Lenat 1993, Resh and Jackson 1993, Scott et al. 1996). For example, Family Richness and EPT Richness are usually inversely related to environmental stress (Lenat 1993, Wallace et al. 1996); % Tolerant included families used by the TVA (Scott et al. 1996) as well as other researchers (Hilsenhoff 1988, Lenat 1993) to indicate poor water-quality conditions. Thus, Family Richness, EPT Family Richness, and % EPT might be expected to increase in response to the RRI modifications, while % Tolerant might decrease. It is less clear how Total Abundance might change, because this metric can be an inconsistent indicator of environmental conditions. For example, an increase in the total number of macroinvertebrates sometimes indicates improvements in water quality, but invertebrates tolerant of poor water quality can also increase in degraded habitats (Resh and Jackson 1993).

Statistical analyses

Dissolved oxygen and temperature.—A one-way ANOVA was used to test the hypothesis that RRI modifications at Upper stations caused a change in yearly mean values for DO and temperature (Chatuge and Nottely were excluded from these analyses because no "before" modification data were available) (Table 2). The RRI modifications were designated as three "treatment" levels in the ANOVA: before any modifications in DO or minimum flow (B), after minimum-flow modifications but before DO modifications (BDO), and after both DO and minimum-flow modifications (A). Although preliminary TVA analyses suggested an increase in DO and minimum flow following RRI changes (Scott et al. 1996), we did not specify a directional response for the abiotic or biotic variables examined because it seemed possible that extraneous factors (e.g., changing land use within the watersheds) could offset possible effects of dam modifications. We only examined a subset of possible comparisons to reduce the magnitude of the experiment-wise error rate (see Jaccard 1998).

DO did not deviate significantly from normality using the Shapiro-Wilk statistic, W, so data were not transformed (Shapiro and Wilk 1965, Zar 1984). Temperature deviated significantly from normality and data were log-transformed, which resulted in distributions that were not significantly different from normal (P =0.15). Neither DO nor temperature exhibited significant heteroscedasticity using Levene's test (DO, P = 0.16; Temperature, P = 0.67).

Minimum velocity and discharge.---A two-way Model I ANOVA tested the hypothesis that minimum velocity differed among mitigation treatments and sampling stations, and exhibited a mitigation treatment \times station interaction (Table 2). Sampling station was considered a fixed factor in this analysis, as well as in the biotic analyses. Although the downstream distances of the Upper, Middle, and Lower stations varied among dams (i.e., some tailwaters are shorter than others), each tailwater was divided into distinct Upper, Middle, and Lower stations. Due to the absence of velocity data for the BDO treatment, we did not perform planned comparisons between pairs of dam treatments. A oneway fixed-effect ANOVA was used to test the hypothesis that minimum discharge changed at the Upper stations following flow modifications; discharge data were not available for other stations. Velocity (in meters per second) and discharge (in cubic meters per second) were log transformed to correct for non-normal distributions. Residual plots were examined for these metrics and suggested no singular large variance for velocity or discharge (see McGuiness 2002).

Biotic responses.—We used correlation analysis to determine whether the five biological metrics (i.e., Total Abundance, Family Richness, EPT Richness, % EPT, % Tolerant) provided independent information about biotic responses to the RRI modifications. Although variables with strong linear relationships are highly redundant, correlated variables that exhibit nonlinear relationships or show considerable scatter in a bivariate plot can contribute unique information (Karr 1991, Barbour et al. 1996). Our strategy for reducing metric redundancy was to eliminate a variable if the absolute value of the product–moment correlation coefficient |r| was greater than 0.9 (Royer et al. 2001) and if bivariate scatterplots demonstrated strong linear relationships (Barbour et al. 1996).

A two-way Model I ANOVA was used to examine how the five biological metrics varied among the three dam-modification treatments (i.e., B, BDO, and A) and among the three sampling stations (i.e., Upper, Middle, and Lower) (see Table 2 for details about the model). A treatment \times station interaction term was also included. For metrics that exhibited a significant treatment effect but no significant interaction term, we used planned comparisons to test for differences between the following treatments: B vs. BDO and BDO vs. A. Similarly, for metrics with a significant station effect but a nonsignificant interaction, planned comparisons tested for differences between Upper vs. Middle stations and Middle vs. Lower stations.

