Gravel dredging alters diversity and structure of riverine fish assemblages

JONATHAN A. FREEDMAN*, ROBERT F. CARLINE† AND JAY R. STAUFFER JR‡

Pennsylvania Cooperative Fish and Wildlife Research Unit, School of Forest Resources, The Pennsylvania State University, University Park, PA, U.S.A.
†*Pennsylvania Cooperative Fish and Wildlife Research Unit, The Pennsylvania State University, University Park, PA, U.S.A.*
‡*Department of Ecosystem Science and Management, The Pennsylvania State University, University Park, PA, U.S.A.*

SUMMARY

1. Human activities affect fish assemblages in a variety of ways. Large-scale and long-term disturbances such as in-stream dredging and mining alter habitat and hydrodynamic characteristics within rivers which can, in turn, alter fish distribution. Habitat heterogeneity is decreased as the natural riffle–pool–run sequences are lost to continuous pools and, as a consequence, lotic species are displaced by lentic species, while generalist and invasive species displace native habitat specialists. Sediment and organic detritus accumulate in deep, dredged reaches and behind dams, disrupting nutrient flow and destroying critical habitat for habitat specialist species.

2. We used standard ecological metrics such as species richness and diversity, as well as stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$, to quantify the differences in fish assemblages sampled by benthic trawls among dredged and undredged sites in the Allegheny River, Pennsylvania, U.S.A.

3. Using mixed-effects models, we found that total catch, species richness and diversity were negatively correlated with depth ($P < 0.05$), while species richness, diversity and proportion of species in lithophilic ('rock-loving') reproductive guilds were lower at dredged than at undredged sites ($P < 0.05$).

4. Principal components analysis and MANOVA revealed that taxa such as darters in brood hider and substratum chooser reproductive guilds were predominantly associated with undredged sites along principal component axis 1 (PC1 and MANOVA $P < 0.05$), while nest spawners such as catfish and open substratum spawners including suckers were more associated with dredged sites along PC2 ($P < 0.05$).

5. Stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$ revealed shifts from reliance on shallow water and benthic-derived nutrients at undredged sites to reliance on phytoplankton and terrestrial detritus at deep-water dredged sites. Relative trophic positions were also lower at dredged sites for many species; loss of benthic nutrient pathways associated with depth and dredging history is hypothesised.

6. The combination of ecological metrics and stable isotope analysis thus shows how anthropogenic habitat loss caused by gravel dredging can decrease benthic fish abundance and diversity, and that species in substratum-specific reproductive guilds are at particular risk. The effects of dredging also manifest by altering resource use and nutrient pathways within food webs. Management and conservation decisions should therefore consider the protection of relatively shallow areas with suitable substratum for spawning for the protection of native fishes.

Keywords: habitat alteration, nutrient pathways, reproductive guilds, sedimentation, stable isotope analysis

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Correspondence: Jonathan A. Freedman, Illinois Natural History Survey, Kaskaskia Biological Station, Sullivan, IL 61951, U.S.A.
E-mail: freedjon@illinois.edu

Introduction

Understanding and untangling the complex effects of human activities on aquatic ecosystems present a challenge to ecologists and resource managers (e.g. Hooper *et al.*, 2005). Habitat loss and degradation have been identified as leading threats to global freshwater biodiversity (Maitland, 1995; Burkhead *et al.*, 1997; Dudgeon *et al.*, 2006); however, such anthropogenic activities provide opportunities as proxies for large-scale manipulative experiments. In-stream substratum removal by dredging or mining are common anthropogenic disturbances in freshwater systems throughout the world (e.g. Kanehl & Lyons, 1992; Meador & Layher, 1998; Davis *et al.*, 2000; Rovira, Batalla & Sala, 2005; Rempel & Church, 2009). While the physical impacts of in-stream substratum removal have been relatively well studied, less is known about the ecological impacts of mining and dredging, particularly on large river fish assemblages (Rempel & Church, 2009).

