

River of the dammed: longitudinal changes in fish assemblages in response to dams

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Abstract Although dams are a common feature on rivers throughout the world, their effects on diversity, composition, and structure of fish assemblages are often unclear. We used electrified benthic trawls and stable isotope analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ to determine the complex relationships between taxonomic diversity and food web structure of fish assemblages among sites in the free-flowing and impounded reaches of the Allegheny River, Pennsylvania, USA. We found higher gamma and beta fish diversity in the free-flowing section, where Brillouin diversity increased in a downstream direction; however, in the impounded section, we found decreasing diversity downstream. Analysis of similarity and non-metric multi-dimensional scaling revealed longitudinal differences in Bray–Curtis similarity between assemblages from

impounded and those from free-flowing sites. Finally, using stable isotope analysis, we showed that fishes in the free-flowing section derived nutrients primarily from benthic sources while fishes in the impounded section had a stronger reliance on pelagic nutrients. Our findings reveal that dams can reduce fish taxonomic diversity, driven primarily by decreases in lotic taxa, while shifting resource use from benthic toward pelagic nutrients. A multi-faceted approach to assess the cumulative effects of dams on aquatic communities is, therefore, recommended.

Keywords Stable isotope analysis · Diversity partitioning · Community ecology · Food web · Nutrient dynamics · Impoundment

Introduction

The majority of large-river systems throughout the world are affected by dams (Nilsson et al., 2005) for purposes that include flood control, hydroelectric power generation, and facilitation of navigation or recreation. Irrespective of their purpose, the presence of dams alters the natural flow of rivers (Graf, 1999, 2006; Poff & Hart, 2002). Nutrient and sediment dynamics are affected, as detritus and sediment accumulate behind dams, thus becoming unavailable downstream (Kondolf, 1997; Vorosmarty et al., 2003; Graf, 2006). By altering flow, dams decrease the natural heterogeneity of rivers (Kondolf, 1997; Poff

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et al., 1997, 2007), as pool and lentic habitats predominate, and the only proxy for riffle habitats is usually immediately downstream of dams where turbulence and oxygen content of the water can be relatively high (Ward & Stanford, 1983). Altered flow regimes, and the transformation from lotic riffle-pool-run sequences to lentic habitats, also leads to subsequent changes in biotic assemblages (Power et al., 1996; Poff et al., 1997; Bunn & Arthington, 2002; Miranda et al., 2008). Species adapted to fast-flowing water are especially susceptible to such changes, while a variety of trophic shifts may occur with the arrival and dominance of lentic species at multiple trophic levels (Poff et al., 1997; Bunn & Arthington, 2002; Lytle & Poff, 2004).

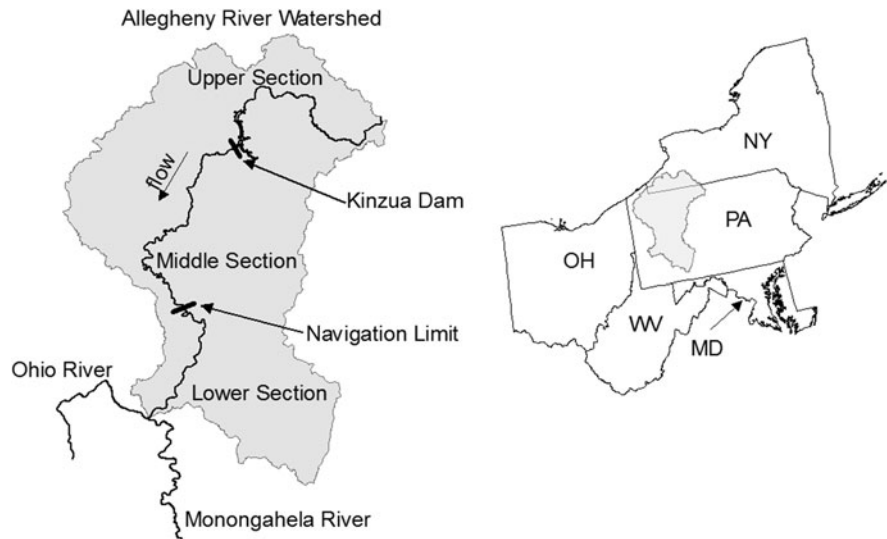
In impounded reaches, aquatic vegetation and periphyton can be negatively affected by higher turbidity and sedimentation rates, and the subsequent reductions in light penetration and changes in substrate composition (Rivier & Segquier, 1985; Poff et al., 1997). Fish species in lithophilic reproductive guilds, such as many darters (Percidae: Etheostomatini), require rocky and gravel habitats, in addition to well-oxygenated, flowing water, in which to spawn and care for their eggs (Page, 1983; Simon, 1998). The loss of these habitats due to increased turbidity and sedimentation can render such habitats unsuitable for reproduction even if adults are able to survive (Berkman & Rabeni, 1987). Sedimentation-induced changes to aquatic invertebrate assemblages can also affect fish foraging behavior and efficiency (Harvey, 1986; Berkman & Rabeni, 1987; Milner & Piorkowski, 2004). Assessing direct effects of these types of disturbance on fish assemblages can be quite challenging, particularly in large-river systems; determining more subtle indirect effects and ecological shifts mediated by dams present a greater challenge still.

Longitudinal patterns along stream river gradients have been described using theoretical models such as the nutrient spiraling concept (Webster & Patten, 1979), river continuum concept (Vannote et al., 1980), process domains concept (Montgomery, 1999), and flood pulse concept (Thorpe & DeLong, 1994); however, these models generally assume uninterrupted continua and do not account for disruptions to water and nutrient flow caused by dams. The serial discontinuity concept (Ward & Stanford, 1983) showed how dams can not only create lentic conditions above the dam, but below the dam can effectively “reset”

environmental conditions to states reflecting lower order streams. Paradoxically, dams can thus provide refugia for lotic species in impounded rivers, with higher flow and oxygenated water immediately below dams (Freedman et al., 2009a; Argent & Kimmel, 2011).

