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Chapter 2

CONTRASTING FISH ASSEMBLAGES IN FREE-FLOWING AND IMPOUNDED TRIBUTARIES TO THE UPPER DELAWARE RIVER: IMPLICATIONS FOR CONSERVING BIODIVERSITY

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ABSTRACT

The Neversink River and the Beaver Kill in southeastern New York are major tributaries to the Delaware River, the longest undammed river east of the Mississippi. While the Beaver Kill is free flowing for its entire length, the Neversink River is subdivided by the Neversink Reservoir, which likely affects the diversity of local fish assemblages and health of aquatic ecosystems. The reservoir is an important part of the New York City water-supply system that provides drinking water to more than 9 million people. Fish population and community data from recent quantitative surveys at comparable sites in both basins were assessed to characterize the differences between free-flowing and impounded rivers and the extent of reservoir effects to improve our capacity to define ecosystem responses that two modified flow-release programs (implemented in 2007 and 2011) should produce in the Neversink River. In general, the continuum of changes in fish assemblages which normally occur between headwaters and mouth was relatively uninterrupted in the Beaver Kill, but disrupted by the mid-basin impoundment in the Neversink River. Fish assemblages were also adversely affected at several acidified sites in the upper Neversink River, but not at most sites assessed herein. The reservoir clearly excluded diadromous species from the upper sub-basin, but it also

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substantially reduced community richness, diversity, and biomass at several mid-basin sites immediately downstream from the impoundment. These results will aid future attempts to determine if fish assemblages respond to more natural, yet highly regulated, flow regimes in the Neversink River. More important, knowledge gained from this study can help optimize use of valuable water resources while promoting species of special concern, such as American eel (*Anguilla rostrata*) and conserving biodiversity in Catskill Mountain streams.

Keywords: impoundment, American eel, Delaware, biodiversity, fish assemblages, flow regime

INTRODUCTION

The Delaware River is the longest undammed river east of the Mississippi allowing native migratory fish access far upstream into a few headwater tributaries. The Neversink River and the Beaver Kill are two major tributaries to the Upper Delaware River and have their origins in the Catskill Mountains of southeastern New York State (Figure 1). Although the Beaver Kill is free flowing, the Neversink River is bisected by the Neversink Reservoir which may affect the long-term sustainability of several fish populations and the structure and function of local stream ecosystems in the upper basin. The Neversink Reservoir not only impedes passage of diadromous species, but affects the water quality, discharge, and thermal and sediment regimes at downstream main stem reaches (Baldigo et al. 2002). While impoundments have been shown to alter the composition of fish communities upstream of, and within reservoirs, often due to fragmentation and the presence of lentic invasive species (Herbert and Gelwick 2003; Jellyman and Harding 2012; Kanno and Vokoun 2010; McCully 1996), the effects on fish assemblages throughout impounded basins have rarely been well documented. The present study was designed to increase our understanding of the effects that impoundments have on local fish assemblages; such information is crucial to effectively conserve and manage natural fishery and water resources within heavily impounded river systems across the Catskill Mountain Region.

Sound fish-management practices require quantitative models to accurately predict the response of fish assemblages to various flow-release scenarios and to better understand the effects of altered hydrologic regimes on the integrity of fish assemblages within natural and compromised riverine ecosystems. Fish communities in large river basins normally follow a predictable succession (longitudinal zonation) from small, cold, low-order headwater reaches to large, warm, high-order reaches following a continuum of abiotic and biotic factors which affect the distributions of individual species (Vannote et al. 1980). Fish species richness and diversity have been shown to increase progressively downstream with increasing stream order often due to addition of more species, rather than replacement of existing species (Hutchinson 1993; Sheldon 1968; Whiteside and McNatt 1972; Zalewski et al. 1990). Some investigations found that changes in physical and chemical factors such as dissolved oxygen, pH, alkalinity, turbidity, conductivity, stream depth, size, order, and habitat heterogeneity explained most of the variability in fish community richness and diversity (Hutchinson 1993; Schlosser 1987; Schlosser 1991; Sheldon 1968). In temperate watersheds, these abiotic factors can also limit the diversity of headwater fish communities to a few species that are tolerant of small/shallow

channels, cold temperatures, rapid changes in discharge, homogeneous habitat, and high water velocities. Although total biomass is often relatively constant in most ecosystems (Tremblay and Richard 1993) and generally does not increase substantially with increasing stream order (Baldigo and Lawrence 2000), increased primary productivity within intermediate-order (mid-reach) segments can support greater secondary and tertiary productivity, thus larger individuals (or increased densities) than in low order streams (Naiman et al. 1987; Vannote et al. 1980). Biotic factors, such as competition and predation, often regulate richness and diversity of fish communities at larger downstream reaches where relatively stable flows, more heterogeneous habitat, and slower and warmer temperatures permit more fish species to coexist (Li et al. 2012; Vannote et al. 1980).

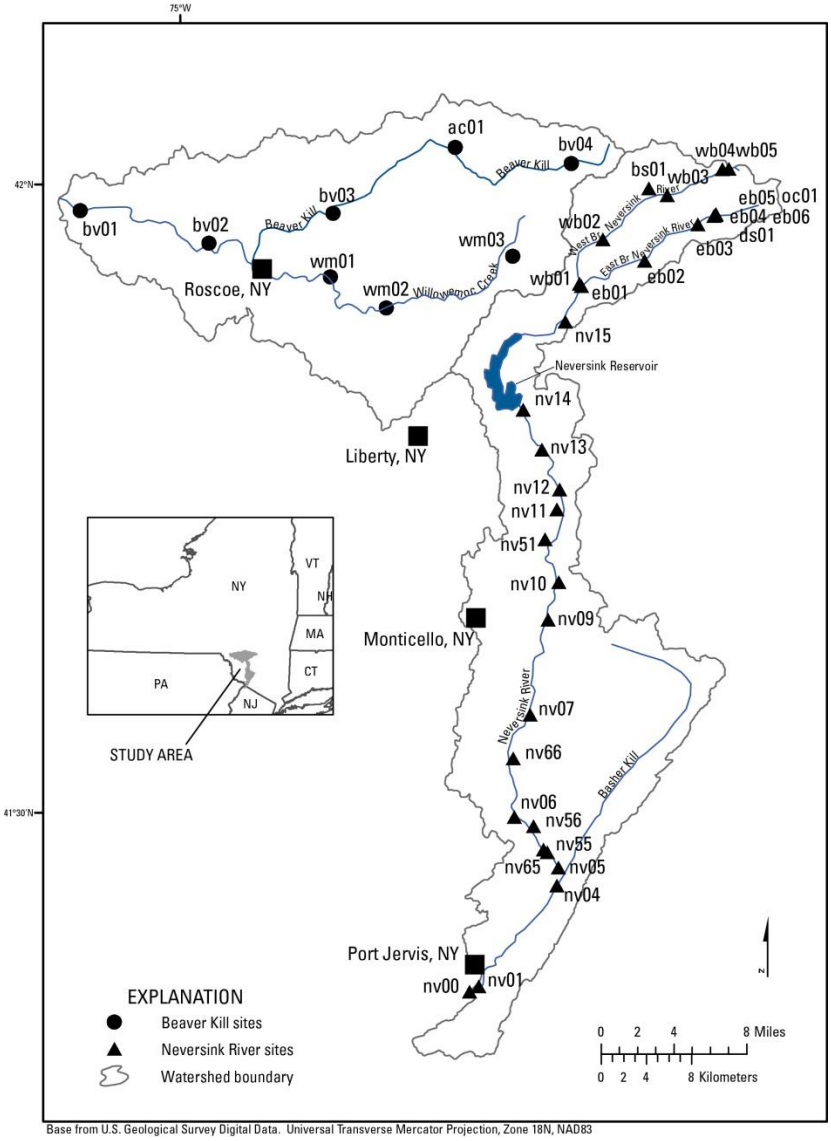

Figure 1. Location of the 31 study sites in the Neversink River and 8 study sites in the Beaver Kill where fish communities were surveyed, 1993-2008 [Site names and characteristics are listed in Table 1].

The impounded Neversink River and free-flowing Beaver Kill systems are comparable and adjacent tributaries to the Upper Delaware River, therefore, their divergent flow (and thermal) regimes allow us to estimate the likely effects that the reservoir has on the normal continuum of fish assemblages expected to occur in the Neversink River. The free-flowing conditions within the Beaver Kill should allow typical species richness and longitudinal succession of fish populations and communities, whereas, the impounded Neversink River should alter biodiversity and the normal headwater-to-mouth succession of fish assemblages in the basin.

This investigation characterizes fish assemblages across the Neversink River Basin and compares differences across sites within this basin and between similarly sized sites in the free flowing Beaver Kill. Qualitative and quantitative fish-community data for 31 sites within the Neversink River and for eight sites on the Beaver Kill are available from surveys conducted by the U.S. Geological Survey (USGS) and The Nature Conservancy (TNC) between 1992 and 2008. These data are evaluated herein in an effort to help define, conserve, and manage natural fishery and water resources within impounded rivers of the Catskill Mountain Region. Specific goals of this study are to: (1) characterize the status of resident and migratory fish populations and communities across both river systems, (2) define the longitudinal changes in fish assemblages between headwaters and confluence in both river systems, (3) quantify and qualify the effects of the impoundment on fish assemblages both upstream and downstream of the Neversink Reservoir, (4) evaluate potential causes (other than the impoundment) for observed differences in fish communities throughout the Neversink River, and (5) consider the ramifications of various management strategies; e.g., how might different release scenarios affect fish biodiversity, the abundance of local populations, and entire river ecosystems.

