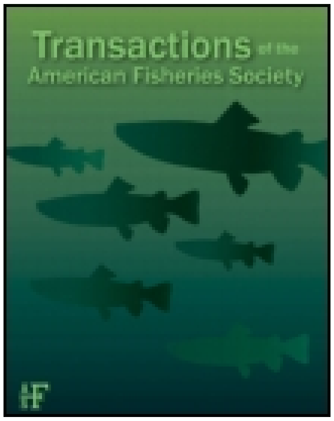


Transactions of the American Fisheries Society
Publication details, including instructions for authors and subscription information:
http://afs.tandfonline.com/loi/utaf20

# Dam Removal Increases American Eel Abundance in Distant Headwater Streams

Nathaniel P. Hitt [a], Sheila Eyler [b] & John E. B. Wofford [c]

[a] U.S. Geological Survey, Leetown Science Center, Aquatic Ecology Branch, 11649 Leetown Road, Kearneysville, West Virginia, 25430, USA

[b] U.S. Fish and Wildlife Service, Maryland Fishery Resources Office, 177 Admiral Cochrane Drive, Annapolis, Maryland, 21401, USA

[c] National Park Service, Shenandoah National Park, 3655 Highway 211 East, Luray, Virginia, 22835, USA

Published online: 20 Jul 2012.

*Transactions of the American Fisheries Society* 141:1171–1179, 2012
American Fisheries Society 2012
ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1080/00028487.2012.675918



**ARTICLE**

# Dam Removal Increases American Eel Abundance in Distant Headwater Streams

**Nathaniel P. Hitt***
*U.S. Geological Survey, Leetown Science Center, Aquatic Ecology Branch, 11649 Leetown Road, Kearneysville, West Virginia 25430, USA*

**Sheila Eyler**
*U.S. Fish and Wildlife Service, Maryland Fishery Resources Office, 177 Admiral Cochrane Drive, Annapolis, Maryland 21401, USA*

**John E. B. Wofford**
*National Park Service, Shenandoah National Park, 3655 Highway 211 East, Luray, Virginia 22835, USA*

***Abstract***
**American eel *Anguilla rostrata* abundances have undergone significant declines over the last 50 years, and migration barriers have been recognized as a contributing cause. We evaluated eel abundances in headwater streams of Shenandoah National Park, Virginia, to compare sites before and after the removal of a large downstream dam in 2004 (Embrey Dam, Rappahannock River). Eel abundances in headwater streams increased significantly after the removal of Embrey Dam. Observed eel abundances after dam removal exceeded predictions derived from autoregressive models parameterized with data prior to dam removal. Mann–Kendall analyses also revealed consistent increases in eel abundances from 2004 to 2010 but inconsistent temporal trends before dam removal. Increasing eel numbers could not be attributed to changes in local physical habitat (i.e., mean stream depth or substrate size) or regional population dynamics (i.e., abundances in Maryland streams or Virginia estuaries). Dam removal was associated with decreasing minimum eel lengths in headwater streams, suggesting that the dam previously impeded migration of many small-bodied individuals (<300 mm TL). We hypothesize that restoring connectivity to headwater streams could increase eel population growth rates by increasing female eel numbers and fecundity. This study demonstrated that dams may influence eel abundances in headwater streams up to 150 river kilometers distant, and that dam removal may provide benefits for eel management and conservation at the landscape scale.**

American eels *Anguilla rostrata* exhibit complex life history strategies characterized by long-distance movements between marine habitats for spawning and freshwater habitats for growth and development (Oliveira 1999). Historically, American eels were widespread throughout the rivers and estuaries of North America's Atlantic coast, but the construction of dams has significantly reduced the amount of accessible habitat for diadromous fishes such as eels (Busch et al. 1998). Significant declines in American eel abundances (Haro et al. 2000; Fenske et al. 2011) have triggered new efforts for fishery management, including new initiatives to improve fish passage (ASMFC 2000). Dams were also recognized as a cause for recognizing American eel as a species of special concern in Canada (COSEWIC 2006) and for the U.S. Fish and Wildlife Service's recent decision to evaluate listing American eels as a threatened species under the Endangered Species Act (USFWS 2011).

Although American eels are capable of passing some significant natural barriers (e.g., the Great Falls of the Potomac River, which has several consecutive falls >6 m), dams may limit the upstream movement of eels such that eel numbers often decrease

*Corresponding author: nhitt@usgs.gov
Received October 17, 2011; accepted February 26, 2012
Published online July 20, 2012

above dams (Goodwin et al. 1999; Machut et al. 2007) and increase immediately below dams (Wiley et al. 2004; Machut et al. 2007). Consequently, barriers may influence stream community composition and population dynamics in upstream and downstream directions. Upstream of dams, decreased eel densities may influence stream fish communities by removing a native piscivore which could otherwise comprise over 25% of the total fish biomass in streams (Smith and Saunders 1955; Ogden 1970). Freshwater mussel distributions may also be limited through restrictions of the fish host movements that are necessary for upstream dispersal of mussel glochidia (Williams et al. 1993; Watters 1996). Downstream of dams, increased eel densities may increase intraspecific competition and decrease per capita growth rates (Machut et al. 2007). Reduced access to headwater streams may also influence eel stock–recruitment dynamics by decreasing the production of female eels (Krueger and Oliveira 1999).

Dam removal has proven effective for restoring historical upstream migrations of diadromous salmonid and clupeid fishes (Hill et al. 1996; Kiffney et al. 2009), but comparatively little is known about American eel responses to dam removal. On one hand, American eels have been observed upstream of dams that are known to limit other migratory fishes (Busch et al. 1998), suggesting that dam removal is relatively unimportant for eel distributions. On the other hand, decreased eel abundances upstream from dams (Goodwin et al. 1999; Machut et al. 2007) suggest that dams permit only a subset of the total migratory population to move upstream. If true, partial barriers to migration could affect eel populations by influencing sex ratios and fecundity. An understanding of the effects of dams could therefore inform conservation and restoration priorities for American eels.

In this study, we used a 15-year data set to evaluate how American eel populations in headwater streams responded to the removal a large downstream dam on the Rappahannock River in Virginia. Our objectives were twofold. First, we evaluated temporal trends in American eel abundance, biomass, and body size before and after dam removal. Second, we evaluated evidence for competing hypotheses involving changes in local physical habitats and population dynamics across larger spatial scales. Our study provides the first analysis of American eel responses to dam removal at the stream network scale (>100 river kilometers [rkm]).