For metrics that exhibited a significant treatment \times station interaction, we used planned comparisons to examine how treatment effects varied with station, and how station effects varied with treatment. Thus, we tested for station-specific treatment differences (e.g., Upper: B vs. BDO; Upper: BDO vs. A) as well as treatment-specific station effects (e.g., B: Upper vs. Middle; B: Middle vs. Lower).

The biological metrics were transformed prior to analysis because of the presence of numerous zeroes in the data matrix (Underwood 1997). Total Abundance, Family Richness, and EPT Richness were log transformed. Percentage metrics were transformed using an arcsine transformation (Underwood 1997). Although *W* did not improve upon transformation for EPT Richness, % EPT, and % Tolerant, plots of residuals indicated no marked heterogeneity of variance so these metrics were retained (see McGuiness 2002).

RESULTS

Abiotic responses

Dissolved oxygen (DO) concentration and temperature at the Upper sampling stations below each dam differed in their responses to the Reservoir Release Improvement (RRI) modifications. DO increased significantly following modifications in both flow and DO, from 4.7 \pm 0.4 mg/L to 7.1 \pm 0.4 mg/L (means \pm SE) ($F_{2,40} = 6.8$, P = 0.01; Fig. 2). Although temperature decreased from ~16.1 to 13.3°C following modifications in DO and flow, this change was not statistically significant ($F_{2,40} = 1.0$, P = 0.39; Fig. 2).

Minimum velocity and discharge increased significantly following modifications in DO and flow. Mean minimum velocity across all stations increased by about 1.5 times ($F_{5,46} = 5.3$, P = 0.03; Fig. 3). Mean minimum discharge at the Upper station increased by >6 times, from an average discharge of 0.7 ± 0.1 m³/ s to 4.3 ± 1.1 m³/s (means ± sE) ($F_{1,16} = 29.4$, P <0.001). Minimum velocity was not significantly different across stations ($F_{5,46} = 2.3$, P = 0.12), and did not exhibit a significant station × interaction ($F_{5,46} =$ 0.2, P = 0.82).

Biotic responses

The strength and pattern of correlations among the benthic macroinvertebrate metrics indicated that each



FIG. 2. Dissolved oxygen (DO) concentration and temperature before DO and flow modifications (B), after flow modifications but before DO modifications (BDO), and after both DO and flow modifications (A) at the Upper sampling stations. Sample sizes are: B, n = 7; BDO, n = 12; A, n = 24. Data are means + sE.

provided unique information about the biological response to dam modifications. Specifically, although 9 of the 10 possible correlation coefficients were statistically significant (critical $\alpha < 0.05$), |r| was greater than 0.7 for only two of these pairs (% EPT and EPT Richness, % EPT and % Tolerant [for definitions, see Methods: Data set structure]). Moreover, bivariate scatterplots indicate that only the relationship between % EPT and % Tolerant was linear. Neither of these pairwise relationships involved $|r| \ge 0.9$, however. Thus, these two metrics (% EPT and % Tolerant) were retained for further analysis, along with the other three metrics (Total Abundance, Family Richness, EPT Richness). The low correlation between Family Richness and Total Abundance indicates that the potential dependence of taxa richness on abundance or sample size (see Hart and Horwitz 1991) was not a complicating factor in our analyses.

The composition of the % Tolerant and % EPT metrics was dominated by Chironomidae and Ephemeroptera, respectively, across all treatments and stations. Chironomidae constituted ~40% of % Tolerant, followed by Oligochaeta, which represented $\sim 30\%$. Ephemeroptera were the most common order within % EPT, representing $\sim 65\%$ of the abundance of % EPT across all stations and treatments. Within Ephemeroptera, Ephemerellidae were the most common family (approximately 86% of Ephemeroptera abundance across all treatments and stations), followed by Baetidae ($\sim 8\%$), Heptageniidae ($\sim 4\%$), and Oligoneuridae $(\sim 1\%)$. Trichoptera was the next most common order within % EPT, representing $\sim 32\%$ aross all stations and treatments. Hydropsychidae was the most abundant family within Trichoptera, constituting 65% of abundance. Brachycentridae represented ~20% of Trichoptera, Hydroptilidae represented $\sim 8\%$ and Glossosomatidae constituted $\sim 1\%$. Plecoptera was the least abundant order of the EPT, representing $\sim 3\%$ of % EPT. Perlodidae and Perlidae were the dominant families for this order, each representing about half of the total Plecoptera abundance.