In-stream removal of substratum affects the physical characteristics of the river as the channel is modified, creating relatively homogenous, deep reaches (Kanehl & Lyons, 1992; Kondolf, 1997; Gob *et al.*, 2005). The removal of coarse gravel and cobble increases river depth, and subsequent accumulation of fine sediment and detritus can thus greatly alter habitat characteristics required by aquatic organisms (Brown, Lyttle & Brown, 1998; Kondolf, 2000; Milner & Piorkowski, 2004; Rinaldi, Wyzga & Surian, 2005). Subsequent bank erosion and head-cutting (the erosion of the upstream end of the dredged area) can also result, further homogenising the aquatic habitat and increasing the loss of littoral and shallow habitats (Kanehl & Lyons, 1992; Rinaldi *et al.*, 2005). Habitat structure for invertebrates and fish is lost as gravel and rocks, coarse woody debris and other structure are removed, and macrophyte beds are destroyed. Increased depth, compounded by turbidity, reduces light penetration to the river bottom and can thus reduce biomass and diversity of submerged vegetation and algae (Rivier & Seguier, 1985), thus altering nutrient dynamics. Changes in substratum composition reduce collector-gatherer and grazer trophic guilds of invertebrates living among rocks while increasing shredders and decomposers burrowing within sediments and terrestrial detritus, thus altering not only invertebrate assemblage composition, but also fish foraging efficiency and habitat use (Harvey, 1986; Brown *et al.*, 1998; Rempel & Church, 2009).

Many fish taxa depend on structured habitats for protection from predators and as refugia from the current (Kanehl & Lyons, 1992). Lithophilic ('rock-loving') spe-cies, such as many darters (Percidae: Etheostomatini) and salmonids (Salmonidae), require rocky and gravel habitats in which to spawn (Page, 1983; Newcombe & Macdonald, 1991; Newcombe & Jensen, 1996; Simon, 1998). The loss of this habitat, as well as increased sedimentation rates due to dredging, can render habitats unsuitable for reproduction even if adults are able to survive (Harvey, 1986; Berkman & Rabeni, 1987). Increased turbidity thus alters fish foraging ability (Cahn, 1929; Abrahams & Kattenfeld, 1997), while high sedimentation can affect spawning (Newcombe & Macdonald, 1991; Newcombe & Jensen, 1996). Species that are tolerant of a range of environmental conditions (eurytopic species) then come to dominate the community in what can be viewed as a form of species regime shift (Kanehl & Lyons, 1992; Brown *et al.*, 1998; Paukert *et al.*, 2008). Small benthic fishes are especially susceptible to anthropogenic disturbances (Angermeier, 1995; Maitland, 1995; Burkhead *et al.*, 1997), but less is generally known about their life-history requirements and distribution relative to adult species, particularly in large rivers.

Assessing direct effects of large-scale disturbances on fish assemblages by presence/absence and relative abundance can be informative, but may reveal little about behavioural and ecological shifts within the community mediated by dredging. Stable carbon isotope signatures (δ^{13}C) vary across different taxa of primary producers, as well as in response to differences in environmental variables such as depth and water velocity (Vander Zanden & Rasmussen, 1999; Post, 2002). Signatures of stable nitrogen isotopes (δ^{15}N) increase with water depth and are enriched at a relatively constant rate (2–5‰, mean 3.4‰) across trophic levels and are therefore used to estimate trophic position (Vander Zanden & Rasmussen, 1999; Post, 2002; Vanderklift & Ponsard, 2003). While stable isotope analysis has been used to gain insights into biotic changes that occurred as a response to anthropomorphic stress, such research has focussed on point- and non-point-source additions to aquatic environments (e.g. Costanzo *et al.*, 2001; Vadeboncoeur *et al.*, 2003; Gray, Cunjak & Munkittrick, 2004; Vander Zanden *et al.*, 2005), but has rarely been combined with the assessment of community metrics (e.g. Freedman, Curry & Munkittrick, in press). Because of this ability to differentiate food sources and detect the changes in trophic positions, stable isotope analysis can also be used to detect the effects of large-scale physical alterations such as dredging on nutrient flow and resource availability.