## METHODS

*Study area*.—Embrey Dam was located near the fall line on the Rappahannock River in Virginia, (Figure 1). Downstream of the dam site, the river is influenced by tidal flows over the course of its 170-rkm distance to the Chesapeake Bay (Figure 1). The dam spanned a width of 235 m and a height of 6.7 m and was constructed in 1910 for hydroelectric production and municipal water supply, replacing a dam built in 1855 (Feeney 2004). On February 23, 2004, the U.S. Army Corps of Engineers breached the dam. The dam removal was the result of many years of work by nonprofit organizations and city, state, and federal government agencies. The dam removal was intended to benefit anadromous clupeids (e.g., American shad *Alosa sapidissima*) and striped bass *Morone saxatilis* as well as catadromous American eels (A. Weaver, Virginia Department of Game and Inland Fisheries, personal communication). In addition to Embrey Dam, a small dam on the Thornton River (Fletcher's Mill Dam, ~1 m high) near the boundary of Shenandoah National Park (SNP) was removed in 2009 to promote fish passage; however, it was not considered further because preliminary analyses indicated no significant differences in eel abundance between the Thornton watershed and other focal watersheds. We evaluated fish community and physical habitat data from headwater streams in SNP (Figure 1) located between 118 and 150 rkm upstream from the former location of Embrey Dam (Table 1).

*Eel population analysis*.—National Park Service personnel sampled fish communities in 117 wadeable stream sites within SNP annually from 1996 to 2010 (rarely excluding years; see Table 1). Of these sites, 32 supported American eels during at least one sampling event. We limited our analysis to 15 sites that had >7 annual collections, including samples before and after 2004 (Figure 1; Table 1). Each site was delimited within standardized 100-m reaches, and fish communities were sampled using standard three-pass backpack electrofishing techniques. Individual eel abundances were recorded for each pass, and the pooled weight of all eels and the minimum individual length (TL) per site were recorded (Atkinson 2002). We estimated eel

TABLE 1. Attributes of sample sites within Shenandoah National Park. The locations of the sites are shown in Figure 1; the watersheds correspond to those in Figures 2–4.

| Site | Watershed | Site elevation (m) | Fluvial distance to dam (km) | Number of sample years before and after dam removal |
|---|---|---|---|---|
| 1F003 | Thornton | 362 | 118 | 8, 4 |
| 1F030 | Thornton | 352 | 119 | 7, 4 |
| 1F145 | Thornton | 415 | 120 | 5, 3 |
| 1FVA2 | Thornton | 382 | 120 | 7, 4 |
| 1FVA3 | Thornton | 428 | 122 | 7, 4 |
| 2F015 | Rose | 340 | 125 | 5, 4 |
| 2F016 | Rose | 414 | 127 | 8, 4 |
| 2F017 | Rose | 642 | 129 | 8, 4 |
| 2F038 | Hughes | 293 | 121 | 8, 4 |
| 2F039 | Hughes | 370 | 122 | 8, 4 |
| 2F040 | Hughes | 402 | 123 | 8, 4 |
| 2F072 | Rapidan | 316 | 146 | 6, 5 |
| 2F093 | Rapidan | 285 | 145 | 8, 7 |
| 2F135 | Rapidan | 412 | 148 | 8, 5 |
| 2FVA4 | Rapidan | 507 | 150 | 7, 7 |