Although longitudinal patterns in relative fish abundance and diversity along a river continuum can thus be affected by the presence of dams (Ward & Stanford, 1983; Miranda et al., 2008). However, most studies have focused on smaller rivers, or on large bodied fish taxa or those that can be sampled in near shore habitats. Furthermore, while there are other studies that separately examine the effects of dams on either taxonomic diversity or nutrient dynamics, the complex relationships between these factors is not well understood. Our objectives were, therefore, to use a novel sampling gear (electrified benthic trawl; Freedman et al., 2009b) in conjunction with stable isotope analysis to examine the effects of dams on benthic fish assemblages and food webs by sampling dam-impacted and free-flowing reaches of the Allegheny River, Pennsylvania. The Allegheny River is important because it is the most northeast extension of the rich Ohio River (and thus also of the Mississippi River watershed); its diverse fauna was derived from the rich Teays/Mississippi valley via the developing Ohio River and from glacial meltwaters of that formed the Great Lakes (Hocutt et al., 1986). We hypothesized that fish diversity would be lower in the impounded section, with shifts from lotic to lentic species dominating the community. As habitat would be less diverse (contiguous deep pools in the impounded section; riffle-pool-run sequences in the free-flowing section), we also expected to see higher biotic homogenization in the impounded section (Olden et al., 2004; Poff et al., 2007). Furthermore, because our impounded sites were located downstream from our free-flowing sites, we expected that differences due to river distance between sites [measured in river kilometers (rkm)] between free-flowing and impounded sites would be greater than within these categories. Regular interruptions in nutrient and water flow caused by navigation dams would also be expected to increase homogeneity and disrupt any longitudinal patterns in diversity. We used diversity partitioning to determine the relative contribution of α (within sample) and beta (among sample) diversity to the overall (gamma) diversity of the river. Finally, we

Fig. 1 Map of Allegheny River watershed (*shaded*), showing the lower section impounded by multiple navigation lock-and-dams, and the free-flowing middle section. For reference, the upper free-flowing section above the Kinzua dam is also denoted



examined how dams affect nutrient flow and food webs using stable isotope analysis; with greater mean depth and habitat homogenization, we expected that fishes at impounded sites would derive fewer nutrients from benthic sources relative to those at free-flowing sites.

Materials and methods

Study area and sampling

The Allegheny River has a total length of 523 km and a watershed of approximately 30,000 km², and is comprised of three main sections (Fig. 1). From its headwaters in Pennsylvania, the upper section of Allegheny River flows into New York State before reentering Pennsylvania, and is unregulated above a hydroelectric and flood-control dam that forms the Kinzua Reservoir at River Kilometer 325. Below the Kinzua Dam, the middle section of the river is free-flowing for 211 km. The lower section's 113 km are regulated by a series of eight navigation lock-and-dam systems until its confluence with the Monongahela River in Pittsburgh forms the Ohio River. Glacial alluvial gravel and rocks comprise the dominant substrate in the Allegheny River. Commercial gravel dredging has occurred throughout most of the nine navigation pools on the Allegheny River (Freedman et al., 2013), but only at one site above the navigation pool influence. Annual mean discharge of the Allegheny River is 189 m³ s⁻¹ at our uppermost site near

Kinzua Dam (USGS Gauging Station 03012550; River Kilometer 316), 623 m³ s⁻¹ at Parker, PA, located 20 km upstream of the navigation limit (USGS Gauging Station 03031500; River Kilometer 133), and 920 m³ s⁻¹ at Lock & Dam 4 at Natrona, PA (USGS Gauging Station 03049500; River Kilometer 39). While subject to some point- and non-point source stressors such as sewage discharges and agriculture, 139 km of the middle section of the Allegheny River is designated as a National Wild and Scenic River, and is yet relatively pristine.

We used electrified benthic trawls (Freedman et al., 2009b) to sample benthic fish assemblages at 66 sites in the middle and lower sections of the Allegheny River (Fig. 1). We sampled 26 sites in the lower, impounded river, with three or four sites in each navigation pool from 2 to 9; these included sites located above and below each dam, with one or two sites located in the middle of the pool (Fig. 2). We sampled 40 sites in the middle, free-flowing section of the river, from below Kinzua dam to just above the upper navigation limit in navigation pool 9. Three to eight (mean ± SD; 4.44 ± 1.63) 2-min timed trawls were conducted at each site depending on the width of the river. All fishes were identified to species in the field when possible; representative samples were retained and photo vouchers were taken for laboratory verification.

Stable isotope sampling and preparation

Stable isotopes can be used to provide information about both realized trophic scenopoetic (environmental

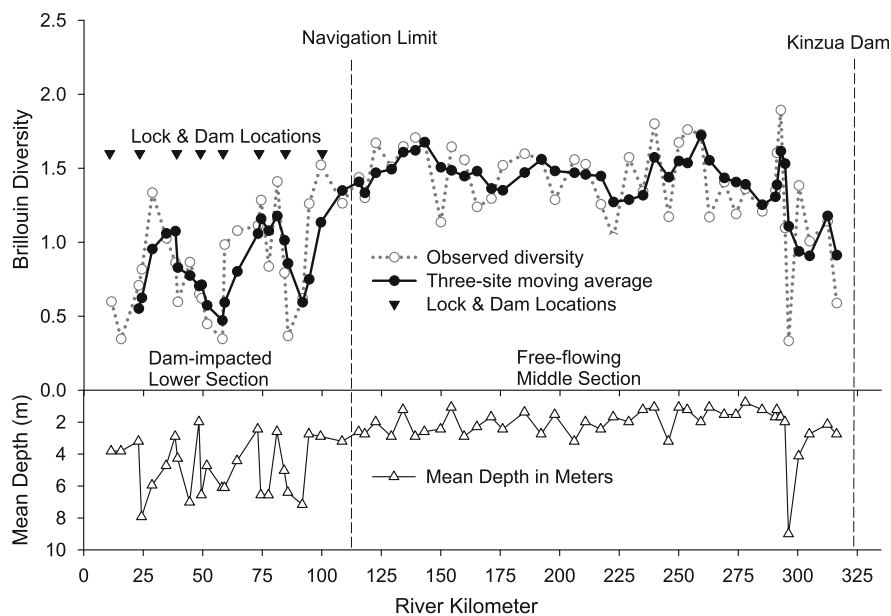


Fig. 2 Fish diversity (*upper panel*) and mean depth (*lower panel*) of sites along a longitudinal gradient in the Allegheny River. *Open circles* and *dotted lines* represent observed Brillouin diversity, while *solid circles* and *lines* were calculated using a three-site moving average. The navigation limit (*dashed*