Most prior studies of the effects of dredging on fish have been conducted in streams and shallow rivers. The effects of dredging on deeper rivers, however, where

methods such as electroshocking, gill nets and seines are ineffective for sampling the channel (Koryak *et al.*, 2008; Freedman, 2010), are unknown. We therefore used an electrified benthic trawl (Freedman *et al.*, 2009) to sample benthic fish assemblages at dredged and undredged sites in a deep, gravel-bed river with a long history of dredging. Unlike streams and shallow rivers, a greater proportion of energy flow in large rivers results from autochthonous sources (Vannote *et al.*, 1980; Finlay, 2001); furthermore, large rivers are complex ecosystems containing unique fish communities that cannot be understood simply by 'scaling-up' the findings from lower-order streams and rivers.

Our objectives therefore were to determine how benthic fish assemblages, nutrient dynamics and resource use differ between deep dredged sites and shallow undredged sites in a large river system. We predicted that there would be lower abundance and diversity of fishes at dredged sites, expecting to see the greatest differences in small, benthic species and those in lithophilic reproductive guilds. To examine the differences in nutrient dynamics and resource use by benthic fish assemblages from undredged and dredged sites, we used stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$. We expected that fishes from dredged sites would have lower reliance on littoral and benthic nutrient pathways (^{13}C-enriched) commensurate with the loss of shallow habitat and increased turbidity reducing benthic productivity, with subsequent increase in reliance on pelagic nutrients and terrestrially derived sources (^{13}C-depleted) including fine particulate organic matter (FPOM) and detritus that accumulate in the deep holes. We also predicted that due to simpler food webs and fewer trophic linkages, fish from dredged sites would feed at lower relative trophic positions than conspecifics from undredged sites. Combining traditional ecological metrics and stable isotope analysis will thus better inform management decisions by improving our resolution for examining the effects of large-scale habitat alteration on large river fish assemblages.

Methods

Study area

We selected the Allegheny River for this study due to its long history of intensive gravel dredging that modified much of the river into long deep reaches. The Allegheny River flows 523 km from its headwaters in Pennsylvania, into New York State, before flowing in a generally southerly direction back into Pennsylvania, where at its confluence with the Monongahela River in Pittsburgh it forms the Ohio

River. Controlled by a series of lock-and-dam structures, the lower 113 km of the Allegheny River maintains a minimum depth of *c.* 4 m (Argent & Kimmel, 2011). Glacial alluvial gravel and rocks comprise the dominant substratum in the Allegheny River, and commercial gravel-dredging operations have operated in seven of the nine navigation pools for decades (Smith & Meyer, 2010). Mean discharge of the Allegheny River at Lock and Dam 7 in Kittanning PA is 455 m^3 s^{-1} (USGS Gauging Station 03036500; river kilometre 73.2). We sampled within Navigation Pools 7 and 8 of the Allegheny River, located between river kilometres 75.3–99.9 (N 40.83732, W 79.53012 to N 40.95537, W 79.54904; Fig. 1). These pools were selected because they have been intensively dredged yet contain sufficient undredged habitat for use as reference sites and, relative to downstream pools, they are subject to fewer cumulative anthropogenic effects, thus minimising potential confounding variables. Sampling sites were selected based on depth profiles within the navigation pools: since definitive dredging history was unavailable, we defined dredged sites those with maximum depths of at least 10 m. We used bathymetric profiles captured by side-scan sonar to examine the river bottom for deep areas with a 'scalloped' pattern characteristic of the clamshell-style grab dredging used for gravel extraction in the Allegheny River. Observed mean and maximum pool depths at normal flow were *c.* 1 m and 3–4 m, respectively, above the influence of navigation dams (J. A. Freedman, pers. obs.). Undredged 'reference' sites were areas at which dredging was not permitted – below dams and under bridges – and a short section of river that had not been dredged. Maximum depths of dredged sites were between 10.4 and 15.2 m (mean 11.8 m ± 2.3 m SD), while those of undredged sites ranged from 3.2 to 7.7 m (4.9 m ± 1.7 m).