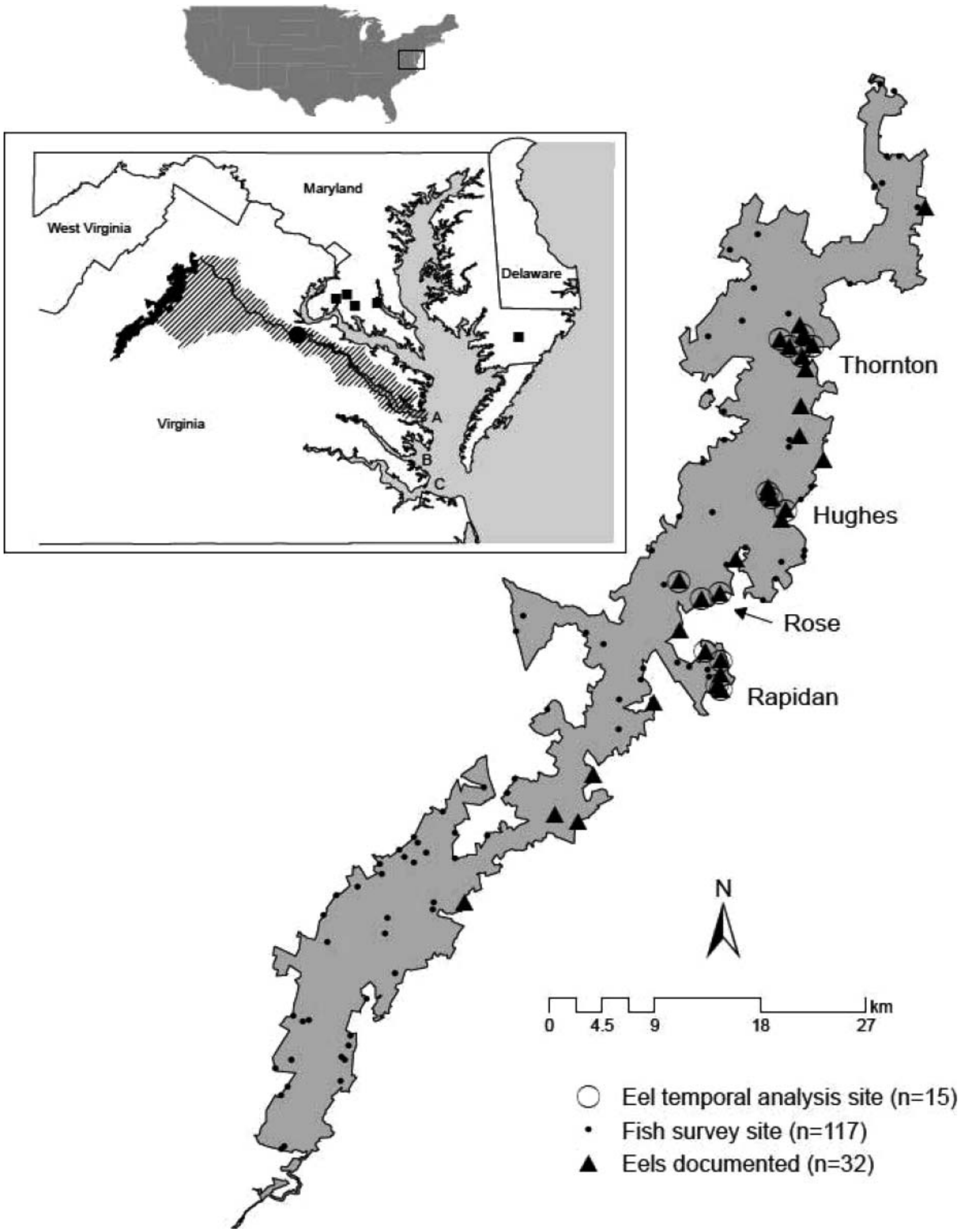


FIGURE 1. American eel distribution within Shenandoah National Park. The regional map indicates the former location of Embrey Dam on the Rappahannock River (circle), the locations of Maryland control stream sites (squares), and the Rappahannock River watershed (cross hatches). Study estuaries are indicated for the Rappahannock River (A), York River (B), and James River (C). Fluvial distances from the Embrey Dam site to Shenandoah National Park sample sites are listed in Table 1.

abundances within sampling reaches as the sum of eel counts across passes and combined site-level data into four focal watersheds for analysis (Table 1). Each of the 15 SNP focal sites in this analysis was located upstream from the Embrey Dam site.

We used time series analysis and nonparametric and parametric statistical tests to evaluate the effects of dam removal on eel abundances in headwater streams. First, we used autoregressive integrated moving average (ARIMA) techniques (Box et al. 2008) to derive a null model for expected eel abundances in the absence of dam removal and to evaluate the significance of observed changes in eel abundances after dam removal. The ARIMA techniques were useful because preliminary analyses revealed potential autocorrelation in eel abundances among years and ARIMA models incorporate such temporal autocorrelation to forecast mean and variance of estimates (Zhang 2003). We parameterized the null model using eel abundance data from 1996 to 2003 (i.e., before dam removal) to forecast abundances from 2004 to 2010 (i.e., after dam removal). Best-fitting ARIMA model parameters (number of autoregressive terms, number of nonseasonal differences, and the number of lagged forecast errors) were selected from the function "auto.arima" in the R library "forecast." We inferred the effects of dam removal based on the departure of observed eel abundances after dam removal from the 95% confidence intervals of the null model predictions. Our analysis of predicted confidence intervals provided a method to estimate the significance of temporal changes without bias due to the nonindependence of residuals common to linear modeling techniques (Box et al. 2008). Koutroumanidis et al. (2006) used similar methods for analysis of fisheries catch rates.

Second, we used Mann–Kendall analysis (Mann 1945; Kendall 1975) to evaluate temporal trends in eel abundances among sites within three time periods: before dam removal (1996–2003), after dam removal (2004–2010), and within the entire period of record. The Mann–Kendall statistics provided a nonparametric analysis of increasing and decreasing eel abundances and ranged from $-1$ (decreasing trends) to $+1$ (increasing trends). We reported Mann–Kendall $P$-values as an index of the relative strength of temporal trends but did not interpret significance based on a critical $\alpha$ level because Mann–Kendall $P$-values are biased by serial autocorrelation (Yue and Wang 2004). Instead, we reasoned that sites would tend to exhibit a random distribution of increasing and decreasing abundances prior to dam removal but would shift to increasing abundances after 2004 if dam removal increased colonization rates. We also plotted average minimum eel lengths and pooled biomass among focal watersheds over time and estimated differences in pre- and postdam mean conditions using $t$-tests.

*Alternative hypotheses*.—We considered local physical habitat and regional population dynamics as alternatives to dam removal to explain temporal changes in eel abundance, size, and biomass. First, we quantified the interannual variation in substrate size and stream depth within SNP sample sites as possible confounding factors from dam removal. National Park Service personnel collected physical habitat samples at three evenly spaced points along 11 equidistant lateral transects within the 100 m reach. At each sample point, stream depth was recorded to the nearest millimeter and the dominant substrate was recorded as silt, sand, gravel, cobble, boulder, or bedrock (Wentworth 1922). To assess substrate size trends, substrate types were numerically coded (i.e., silt = 0, sand = 1, etc.) to calculate mean conditions (Bain and Stevenson 1999). American eels are typically associated with pools in lotic environments (Jenkins and Burkhead 1994), and we assumed that changes in pool habitat would be reflected by changes in mean stream depth and substrate size over time.

Second, we evaluated eel abundances in additional streams of the Chesapeake Bay region to control for the effects of dam removal in the SNP sites. We reasoned that if oceanic-scale processes were influencing headwater eel numbers (i.e., mass effects; sensu Shmida and Wilson 1985), eel numbers would exhibit similar trends outside the Rappahannock River watershed. We examined eel time series data from the Maryland Biological Stream Survey (MBSS). The MBSS fish community data were collected by Maryland Department of Natural Resources personnel annually from 2000 to 2010. Stream sites were sampled using two-pass backpack electrofishing techniques during summer base-flow conditions within blocknetted 75-m sample reaches (MDNR 2010). We evaluated five sites that contained eel records and were not separated from the ocean by dams. Sites were located within watersheds of the lower Potomac River, Pocomoke River, and Patuxent River in the southwestern portion of the Chesapeake Bay (Figure 1). Mean stream widths of the selected MBSS stream sites ranged from 1.7 to 6.6 m (average = 3.8 m) and were located within 10 rkm of the tidal-influence zone (Figure 1).