line) forms the break between the impounded lower section and free-flowing middle section, while the Kinzua dam (*dashed line*) is the upstream limit of the middle section of river. Navigation lock-and-dam structures are denoted by *solid triangles*, and mean depths by *open triangles*

conditions) and bionomic (interactions with other organisms) niche dimensions (Newsome et al., 2007). In other words, we used them not only to determine what an organism was eating, but also whether it was deriving nutrients from benthic or pelagic sources (e.g., Post, 2002b; Vander Zanden & Vadeboncoeur, 2002; Vander Zanden et al., 2005; Newsome et al., 2007). Stable carbon isotope signatures ($\delta^{13}\text{C}$) vary across both primary producers and in response to differences in environmental variables. For instance, periphyton and phytoplankton differ in $\delta^{13}\text{C}$ signatures, as do producers from deep or shallow water (Vander Zanden & Rasmussen, 1999; Post, 2002b). Variation in primary producer $\delta^{13}\text{C}$ in streams and rivers is largely driven by CO_2 availability: in shallow or turbulent water, the boundary layer effect increases the availability of “fresh” CO_2 , while in slow or deep water CO_2 is less available and is, therefore, “recycled” by primary producers (Peterson & Fry, 1987; Finlay et al., 1999; Trudeau & Rasmussen, 2003). The heavier stable isotope of nitrogen (^{15}N) is conserved in organic tissues, and passes to higher consumers via bioaccumulation. Thus, $\delta^{15}\text{N}$ is enriched at a relatively constant rate (2–5‰, mean 3.4‰) across trophic levels, and,

therefore, serves to estimate trophic position within a food-web (Vander Zanden & Rasmussen, 1999; Vander Zanden & Rasmussen, 2001; Post, 2002a; Vanderklift & Ponsard, 2003). While stable isotope analysis has been used to gain insights into biotic changes that occur as a response to anthropomorphic stress, such research has tended to focus on point- and non-point-source additions to aquatic environments (Costanzo et al., 2001; Vadeboncoeur et al., 2003; Gray et al., 2004; Grey et al., 2004; Anderson & Cabana, 2005; Vander Zanden et al., 2005) rather than physical alterations to the environment. The ability of stable isotope analysis to differentiate food sources and detect trophic positions thus makes it a powerful tool for examining the effects of dams on riverine fish assemblages.

Two sites were sampled above the influence of navigation dams (free-flowing sites), and three sites were sampled in the upper navigation pools of the Allegheny River (Pools 7–8) during late summer, 2007. Adult fishes were collected using a combination of Missouri- and PSU-benthic trawls (Herzog et al., 2005; Freedman et al., 2009b). Fish samples were immediately frozen until processed in the laboratory. All fishes were identified to species, with the exception

of shiners (*Notropis* spp.) which were not identified to species prior to stable isotope sampling, and were, therefore, grouped together and analyzed as shiner spp. Several individuals of each fish taxon (range 2–48 individuals per site) to compensate for inherent inter-individual variability, and of different size-classes where relevant, were sampled for stable isotope analysis. White muscle tissue was used if sufficient material could be obtained for fish samples as previous studies have shown it to be less variable than other tissues, with a moderate stable isotope turnover rate on the order of weeks to months (Hobson, 1999); smaller fishes were eviscerated and decapitated. To compensate for inherent differences among sites, samples were pooled by taxon for both the two free-flowing and the three dam-impacted sites.

All samples were rinsed with deionized water, placed into a clean glass vial, and dried in a drying oven at 60°C for 24–48 h. Dried samples were homogenized to a fine powder using mortar-and-pestle, or using a glass stirring rod within the vial. Samples were weighed into 0.2 mg ($\pm 10\%$) aliquots, placed into 5 mm \times 3.5 mm tin capsules, and analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ using either a Thermo-Finnigan Delta Plus or Delta XP isotope-ratio mass spectrometer interfaced with a Carlo Erba NC2500 Elemental Analyzer via the Conflo II or Conflo III at the Stable Isotopes in Nature Laboratory at the University of New Brunswick, Canada.

From each sample, the ratios of ^{14}N to ^{15}N and of ^{12}C to ^{13}C were determined, and used to calculate $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ using the formula:

$$\delta X = \left[\left(R_{\text{sample}} / R_{\text{standard}} \right) - 1 \right] \times 1,000,$$

where X refers to the rare, heavy isotope, and R is the ratio of the heavy isotope (^{15}N , ^{13}C) to the light isotope (^{14}N , ^{12}C) in the sample and in a standard. The standard for nitrogen is atmospheric nitrogen (AIR), and for carbon is carbon dioxide derived from calcium carbonate in the Pee Dee Bee formation of South Carolina (PDB). As lipids are rich in carbon relative to tissues, variable tissue-lipid contents among samples can increase overall variability of samples; we, therefore, used a lipid correction factor to standardize across samples (Eq. 3, Table 1 from Post et al., 2007). For isotopic standards, standard deviations were 0.15‰ for $\delta^{13}\text{C}$ and 0.24‰ for $\delta^{15}\text{N}$, for elemental standards standard deviations ranged from 0.13 to

0.15‰ for $\delta^{13}\text{C}$ and 0.14 to 0.25‰ for $\delta^{15}\text{N}$, and for biologic standards, the standard deviations ranged from 0.11 to 0.14‰ for $\delta^{13}\text{C}$ and from 0.12 to 0.14‰ for $\delta^{15}\text{N}$. Replicate fish tissue samples varied by an average of 0.22‰ (SD 0.24‰) for $\delta^{13}\text{C}$ and 0.19‰ (SD 0.18‰) for $\delta^{15}\text{N}$.

Statistical analysis

We calculated both observed site-to-site differences, and used three-site moving averages to visualize longitudinal trends, in Brillouin diversity of fish assemblages along the river (Fig. 2); however, all analyses were conducted on the observed data. We performed both non-metric multidimensional scaling (nMDS) and analysis of similarity (ANOSIM) based on a Bray–Curtis dissimilarity matrix of fish assemblages to examine differences among sites, using Primer 5.2.2 (Primer-E Ltd., Plymouth, UK). River sections (free-flowing middle and impounded lower) were used as factors.