Fish community sampling

To sample diversity of small benthic fishes, we conducted 10, 2-min electrified benthic trawls (PSU trawl sensu Freedman *et al.*, 2009) at each of five undredged and four dredged sites, from 13 to 15 July 2009 (Fig. 1). Analysis of species saturation data showed that at eight of the sites, seven trawls were required to provide maximum species richness, while at one site an additional species was captured in the tenth trawl sample. Two sites were located immediately below dams and had no history of gravel dredging; three sites were located away from dams and had not been dredged; and four sites had been dredged. The PSU trawl is a modified Missouri trawl (Herzog *et al.*, 2005) with a 2.44-m headrope, weighted otter-boards, a
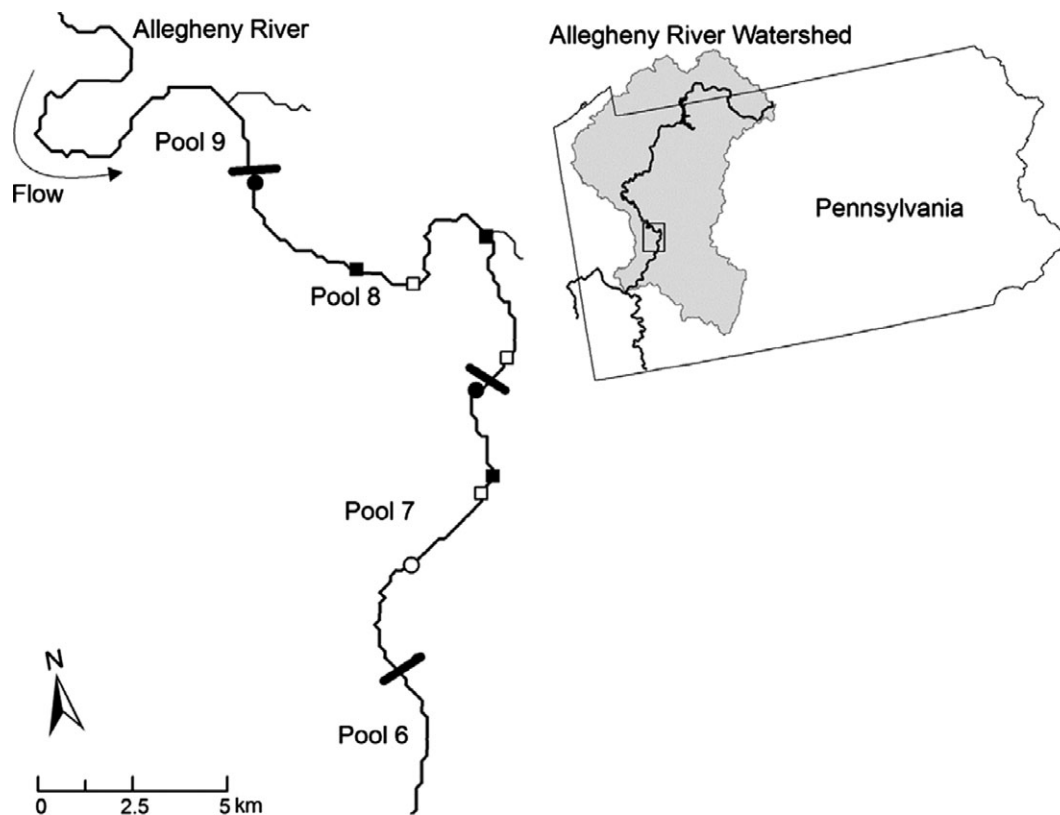
Fig. 1 Map of the Allegheny River, Pennsylvania, U.S.A. Squares represent sites sampled for both stable isotopes and community metrics, while sites indicated by circles were sampled only for community metrics. Shaded symbols in Navigation Pools 7 and 8 represent undredged sites, while open symbols are dredged sites; solid cross-bars indicate navigation lock and dams. The Allegheny River catchment (shaded) and the study area (box) are delineated in the inset map.