Two hypotheses concerning the effects of impoundments may be addressed using fish data collected from study sites within both river systems over the 16 period. The first hypothesis is that the normal low-order to high-order continuum of fish assemblages will not change downstream of the impoundment in the Neversink River. This is evaluated herein by comparing changes in fish community metrics across the Neversink River alone and by the differences between community metrics for sites in the Neversink River and in the Beaver Kill that are similar in drainage area (size). The second hypothesis is that fish communities upstream of the reservoir will be minimally affected (only by the loss of diadromous species). Assuming that the condition or health of aquatic ecosystems (or simply local fish communities) can be loosely defined by differences in species richness, diversity, density, and biomass (standing crop) (Hawksworth 1995), then the potential effects of reservoirs on communities upstream and downstream from impoundments may be qualified and (or) quantified by differences or changes in key fishery metrics from analogous study sites within both river systems. By defining the actual impacts of an impoundment on fish assemblages throughout the Neversink River, these findings will provide a better gauge of the tradeoffs (e.g., loss of fishery resources) that occur when indispensable water-supply reservoirs are built. More important, these results help identify specific factors that may regulate fish assemblages; as such, they can be used to predict how alternative water-management strategies might benefit degraded fish assemblages across impounded river systems.

METHODS

Data from four sets of surveys completed at 39 sites across the two basins (Figure 1) were evaluated for this analysis; each round of surveys were collected for specific purposes, and thus, differ slightly in content. Fish communities were inventoried at more than 31 main stem and tributary sites throughout the Neversink River Basin during 2002, 2003, and 2004 to qualify community composition (abundance of fish species, richness, and diversity). Two or three quantitative fish surveys were also done annually at 15 of these sites upstream of the reservoir during 1992-93 as part of an investigation of the effects of acid deposition on stream chemistry and ecosystems (Baldigo and Lawrence 2000; Baldigo and Lawrence 2001) and at five sites downstream of the reservoir during 2006-08 to generate fish population and community metrics for the present assessment of intra-basin differences. Quantitative surveys were also done at eight sites across the Beaver Kill during 2006-08 to generate fishery metrics at sites that were unaffected by an impoundment and comparable (in drainage area) to several sites in the Neversink River.

Fish-community data from surveys done at all acidified sites in the East Branch Neversink River were excluded from the present analyses, and from much of the discussion, because those assemblages were limited mainly by poor water quality (Baldigo and Lawrence 2000; Baldigo and Murdoch 1997). Acid deposition did not affect chemistry and fish assemblages at most study sites in the West Branch Neversink River and all sites in the Beaver Kill due to the moderate to high acid neutralizing capacity (ANC) of waters at those sites.

Study Area

This paper focuses on data collected from 39 study sites (Table 1, Figure 1) throughout the Neversink River and the Beaver Kill, which both empty into the Delaware River. The key difference between the two basins is that the Beaver Kill is free-flowing and the Neversink River contains an impoundment located mid-basin (upstream of site nv14 and downstream of site nv15) that completely blocks fish movement. Although fishery data are available from numerous sites within the Neversink River, eight sites recently surveyed in the Beaver Kill were chosen to envelop the range in drainage areas that occur across the Neversink River study sites. Thus, data from the Beaver Kill represent an unaffected or control condition; and differences in fish metrics between similarly sized (drainage areas and channel widths and depths) sites can be used to quantify or qualify impacts that the impoundment may have on fish assemblages in parts of the Neversink River.

The Neversink River watershed is mostly forested and relatively undeveloped with only one city (Monticello, NY) totally within its boundary. The drainage area for the basin is about 900 km^2 and its waters flow from north to south through four distinct physiographic regions between its headwaters and confluence with the Delaware River at Port Jervis, NY. The 240 km^2 upper Neversink River Basin is mountainous and terminates at the Neversink Reservoir. The upper sub-basin is split fairly evenly into two branches, the West Branch Neversink River and the often-acidified East Branch Neversink River. The 364 km^2 middle sub-basin is

Table 1. Study site names, codes, and USGS station IDs for fish surveys conducted in the Neversink River and Beaver Kill, 1992-2008. [na = not available]

USGS Station name	Site code	USGS Station ID	Latitude, Longitude	Drainage area (km^2)	Elevation (m)
Beaver Kill sites					
BEAVER KILL AT BALSAM LAKE CLUB	bv04	na	42 01 01.2, 74 34 54.7	15.6	719
ALDER CREEK AT TURNWOOD NY	ac01	01417994	42 01 46.1, 74 42 23.5	16.0	560
WILLOWEMOC CR ABOVE BUTTERNUT BK NR WILLOWEMOC NY	wm03	01418798	41 56 33.5, 74 38 44.1	22.5	579
WILLOWEMOC CREEK AT PARKSTON NY	wm02	01419250	41 54 05.0, 74 46 48.0	127.4	463
BEAVER KILL AT COVERED BRIDGE	bv03	na	41 58 38.2, 74 50 13.7	179.0	451
WILLOWEMOC CREEK AT DECKERTOWN NY	wm01	01420355	41 55 35.1, 74 50 26.1	282.3	414
BEAVER KILL ABOVE RT 17 BRIDGE AT COOKS FALLS NY	bv02	01420497	41 57 09.3, 74 58 10.0	613.8	355
BEAVER KILL AT PEAKVILLE NY	bv01	01420805	41 58 48.7, 75 06 25.0	766.6	305
Neversink River sites					
E BR NEVERSINK R TRIB, EAST-DEER SHNTY BK, DENNING	oc02	0143400360	41 58 28.0, 74 25 44.0	0.3	683
DEER SHANTY BROOK AT MOUTH NEAR DENNING NY	ds01	0143400505	41 58 31.0, 74 25 45.0	5.5	683
E BR NEVERSINK @ TRIB, EAST-DEER SHNTY BK, DENNING	eb06	01434003	41 58 28.0, 74 25 45.0	15.2	683
E BR NEVERSINK R AB DEER SHANTY BR NR DENNING NY	eb05	0143400350	41 58 28.0, 74 25 47.0	15.4	683
E BR NEVERSINK R BLW DEER SHANTY BK NR DENNING NY	eb04	0143400620	41 58 25.0, 74 25 52.0	20.9	683
E BR NEVERSINK R NORTHEAST OF DENNING NY	eb03	0143400680	41 58 01.0, 74 26 53.0	23.1	653
EAST BRANCH NEVERSINK RIVER EAST OF LADLETON NY	eb02	01434013	41 56 18.0, 74 30 19.0	48.2	628
EAST BRANCH NEVERSINK AT CLARYVILLE	eb01	01434020	41 55 06.0, 74 34 23.0	59.6	543
W BR NEVERSINK R AT WINNISOOK L NR FROST VALLEY NY	wb05	01434021	42 00 40.0, 74 24 52.0	2.0	815
W BR NEVERSINK @ DEC SLIDE MT PKG LOT, NR BRANCH	wb04	0143402110	42 00 39.0, 74 25 17.0	3.2	774
BISCUIT BK ABOVE PIGEON BK AT FROST VALLEY NY	bs01	01434025	41 59 45.9, 74 30 00.8	9.6	635
W BR NEVERSINK R AT BRANCH NR FROST VALLEY NY	wb03	0143402265	41 59 25.0, 74 28 51.0	20.4	573
WEST BR NEVERSINK RIVER NR CLARYVILLE NY	wb01	01434176	41 57 20.0, 74 32 59.0	65.5	552
WEST BRANCH NEVERSINK R AT CLARYVILLE NY	wb01	01434498	41 55 13.0, 74 34 29.0	87.5	494
NEVERSINK RIVER NEAR CLARYVILLE NY	nv15	01435000	41 53 24.0, 74 35 24.0	172.5	464
NEVERSINK RIVER AT NEVERSINK NY	nv14	01436000	41 49 12.0, 74 38 08.0	239.8	383
NEVERSINK RIVER NORTH OF WOODBOURNE NY	nv13	01436450	41 47 18.0, 74 36 57.0	274.5	360
NEVERSINK RIVER AT WOODBOURNE NY	nv12	01436500	41 45 24.3, 74 35 48.4	292.7	560
NEVERSINK RIVER NORTH OF	nv11	01436511	41 44 27.0,	303.0	347

USGS Station name	Site code	USGS Station ID	Latitude, Longitude	Drainage area (km^2)	Elevation (m)
FALLSBURG NY			74 36 01.0		
NEVERSINK RIVER SOUTH OF WOODRIDGE NY	nv10	01436559	41 40 58.0, 74 35 55.0	326.3	337
NEVERSINK RIVER NORTH OF BRIDGEVILLE NY	nv09	01436661	41 39 10.0, 74 36 37.0	435.1	318
NEVERSINK RIVER SOUTH OF BRIDGEVILLE NY	nv07	01436749	41 34 38.0, 74 37 47.0	479.1	298
NEVERSINK RIVER NEAR PHILWOLD NY	nv66	01436766	41 32 33.0, 74 38 52.0	507.6	250
NEVERSINK RIVER AT OAKLAND VALLEY NY	nv06	01437000	41 29 45.0, 74 38 47.0	577.6	219
NEVERSINK RIVER NEAR OAKLAND VALLEY NY	nv56	na	41 29 18.3, 74 37 45.5	591.3	177
NEVERSINK R UPSTREAM FROM CUDDEBACKVILLE DAM NY	nv65	01437016	41 28 11.0, 74 36 58.0	598.3	165
NEVERSINK R DOWNSTREAM FROM CUDDEBACKVILLE DAM NY	nv55	01437019	41 28 04.0, 74 36 44.0	598.3	158
NEVERSINK RIVER AT CUDDEBACKVILLE NY	nv05	01437025	41 27 20.0, 74 36 02.0	603.5	146
NEVERSINK RIVER AT GODEFFROY NY	nv04	01437500	41 26 28.0, 74 36 07.0	795.1	140
NEVERSINK RIVER AT PORT JERVIS NY	nv01	01438000	41 21 40.0, 74 41 07.0	870.2	109
NEVERSINK R AT MOUTH AT PORT JERVIS NY	nv00	01438109	41 21 24.0, 74 41 42.0	896.1	108