Three biological metrics (Family Richness, % Tolerant, and Total Abundance) exhibited significant effects of the dam-modification treatments, and two of these (Family Richness and % Tolerant) exhibited significant among-station variation. There was no significant treatment \times station interaction for these metrics, however. The absence of significant interactions for Family Richness and Total Abundance is unlikely to be an artifact of log transformation because the interaction term was nonsignificant using the raw data as well as the transformed data (Neter et al. 1996). Family Richness increased significantly after flow was increased but before DO was changed, and was significantly greater at the Lower stations than at the Middle stations (Table 3, Fig. 4a). % Tolerant declined significantly after DO was increased, and was significantly greater at the Upper stations than at the Middle stations (Table 3, Fig. 4d). Total Abundance increased significantly following the increase in flow, but then decreased significantly after DO was increased (Table 3, Fig. 4e).

For EPT Richness and % EPT, we detected significant treatment and stations effects, as well as significant treatment \times station interactions. Thus, planned comparisons were used to test for station-specific treatment differences and treatment-specific station differences. At each station, EPT Richness was significantly greater after both flow and DO were increased than after just the flow increase (Table 3, Fig. 4b). In contrast, station differences for this metric varied depending on the treatment. For both the B (before DO and flow modifications) and A (after both DO and flow modifications) treatments, EPT Richness was significantly greater at the Lower stations than the Middle stations, and significantly greater at the Middle stations than the Upper stations. Although EPT Richness was also significantly



FIG. 3. Minimum velocity before and after modifications in minimum flow for all three sampling stations (Upper, Middle, Lower). Sample sizes (no. stations) for Upper and Middle stations are: B, n = 9; BDO, n = 9; for Lower station: B, n = 8, BDO, n = 8. Treatments are as defined in Fig. 2.

Source of variation and comparison	df	Family richness, FR (0.009)	EPT FR (0.007)	%EPT (82.61)	%Tolerant (123.22)	Abundance (0.13)
Dam treatment	20	7.3**	23.1**	10.7**	6.6**	5.1**
B vs. BDO	1	$10.4^{**}+$	0.3	1.4	< 0.1	$11.1^{**}+$
BDO vs. A	1	1.0	19.9^{**} +	$14.5^{**}+$	7.4**-	4.2*-
Sampling station	2	12.7**	80.9**	25.7**	13.8**	3.0
Upper vs. Middle	1	3.5	54.1**+	24.7**+	15.0 * * -	4.9
Middle vs. Lower	1	9.8*+	28.3**+	4.0* +	1.3	0.1
Treatment \times station	40	1.2	2.3**	1.5*	1.3	1.1
Upper B vs. BDO	1		0.2	0.3		
Upper BDO vs. A	1		6.4* +	7.9^{**} +		
Middle B vs. BDO	1		< 0.1	1.1		
Middle BDO vs. A	1		5.2*+	3.4		
Lower B vs. BDO	1		2.0	0.3		
Lower BDO vs. A	1		$8.7^{**} +$	3.7		
B: Upper vs. Middle	1		22.7**+	13.8^{**} +		
B: Middle vs. Lower	1		$14.6^{**} +$	0.5		
BDO: Upper vs. Middle	1		$11.8^{**} +$	$6.6^{*}+$		
BDO: Middle vs. Lower	1		3.5	1.2		
A: Upper vs. Middle	1		20.0**+	5.7* +		
A: Middle vs. Lower	1		$11.4^{**}+$	2.5		

TABLE 3. *F* ratios from a two-way ANOVA testing for differences among dam treatments (B, BDO, A) and stations (Upper, Middle, Lower) for five biological metrics in nine dam tailwaters.

Notes: FR = Family Richness. Mean-square error values are listed in parentheses below each variable heading. For each station, N = 13 samples sites for B, N = 12 samples for BDO, N = 27 samples for A. Key to other symbols: "+" = increase (e.g., BDO > B or A > BDO); "-" = decrease (e.g., BDO < B or A < BDO). For treatment codes see Fig. 2 legend. $*P \le 0.05$; $**P \le 0.01$.

greater at the Middle stations than the Upper stations for the BDO (after flow modifications but before DO modifications) treatment, there was no significant difference between the Middle and Lower stations. % EPT exhibited a consistent longitudinal pattern for all treatments, with significantly greater average values at the Middle than Upper stations, but there was no significant difference between Middle and Lower stations (Fig. 4c). On the other hand, planned comparisons demonstrated that the only significant treatment difference was between BDO and A, and this only occurred at the Upper stations.