Third, we evaluated eel abundances within estuaries of the Rappahannock River, York River, and James River (Figure 1) to understand whether or not the Embrey Dam removal coincided with unusually high or low rates of recruitment from marine areas (i.e., mass effects). Estuary data were collected by the Virginia Institute of Marine Science using a trawl survey designed to estimate the abundance of juvenile fish in the Virginia portion of the Chesapeake Bay (Tuckey and Fabrizio 2010). The trawl surveys sampled eel abundances within estuaries of the Rappahannock River, York River, and James River during spring months (April to June), and we evaluated annual data collected between 1996 and 2010. Sampling was conducted monthly at both fixed and randomly selected stations within each estuary. The index for American eels is an annual weighted geometric mean catch per tow of all eels greater than 152 mm TL (Tuckey and Fabrizio 2010). All analyses were conducted in R version 2.13.1 (R Development Core Team 2011).

## RESULTS

Mean American eel abundances within SNP watersheds increased from 1.6 to 3.9 eels/100 m after the removal of Embrey Dam in 2004 (Table 2). Postdam eel abundances exceeded

TABLE 2. Eel population attributes and environmental conditions in Shenandoah National Park watersheds pre- and postremoval of Embrey Dam. Values are means, with SDs in parentheses. Differences between pre- and postdam means are indicated by different lowercase letters ($t$-tests assuming unequal variance) using a Bonferroni correction for $\alpha = 0.05/5 = 0.01$ ($t = -2.79$, $P = 0.006$). Sample sizes are listed in Table 1.

| | Eel abundance / 100 m | | Minimum total length (mm) | | Pooled eel biomass (g) | | Mean stream depth (m) | | Mean substrate size-class | |
|---|---|---|---|---|---|---|---|---|---|---|
| Watershed | Pre | Post | Pre | Post | Pre | Post | Pre | Post | Pre | Post |
| Hughes | 2.4 | 3.8 | 389 | 313 | 522 | 707 | 0.17 | 0.16 | 3.1 | 3.0 |
| | (1.3) | (2.9) | (96) | (168) | (321) | (400) | (0.02) | (0.03) | (0.4) | (0.4) |
| Rapidan | 1.4 | 4.7 | 452 | 226 | 783 | 819 | 0.18 | 0.21 | 3.2 | 3.1 |
| | (0.7) | (4.4) | (52) | (136) | (282) | (461) | (0.02) | (0.02) | (0.3) | (0.1) |
| Rose | 0.6 | 2.3 | 545 | 323 | 725 | 335 | 0.13 | 0.18 | 3.1 | 3.0 |
| | (0.7) | (1.7) | (104) | (160) | (222) | (293) | (0.02) | (0.03) | (0.3) | (0.2) |
| Thornton | 2.0 | 4.2 | 368 | 234 | 538 | 520 | 0.11 | 0.10 | 2.9 | 2.5 |
| | (0.6) | (3.6) | (40) | (78) | (255) | (205) | (0.02) | (0.01) | (0.4) | (0.3) |
| All | 1.6 y | 3.9 z | 426 | 269 | 628 | 620 | 0.15 | 0.17 | 3.0 | 2.9 |
| | (1.6) | (5.0) | (96) | (135) | (287) | (388) | (0.04) | (0.05) | (0.3) | (0.4) |

ARIMA null model predictions for all focal watersheds (Figure 2) and exhibited a time-lag response to dam removal: observed abundances exceeded predicted values (>95% confidence intervals) within 4 years after dam removal in the Hughes, Rapidan, and Thornton River watersheds and within 2 years in the Rose River watershed (Figure 2). Mann–Kendall analysis supported the ARIMA model results, indicating nine sites (60%) with decreasing abundance trends prior to dam removal (i.e., $\tau < 0$) but all sites with increasing abundance trends after dam removal ($\tau > 0$) (Table 3). Analysis of the combined data set (1996–2010) showed 13 sites with increasing trends and 2 sites with decreasing trends in eel abundance (Table 3).

Headwater streams generally supported smaller eels after dam removal than before dam removal (Figure 3; Table 2). Prior to dam removal, average minimum eel lengths ranged from 545 mm (Rose River watershed) to 368 mm (Thornton River watershed); after dam removal, the range of average minimum total lengths dropped to between 323 mm (Rose River watershed) and 226 mm (Rapidan River watershed) (Table 2). Moreover, no eels less than 300 mm TL were detected in any SNP watershed before 2004, but eels of that length were present in each watershed after dam removal (Figure 3). Average total eel biomass decreased on average from 401 g to 159 g after dam removal (Table 2) but exhibited substantial spatial and temporal

TABLE 3. Mann–Kendall $\tau$-statistics for time series analysis of American eel abundances.

| | Before dam removal | | After dam removal | | Whole data set | |
|---|---|---|---|---|---|---|
| Site | $\tau$ | $P$ | $\tau$ | $P$ | $\tau$ | $P$ |
| 1F003 | −0.189 | 0.612 | 0.667 | 0.308 | 0.469 | 0.045 |
| 1F030 | −0.150 | 0.759 | 0.667 | 0.308 | 0.135 | 0.633 |
| 1F145 | −0.738 | 0.130 | 0.816 | 1.000 | −0.433 | 0.195 |
| 1FVA2 | 1.000 | 1.000 | 0.548 | 0.470 | 0.526 | 0.061 |
| 1FVA3 | 0.265 | 0.525 | 0.183 | 1.000 | 0.060 | 0.871 |
| 2F015 | 0.316 | 0.613 | 0.913 | 0.149 | 0.509 | 0.085 |
| 2F016 | 0.504 | 0.148 | 0.548 | 0.470 | 0.627 | 0.011 |
| 2F017 | 1.000 | 1.000 | 0.707 | 0.371 | 0.408 | 0.148 |
| 2F038 | −0.390 | 0.272 | 0.913 | 0.149 | 0.116 | 0.670 |
| 2F039 | −0.222 | 0.530 | 0.548 | 0.470 | −0.032 | 0.944 |
| 2F040 | 0.197 | 0.605 | 0.548 | 0.470 | 0.201 | 0.430 |
| 2F072 | 1.000 | 1.000 | 0.632 | 0.289 | 0.426 | 0.155 |
| 2F093 | −0.591 | 0.070 | 0.781 | 0.023 | 0.217 | 0.308 |
| 2F135 | −0.321 | 0.385 | 0.800 | 0.086 | 0.530 | 0.019 |
| 2FVA4 | −0.233 | 0.610 | 0.476 | 0.204 | 0.198 | 0.403 |