located between the reservoir and the confluence with the Basher Kill. In this reach, the Neversink flows through a broad floodplain, but then passes through a narrow gorge for most of its length. The 111 km^2 lower sub-basin is a broad river with an ancient and relatively large alluvial floodplain. The 189 km^2 Basher Kill sub-basin is the largest tributary to the lower Neversink and consists of a 12 km^2 emergent marsh through which the Basher Kill flows as well as several small tributaries. Discharge for the downstream-most USGS streamgage on the Neversink River at Godeffroy (USGS station 01437500) averaged 18.3 m^3/s during the 2008 water year and 12.5 m^3/s between 1954 and 2008 (http://ny.water.usgs.gov/pubs/wdr/wdrny081/troy.listing08.pdf). The Neversink Reservoir has a surface area of about 6.0 km^2, and it impounds about 132,000,000 m^3/s of water. During the 2008 water year, the reservoir released an average of 4.2 m^3/s into the Neversink River (average daily flows varied from 1.2 to 84.4 m^3/s) determined at a USGS streamgage immediately downstream from the dam (USGS station 01436000 or 01435900), with an additional 4.0 m^3/s diverted continuously to the New York City water-supply system (http://ny.water.usgs.gov/pubs/wdr/wdrny081/troy.listing08.pdf). After the impoundment was completed in 1953, the annual mean discharge of the Neversink River at these stations (study site nv14) fell from 7.5 m^3/s to just over 1.4 m^3/s, the average length of low-flow pulses increased from 6 to 44 days, and the average length of high-flow pulses dropped from 5.3 to 2.7 (personal communication; T. Moberg, The Nature Conservancy, December 2013).

The watershed of the Beaver Kill, like the Neversink River, is mountainous with steep and narrow valleys, mostly forested, and undeveloped with several small hamlets within its watershed boundary. A 4-lane highway (State Route 17), with numerous bridges, was constructed along a 42 km section of the river during the 1960s, but appears to have had little or no effect on hydrology within the basin (Baldigo 1999). The drainage area of the Beaver

Kill is 774 km^2 at its confluence with the East Branch Delaware River at East Branch, NY. The Beaver Kill flows generally from east to west and may be divided into three sub-basins, the lower Beaver Kill, Willowemoc Creek, and upper Beaver Kill. The upper basin consists of the main stem with a drainage area of 252 km^2 upstream of its confluence with Willowemoc Creek near Roscoe, NY. One 15-m waterfall is located downstream of bv04, and appears to have restricted all but two species (brook trout *Salvelinus fontinalis* and slimy sculpin *Cottus cognatus*) from this uppermost site. Willowemoc Creek, with a drainage area of 339 km^2, is the largest tributary to the Beaver Kill. The lower basin consists of the main stem Beaver Kill between Roscoe and East Branch, NY. Daily discharge for the furthest downstream USGS streamgage on the Beaver Kill at Cooks Falls (USGS station 01420500) varied from 2.1 to 204.8 m^3/s and averaged 21.8 m^3/s during the 2008 water year; daily discharge averaged 16.1 m^3/s between 1913 and 2008 (http://ny.water.usgs.gov/pubs/wdr/wdrny081/troy. listing08.pdf).

Field Methods

The methods used to collect fish for both qualitative and quantitative surveys were relatively similar. Survey reaches (study sites) were generally chosen to include two or more complete geomorphic channel-unit sequences (Fitzpatrick et al. 1998; Meador et al. 2003; Simonson et al. 1994). Most sampled reaches were from 20 to 35 mean channel widths long and generally ranged from 100 m to a maximum of 400 m. At each reach, fish were collected using a backpack electrofisher and two or three netters. Boat electrofishing was used only at the two downstream-most sites on the Neversink River. All qualitative surveys were timed and consisted of two or three electrofishing passes through each unblocked sample reach. Quantitative surveys consisted of three or four electrofishing passes through seine-blocked reaches. The sample area dimensions were measured on site. At sites with channels less than 15 m wide, seines were set shore to shore, completely blocking the upstream and downstream ends of the reach. At wider sites, three (replicate) surveys were done in somewhat rectangular near-shore subreaches. At each sub-reach, one blocking seine was affixed to the bank and then stretched perpendicular to the bank and attached to a rock or rebar (6 to 8 m from shore); a second 25 m seine was set downstream and parallel to shore and then attached to a second rock or rebar (also 6 to 8 m from shore); and a third seine was placed between the second rebar and shore. Fish collected during each sub-reach and pass were processed separately. Each fish was identified to species and the lengths and weights for all fish longer than 150 mm were recorded. The lengths and weights for abundant species (some minnows), which were usually smaller than 150 mm, were obtained from 40 to 50 individuals; thereafter, total weights and counts were recorded by species in batches of 10 to 50. All processed fish were returned to the stream after the final survey pass.

Community and Population Metrics

Data collected during qualitative and quantitative surveys were used to estimate three ecosystem diversity metrics that characterize components of community breadth or size (total species richness), heterogeneity (Simpson's diversity index), and balance (evenness) at each study site. Richness (S) is simply the number of different fish species collected in the sampled

areas at each study site. Simpson's diversity index (reinterpreted as 1-*D*) uses the number of species present and the relative abundance of each species to calculate a metric that ranges from 0 to 1; zero indicates no diversity (e.g., 1 or 0 species) and higher values indicate a large number of species and similar abundance of each (Simpson 1949; Whittaker 1975). Evenness is a diversity metric which quantifies how well balanced, or how equal the numbers of each fish species are within a community. It is denoted by Pielou's evenness index (*J'*) which ranges from 0 to 1 and is estimated from the Shannon diversity index (*H*') divided by the maximum value of *H'* or H'_{max} (Shannon 1948; Whittaker 1975).

Estimates of density and biomass for the fish community and individual species populations could only be determined using data from the quantitative surveys. The number of fish captured during each pass was used to estimate density, biomass, and 95% confidence intervals (CIs) for the entire fish community and for each species population using the Moran-Zippin method of proportional reduction (Van Deventer and Platts 1985; Zippin 1958). These values were divided by the total area sampled at each study site to estimate the number of fish or the biomass (grams) of fish in the local community or species population per unit area.

Data Analysis

The effects of the impoundment on fish communities and populations in the Neversink River were evaluated through an analysis of longitudinal trends in metrics within the Neversink River, and by differences in the metrics between sites of similar drainage area in the Neversink River and Beaver Kill Basins. Estimates of community and population density and biomass from quantitative surveys, and richness and diversity from quantitative and qualitative surveys were evaluated through non-linear regression and graphical analyses to semi-quantify the potential effects of the reservoir on fish communities both upstream and downstream of the impoundment.

RESULTS

Fish Communities

Species richness at study sites (site IDs are provided in Table 1 and Figure 1) in the Beaver Kill ranged from 2 species at bv04 to 15 species at bv01, near its confluence with the East Branch Delaware River (Table 2). Richness at study sites in the Neversink River ranged from no (0) species at wb05 to 8 species upstream of the Neversink Reservoir, and to as many as 22 species at nv05, near its confluence with the Basher Kill (Table 2). Richness in the Beaver Kill increased rapidly from 2 to 7 species at sites with drainages smaller than 100 km^2 to an asymptote of 13 to 15 species at all sites with drainages larger than 100 km^2 (Figure 2A). Richness increased more gradually with drainage area in the Neversink River (Figure 2A); richness ranged from 0 to 3 species at sites with drainages smaller than 50 km^2 to an asymptote of about 15 to 17 species when drainages exceeded 300 km^2. Several additional fish species also occurred at larger sites (drainages between 400 and 900 km^2) located farther downstream.