DISCUSSION

Abiotic and biotic responses to dam mitigation

Dam modifications successfully increased dissolved oxygen (DO) concentrations, as well as minimum discharge and velocity. For example, DO increased by about 34% following the DO modifications. The average increase in minimum discharge and velocity was about 528% and 59%, respectively. Although the RRI (Reservoir Release Improvement) program produced higher minimum flows, it was not designed to establish a natural flow regime. Most TVA (Tennessee Valley Authority; Tennessee, USA) tailwaters still experienced large fluctuations in discharge associated with peaking hydropower operations, which probably limited the potential degree of improvement in ecological integrity that occurred in these rivers (Poff et al. 1997).

The observed changes in biotic metrics also indicated that the dam modifications resulted in improved ecological integrity within tailwaters. Across all sampling stations, Family Richness (number of families) increased 36% and % Tolerant (percentage of total number of macroinvertebrates tolerant of low water quality) decreased by about 13% from B (before any flow or DO modification) to A (after both flow and DO modifications). At the Upper stations, % EPT and EPT Family Richness increased 325% and 119%, respectively, following flow and DO changes (i.e., from B to A). Weisberg et al. (1990) also observed increases in the proportion of flow-dependent EPT taxa (e.g., hydropsychid caddisflies) in response to increased minimum flows.

Total Abundance (total number of macroinvertebrates) exhibited a more complicated response to dam modifications than the other four metrics. Although this metric increased by 163% after flow was increased, it declined by nearly 60% following increased DO. Studies of macroinvertebrates as indicators of water quality have indicated that Total Abundance can either increase or decrease as environmental conditions improve (Resh and Jackson 1993). These complex relationships suggest that Total Abundance may behave too inconsistently to support reliable inferences about changes in ecological integrity. Alternatively, a greater understanding of biological interactions among the different taxa that comprise the metric may be needed to interpret its response. For example, the initial flow increase in the absence of increased DO may have simply provided more suitable habitat for small-bodied, pollution-tolerant taxa such as chironomid midges, which led to an increase in their abundance. In contrast, the decline in Total Abundance following the DO increase might stem



FIG. 4. (a) Family Richness, (b) EPT Richness (no. Ephemeroptera, Plecoptera, and Trichoptera families), (c) % EPT, (d) % Tolerant (percentage of Total Abundance comprised by invertebrates considered tolerant of low water quality), and (e) Total Abundance (total no. of macroinvertebrates) before DO and minimum-flow modifications (B), after flow modifications but before DO modifications (BDO), and after both DO and flow modifications (A) at all three sampling stations (Upper, Middle, Lower). Sample sizes are: B, n = 13; BDO, n = 12; A, n = 27. Data are means and 1 se.

from the observed increase in % EPT, which consists of more pollution-intolerant and larger-bodied taxa compared to midges. Thus, if the availability of limiting food resources (e.g., particulate organic matter per unit area) used by benthic macroinvertebrates remained relatively constant during the dam-mitigation changes, and if such food limitation sets an upper limit to the total biomass of benthic macroinvertebrates, then a shift to larger bodied individuals such as EPT could cause a reduction in Total Abundance (Begon et al. 1986). Our results suggest that these RRI modifications facilitated a shift toward conditions that existed before the TVA dams were constructed. Although pre-dam data and published reports are limited, available studies indicate that temperature and flow decreased and the composition of the biological assemblages changed after dam construction (Krenkel et al. 1979). For example, following the closure of Norris Dam, its tailwater experienced a decrease in Trichoptera, Ephemeroptera, Plecoptera, and Odonata (which were all previously abundant) and an increase in Simuliidae and Chironomidae (Tarzwell 1938). Unfortunately, there are too few data to permit quantitative comparisons of pre- and post-dam conditions (both pre-RRI and post-RRI).

Disentangling the ecological effects of flow and DO

It was difficult to ascertain the relative contribution of increases in flow and DO to the overall change in the benthic macroinvertebrate assemblage. Three metrics (EPT Richness, % EPT, and % Tolerant) exhibited significant responses only after increased DO, whereas Family Richness responded significantly to increased flow but not to increased DO. The significant response of the three metrics following the DO increase is consistent with the fact that many EPT taxa cannot tolerate DO concentrations <5 mg/L, whereas the chironomid midges that were numerically dominant in most of the tailwaters can tolerate DO concentrations as low as 1 mg/L (Nebeker 1972, Lowell and Culp 1999). It is less clear why Family Richness did not respond to the increase in DO, although this metric includes several non-EPT taxa (e.g., Chironomidae, Simuliidae, Elmidae) that are relatively tolerant of low DO (Hilsenhoff 1988).