To quantify the effects of dams in structuring diversity, we examined the relative contributions of alpha (α , within sample) and beta (β , among sample) diversity to the gamma (γ , total) diversity of the Allegheny River (sensu Crist et al., 2003). We performed complete randomization of 10,000 iterations using additive partitioning (Partition 3.0; Veech & Crist, 2009) wherein

$$\gamma_{(\text{totaldiversity})} = \alpha_{1(\text{withinsite})} + \beta_{1(\text{amongsite})} + \beta_{2(\text{amongsection})}$$

to test for the presence of patterns across these hierarchical levels in the Allegheny River. We tested the null hypothesis that observed fish species richness at each hierarchical level was not significantly different from a random distribution of these fish species among samples at each of these levels.

We used circular statistics (Schmidt et al., 2007) to assess differences between fish stable isotope signatures by assessing directional changes from free-flowing to impounded sites using the software package Oriana 3.0 (Kovach, 2009). In circular statistics, the stable isotope data are transformed into linear vectors for each fish species, with an origin that is standardized as 0.0. $\delta^{13}\text{C}$ is plotted on the X-axis, with ^{13}C -depletion (indicative of pelagic carbon sources) to the left (270°), and ^{13}C -enrichment (benthic carbon

Table 1 Fish species captured and relative abundance (number per trawl sample) in the impounded lower section and free-flowing middle section of the Allegheny River

Scientific name	Common name	Catch-per-sample	
		Impounded	Free-flowing
Petromyzontidae			
<i>Ichthyomyzon bdellium</i>	Ohio Lamprey	0	0.02
<i>Petromyzontid</i> sp.	Lamprey Larvae	0	0.01
Cyprinidae			
<i>Campostoma anomalum</i>	Central Stoneroller	0	0.01
<i>Cyprinus carpio</i>	Common Carp	0.01	0
<i>Erimystax dissimilis</i>	Streamline Chub	0.57	3.11
<i>Exoglossum laurae</i>	Tonguetied Minnow	0	0.02
<i>Hybopsis amblops</i>	Bigeye Chub	0	0.15
<i>Luxilus chrysocephalus</i>	Striped Shiner	0	0.02
<i>Nocomis micropogon</i>	River Chub	0	0.07
<i>Notropis atherinoides</i>	Emerald Shiner	0	0.03
<i>Notropis photogenis</i>	Silver Shiner	0	0.16
<i>Notropis volucellus</i>	Mimic Shiner	0.13	7.50
<i>Notropis</i> spp.	Shiner Species	0.03	0
<i>Pimephales notatus</i>	Bluntnose Minnow	0	0.38
Catosomidae			
<i>Catostomus commersonii</i>	White Sucker	0	0.01
<i>Hypentelium nigricans</i>	Northern Hogsucker	0	0.03
<i>Moxostoma anisurum</i>	Silver Redhorse	0.02	0
<i>Moxostoma duquesnei</i>	Black Redhorse	0	0.01
<i>Moxostoma erythrurum</i>	Golden Redhorse	0.01	0
<i>Moxostoma</i> spp.	Redhorse Species	0.02	0
Ictaluridae			
<i>Ictalurus punctatus</i>	Channel Catfish	0.28	0.02

Table 1 continued

Scientific name	Common name	Catch-per-sample	
		Impounded	Free-flowing
<i>Noturus eleutherus</i>	Mountain Madtom	0	0.05
<i>Noturus flavus</i>	Stonecat	0.03	0.01
<i>Noturus stigmosus</i>	Northern Madtom	0.01	0.01
<i>Pylodictis olivaris</i>	Flathead Catfish	0.03	0.02
Percopsidae			
<i>Percopsis omiscomaycus</i>	Trout-Perch	0.06	0.11
Atherinopsidae			
<i>Labidesthes sicculus</i>	Brook Silverside	0	0.01
Centrarchidae			
<i>Ambloplites rupestris</i>	Rock Bass	0.01	0.07
<i>Lepomis cyanellus</i>	Green Sunfish	0	0.01
<i>Lepomis macrochirus</i>	Bluegill	0	0.05
<i>Micropterus dolomieu</i>	Smallmouth Bass	0.37	1.63
<i>Micropterus punctulatus</i>	Spotted Bass	0.01	0
<i>Micropterus salmoides</i>	Largemouth Bass	0.02	0
<i>Micropterus</i> sp.	Black Bass Species	0.02	0
Percidae			
<i>Etheostoma blennioides</i>	Greenside Darter	0.61	4.65
<i>Etheostoma caeruleum</i>	Rainbow Darter	0.68	6.87
<i>Etheostoma camurum</i>	Bluebreast Darter	1.01	1.17
<i>Etheostoma flabellare</i>	Fantail Darter	0.09	0.34
<i>Etheostoma maculatum</i>	Spotted Darter	0.01	0.21
<i>Etheostoma nigrum</i>	Johnny Darter	3.36	0.17
<i>Etheostoma tippecanoe</i>	Tippecanoe Darter	0.80	0.39
<i>Etheostoma variatum</i>	Variegated Darter	0.02	1.17
<i>Etheostoma zonale</i>	Banded Darter	0.42	5.19

Table 1 continued

Scientific name	Common name	Catch-per-sample	
		Impounded	Free-flowing
<i>Percina caprodes</i>	Logperch	2.44	1.32
<i>Percina copelandi</i>	Channel Darter	6.41	1.52
<i>Percina evides</i>	Gilt Darter	0.72	3.05
<i>Percina macrocephala</i>	Longhead Darter	0.30	1.44
<i>Percina maculata</i>	Blackside Darter	0	1.51
<i>Percina (hybrid)</i>	Darter hybrid	0	0.01
<i>Perca flavescens</i>	Yellow Perch	0.02	0
<i>Sander vitreus</i>	Walleye	0.04	0.02
<i>Sander sp.</i>	Walleye or Sauger	0.07	0.04
Sciaenidae			
<i>Aplodinotus grunniens</i>	Freshwater Drum	0.19	0
Cottidae			
<i>Cottus bairdi</i>	Mottled Sculpin	0	4.01
Mean Number of Fish per Trawl		18.8	46.6

sources) to the right (90°). $\delta^{15}\text{N}$ is plotted on the Y-axis, with ^{15}N -enrichment (higher trophic level) at 0° and ^{15}N -depletion (lower trophic level) at 180° . We defined the origin as being the free-flowing site, while the other end of the vector represents the impounded sites. The length of each vector represents the magnitude of change of stable isotopic signatures for that species, while the angle of the vector represents the directionality of that change. We used Rayleigh's Test for Circular Uniformity to test whether the distribution of vectors was random or uniform. Alpha levels of 0.05 were used to assess significance for all analyses.