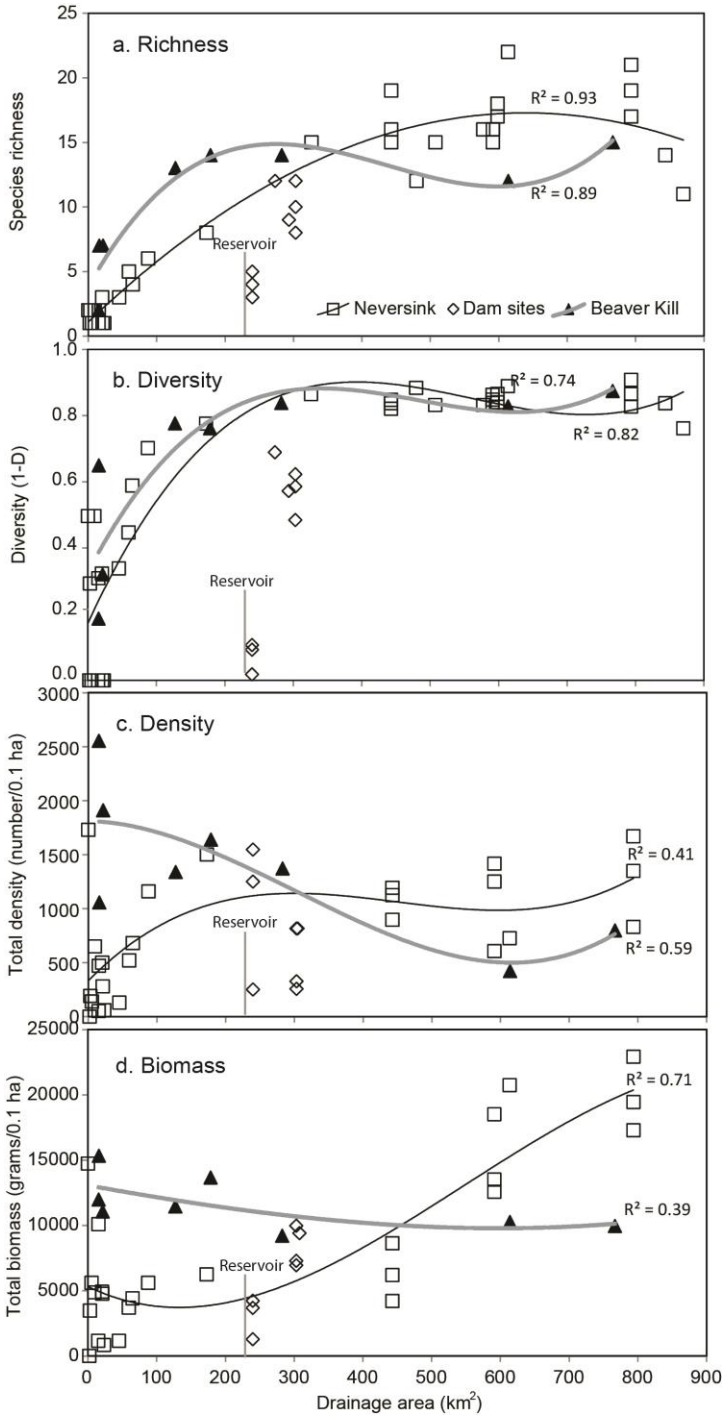

Figure 2. Best-fit polynomial lines (and R^2 values) for estimates of (a) richness, (b) diversity, (c) density, and (d) biomass from quantitative fish-community surveys done at 31 study sites in the Neversink River and 8 study sites in the Beaver Kill, 1993-2008 [Data from four sites downstream from the Neversink Reservoir influenced by the Dam (Dam sites) were omitted from the Neversink best-fit lines].

Table 2. Fish-community metrics from all study sites surveyed in the Neversink River and Beaver Kill, 1992-2008 [Five Neversink River sites were sampled annually from 2006 to 2008; site names and characteristics are listed in Table 1; na = not available]

Site ID	Richness (*S*)	Density (No/0.1ha)	Biomass (g/0.1ha)	Index of Diversity (1-*D*~)	Evenness (*J'*)
			Beaver Kill sites		
bv04	2	2555	11970	0.19	0.48
ac01	7	1058	15329	0.65	0.62
wm03	7	1909	11062	0.32	0.32
wm02	13	1339	11440	0.78	0.69
bv03	14	1638	13666	0.76	0.69
wm01	14	1371	9208	0.84	0.78
bv02	12	422	10254	0.83	0.79
bv01	15	798	9945	0.87	0.85
			Neversink River sites		
oc02	2	1730	14730	0.50	0.99
ds01	1	140	5590	0.00	0.00
eb06	1	50	1150	0.00	0.00
eb05	2	470	10080	0.31	0.70
eb04	1	280	4770	0.00	0.00
eb03	1	60	840	0.00	0.00
eb02	3	130	1150	0.34	0.54
eb01	5	520	3690	0.45	0.60
wb05	0	0	0	0.00	0.00
wb04	2	190	3470	0.29	0.68
bs01	2	650	4870	0.50	0.99
wb03	3	500	4910	0.32	0.50
wb01	4	680	4400	0.59	0.78
wb01	6	1160	5590	0.70	0.77
nv15	8	1500	6250	0.78	0.81
nv14(2006)	5	1250	3674	0.09	0.15
nv14(2007)	3	250	1274	0.11	0.23
nv14(2008)	4	1547	4217	0.02	0.04
nv13	12	na	na	0.69	0.60
nv12	9	na	na	0.57	0.57
nv11(2006)	10	326	6934	0.48	0.49
nv11(2007)	8	256	7287	0.62	0.63
nv11(2008)	12	817	9972	0.59	0.46
nv10	16	na	na	0.87	0.81
nv09(2006)	19	1124	8621	0.84	0.70
nv09(2007)	16	896	4204	0.85	0.75
nv09(2008)	15	1193	6197	0.82	0.74
nv07	13	na	na	0.88	0.89
nv66	15	na	na	0.83	0.81
nv56	16	na	na	0.83	0.74
nv06(2006)	16	605	12578	0.85	0.78
nv06(2007)	16	1250	13503	0.84	0.76
nv06(2008)	15	1416	18509	0.86	0.81
nv65	17	na	na	0.84	0.74
nv55	18	na	na	0.87	0.78
nv05	22	726	20726	0.89	0.83
nv04(2006)	21	831	22912	0.86	0.78
nv04(2007)	17	1669	19435	0.83	0.74
nv04(2008)	19	1349	17282	0.91	0.88
nv01	14	na	na	0.84	0.79
nv00	11	na	na	0.76	0.75

The best-fit lines for both systems (Figure 2A) indicate that 3 to 5 fewer species occurred at sites upstream from the Neversink Reservoir (drainages < 200 km^2) than could be expected from the surveys at comparable Beaver Kill sites. The four sites immediately downstream of the reservoir (drainages of 225 to 300 km^2) contained as many as 8 fewer species than predicted by the best-fit line (which excluded data from those sites) (Figure 2A). Data from sites nv11 to nv09 were omitted from the best-fit line, but comparisons between data from these sites and the Beaver Kill best-fit line indicate that species richness was reduced by 7 to 10 species in the main stem Neversink River for at least 10 km downstream from the reservoir.

With minor exceptions, diversity at study sites in the Beaver Kill and Neversink River followed the trends observed in richness (Figure 2). Diversity in the Beaver Kill ranged from 0.19 at bv04 to 0.87 at bv01; in the Neversink River it ranged from 0 at several sites upstream from the reservoir to 0.91 at nv04 during the 2008 survey (Table 2). In both rivers, diversity increased rapidly to an asymptote of about 0.85 to 0.90 at most sites with drainages larger than 200 km^2 (Figure 2B). The best-fit lines for both systems show that diversity was 10 to 50 percent lower at Neversink River sites upstream from the reservoir; and 50 to 100 percent lower at the four sites immediately downstream from the reservoir (excluding data from those sites), than observed at comparable sites in the Beaver Kill (Figure 2B). Diversity data from sites nv11 to nv09 were not used in the best-fit line, but comparisons between data from these sites and the Beaver Kill best-fit line indicate that diversity was reduced by as little as 13 percent to as much as 98 percent in the main stem Neversink River for at least 10 km downstream from the reservoir.

The trends in total density and biomass of fish communities between upstream and downstream study sites were generally comparable, but differed between the two river systems. The density of fish communities in the Beaver Kill generally decreased from 1000 to 2600 fish/0.1ha at high elevation sites with small drainages, to 400 to 800 fish/0.1ha at low elevation sites, with large drainages (Figure 2C, Table 2). Except for one site (oc02) with more than 1700 fish/0.1ha, the trend in density was reversed in the Neversink River; density increased from 0 to 600 fish/0.1ha at small high-elevation sites to 1200 to 1500 fish/0.1ha at large, low-elevation sites (Figure 2C, Table 2). The densities of fish communities at several sites downstream of the reservoir were depressed slightly (5 out of 7 surveys) when compared to the overall trend (Figure 2C). Community biomass in the Beaver Kill was not as variable as density, but decreased slightly from 12,000 to 15,000 g/0.1ha at high elevation sites to 9000 to 10,000 g/0.1ha at low-elevation sites (Figure 2D, Table 2). Except for sites oc02 and eb05 (10,000 to 15,000 g/0.1ha), the biomass trend was reversed in the Neversink River; biomass increased from 0 to 5000 g/0.1ha at most upstream sites to 13,000 to 23,000 g/0.1ha at downstream sites (Figure 2D, Table 2). Community biomass appeared to be depressed slightly only at one site (nv14) immediately downstream of the reservoir (Figure 2D). In general, density and biomass of fish communities in the Neversink River upstream from the reservoir were considerably lower than found at comparably sized sites in the Beaver Kill.

Species Populations

The presence or absence of many fish species accounted for the shifts in community metrics observed among sites across both rivers (Table 3). In the Beaver Kill, brook trout and

slimy sculpin only occurred at sites with drainages smaller than 200 km^2, whereas, common shiner *Luxilus cornutus*, fallfish *Semotilus corporalis*, smallmouth bass *Micropterus dolomieu*, and two sunfish species (*Lepomis gibbosus* and *L. auritus*) only occurred at sites with drainages larger than 200 km^2. White sucker *Catostomus commersonii*, longnose sucker *Catostomus catostomus*, cutlips minnow *Exoglossum maxillingua*, margined madtom *Noturus insignis*, and tessellated darter *Etheostoma olmstedi* were generally found at sites with intermediate to large drainages (greater than 100 km^2). Brown trout *Salmo trutta*, American eel *Anguilla rostrata*, sea lamprey *Petromyzon marinus*, eastern blacknose dace *Rhinichthys atratulus*, and longnose dace *R. cataractae* were largely ubiquitous. A15-m waterfall situated well downstream of bv04, however, restricted all but two species (brook trout and slimy sculpin) from this site.