Efforts to distinguish the effects of flow and DO changes were further complicated by the design of the RRI program. Rather than operating dams so that these two treatments were changed independently, the DO increase always occurred in combination with increased flow or followed a period when the flow increase occurred. Moreover, the combined influence of flow and DO could be non-additive, which would further complicate efforts to evaluate their individual effects. For instance, increased velocities can offset some negative effects of low DO on benthic macroinvertebrates by enhancing oxygen uptake, feeding rates, fecundity, and survival (Eriksen et al. 1984, Lowell and Culp 1999).

Variations in sampling frequency and data availability between the abiotic and biotic data also limited explanations of the links between changes in DO, flow, and biological assemblages. Information on seasonal patterns in DO, temperature, and flow were not available due to variations in data availability within the data set, nor were these data always collected consistently with respect to time of day. Instead, we used mean monthly values for DO, temperature, and flow within the time frame during which benthic macroinvertebrates were sampled, but this constrained our ability to explain benthic macroinvertebrate responses. DO and flow levels can fluctuate daily, monthly, and annually and benthic macroinvertebrates may respond more to maximum or minimum levels of these variables than to mean monthly or annual values (Poff et al. 1997).

Although it is difficult to identify the specific mechanisms governing observed biotic responses, the fact that statistically significant responses to dam mitigation emerged across the entire set of tailwaters and time periods strongly supports the idea that these changes are linked to the DO and flow modifications. Moreover, the design of the RRI program did provide some ability to control for potential temporal changes in background conditions because the dam modifications were implemented at different times for different dams (see Table 1). Thus, the time intervals for the periods before and after flow and DO changes varied among the dams, which may have created a quasi-randomization in among-year variations in weather, fish abundance, and other potential confounding factors. Changes in both DO and flow over a range of temporal scales can have direct and indirect effects on a variety of other physical, chemical, and biological variables, however. Thus, additional studies would be needed to elucidate the actual causal pathways governing the responses of different biota, and the ways in which such responses interact to produce the observed responses in macroinvertebrate metrics.

Longitudinal gradients in abiotic and biotic conditions

Valuable insights about the potential responses of a river ecosystem to modified dam operations can be gained by examining the form and magnitude of ecological changes that exist along a downstream gradient below the dam. For example, abiotic conditions in TVA tailwaters are likely to improve with increasing distance below the dams and this could lead to a corresponding change in the biota. Ecological impacts below hydropower dams with hypolimnetic releases are often greatest immediately below the dam due to marked reductions in DO and water temperature as well as large flow alterations. These extreme conditions are usually ameliorated farther downstream due to reaeration and solar heating, as well as hydraulic storage processes and tributary inputs that moderate short-term flow variations (Ward and Stanford 1983, Stevens et al. 1997, Camargo and Voelz 1998).

Several factors made it difficult to characterize these longitudinal gradients in TVA tailwaters, however. Most importantly, limited multi-station abiotic data made it impossible to test for gradients in DO, temperature, or discharge. Although multi-station data were available for minimum velocity, no significant station effect was detected. Minimum velocity at the Lower station was about 75% higher than at the Upper station (across both treatments), however, which suggests that this lack of significance may be due in part to low statistical power. For example, in contrast to biological data, data on minimum velocity were not available for multiple years before and after flow modification at each dam. Moreover, these data were generated from a one-dimensional hydraulic model rather than from direct measurements, which may have reduced their accuracy.

Although there was little evidence of improvement in abiotic conditions with increasing downstream distance, striking longitudinal gradients were evident in the benthic macroinvertebrate assemblage. Indeed, planned comparisons detected significant station differences for four of the five biological metrics. These differences were more frequent between Upper and Middle stations than between Middle and Lower stations. For instance, seven of the nine planned comparisons between the Upper and Middle stations were significant (% Tolerant; EPT Richness and % EPT: B, BDO, and A), whereas only three of nine comparisons between Middle and Lower stations were significant (Family Richness; EPT Richness and % EPT: B and A) (Table 3).