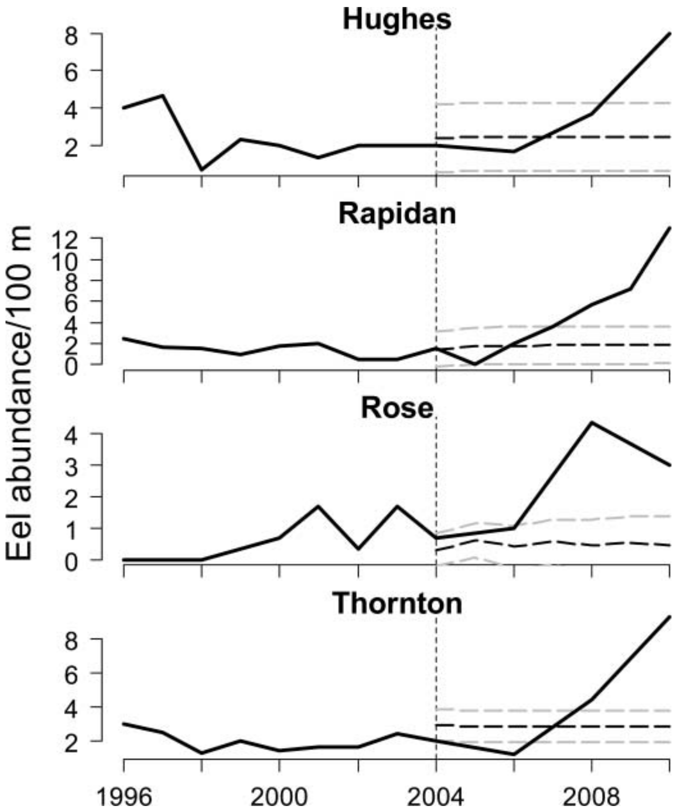


FIGURE 2. Interannual variation in American eel abundance within Shenandoah National Park watersheds. Solid lines show the average observed abundances within focal watersheds. Black dashed lines indicate the autoregressive integrated moving average (ARIMA) model predictions for 2004–2010 (parameterized from 1996 to 2003 data; see text). Gray dashed lines indicate the upper and lower 95% confidence limits for mean predicted abundances. Sites within watersheds are listed in Table 1.

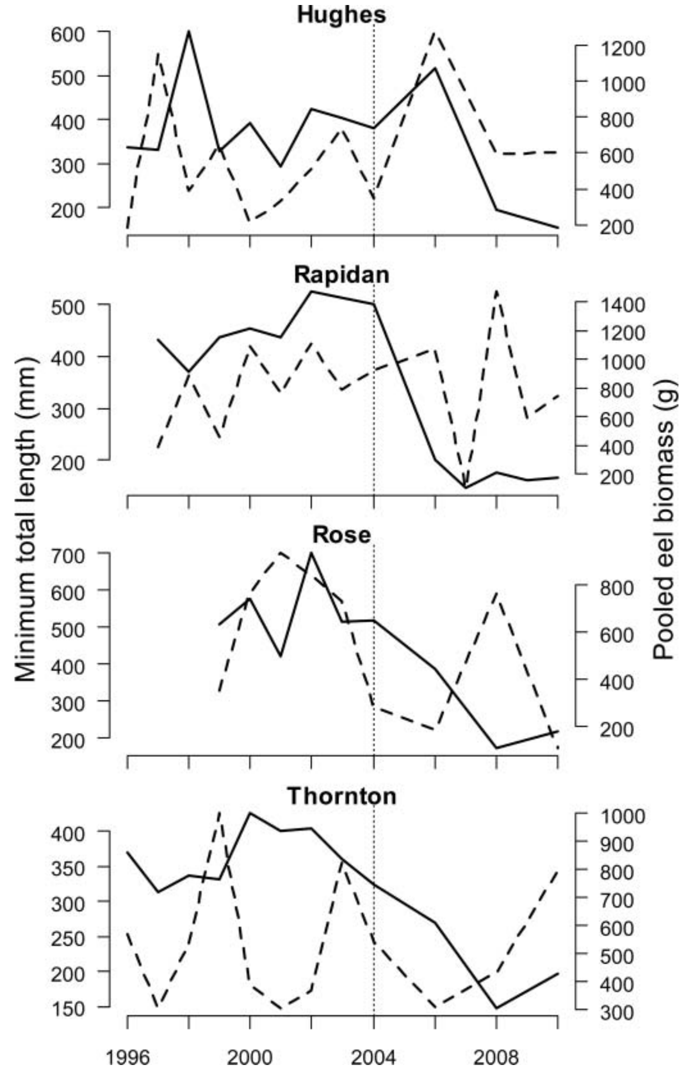


FIGURE 3. Interannual variation in American eel minimum total length (solid line, left axis) and pooled biomass (dashed line, right axis) within Shenandoah National Park watersheds. Sites within watersheds are listed in Table 1.

variation (Figure 3). Although individual length data were not available, the minimum length, total number of eels collected, and biomass data indicate that eel abundances increased due primarily to the immigration of eels <300 mm TL.

Mean depth and substrate size-classes were highly variable across SNP watersheds and exhibited no significant differences between pre- and postdam conditions (Table 2; Figure 4). Across SNP watersheds, mean depths ranged from 0.04 to 0.20 m and showed inconsistent temporal patterns (Figure 4). For instance, 2004 yielded some of the lowest mean depths in the Hughes and Thornton River watersheds but the highest in the Rapidan River watershed (Figure 4). Mean depths in the Rose River watershed showed an increasing trend (Figure 4) but increased by only 0.05 m on average after dam removal (Table 2). Among watersheds, mean substrate size ranged from approximately 2.5 to 3.5 across years, suggesting substrate fluctuations around cobble-dominated systems (cobble = 3; Figure 4). Pre- versus postdam comparisons of mean substrate size-class within watersheds indicated that substrate size has not changed in a systematic direction (Table 2). It is therefore unlikely that physical habitat changes could explain the observed increases in eel abundance over time.

American eel abundances within Maryland streams and Virginia estuaries exhibited no distinct changes coincident with dam removal on the Rappahannock River (Figure 5). Mean eel abundances in Maryland streams ranged from 3.2 to 22.0 individuals/75 m between 2000 and 2010 and exhibited no consistent increases after 2004 (Figure 5A). In contrast, estuarine eel abundances generally decreased over time in the Rappahannock River (Figure 5B) as well as in the York River (Figure 5C) and James River (Figure 5D). It is therefore unlikely that oceanic-scale dynamics could explain the observed population increases in the Rappahannock River tributaries. Instead, we observed increasing eel numbers in headwater streams despite decreasing regional trends.