In the Neversink River, only brook trout, brown trout, slimy sculpin, eastern blacknose dace, and longnose dace were consistently collected upstream of the Neversink Reservoir during our surveys (Table 4). All five species were absent from wb05 (Baldigo and Lawrence 2001), but the composition of communities was similar in most other low-order reaches of both systems. Several Atlantic salmon *Salmo salar* (stocked into the reservoir since the 1970s) were also collected from nv15 during surveys done in the early 1990s. American eel, sea lamprey, longnose sucker, cutlips minnow, margined madtom, several minnow species, and numerous warm water species were absent at all sites upstream from the impoundment with drainages less than 200 km^2. White sucker and tessellated darter were also absent in our surveys, however, both species were collected sporadically upstream from nv15 during the 2000s (Karen Murray, USGS personal communication, May 2013). Except for the loss of longnose dace and American eel (and the presence of one or two white suckers or pumpkinseed sunfish), the same species found upstream from the reservoir were generally encountered at low densities immediately downstream from the reservoir. Only one brook trout and three slimy sculpin were collected at the next two sites downstream from nv14. In addition to the seven species observed at nv14, another seven species were collected at nv11 with a drainage area of 303 km^2 (Table 1, 3). The species which only occurred at Neversink River sites downstream of the reservoir (drainages of 300 km^2 or larger) included American eel, sea lamprey, creek chub *Semolitus atromaculatus*, common shiner, fallfish, sunfish (bluegill *Lepomis macrochirus*, pumpkinseed, and redbreast), white sucker, cutlips minnow, margined madtom, tessellated darter, and shield darter *Percina peltata*. Several other fishes, including rock bass *Ambloplites rupestris*, yellow perch *Perca flavescens*, and chain pickerel *Esox niger* were encountered at downstream sites with drainages larger than 400 km^2. Only brown trout were ubiquitous to most sites in the Neversink River, however, they were absent from at least two acidified sites in the upper basin. While the Neversink Reservoir clearly limited the distribution of several fish species from the upper basin, its effect on the density and distribution of many species at sites downstream of the reservoir was less obvious.

Although species densities were highly variable in both rivers, the differences in biomass of individual species (and in groups of species) across the Neversink River and between comparable sites in the Neversink River and in the Beaver Kill quantified the impact of the impoundment on the structure and function (health) of fish communities both upstream and downstream from the reservoir. In fact, the trends (and levels) in estimated density and biomass of species populations differed considerably among sites with small, intermediate, and large drainage-areas in the Beaver Kill (Table 3, Figure 3C) and between sites located

upstream and downstream from the reservoir in the Neversink River (Table 4, Figures 3A, 3B).

Table 3. Estimated density and biomass for species populations from all study sites surveyed in the Beaver Kill, 2006-2008 [Site names and characteristics are listed in Table 1; genus and species names are provided in the manuscript text]

Fish species	bv04	ac01	wm03	wm02	bv03	wm01	bv02	bv01
				Species density (No./0.1 ha)				
American eel	0	28	13	11	25	14	25	28
sea lamprey	0	0	5	26	15	59	5	56
creek chub	0	6	0	5	0	50	0	0
common shiner	0	0	0	0	148	81	69	32
fallfish	0	0	0	0	0	0	0	58
pumpkinseed sunfish	0	0	0	0	0	2	2	0
redbreast sunfish	0	0	0	0	0	0	0	6
creek chubsucker	0	0	0	0	2	0	0	0
white sucker	0	0	0	16	21	380	47	10
longnose sucker	0	0	0	8	0	7	0	0
cutlips minnow	0	0	0	195	281	147	121	105
margined madtom	0	0	0	5	173	74	69	191
brown trout	0	438	9	47	33	0	14	6
brook trout	281	8	294	3	2	0	0	0
eastern blacknose dace	0	154	34	198	769	299	9	16
longnose dace	0	8	5	232	131	204	51	133
tessellated darter	0	0	0	79	135	64	2	60
shield darter	0	0	0	0	8	12	4	36
smallmouth bass	0	0	0	0	0	12	0	70
slimy sculpin	2410	432	1544	506	46	0	0	0
unidentified minnows	0	0	0	0	0	0	0	8
				Species biomass (g/0.1 ha)				
American eel	0	5089	2475	1674	5400	1549	6239	6868
sea lamprey	0	0	22	79	32	143	12	178
creek chub	0	8	0	55	0	621	0	0
common shiner	0	0	0	0	326	129	390	75
fallfish	0	0	0	0	0	0	0	83
pumpkinseed sunfish	0	0	0	0	0	24	7	0
redbreast sunfish	0	0	0	0	0	0	0	99
creek chubsucker	0	0	0	0	2	0	0	0
white sucker	0	0	0	280	11	3807	796	40
longnose sucker	0	0	0	121	0	81	0	0
cutlips minnow	0	0	0	1272	1579	770	929	584
margined madtom	0	0	0	84	2706	958	608	1011
brown trout	0	7742	712	4153	802	0	1000	243
brook trout	4706	430	3498	11	7	0	0	0
eastern blacknose dace	0	368	68	464	1658	445	5	8
longnose dace	0	55	31	1390	707	539	245	264
tessellated dart	0	0	0	156	225	73	1	53
shield darter	0	0	0	0	26	20	22	141
smallmouth bass	0	0	0	0	0	50	0	289
slimy sculpin	7264	1637	4256	1699	184	0	0	0
unidentified minnows	0	0	0	0	0	0	0	9

The density of fish communities in the Beaver Kill was typically dominated by: (a) slimy sculpin and either brook trout or brown trout at the three smallest upstream sites; (b) sculpin, cutlips minnow, white suckers, and longnose and eastern blacknose dace at the three intermediate sites; and (c) margined madtom, cutlips, and longnose dace at the two largest downstream sites. Biomass of fish communities in the Beaver Kill was generally dominated by: (a) American eel, slimy sculpin, brook trout, and brown trout at the three smallest

upstream sites; (b) American eel, white sucker, cutlips minnow, margined madtom, and brown trout at the three intermediate sites; and (c) solely by American eel at the two largest downstream sites.

Table 4. Estimated density and biomass for species populations from selected Neversink River study sites, 1992-2008 [Five Neversink River sites were sampled annually from 2006 to 2008; site names and characteristics are listed in Table 1; genus and species names are provided in the manuscript text; na = not available]

Fish species	wb05	wb04	wb03	wb02	wb01	nv15	nv14	nv11	nv09	nv06	nv05	nv04
Species density (No./0.1 ha)												
American eel	0	0	0	0	0	0	1	13	20	82	72	130
sea lamprey	0	0	0	0	0	0	0	1	146	60	10	81
creek chub	0	0	0	0	0	0	0	0	1	0	0	42
common shiner	0	0	0	0	0	0	0	1	0	128	21	55
spottail shiner	0	0	0	0	0	0	0	0	0	0	3	0
fallfish	0	0	0	0	0	0	0	0	1	50	3	234
pumpkinseed sunfish	0	0	0	0	0	0	1	14	6	0	26	2
bluegill sunfish	0	0	0	0	0	0	0	0	2	0	174	19
redbreast sunfish	0	0	0	0	0	0	0	1	11	2	28	12
white sucker	0	0	0	0	0	0	1	163	219	136	44	141
cutlips minnow	0	0	0	0	0	0	0	0	45	80	115	54
margined madtom	0	0	0	0	0	0	0	0	1	36	31	58
brown trout	0	0	10	20	50	40	9	231	11	9	15	11
brook trout	0	180	120	60	10	40	14	0	0	1	0	0
eastern blacknose dace	0	0	0	30	310	210	4	2	134	338	31	85
longnose dace	0	0	0	0	180	120	0	4	134	194	8	137
tessellated darter	0	0	0	0	0	0	0	15	249	23	31	127
shield darter	0	0	0	0	0	0	0	0	33	19	26	35
largemouth bass	0	0	0	0	0	0	0	9	2	0	28	5
smallmouth bass	0	0	0	0	0	0	0	0	1	5	3	19
rock bass	0	0	0	0	0	0	0	0	8	0	23	10
black crappie	0	0	0	0	0	0	0	0	0	0	28	9
yellow perch	0	0	0	0	0	0	0	5	60	1	3	1
chain pickerel	0	0	0	0	0	0	0	0	5	0	0	7
brown bullhead	0	0	0	0	0	0	0	1	1	0	0	1
slimy sculpin	0	10	370	570	610	1080	989	3	0	0	0	0
unidentified minnows	0	0	0	0	0	0	0	0	116	135	5	142
Atlantic salmon	0	0	0	0	0	10	0	0	0	0	0	0
Species biomass (g/0.1 ha)												
American eel	0	0	0	0	0	0	8	1307	1747	9544	6928	11820
sea lamprey	0	0	0	0	0	0	0	2	436	192	72	159
creek chub	0	0	0	0	0	0	0	0	2	0	0	29
common shiner	0	0	0	0	0	0	0	1	0	531	74	233
spottail shiner	0	0	0	0	0	0	0	0	0	0	5	0
fallfish	0	0	0	0	0	0	0	0	0	272	5	307
pumpkinseed sunfish	0	0	0	0	0	0	13	57	47	0	77	29
bluegill sunfish	0	0	0	0	0	0	0	0	10	0	2417	82
redbreast sunfish	0	0	0	0	0	0	0	1	238	44	786	432
white sucker	0	0	0	0	0	0	17	253	1341	877	773	2488
cutlips minnow	0	0	0	0	0	0	0	0	502	676	787	522
margined madtom	0	0	0	0	0	0	0	0	22	387	338	678
brown trout	0	0	810	1600	930	540	32	6307	578	947	469	370

Table 4. (Continued)

Fish species	wb05	wb04	wb03	wb02	wb01	nv15	nv14	nv11	nv09	nv06	nv05	nv04
brook trout	0	3390	2890	1560	270	760	235	0	0	65	0	0
eastern blacknose dace	0	0	0	50	990	650	5	7	164	487	53	110
longnose dace	0	0	0	0	1820	920	0	23	293	505	51	462
tessellated darter	0	0	0	0	0	0	0	12	363	40	76	212
shield darter	0	0	0	0	0	0	0	0	92	60	108	125
largemouth bass	0	0	0	0	0	0	0	10	1	0	4644	9
smallmouth bass	0	0	0	0	0	0	0	0	6	171	56	325
rock bass	0	0	0	0	0	0	0	0	214	0	2633	1166
black crappie	0	0	0	0	0	0	0	0	0	0	364	125
yellow perch	0	0	0	0	0	0	0	3	169	1	5	2
chain pickerel	0	0	0	0	0	0	0	0	54	0	0	176
brown bullhead	0	0	0	0	0	0	0	46	20	0	0	72
slimy sculpin	0	80	1210	1190	1580	2930	2744	35	0	0	0	0
unidentified minnows	0	0	0	0	0	0	0	0	40	66	3	26
Atlantic salmon	0	0	0	0	0	450	0	0	0	0	0	0

Estimated density and biomass of species populations were generally alike at sites upstream from the Neversink Reservoir, but highly variable downstream from the reservoir (Table 4). The density of fish communities was dominated by: (a) slimy sculpin, eastern blacknose dace, or brook trout at small sites upstream from the reservoir; (b) slimy sculpin immediately downstream of the reservoir; (c) white sucker, brown trout, longnose dace, eastern blacknose dace, and tessellated darter at most large downstream sites, and (d) fallfish at the furthest downstream site, nv04. No species occurred at wb05 (zero density and biomass). The biomass of fish communities was generally dominated by slimy sculpin, brook trout, and brown trout at most sites upstream from the reservoir, however, longnose dace and eastern blacknose dace dominated the two larger sites with drainages areas approaching or exceeding 100 km^2. Slimy sculpin dominated community biomass at the first site downstream from the reservoir (nv14) and American eel dominated community biomass at most of the remaining sites located downstream from the reservoir. The biomass of brown trout was unusually high at nv11 and the biomass of three warm water fish species and white suckers also reached relatively high levels at nv05 and nv04.