The basic pattern of these longitudinal gradients in macroinvertebrate metrics did not differ before vs. after dam mitigation, however. For example, we observed no significant treatment × station interaction for Family Richness, % Tolerant, and Total Abundance. Although EPT Richness and % EPT exhibited significant treatment \times station interactions, the results of planned comparisons indicate that the pattern of station differences did not differ before vs. after the dam modifications. In particular, EPT Richness and % EPT at Middle stations were significantly greater than at Upper stations during each of the three dam-modification treatments. Furthermore, although the increase in % EPT following flow and DO modifications was much greater at Upper stations (~10-fold) than Lower stations (\sim 2-fold), the longitudinal gradient for this metric was still evident after dam modifications.

Many ecological impacts of dams are likely to be greatest immediately downstream of the dam, and to diminish asymptotically with increasing downstream distance (Ward and Stanford 1983). Indeed, the largest differences between macroinvertebrate assemblages occurred consistently between Middle and Upper stations rather than between Middle and Lower stations, even though both station pairs were separated by about the same distance. Because ecological integrity at Lower and Upper stations generally increased by similar amounts following dam mitigation (i.e., there were few treatment \times station interactions), this suggests that even the Lower stations were not far enough downstream to be unaffected by dam impacts. Alternatively, the power of our statistical analyses may have been too low to detect a diminished ecological response to dam mitigation with increasing downstream distance. Even though minimum flows were increased following dam mitigation, hydropower operations still produce large short-term fluctuations in discharge that are dramatically different from the natural flow regime. Thus, these dams probably continue to be a significant source of impairment to benthic macroinvertebrate assemblages despite TVA's success at increasing minimum flow.

Conclusion

These results demonstrate that changes to dam operations can improve the ecological integrity of rivers. Because many dam operations in the United States and throughout the world may be changed in the future to achieve a better balance between human and ecosystem needs for water (e.g., via "green power" designations, dam relicensing, and adaptive-management experiments; Moxon 1999, Rhodes and Brown 1999, Powell 2002), it is useful to examine how our findings could improve the ability to detect and understand the causes of ecological changes from dam mitigation. First, there were significant improvements in several key components of ecological condition in response to the increase in minimum flows, yet the flow regime remained highly modified. This result raises the hope that dam-mitigation efforts that produce more natural flow regimes than those achieved in TVA tailwaters could potentially lead to even larger increases in ecological integrity. Second, although our study could not unequivocally identify the relative ecological benefits of changes to flow and DO, it was clear that flow alone usually had a smaller beneficial effect than the combined effects of flow and DO increases together. This suggests that efforts to improve dam management must be based on an integrated understanding of the ways that ecological integrity can potentially be impaired by multiple stressors, including poor water quality and limited availability of suitable habitat, as well as altered flow regimes. Moreover, if changes to flow and DO were applied using a true factorial design, it would then be possible to distinguish the independent and interactive effects of these two factors. Third, the experimental design could potentially be strengthened by simultaneous monitoring at sites that represent independent spatial controls (e.g., dam sites at which dam management remains unchanged as well as undammed sites) (Downes et al. 2002). Fourth, interpretation of the TVA results would have been enhanced if data on DO, velocity, and other possible explanatory variables (e.g., nutrients, seston, substrate characteristics) were available for all dams, stations, and years for which biological samples were collected. Closely coordinating the monitoring of biotic and abiotic characteristics would facilitate the interpretation of potential causes of observed biological changes.

Given our incomplete understanding of the way that river ecosystems "work," many researchers have argued that strategies for improving dam operations will require the use of ecosystem-level experiments and adaptive ecosystem management (Lee 1993, Poff et al. 2003, Postel and Richter 2003, Richter et al. 2003). This "learning by doing" approach is critically dependent on the ability to monitor ecosystem responses to alternative management "experiments," and uses any divergence between observed and expected responses as the basis for improving both ecosystem models and management practices. Thus, if future dam reoperation programs are to be guided by adaptive management, it would also be useful to make quantitative predictions about the magnitude and time scale of expected ecological responses to reoperation. Such expectations could be used to determine when and how additional changes to dam operations might be instituted if observed ecological responses begin to diverge from expected responses. Moreover, future attempts at dam reoperation might benefit from a coordination of monitoring and analysis across a number of dams. Although such large-scale experiments can be difficult to design, implement, and interpret, our experience suggests that much can be learned by examining ecological responses to alternative dam-management practices across many rivers.

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