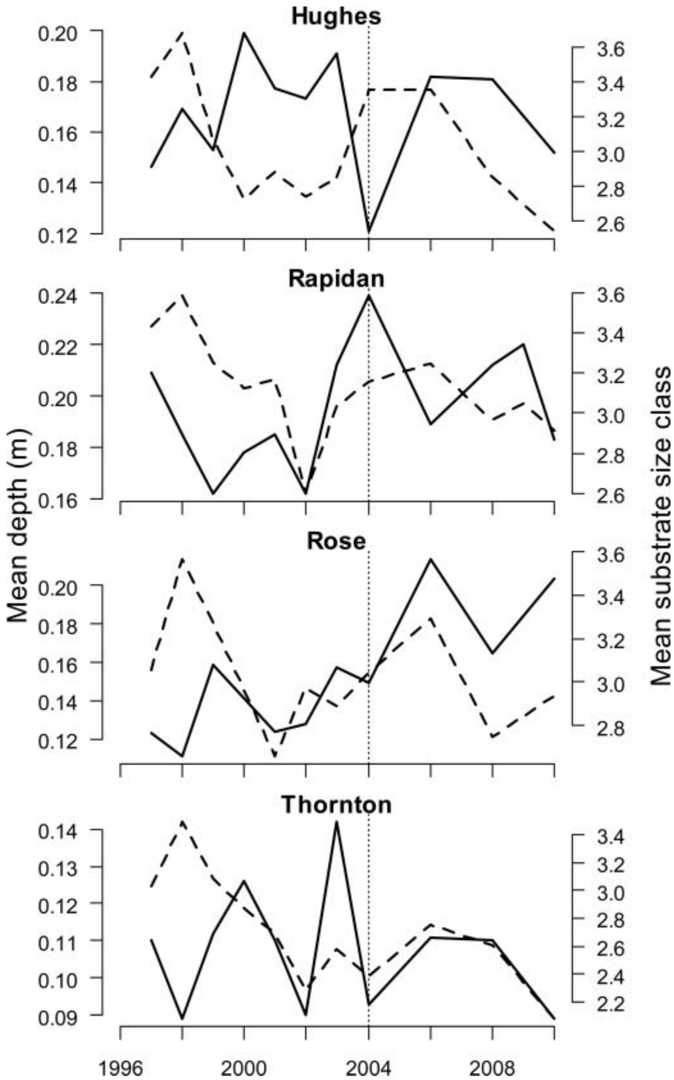


FIGURE 4. Interannual variation in mean stream depth (solid line, left axis) and substrate size-class (dashed line, right axis) within watersheds used for American eel analysis in Shenandoah National Park. See text for substrate class definitions.

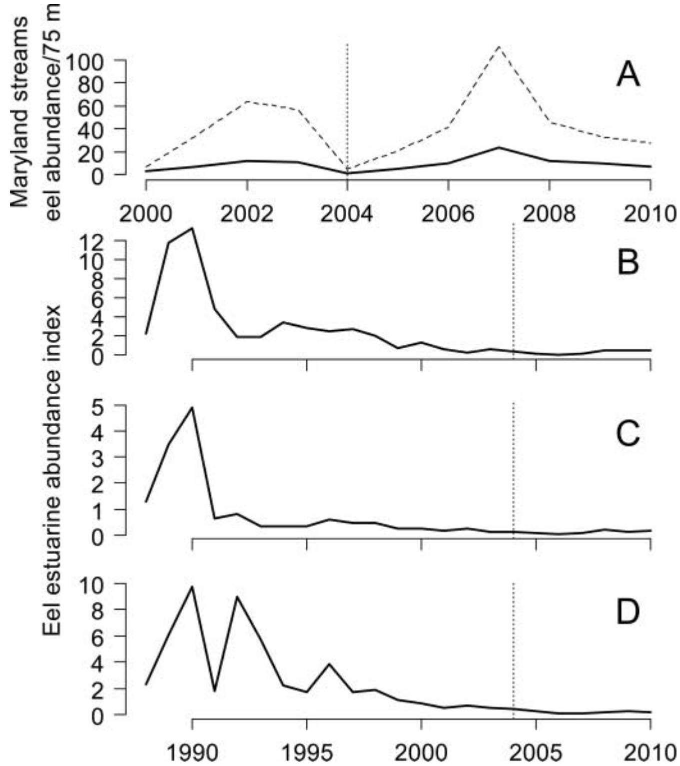


FIGURE 5. Interannual variation in American eel abundances within **(A)** Maryland nontidal wadeable streams and the estuaries of **(B)** the Rappahannock River, **(C)** the York River, and **(D)** the James River, Virginia. Vertical dotted lines indicate the year of dam removal on the Rappahannock River. In panel (A), the horizontal dashed line indicates 2 SDs from the mean abundances (solid line).

## DISCUSSION

Our study provides new inferences regarding the landscape-level effects of dam removal. Prior studies have shown localized effects of dam removal on fish populations, but our analysis is the first to our knowledge to demonstrate such influences on fish populations far upstream (i.e., 150 rkm). Our results also show that the immigration of small-bodied individuals (<300 mm TL) was primarily responsible for the observed increases in eel numbers. Although Embrey Dam did not prevent eel passage, our results indicate that it depressed eel abundances and altered eel size structure within connected headwater catchments. The benefits of dam removal may therefore extend far into headwater areas.

Although SNP sites showed increasing eel numbers over time, total eel abundances remained relatively low. For instance, Ogden (1970) reported that American eels were the most abundant species in a New Jersey stream, comprising 20% of all observed fishes (and 37% of biomass, second only to white suckers *Catostomus commersonii*, at 47% of total biomass). In contrast, eel numbers in the SNP study sites never exceeded 2% of the total catch because fish assemblages were numerically dominated by eastern blacknose dace *Rhinichthys atratulus* (up to 52% of the total catch) and brook trout *Salvelinus fontinalis* (up to 77% of the total catch) (J. E. B. Wofford, National Park Service, unpublished data). Thus, we would expect eel abundances to increase over the near term in SNP streams without limitations due to intraspecific competition for food or microhabitats. Moreover, measures of regional connectivity are generally more powerful than local physical habitat variables for modeling anguillid distributions and abundance (Smogor et al. 1995; Domingos et al. 2006).