Differences in the number of fish species or groups, and in the total biomass of fish assemblages at sites located upstream from the Neversink Reservoir (Figure 3B) and at comparable sites in the Beaver Kill (Figure 3C) clearly show that fish communities in the upper Neversink River are relatively unbalanced and lack diversity. Neversink River sites upstream from the reservoir (nv15 to wb03) generally contained three to five species (and often fewer) represented by two to three species groups, whereas comparable sites on the Beaver Kill (bv03 to bv04) had two to 17 species (typically seven or more) and were usually diverse and well balanced. The reservoir obviously restricts diadromous species such as American eel and sea lamprey from the upper reaches of the Neversink River, but it also appears to impede populations of other species, such as common shiner, creek chub, margined madtom, longnose sucker, cutlips minnow, shield darter, and possibly tessellated darter and white sucker. The absence of two to 12 species at upper Neversink River sites reduces biodiversity substantially (Figure 2B) and leads to a poorly balanced mix of large predators

(trout species) and small prey (mostly sculpin and minnows species) at several sites (e.g., nv15 and wb01) (Figure 3B).

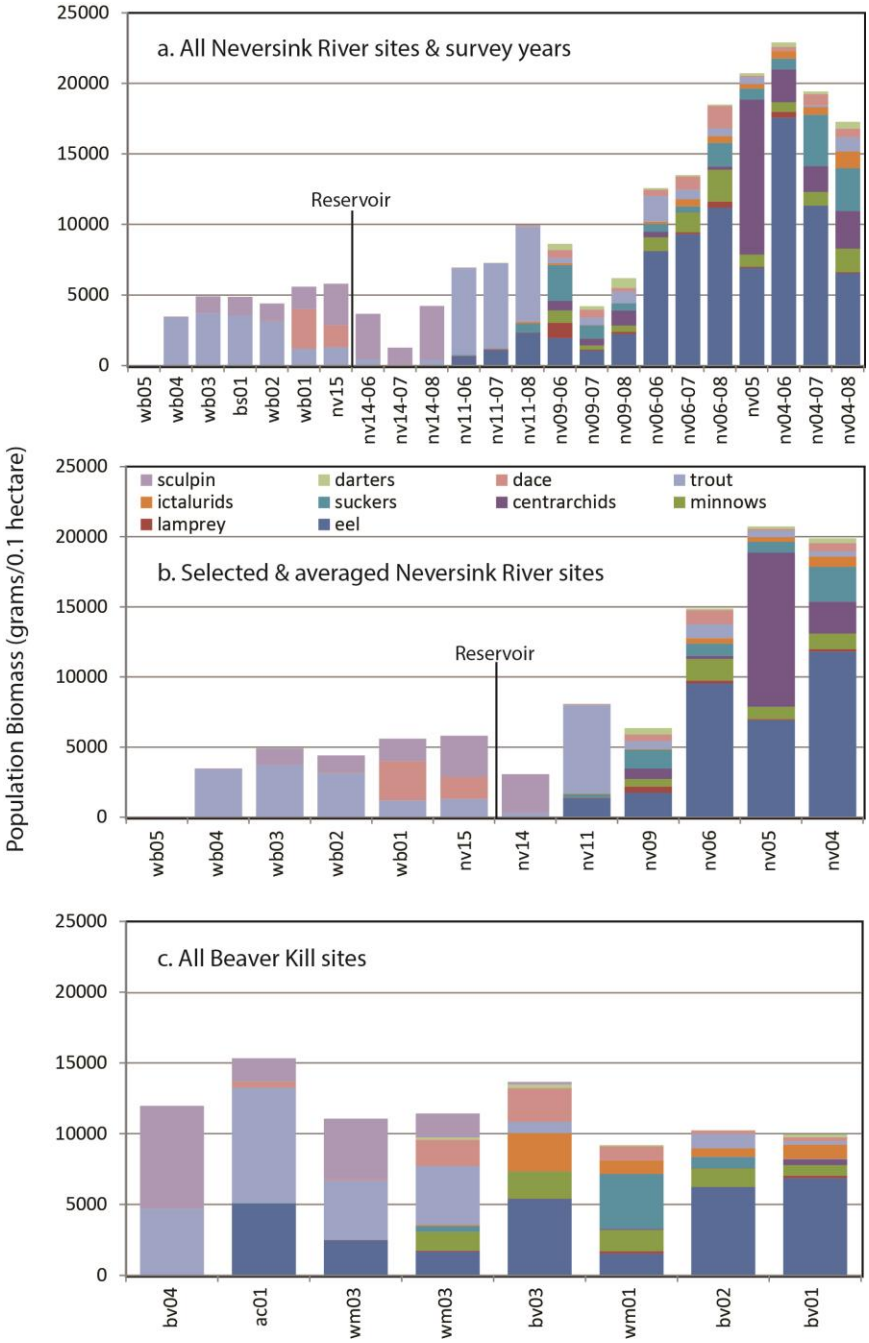

Figure 3. Estimated biomass for major groups of fish from (a) individual and annual surveys completed at 13 sites in the Neversink River, (b) individual and annual surveys (averaged across three years) done at 12 main stem sites in the Neversink River, and (c) individual surveys done at 8 main stem sites in the Beaver Kill, 2006-2008 [The values of 06, 07, and 08 at the end of the site code identify year (2006-2008) when annual fish surveys were completed].

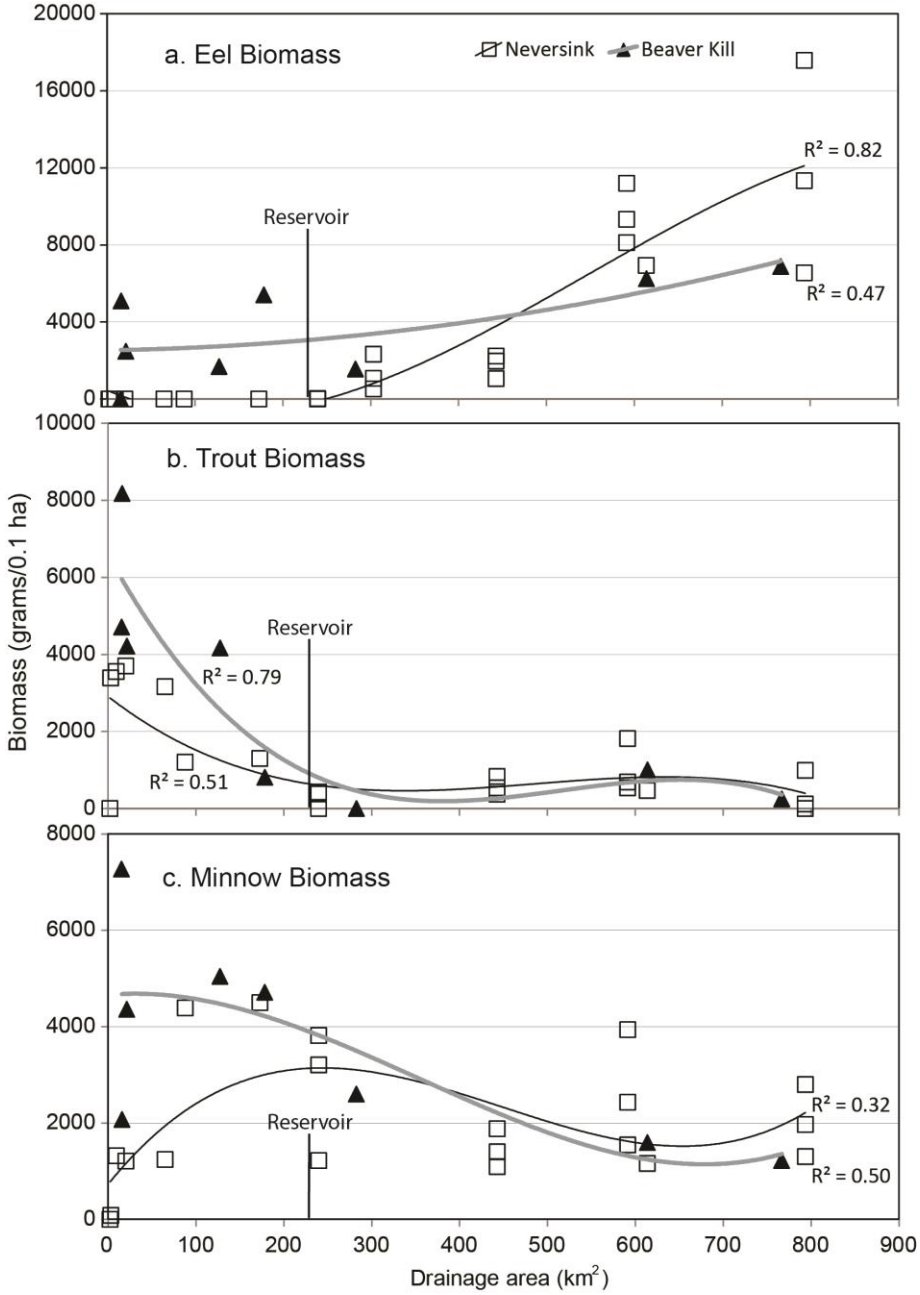

Figure 4. Best-fit polynomial lines (and R^2 values) for estimates of (a) biomass for American eel, (b) biomass for all trout species, and (c) biomass for all minnow species from quantitative surveys done at 12 study sites in the Neversink River and 8 study sites in the Beaver Kill, 2006-2008 [Data from nv11 were omitted from the Neversink best-fit lines].