Results

Fish distribution, abundance, and diversity

Diversity in the free-flowing middle section generally increased from the Kinzua dam until the dam influence near 116 rkm and was variable in the dam-impacted

lower section, but generally declined downstream (Fig. 2). We caught more fishes in the free-flowing section (46.6 fish per trawl) than in the impounded section (18.8 fish per trawl), as well as higher taxonomic richness with 44 taxa in the free-flowing section compared to 34 taxa in the impounded section (Table 1). Mean diversity was lower in the impounded section (mean Brillouin diversity 1.04 ± 0.34 SD) than in the free-flowing section (1.44 ± 0.35 ; t test, $df = 64$, $t\text{-stat} = -4.59$, $P < 0.00002125$; Fig. 2). Mean depth of sites in the impounded section was 4.7 m (range 0.3–14.9 m) and in the free-flowing section was 2.2 m (range 0.3–10.0 m; Fig. 2).

We caught a total of 10,038 fishes comprising 54 taxa: 53 species and 1 hybrid (Table 1). Fishes from the family Percidae (primarily darters) comprised 90.5% of the total catch in the impounded section, while catch from the free-flowing section comprised 62.4% percids and 24.6% cyprinids (minnow family). However, percids were more abundant in the free-flowing section, with a catch rate of percids (29.1 per trawl) almost double that in the impounded section (17.0 per trawl; Table 1). The most prevalent percids in the impounded section were tolerant species such as Channel Darter (34.2% of total catch), Johnny Darter (17.9%), and Logperch (13.0%). In the free-flowing section, the most prevalent percids were species with more lotic requirements such as Rainbow Darter (14.7% of total catch), Banded Darter (11.1%), and Greenside Darter (10.0%; Table 1). Overall, the most prevalent species in the free-flowing section was Mimic Shiner (16.1% of total catch; Table 1), while Mottled Sculpin (8.6%) were also prevalent, particularly in the upper reaches of the section. The free-flowing site with the lowest diversity (0.33) was located at river km 296.1. This site was the deepest in the free-flowing section (9.0 m deep) and we captured just 22 fishes: 19 Trout-Perch and three Mottled Sculpin. This site was also characterized by sandy substratum, which was also noted at the other three sites in the impounded section where Trout-Perch were collected.

Twenty taxa (19 species and one hybrid) were found only in the free-flowing section, while 10 taxa were found only in the impounded section (Table 1). These contributed to a section beta diversity (β_2) of 14.5 which represented 26.9% of gamma species richness but was not significantly different than expected using diversity partitioning ($P > 0.05$; 10,000 iterations;

Table 2 Additive partitioning results for fish communities among sites in impounded and free-flowing sections of the Allegheny River

Spatial scale	Diversity component	Observed mean diversity	Expected mean diversity	Contribution to gamma diversity (%)
River	γ	54		
Section	α_2	39.5	39.5	73.1
	β_2	14.5	14.5	26.9
Site	α_1	10.94	17.11	27.7
	β_1	28.56	22.39	72.3

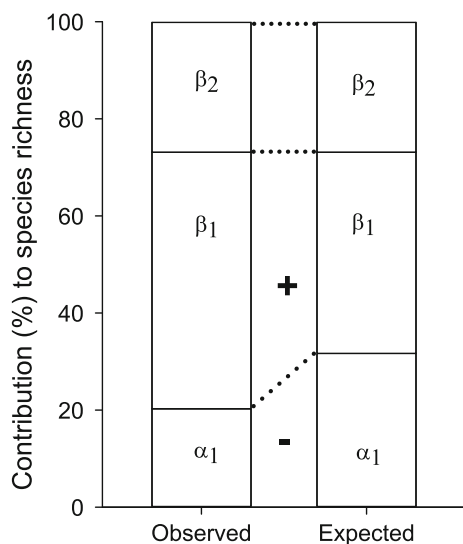
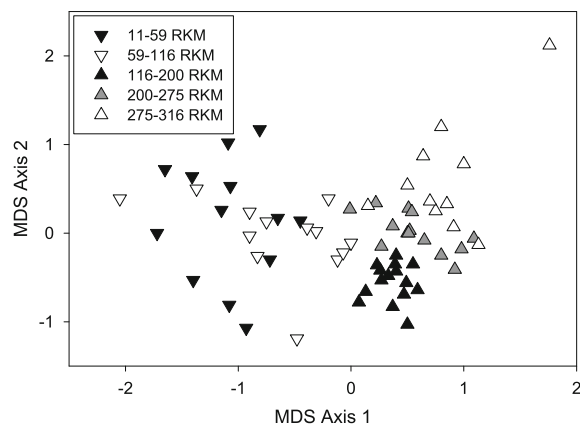
**Fig. 3** Diversity partitioning results (10,000 iterations) for the Allegheny River showing species richness between the free-flowing middle and impounded lower sections (β_2), among sites (β_1), and within sites (α_1). The symbol *plus* indicates that observed diversity was greater than expected, while *minus* indicates that observed diversity was lower than expected

Table 2; Fig. 3). The mean numbers of species that were not shared among sites (β_1) were higher than expected from the 10,000 randomizations (72.3% of gamma diversity versus 56.7%; $P < 0.001$). The mean numbers of species shared among sites (α_1) were lower than expected (27.7% versus 43.3% expected; $P < 0.001$; Table 2; Fig. 3).