19.05-mm inner mesh bag and 4.76-mm outer mesh bag manufactured by Innovative Net Systems (Milton, LA, U.S.A.). The trawl was modified by adding a cathode–anode electrical array connected to a Smith-Root Type VI-A electrofishing shock box. The trawl was towed with the current twice along each bank, twice in the centre channel and twice each to the right and left of the mid-channel. Tow-line length was adjusted for water depth. The crew monitored the tow lines by feeling for bumps and tugs characteristic of the trawl being in contact with the substratum, to ensure that it remained on the bottom. If the trawl was not dragging the bottom, or was twisted or snagged, the sample was discounted and the trawl was redeployed. Where possible, all fishes were identified to species in the field; representative samples of smaller species and juveniles were retained for laboratory verification and as voucher specimens; photo vouchers were also taken. Lamprey ammocoete larvae (*Ichthyomyzon spp.* and *Lampetra* spp.) were not identifiable to species and were thus grouped as ammocoete larvae.

Stable isotope sampling

For stable isotope analysis, we sampled three undredged sites and three dredged sites during early autumn, 2007 (Fig. 1). Fishes from each site were sampled at three habitats, defined as (i) near-shore, (ii) near-channel and (iii) mid-channel, and were collected using both Missouri- and PSU-benthic trawls (minimum of two trawls at each habitat) and 10-m-long, 5-mm mesh beach-seines pulled along the bank. All fishes were identified to species, and the total length was measured (mm). Minnows of the genus *Notropis* were not definitively identified to species prior to processing and were thus grouped together as shiner spp. for the stable isotope analysis. Several individuals of each fish species (to compensate for inherent interindividual variability), and of a range of sizes when available, were sampled for stable isotope analysis. White muscle tissue was used where possible 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). This meant that the stable isotope signatures of the fish were representative of fish diets in mid- to late summer, thus complementing the timing of our fish community sampling. Fillets were taken from larger fishes, while for the smallest individuals (<30 mm), samples consisted of whole or decapitated and gutted fishes. Fish samples were immediately frozen until processing in the laboratory.

All samples were prepared as follows: each sample was placed into a clean glass vial and dried in an oven at 60 °C for 24–48 h and then homogenised to a fine powder using mortar and pestle, or within the vial using a glass stirring rod. Samples were weighed into 0.2 mg (±10%) aliquots, placed into 5-mm × 3.5-mm tin capsules and analysed for $\delta^{13}C$ and $\delta^{15}N$ 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 $\delta^{15}N$ and $\delta^{13}C$ were calculated using the formula:

$$\delta X = [(R_{sample}/R_{standard}) - 1 \times 1000$$

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 that for carbon is carbon dioxide derived from calcium carbonate in the Pee Dee Bee formation of South Carolina (PDB). Lipids are rich in carbon relative to other tissues; therefore, variable tissue lipid contents among samples can increase overall variability of samples. To account for this, we used a lipid correction factor that uses the C : N ratio to standardise lipid content across samples (Post *et al.*, 2007). Standard deviations of isotopic standards were 0.15‰ for $\delta^{13}C$ and 0.24‰ for $\delta^{15}N$, for elemental standards ranged from 0.13 to 0.15‰ for $\delta^{13}C$ and 0.14 to 0.25‰ for $\delta^{15}N$, and for biological standards ranged from 0.11 to 0.14‰ for $\delta^{13}C$ and from 0.12 to 0.14‰ for $\delta^{15}N$. A subset of samples were replicated and varied by an average of 0.22‰ for $\delta^{13}C$ and 0.19‰ for $\delta^{15}N$, with standard deviations of 0.24 and 0.18‰, respectively.

Data analysis

We used linear mixed-effects models to account for the hierarchical sampling design of multiple benthic trawls at each site. We used the lme4 package (Bates, Maechler &

Bolker, 2011) for R 2.8.1 (R Development Core Team, 2008) to test the effects of dredging and depth on total catch, species richness, Brillouin Index diversity and proportion of lithophilic species (those in lithophilic or 'rock-loving' reproductive guilds) among trawl samples. Each data point represents one-two-minute trawl sample, nested within sites which were categorised as dredged or undredged. The linear mixed-effects model used in the analyses was

$$Y_{ij} = \beta_0 + \beta_1 Depth_{ij} + \beta_2 Dredged_{ij} + b_{ij} + \varepsilon_{ij}$$

where Y_{ij} is the catch, species richness, Brillouin diversity or proportion of lithophilic species from Trawl j at Site i. β_0 is the fixed intercept, while β_1 and β_2 are coefficients for the fixed effects of depth and dredged, respectively; b is the coefficient for the random effect of site, and ϵ is the error term for the model. Likelihood ratio tests were used to compare model fit between the full model and reduced models which excluded either dredged or depth effects. Significant increase in the likelihood ratio test at $P < 0.05$ indicates that the excluded effect is significant and should be retained in the model.