Though biomass of American eel upstream of the Neversink Reservoir is zero (Figure 4A), total trout biomass upstream of the reservoir is about 50% lower than in comparable sites in the upper Beaver Kill (Figure 4B). The biomass of small fish species at upstream sites in

both rivers also reflects this pattern, especially at sites with drainages of less than 65 km^2 (Figure 4C).

The effects of the Neversink Reservoir on downstream fish communities were nearly as strong as they were in the upper sub-basin. The number of species or species groups, as well as total biomass of fish communities downstream from the Neversink Reservoir (Figure 3B) and at comparable sites in the Beaver Kill (Figure 3C) indicate that fish communities in the middle Neversink River were relatively unbalanced and lacked diversity. Only one to three species (from one or two species groups) were abundant at Neversink River sites downstream from the reservoir (sites nv14 and nv11), whereas four to six species (representing five or six species groups) were abundant at comparable sites in the Beaver Kill (sites bv03 to wm01). Waters from reservoir apparently altered the physical habitat and hydrologic or thermal regime sufficiently to restrict diadromous species such as American eel and sea lamprey, but also appeared to inhibit populations of other species, such as common shiner, creek chub, margined madtom, cutlips minnow, shield darter, smallmouth bass, rock bass, and chain pickerel from one or two of the uppermost middle-reach sites in the Neversink River. Similar to upstream reaches, the absence of 7 to 10 species at the two uppermost middle Neversink River sites reduces diversity substantially and also leads to a poorly balanced mix of predator (trout and American eel) and prey (minnows) at nv14 and nv11 (Figure 3B). Except for low biomass of American eel at two or three mid-basin sites immediately downstream from the reservoir, biomass of American eel at the lower Neversink River sites was roughly 50% higher than in comparable Beaver Kill sites (Figure 4A). Biomass of American eel in the Beaver Kill was remarkably consistent among almost all study sites (Figure 4C). Trout and minnow biomass at sites with drainage areas larger than about 330 km^2, however, did not differ greatly among comparable sites in both river systems (Figure 4B, 4C).

DISCUSSION

Fish assemblages in parts of the Neversink River are affected to various degrees by several stressors. The Neversink Reservoir is obviously the main reason for the absence of migratory fish species at upstream sites, but it also appears to cause decreases in richness, diversity and biomass at fish communities from several mid-basin sites immediately downstream from the impoundment. Fish-community metrics were so low at several sites immediately below the reservoir that they could not be included in the models that describe their relations with drainage area (Figure 2). The absence of non-migratory fish species and reduced community richness, density, and biomass at several headwater sites can also be attributed to impaired water quality. Trout survival and fish populations at several sites in the West Branch Neversink River (e.g., wb05) and across most of the East Branch Neversink River were moderately to severely affected by acidification (Baldigo and Lawrence 2001; Baldigo and Murdoch 1997; Lawrence et al. 2001). This water-quality issue is well described by other investigations and not discussed herein.

The normal succession or continuum of fish-species assemblages (Vannote et al. 1980) characteristic of small, cold-water, and unproductive headwater sites to those typical of large, warm-water, and productive downstream sites is disrupted in the Neversink River. This discontinuum is not unexpected because analogous trends and species shifts were noted for

macroinvertebrate communities downstream from the reservoir (Ernst et al. 2008). The Neversink Reservoir essentially "resets" riverine habitat from those conditions which would be expected for drainages of 240 km^2 to that those which currently occur at mid-basin or headwater sites with drainages of 2 to 100 km^2. The altered conditions and resulting reductions in community richness, diversity, and biomass downstream from the reservoir (sites nv11 and nv14) are nearly as profound as those noted upstream from the reservoir. For example, the exceptionally low richness and diversity at nv14 (with a drainage area of 240 km^2) is comparable to other headwater Neversink River sites (Figure 2B) that only contain slimy sculpin and trout populations. Hypolimnetic reservoir releases have shifted temperatures in the tailwaters from a formerly warm or cool-water regime to a cold-water regime. The predominance of sculpin at nv14 may be due to the fact that sculpin are particularly well suited to cold, sterile waters (Scott and Crossman 1973, Lyons et al. 1996) and are not subjected to heavy predation because large piscivorous trout and American eel are essentially absent immediately downstream from the reservoir (Figures 3A, 4B). The dominance of sculpin at downstream reaches may also be related to density-dependent predator and prey interactions. Although trout can prey on sculpin (Hanson et al. 1992), sculpin may also regulate trout populations at high densities because they can compete with trout for the same benthic foods (Ruetz et al. 2003; Zimmerman and Vondracek 2007) and consume trout eggs (Clary 1972). Regardless of the reason, the suitable habitat and lack of predation pressures permit one species, slimy sculpin, to dominate fish communities (numbers and biomass) in reaches that are in close proximity to the reservoir, as they typically do in headwater sites.

The contemporary absence of two native diadromous species (American eel and sea lamprey) from many kilometers of potential spawning, rearing, and growth habitat in the reaches upstream from the reservoir has several important implications for the health of ecosystems in the upper Neversink River. First, the Neversink Reservoir dam currently prevents sea lamprey, which historically resided in the upper sub-basin, from providing any ecosystem services in these reaches. In the Beaver Kill, sea-run adult lamprey die after spawning and add marine-derived nutrients (MDNs) to local aquatic ecosystems (Nislow and Kynard 2009). Additionally, the filter feeding lamprey ammocoetes do not compete with other fish species and provide food for predatory species which are large enough to consume them. The absence of lamprey in the upper Neversink River may leave these reaches less productive than they would have been under pre-dam circumstances. In fact, nutrient "enrichment" related to lampreys might contribute to the relatively high total fish biomass observed at all upper Beaver Kill sites (average of about 12,000 g/0.1ha) and lower Neversink River sites (average of about 18,000 g/0.1ha). Conversely, the absence of lamprey could potentially limit community biomass to the low levels observed at most upper Neversink River sites (average less than 5000 g/0.1ha) (Figures 3A, 3C). Although the reservoir may not directly affect fish production in the upper basin, it could have an indirect effect by blocking potential sources of MDNs and ammocoetes. Second, the biomass of the fish communities (Figure 2D) and both predator (trout) and prey species (minnows) at sites in the uppermost Neversink River were much lower than expected based on biomass estimates from comparable sites in the Beaver Kill (Figure 4B, 4C). The concept of biomass stability (Tremblay and Richard 1993) suggests that total community biomass, or at least the biomass of the top predators at upper Neversink River sites should be similar to that found at comparable sites in the Beaver Kill. American eel were absent from all upper Neversink

River sites, but eel and trout consume many of the same benthic fish (and macroinvertebrate) species (Carlander 1969; Denoncourt and Stauffer 1993; Facey and Labar 1981). Given the absence of an effective competitor such as American eel, trout biomass at sites in the upper Neversink River should be more similar to, or possibly higher than, trout biomass levels observed at headwater sites in the Beaver Kill. Low species richness and the discrepancy in biomass among comparable sites suggests that other factors, such as impaired water quality (Baldigo and Lawrence 2000; Baldigo and Lawrence 2001) also affect fish communities at some reaches in the upper Neversink River. Our results clearly show that the reservoir affects the structure of local ecosystems, yet associated effects of the reservoir on the function of aquatic ecosystems are more difficult to characterize using fish inventories.

The adverse effect of Neversink Reservoir on richness and diversity at most upstream sites, and at several downstream sites, has some broad ecological ramifications. Species richness and diversity may be considered primary indicators of ecosystem health (Bunn et al. 2010; Hawksworth 1995). Species assemblages at stressed or environmentally degraded sites are often less diverse and balanced, and thus, less stable than they would be at unimpacted sites (Davis and Robinson 2012; Schaefer et al. 2012; Whittaker 1975). Consequently, ecosystem function and structure at many sites in the Neversink River should be less resilient or resistant to disturbances, and will likely degrade further when subjected to additional environmental stresses**.** For instance, a contaminant spill, severe flooding, or more gradual (long-term) shifts in habitat quality or hydrologic and thermal regimes could extirpate intolerant species. Lost species might not be replaced in the upper Neversink River, however, because other species with similar niches have already been eradicated and the species pool is limited. Accordingly, the loss of any of the dominant species found at Neversink River sites wb03, nv15, or nv14 (Table 3, Figure 3A) might have a serious impact on species interactions at these sites; whereas, a similar loss at Beaver Kill sites ac01 or bv03 (Table 2, Figure 3C) might affect community function less severely because four to seven species are relatively common and one tolerant species could potentially replace the function provided by the lost species. The divergent consequences of such losses in each sub-basin may be estimated by comparing the biomass of primary predators (trout and eel) at sites in the upper reaches of both rivers. Biomass of all trout (primarily brown trout) at sites in the upper Beaver Kill (drainages less than 200 km^2) average about twice as high as trout biomass at Neversink River sites with the same size drainages (Figure 4B). In addition, biomass of American eel at the same Beaver Kill sites average near 2600 g/0.1 ha and no eel (zero biomass) occur at comparable sized sites in the upper Neversink River. The loss of trout at most sites in the upper Beaver Kill might have only minimal effects on the local food web, but a comparable loss of trout populations at sites the upper Neversink River would eliminate the apex predators and significantly alter the aquatic food web and energy flow across trophic levels. Additional declines or the complete loss of an important native species such as brook trout, which has already experienced severe declines across the Northeast (Hudy et al. 2008), would further weaken prospects for the species' long-term sustainability.