Increasing eel abundances may influence stream fish communities by altering predation and competition pressures. Although brook trout are currently the dominant piscivore in most SNP streams, fish typically comprise a relatively small portion of lotic brook trout diets (Reed and Bear 1966). As a result, increasing eel numbers could affect the predation rates on benthic fishes, which comprise the majority of American eel fish diets (Ogden 1970). Such increased predation on benthic fishes may influence the top-down regulation of stream food webs (Power et al. 1985), and thus migration barriers which reduced American eel numbers could have ecosystem-level consequences (e.g., Pringle 1997). However, such effects would take several years to observe because American eels typically shift from invertebrates to fish and crayfish diets at approximately 400 mm TL (Ogden 1970; Lookabaugh and Angermeier 1992) and small-bodied eels were primarily responsible for the increased abundances we observed. Moreover, because American eels spend several years in freshwater habitats before their spawning outmigration (i.e., 6–21 years; Jessop 2010), additional sampling will be necessary to assess fish community responses to changing eel abundances.

Increasing the headwater stream abundances of American eels could affect regional population dynamics because headwater reaches provide vital habitats for the growth and development of female eels. First, access to headwater streams could increase per capita fecundity because American eel body sizes typically increase with distance from the ocean (Lookabaugh and Angermeier 1992; Smogor et al. 1995) and eel fecundity increases with body size (Barbin and McCleave 1997). Second, only female American eels are typically observed in headwater streams (Goodwin and Angermeier 2003), and so the relative abundance of females could increase if restored headwater connectivity reduced the downstream crowding associated with high abundances of male fish (Krueger and Oliveira 1999). Conservation and restoration efforts for American eels could therefore benefit by considering headwater connectivity as a possible mechanism by which to increase eel numbers throughout their range.

Dam removal presents several ecological trade-offs for consideration in fisheries management. Over the short term, dam removal may increase downstream sedimentation and decrease water quality, but fish populations and communities may benefit from increased abundance and resilience with restored stream network connectivity (Bednarek 2001; Hart et al. 2002; Stanley and Doyle 2003). In some cases, barriers may be used as a management tool to prevent the immigration of undesirable species (Fausch et al. 2009). Although American eels are well known for their long-distance catadromous migrations, barrier removal could also benefit nondiadromous freshwater fishes by permitting fish movement and recolonization within stream networks (Winston et al. 1991; Catalano et al. 2007; Hitt and Angermeier 2008, 2011). Dams are ubiquitous in river systems worldwide (Poff and Hart 2002), but the rate of dam removal is increasing through time (Stanley and Doyle 2003) and our analysis suggests that dam removal confers ecological benefits for fish conservation and management across large spatial scales.

## ACKNOWLEDGMENTS

We thank T. Tuckey, K. Whiteford, M. Kashiwagi, A. Weaver, N. Dammeyer, A. Williams, C. Snyder, J. Schaberl, S. Faulkner, and K. Cooper for assistance with the development and review of this paper. This research was supported by Shenandoah National Park, the National Park Service's Inventory and Monitoring Program, and the U.S. Geological Survey. Use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

## REFERENCES

ASMFC (Atlantic States Marine Fisheries Commission). 2000. Interstate fishery management plan for American eel (*Anguilla rostrata*). ASMFC, Fisheries Management Report 36, Washington, D.C.

Atkinson, J. B. 2002. Shenandoah National Park fisheries: monitoring protocol. Shenandoah National Park, Luray, Virginia.

Bain, M. B., and N. J. Stevenson, editors. 1999. Aquatic habitat assessment: common methods. American Fisheries Society, Bethesda, Maryland.

Barbin, G. P., and J. D. McCleave. 1997. Fecundity of the American eel *Anguilla rostrata* at 45° N in Maine, U.S.A. Journal of Fish Biology 51:840–847.

Bednarek, A. T. 2001. Undamming rivers: a review of the ecological impacts of dam removal. Environmental Management 27:803–814.

Box, G. E. P., G. M. Jenkins, and G. C. Reinsel. 2008. Time series analysis: forecasting and control, 4th edition. Wiley, New York.

Busch, W. D. N., S. J. Lary, and C. M. Castiglione. 1998. Evaluating stream habitat for diadromous fish in Atlantic coast watersheds: a preliminary assessment. Habitat Hotline Atlantic (November):1–3.

Catalano, M. J., M. A. Bozek, and T. D. Pellett. 2007. Effects of dam removal on fish assemblage structure and spatial distributions in the Baraboo River, Wisconsin. North American Journal of Fisheries Management 27: 519–530.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2006. Assessment and status report on the American eel *Anguilla rostrata* in Canada. COSEWIC, Ottawa.

Domingos, I., J. L. Costa, and M. J. Costa. 2006. Factors determining length distribution and abundance of the European eel, *Anguilla anguilla,* in the River Mondego (Portugal). Freshwater Biology 51:2265–2281.

Fausch, K. D., B. E. Rieman, J. B. Dunham, M. K. Young, and D. P. Peterson. 2009. Invasion versus isolation: trade-offs in managing native salmonids with barriers to upstream movement. Conservation Biology 23:859–870.

Feeney, B. 2004. Embrey Dam removal opens 100s of miles of river to fish. Chesapeake Bay Journal 14(2):5.

Fenske, K. H., M. J. Wilberg, D. H. Secor, and M. C. Fabrizio. 2011. An age- and sex-structured assessment model of American eels (*Anguilla rostrata*) in the Potomac River, Maryland. Canadian Journal of Fisheries and Aquatic Sciences 68:1024–1037.

Goodwin, K. R., and P. L. Angermeier. 2003. Demographic characteristics of American eel in the Potomac River drainage, Virginia. Transactions of the American Fisheries Society 132:524–535.

Goodwin, K. R., P. L. Angermeier, and D. J. Orth. 1999. Assessing impacts of hydropower dams on upstream migration of American eel. Final Report to the Virginia Department of Game and Inland Fisheries, Richmond, Virginia.