There was differentiation between fish assemblages from the free-flowing and impounded sections of the Allegheny River along Axis 1 of the nMDS, with all fish assemblages from impounded sites having values of <0 , while only one free-flowing site value of <0 along this axis (nMDS, Stress 0.17; Fig. 4). ANOSIM

**Fig. 4** nMDS plot of Bray-Curtis similarity among sites in the Allegheny River. *Downward triangles* represent impounded lower section sites, while *upward triangles* represent free-flowing middle section sites. Symbol *shading* represents subsections defined by rkm

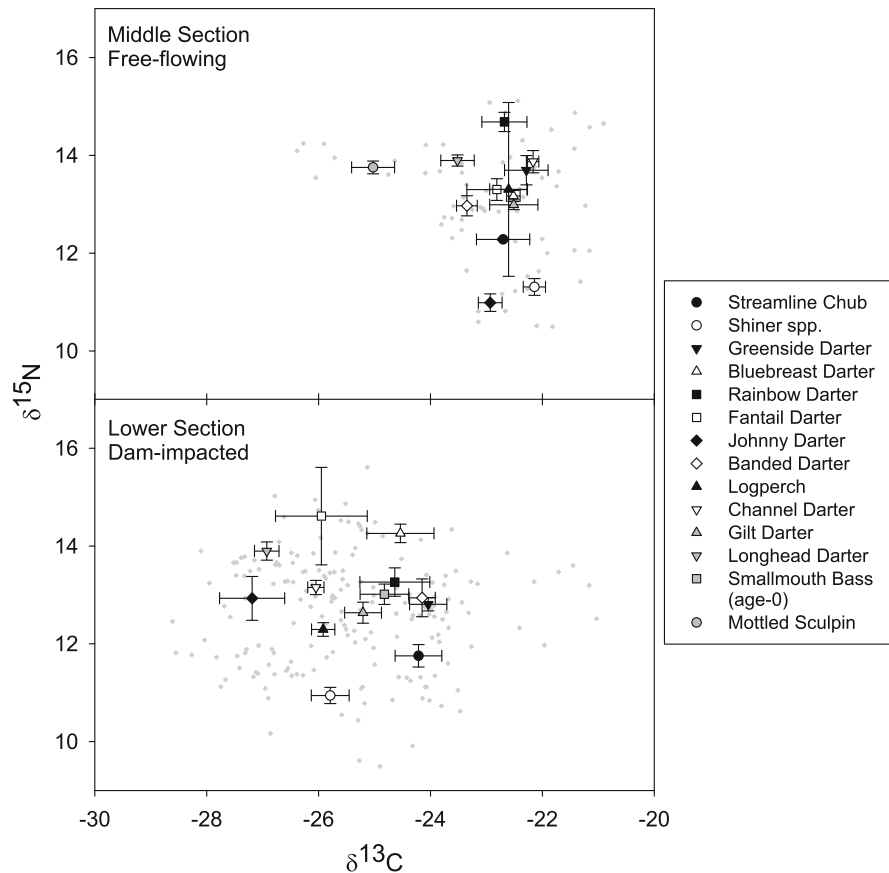
also revealed significant differences in site similarity between free-flowing and impounded sites (Global R : 0.62, significance level 0.1). Fish assemblages in the impounded section were equally dissimilar between 0 and 59 rkm (navigation pools 2–5) and 59–115 rkm (navigation pools 6–9) subsections. Fish assemblages from the free-flowing section were progressively more dissimilar from impounded section assemblages with the increasing distance upstream (Fig. 4). Fish assemblages from sites located below dams in both the 0–59 and 59–116 rkm subsections were not more similar to free-flowing sites than that of sites located mid-pool or above dams.

Food webs and nutrient dynamics

Small fishes from free-flowing sites were less depleted in ^{13}C , consistent with reliance on benthic-derived nutrients (Fig. 5). Fishes from impounded sites had ^{13}C depleted $\delta^{13}\text{C}$ signatures, consistent with increased reliance on pelagic-derived nutrients rather than benthic-derived nutrients. Only Mottled Sculpin from free-flowing sites had $\delta^{13}\text{C}$ signatures more negative than -24.00% .

There was a directional shift in $\delta^{13}\text{C}$ from free-flowing to impounded sites. Circular statistics revealed that fishes from the lower section (Rayleigh's Test, $Z = 11.437$, $P = 0.00000143$; Fig. 6) shifted to increased reliance on pelagic-derived nutrients at impounded sites. There was no significant effect of

Fig. 5 Bivariate plots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for fish assemblages in the free-flowing middle section (*upper plot*) and impounded lower section (*lower plot*) of the Allegheny River. Symbols indicate mean stable isotope values (\pm s.e.) of individual species while *light gray crosses* represent stable isotope values for individual fish



dam influence on the trophic position of fishes. Fantail Darter (from mean $\delta^{15}\text{N}$ 13.30 ± 0.38 SD at free-flowing sites to 14.61 ± 1.41 at undredged sites) and Johnny Darter (from $\delta^{15}\text{N}$ 10.99 ± 0.25 to 12.93 ± 1.00) appeared to be exceptions as they both increased mean trophic position from free-flowing to undredged sites.

Discussion

Effects of dams on fish distribution, abundance, and diversity

We detected significant differences between fish communities in the impounded lower section and free-flowing middle sections of the Allegheny River. These were largely influenced by higher fish abundance and taxonomic diversity at sites in the free-flowing section. Mottled Sculpins were captured at 23 of the 24 uppermost sites; they were among the

most abundant taxa in the free-flowing section, but were not captured below river km 210. This may be due to thermal limitations and habitat preference, as this species is generally associated with cool, clear, flowing water (Scott & Crossman, 1973; Trautman, 1981). Lotic-adapted darters such as Greenside, Rainbow, Banded, and Gilt darters were more abundant in the free-flowing section than in the impounded section. Darter species that were more abundant in the lower section included Johnny Darter, Channel Darter, and Logperch, all of which are better adapted to slower-moving and lentic conditions than most darters (Page, 1983). Streamline Chub and Mimic Shiners were also more prevalent in the free-flowing section although they have different habitat preferences. Both species are found in streams and rivers, but while Mimic Shiners are more tolerant of both silt and lotic conditions than Streamline Chub, neither species thrives in high-silt environments that characterizes much of the impounded section (Trautman, 1981).