Although the remarkably high species richness, diversity, and biomass observed at several sites in the lower Neversink River are not a primary focus of this study, there are several possible explanations for these unusual findings. Most of the lower Neversink River study sites were located near: (a) major tributaries, (b) its confluence with the Basher Kill and the Bashakill marsh, or (c) its terminus with the main stem Delaware River. The proximity of main stem Neversink River study sites to the main stem of the Delaware River, which

contains different habitats and fish assemblages, evidently is a source for more species than are found in the lower Beaver Kill; including several native and nonnative species that are not typically found in mountain streams. The large number of species and high evenness (Table 2) also increases diversity which produces relatively well-balanced fish communities. The unusually high biomass of these fish communities is likely a result of warmer water temperatures, the contribution of MDNs (see discussion above), and additional nutrients from several small waste-water treatment plants (WWTPs) which empty into the Neversink River near sites nv11, nv09, and nv01. Warmer temperatures are partly due to the elevations of Neversink River sites nv00 to nv07, which are as much as 200 m lower than the lowest site (bv01) in the Beaver Kill. The WWTP effluents from the municipalities of Monticello, Fallsburg, and Port Jervis appear to contribute to elevated concentrations of nitrate, ammonia, and phosphorus in waters of the middle and lower Neversink River (Baldigo et al. 2004; Baldigo et al. 2002).

Management Implications

Our findings have several important implications for management of fishery and water resources in both study basins and in other impounded systems. The functionally impaired ecosystems encountered at many sites in the upper and middle Neversink River were not surprising considering that the impoundment completely blocks fish migration and alters downstream water quality, hydrology and thermal regimes, channel stability, and sediment loads. The hydrologic regime, however, is a 'master variable' that generally drives many physical, chemical and biological processes, and affects riverine ecosystems (Poff et al. 1997; Power and Power 1995). Changes in habitat due to flow alteration are known to disrupt native biodiversity and ecological integrity (Anonymous 1997; Poff et al. 1997; Richter et al. 1996; Richter et al. 1997). Reservoir operations also tend to increase hydrologic and channel stability, decrease sediment loads and alter the thermal and flow cues that many species rely on for spawning, migration, and fry emergence (Baldigo et al. 2004). The flow and thermal regime of the Neversink River downstream from the reservoir is currently much different from the regime that existed prior to dam construction. An assessment of daily flow records under four reservoir-management periods at two USGS streamgages immediately downstream of the dam (near site nv14) determined that the: (a) median monthly flows from November to June were reduced by more than 7%, (b) timing of low flows shifted from late summer and early fall to late fall and early winter, (c) magnitude of winter and spring low flow events (the 7- and 30-day minimum flows) decreased by more than 80%, (d) frequency and duration of winter and spring low flow pulses increased more than 80%, (e) magnitude of high flow events (3- and 90-day maximum flows) decreased by more than 70%, and (f) frequency of high flow pulses decreased by more than 80% after the Neversink Reservoir was fully operational (personal communication; T. Moberg, The Nature Conservancy, December 2013). In fact, the daily discharges in the Neversink River below the reservoir (USGS stations 01435900 and 01436000) were less than the pre-reservoir (1941-52) 10th percentile flow of 1.47 m^3/s approximately 82 and 74 percent of time during the initial dam operation (1953-83) and the reservoir release program (1984-2006) years, respectively (Figure 5). Encouragingly, the daily flows during the Flexible Flow Management Program (FFMP) (2007-10) and Operations Support Tool (OST) (2011-14) years were less than the pre-reservoir 10th

percentile flow approximately 5 and 2 percent of the time, respectively (Figure 5). These changes suggest that the flow regime in the Neversink River downstream of the reservoir has become more comparable to past (pre-reservoir) conditions. Such flow-management strategies should, in theory, help native fish species reoccupy reaches where stable and (or) low flows and extremely cold waters have reduced or eliminated their populations.

The differences in fish assemblages of the two basins illustrate the potential benefits that flow modifications, dam removals, and fish passageways might provide to ecosystems in dammed river systems. Restored connectivity in the Neversink River (or in comparable systems) would also help conserve species of special concern (i.e., threatened or endangered) and promote more diverse and resilient fish communities. In the absence of the reservoir or the presence of a fish-passage device, catadromous American eel (resident in the upper Beaver Kill and lower Neversink River) and the anadromous sea lamprey (observed in the lower Neversink River), would likely ascend to further upstream reaches. Additional anadromous species such as American shad *Alosa sapidissima* and blueback herring *A. aestivalis*, observed seasonally in both systems (but not during our summer surveys), might also be able to traverse reaches further upstream in the Neversink River. The restoration of extirpated migratory native species to reconnected (upstream) reaches could help return biodiversity to near-normal levels that have not been possible for decades.

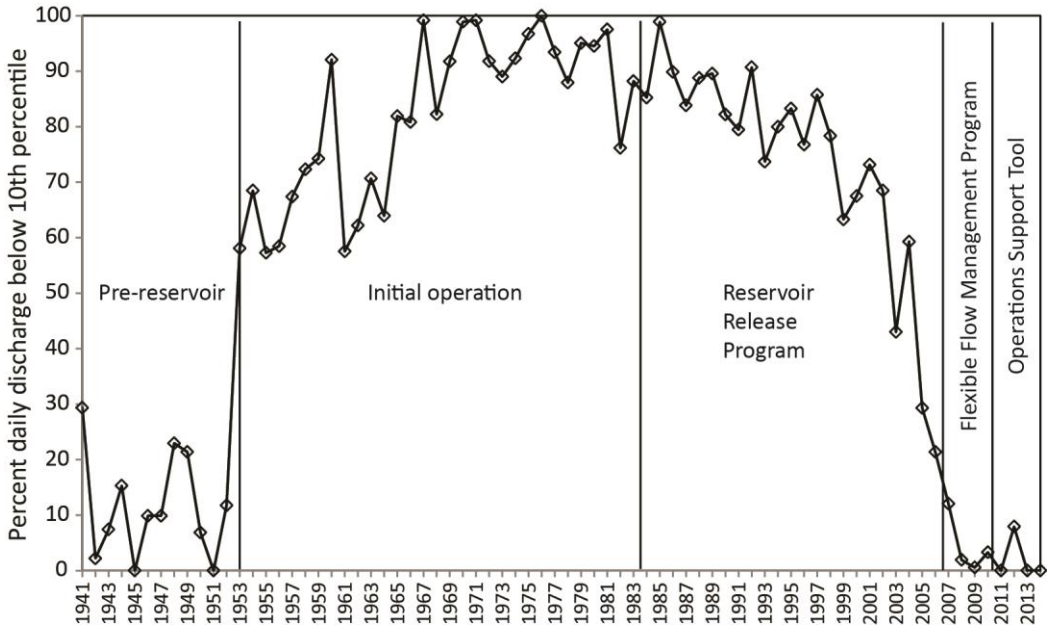

Figure 5. Percent of daily discharge estimates (for each calendar year) that were less than the pre-reservoir 10th flow percentile in the Neversink River below the reservoir (USGS stations 01435900 and 01436000) during five reservoir-management periods, 1941-2014.

The primary mandate for managing waters in the Neversink Reservoir is to provide high-quality drinking water for the residents of New York City (NYC). Nonetheless, ongoing attempts to balance environmental needs with this directive have been evolving since the late 1970s. From 1983 to 2007, the New York City Department of Environmental Protection (NYCDEP) managed the reservoir under a "Reservoir Release Program" (Figure 5) that

attempted to protect the cold-water fishery and other native species at downstream reaches by using a minimum flow standard of 1.7 m^3/s (60 ft^3/s) during the warm summer months. Little attention, however, was given to the variability that riverine systems normally experience. In late 2007, the NYCDEP implemented the FFMP, which was developed by the Nature Conservancy (Gong et al. 2010). The FFMP incorporated several flow-variability elements into the release program while balancing the needs of the NYCDEP water-supply system. The FFMP was a framework to more effectively coordinate diversions and releases from all of the reservoirs in New York City's Upper Delaware Basin to (a) meet core water-supply need, (b) address multiple ecological-flow issues, and (c) meet a United States Supreme Court decree which dictates operation of impoundments in the Delaware River watershed. The issues identified were: "to help control temperatures in the tailwaters to help sustain cold water fisheries; to assist in mitigating the impacts of flooding; and to provide flows in the main stem and the Delaware Bay to help protect ecological health, support withdrawal and non-withdrawal" (NYSDEC 2012). Since the FFMP ended in 2011, the NYCDEP began using the new OST to make predictive decisions for water-supply planning and operations. Although no biology data have been collected to determine whether the new release regimes have benefited fish communities at the impacted sites below the reservoir, these efforts are the first steps in reconstituting a more natural flow regime and restoring some semblance of the original biodiversity and ecosystem health in the lower Neversink River. This modified flow-release program offers an example of how environmental and water-use entities can synchronize seemingly independent missions to not only benefit riverine ecosystems, but to also maintain the quantities of clean drinking water that rivers of this region supply to more than 9 million people in New York City.

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