Haro, A., W. Richkus, K. Whalen, A. Hoar, W. D. Busch, S. Lary, T. Brush, and D. Dixon. 2000. Population decline of the American eel: implications for research and management. Fisheries 25(9):7–16.

Hart, D. D., T. E. Johnson, K. L. Bushaw-Newton, R. J. Horowitz, A. T. Bednarek, D. F. Charles, D. A. Kreeger, and D. J. Velinsky. 2002. Dam removal: challenges and opportunities for ecological research and river restoration. BioScience 52:669–681.

Hill, M. J., E. A. Long, and S. Hardin. 1996. Effects of a dam removal on Dead Lake, Chipola River, Florida. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 48(1994): 512–523.

Hitt, N. P., and P. L. Angermeier. 2008. Evidence for fish dispersal from spatial analysis of stream network topology. Journal of the North American Benthological Society 27:304–320.

Hitt, N. P., and P. L. Angermeier. 2011. Fish community and bioassessment responses to stream network position. Journal of the North American Benthological Society 30:296–309.

Jenkins, R. E., and N. M. Burkhead. 1994. Freshwater fishes of Virginia. American Fisheries Society, Bethesda, Maryland.

Jessop, B. M. 2010. Geographic effects on American eel (*Anguilla rostrata*) life history characteristics and strategies. Canadian Journal of Fisheries and Aquatic Sciences 67:326–346.

Kendall, M. G. 1975. Rank correlation methods. Griffin Publishers, London.

Kiffney, P. M., G. R. Pess, J. H. Anderson, P. Faulds, K. Burton, and S. C. Riley. 2009. Changes in fish communities following recolonization of the Cedar River, WA, USA by Pacific salmon after 103 years of local extirpation. River Research and Applications 25:438–452.

Koutroumanidis, T., L. S. Iiadis, and G. K. Sylaios. 2006. Time-series modeling of fishery landings using ARIMA models and fuzzy expected intervals software. Environmental Modelling and Software 21:1711–1721.

Krueger, W. H., and K. Oliveira. 1999. Evidence for environmental sex determination in the American eel, *Anguilla rostrata*. Environmental Biology of Fishes 55:381–398.

Lookabaugh, P. S., and P. L. Angermeier. 1992. Diet patterns of American eel, *Anguilla rostrata,* in the James River drainage, Virginia. Journal of Freshwater Ecology 7:425–431.

Machut, L. S., K. E. Limburg, R. E. Schmidt, and D. Dittman. 2007. Anthropogenic impacts on American eel demographics in Hudson River tributaries, New York. Transactions of the American Fisheries Society 136:1699–1713.

Mann, H. B. 1945. Nonparametric tests against trend. Econometrica 13:245–259.

MDNR (Maryland Department of Natural Resources). 2010. Maryland biological stream survey, sampling manual: field protocols. MDNR, Report 12-2162007-19, Annapolis.

Ogden, J. C. 1970. Relative abundance, food habits, and age of the American eel, *Anguilla rostrata* (LeSueur), in certain New Jersey streams. Transactions of the American Fisheries Society 99:54–59.

Oliveira, K. 1999. Life history characteristics and strategies of the American eel, *Anguilla rostrata*. Canadian Journal of Fisheries and Aquatic Sciences 56:795–802.

Poff, N. L., and D. D. Hart. 2002. How dams vary and why it matters for the emerging science of dam removal. BioScience 52:659–668.

Power, M. E., W. J. Matthews, and A. J. Stewart. 1985. Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. Ecology 66:1448–1456.

Pringle, C. M. 1997. Exploring how disturbance is transmitted upstream: going against the flow. Journal of the North American Benthological Society 16:425–438.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: www.R-project.org/. (October 2011).

Reed, E. B., and G. Bear. 1966. Benthic animals and foods eaten by brook trout in Archuleta Creek, Colorado. Hydrobiologia 27:227–237.

Shmida, A., and M. V. Wilson. 1985. Biological determinants of species diversity. Journal of Biogeography 12:1–20.

Smith, M. W., and J. W. Saunders. 1955. The American eel in certain fresh waters of the maritime provinces of Canada. Journal of the Fisheries Research Board of Canada 12:238–269.

Smogor, R. A., P. L. Angermeier, and C. K. Gaylord. 1995. Distribution and abundance of American eels in Virginia streams: tests of null models across spatial scales. Transactions of the American Fisheries Society 124:789–803.

Stanley, E. H., and M. W. Doyle. 2003. Trading off: the ecological effects of dam removal. Frontiers in Ecology and the Environment 1:15–22.

Tuckey, T. D., and M. C. Fabrizio. 2010. Estimating relative juvenile abundance of ecologically important finfish in the Virginia portion of Chesapeake Bay. Annual Report to the Virginia Marine Resources Commission, Project F-104-R-14, Virginia Institute of Marine Science, Gloucester Point.

USFWS (U.S. Fish and Wildlife Service). 2011. Endangered and threatened wildlife and plants; 90-day finding on a petition to list the American eel as threatened. Federal Register 76:189(29 September 2011):60431–60444.

Watters, G. T. 1996. Small dams as barriers to freshwater mussels (Bivalvia, Unionoida) and their hosts. Biological Conservation 75:79–85.

Wentworth, C. K. 1922. A scale of grade and class terms for clastic sediments. Journal of Geology 30:377–392.

Wiley, D. J., R. P. Morgan II, R. H. Hilderbrand, R. L. Raesly, and D. L. Shumway. 2004. Relations between physical habitat and American eel abundance in five river basins in Maryland. Transactions of the American Fisheries Society 133:515–526.

Williams, J. D., M. L. Warren Jr., K. S. Cummings, J. L. Harris, and R. J. Neves. 1993. Conservation status of freshwater mussels of the United States and Canada. Fisheries 18(9):6–22.

Winston, M. R., C. M. Taylor, and J. Pigg. 1991. Upstream extirpation of four minnow species due to damming of a prairie stream. Transactions of the American Fisheries Society 120:98–105.

Yue, S., and C. Wang. 2004. The Mann-Kendall test modified by effective sample size to detect trend in serially correlated hydrological series. Water Resources Management 18:201–218.

Zhang, G. P. 2003. Time series forecasting using a hybrid ARIMA and neural network model. Neurocomputing 50:159–175.