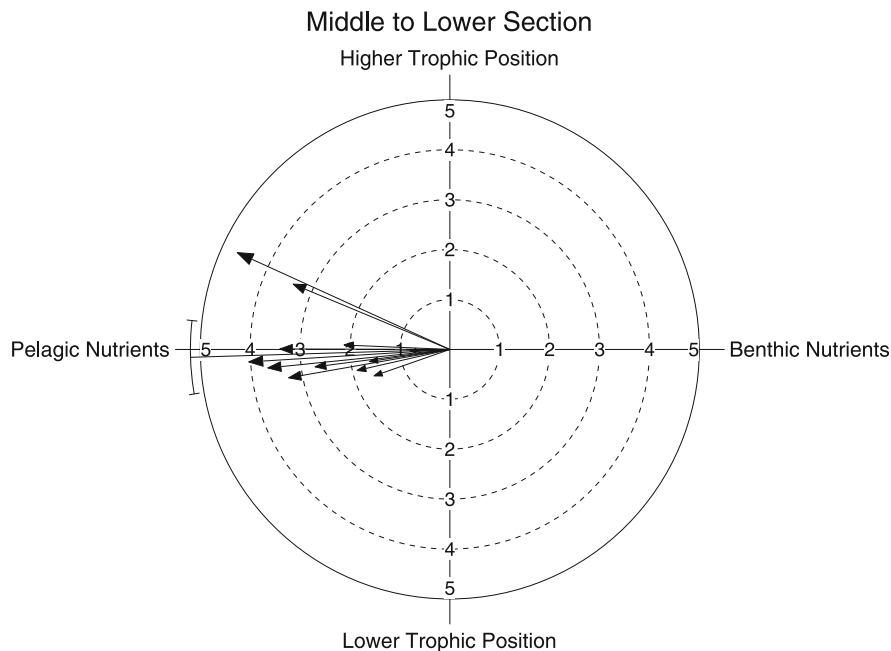


Fig. 6 Circular plots of $\delta^{13}\text{C}$ (horizontal axis) and $\delta^{15}\text{N}$ (vertical axis). Enriched $\delta^{13}\text{C}$ indicative of benthic-derived nutrients is to the right and depleted $\delta^{13}\text{C}$ representing pelagic-derived nutrients is to the left. Higher and lower $\delta^{15}\text{N}$ values are indicative of higher and lower trophic positions and are oriented to the top and bottom of the plot, respectively. Individual arrows

represent mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of individual species: vector direction indicates shifts in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between sites in the free-flowing middle section and impounded lower section, while the length of the vector indicates the magnitude of the difference. The solid line is the overall mean, and the line at the circumference is the 95% confidence interval

Fish assemblages from below dams were dissimilar to above-dam sites. Contrary to our expectations, however, below-dam sites were not more similar to free-flowing sites. Species that are adapted to lotic conditions may find refugia below dams within rivers where turbulence is greatest (Freedman et al., 2009a; Argent & Kimmel, 2011). For instance, lotic fish species listed as threatened by the state of Pennsylvania were found at higher abundances in dam tailwaters on the Ohio River (Freedman et al., 2009a), and a similar trend was noted for dams in the Allegheny River (Argent & Kimmel, 2011). Despite providing refugia for lotic species, fish assemblages from habitats immediately below dams were equally dissimilar to free-flowing sites as were other dam-impacted sites. This indicates a fundamental impact of dams on these fish assemblages.

This may be driven, in part, by the lower diversity in the impounded section than the free-flowing section. Additive partitioning revealed higher heterogeneity in fish assemblages between impounded and free-flowing sites than expected. There was no evidence of increased homogeneity *per se* among the

impounded sites relative to free-flowing sites. At the same time, despite generally lower diversity at lower river km in the impounded section, there was no pattern of longitudinal changes in this section apparent in the MDS analysis. The free-flowing section, however, showed a downstream pattern in increased diversity that was also apparent in MDS analysis. Fish assemblages in the free-flowing section are thus generally consistent with the river continuum concept (Vannote et al., 1980) in that there were increases in taxonomic diversity and mixed assemblages of lotic and lentic species at downstream sites. The disruption of this pattern, with generally lower taxonomic diversity and a sharp drop in lotic species, and a lack of longitudinal changes in the dam-impacted section are consistent with the serial discontinuity concept (Ward & Stanford, 1983).

While the locks in navigation lock-and-dam systems provide access between pools, the dams inhibit fish movement. For instance, river darter, *Percina shumardi*, has been captured to the base of the second lock-and-dam of the Ohio River (DaShields lock-and-dam in the Montgomery Pool; Freedman et al., 2009a).

Extensive sampling has not collected this species upstream of this dam in the Ohio River or in the Allegheny or Monongahela rivers (Freedman et al., 2009a, b; Stauffer et al., 2010; Argent & Kimmel, 2011), suggesting that it is recolonizing the Pennsylvania section of the Ohio River from downstream refugia rather than simply having been missed in prior surveys. The range of this species may expand upstream into the Allegheny and Monongahela rivers, but this dispersal will likely be slowed by the presence of navigation dams. The extirpation from the Ohio River of anadromous species such as Lake Sturgeon, *Acipenser fulvescens*, can be at least partially explained by the presence of dams (Pearson & Pearson, 1989). The presence of locks may help to mediate this issue, as juvenile paddlefish, *Polyodon spathula*, stocked in the Ohio River were confirmed to have passed through locks in both upstream and downstream directions (Barry et al., 2007). The use of navigation lock chambers by fishes can also be confirmed by lock chamber rotenone surveys on The Ohio River in which almost 3×10^6 fishes comprising 116 fish taxa were collected in 377 sampling events: an average of almost 8,000 fishes per collection (Thomas et al., 2005).

Effects of dams on food webs and nutrient dynamics

Stable isotope analysis revealed a shift toward increased reliance on pelagic-derived nutrients by fishes at impounded sites relative to the free-flowing sites above the navigation dam influence. This shift is consistent with shifts from allochthonous to autochthonous and benthic to pelagic nutrients from low-order streams to high-order rivers predicted and observed in other studies (e.g., Vannote et al., 1980; Finlay, 2001), and also with patterns of increased depth caused by the downstream presence of dams at these sites. These results are also consistent with shifts from benthic-driven primary production (e.g., periphyton) to pelagic production (e.g., phytoplankton) as a result of cultural eutrophication (Vadeboncoeur et al., 2003; Chandra et al., 2005; Vander Zanden et al., 2005). Such shifts are generally considered to be the result of eutrophication increasing concentration and productivity of pelagic primary producers, thus starving benthic producers of both nutrients for growth and sunlight for photosynthesis (Vadeboncoeur et al.,

2003; Chandra et al., 2005). Anthropogenically increased depth and turbidity may have similar effects (Freedman et al., 2013). As average depth increases from headwater streams to high-order rivers, relatively less light reaches the river floor, from near 100% of non-refracted light in small clear streams to zero in turbid and deep water, thus decreasing benthic production. Dams increased the mean depth from <3 m in pools in the free-flowing Allegheny River to a constant minimum of 4–5 m (or more) in dam-impacted reaches, and can, therefore, decrease benthic production without any influences from eutrophication or other increases in relative turbidity. Since the free-flowing reach of the river includes runs and riffles as well as pools, while the homogenous impounded reaches effectively consist only of long pools possibly with minimal lotic habitat immediately downstream of dams, a loss of some benthic nutrient pathways becomes even more likely.

Reliance on benthic-derived nutrients at free-flowing sites appears to be high while at dam-impacted sites $\delta^{13}\text{C}$ signatures suggest a trend toward increasing reliance on pelagic-derived nutrients. While a full range of benthic and pelagic nutrients seem to be available, fishes are relying more on pelagic nutrients; this is consistent with the theory that reliance on pelagic nutrients (and decreased reliance on benthic nutrients) would increase with the increased depth due to the navigation dams. Pelagic production is also lower in lower order rivers, with zooplankton diversity and biomass consequently increasing downstream (e.g., Vannote et al., 1980; Ward & Stanford, 1983). The relative reliance on pelagic nutrient sources in the free-flowing section may, therefore, be a combination of higher availability of benthic nutrients and lower availability of pelagic nutrients.

Rafinesque (1820) referred to the Allegheny River as being “almost perfectly clear,” while our Secchi depths ranged from 142 to 145 cm downstream of an active dredging operation and 157–198 cm in other impounded areas of the river (JAF, unpublished data), thus offering supporting evidence that this is no longer the case. We found Secchi depths in the range of 330 cm, however, in a pool above the dam influence, so there does appear to be a negative effect of dams on water clarity. Although other studies have found that dams can decrease turbidity through retention of fine sediments (e.g., Kondolf, 1997), the Allegheny River system may differ due to the size of the dams

(relatively small compared to dams constructed for hydroelectric power generation, flood-prevention, and similar purposes) and locks, both of which may allow for the passage and resuspension of fine sediments. Land use does not differ greatly between the upper navigation pools and lower free-flowing section, consisting primarily of forested land with some residential properties. The approximately 214 km of the Allegheny River between the Kinzua Dam and the end of the navigation dam influence near East Brady PA, likely experience full light penetration except during times of high discharge due to shallow depths and lower turbidity. Despite the upstream presence of the Kinzua dam, free-flowing sites likely represent similar reference states to the historical condition, and with similar fish assemblages and food-web structure.

According to the river continuum concept, nutrient sources shift from allochthonous inputs to autochthonous primary production along the longitudinal river gradient (Vannote et al., 1980). These gradients can be reset by dams, creating higher-flow downstream conditions that mimic higher order streams. Conversely, deeper and slower flowing conditions above dams can be more similar to lower order rivers. Plankton communities are sparse in higher order streams and rivers relative to lower order rivers and impoundments. In the Allegheny River, therefore, nutrient inputs in the free-flowing section would comprise primarily benthic sources, possibly with increased allochthonous inputs. In the dam-impacted section, however, increased phytoplankton production due to environmental conditions combined with lower benthic production would lead to increased reliance on such pelagic producers. The Allegheny River also has a long history of extractive gravel dredging. Dredged portions can exceed 20 m depth, with no light penetration deeper than approximately 10 m. We focused our sampling on undredged areas <7 m deep; however, in another study, we found that dredged areas accumulate terrestrial detritus, and to alter nutrient and sediment flow (Freedman et al., 2013).

Conclusions

We found significant differences among fish community compositions at sites in impounded and free-flowing sections of the Allegheny River. Furthermore, the shift from communities characterized by lotic-

adapted species and those intolerant of silt, to those dominated by generalist and tolerant large-river species was very abrupt. In particular, the longitudinal gradient in fish community similarity and downstream trend toward increasing taxonomic diversity was disrupted in the impounded section, where we found decreasing downstream diversity but no concurrent trend in similarity. These findings were consistent with the stable isotope results, which showed shifts away from the benthic production that characterized the free-flowing section toward increasing reliance on pelagic-derived nutrients in the impounded section. These shifts were likely due to a decrease in benthic production due to increased depth, turbidity, and siltation (Freedman et al., 2013), and would also be consistent with a decline of lotic and intolerant species. By using an electrified benthic trawl, we were able to sample small benthic fishes that are difficult to sample using traditional methods. However, although we did also capture some non-benthic taxa, our sampling method was biased toward the capture of benthic rather than pelagic or littoral fishes. Since benthic fishes may be particularly impacted by habitat alterations due to increased depth (Freedman et al., 2013), our findings cannot necessarily be extrapolated to the entire fish community.

While dams can provide economic benefits, it is necessary to understand the effects that they can have on individual fish species, populations, and communities. While dam removal can restore habitats, and subsequently invertebrate and fish populations (Maloney et al., 2008), many factors need to be considered prior to restoration (Poff & Hart, 2002). Stable isotope analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ is an appropriate tool for assessing differences in fish assemblages between sites with varying degrees of influence from dams, and should be considered for before-after-control-impact (BACI) study designs. It is, therefore, important for managers and policy makers to consider not only the direct effects of habitat alterations on taxonomic diversity, but also indirect effects on ecosystem functioning. Furthermore, alterations in water flow, prey availability, and migration due to dams can even effect changes in fish ecomorphology and functional morphology in certain species (Curry et al., 2004; Palkovacs et al., 2007; Langerhans, 2008; Freedman, 2010; Haas et al., 2010), further confounding these issues. Dams influence riverine fish in many ways; a complete understanding of ecological processes is,

therefore, necessary for informed conservation and management decisions.

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