To assess whether the reproductive guild is a factor in determining which fish are more susceptible to dredging, and thus structuring fish assemblages, we used established reproductive guilds from Simon (1998; Table 1). Because we hypothesised that small fishes that breed in and around gravel and rocks ('lithophilic species') are most susceptible to gravel dredging, we calculated the proportion of the catch in each trawl that was composed of lithophilic brood hiders, open substratum and substratum chooser reproductive guilds. The relative abundances of fishes in different reproductive guilds between dredged and undredged sites were analysed using principal components analysis (PCA) in the ade4 package (Dray & Dufour, 2007) and a multivariate analysis of variance (MANOVA) in R 2.8.1. Graphs were made in SigmaPlot 12.0 (Systat, 2011).

We used circular statistics (Schmidt *et al.*, 2007) to assess the differences in fish stable isotope signatures by assessing directional changes from undredged to dredged sites, using the software package Oriana 3.0 (Kovach Computing Services 2009). For circular statistics, the stable isotope data are transformed into linear vectors for each fish species, with an origin that is standardised as 0, $\delta^{13}C$ is plotted on the *X*-axis, with ^{13}C-depletion (indicative of pelagic and terrestrial carbon sources) to the left (270°) and ^{13}C-enrichment (littoral and shallow benthic carbon sources) to the right (90°). $\delta^{15}N$ is plotted on the *Y*-axis, with ^{15}N-enrichment (higher trophic level) at 0° and

Table 1 Reproductive guilds of fish species captured during benthic trawling in the Allegheny River, Pennsylvania, U.S.A.

Family and scientific name	Common name	Reproductive guild
Petromyzontidae		
Petromyzon or *Ichthyomyzon* spp.	Lamprey species ammocoete larvae	Brood Hider – Lithophil
Cyprinidae		
Erimystax dissimilis (Kirtland)	Streamline chub	Open Substratum – Lithophil
Notropis volucellus (Cope)	Mimic shiner	Open Substratum – Phytophil
Pimephales notatus (Rafinesque)	Bluntnose minnow	Nest Spawner – Speleophil
Catostomidae		
Catostomidae spp.	Sucker larvae	Open Substratum – Lithophil
Ictiobus bubalus (Rafinesque)	Smallmouth buffalo	Open Substratum – Lithopelagophil
Moxostoma carinatum (Cope)	River redhorse	Open Substratum – Lithophil
Moxostoma erythrurum (Rafinesque)	Golden redhorse	Open Substratum – Lithophil
Moxostoma macrolepidotum (Lesueur)	Shorthead redhorse	Open Substratum – Lithophil
Ictaluridae		
Ictalurus punctatus (Rafinesque)	Channel catfish	Nest Spawner – Speleophil
Noturus flavus Rafinesque	Stonecat madtom	Nest Spawner – Speleophil
Pylodictis olivaris (Rafinesque)	Flathead catfish	Nest Spawner – Speleophil
Percopsidae		
Percopsis omiscomaycus (Walbaum)	Trout-perch	Open Substratum – Lithophil
Moronidae		
Morone chrysops (Rafinesque)	White bass	Open Substratum – Phytolithophil
Centrarchidae		
Ambloplites rupestris (Rafinesque)	Rockbass	Nest Spawner – Polyphil
Lepomis macrochirus Rafinesque	Bluegill sunfish	Nest Spawner – Polyphil
Micropterus dolomieu Lacepède	Smallmouth bass	Nest Spawner – Polyphil
Percidae		
Etheostoma blennioides Rafinesque	Greenside darter	Substratum Chooser – Phytophil
Etheostoma caeruleum Storer	Rainbow darter	Brood Hider – Lithophil
Etheostoma camurum (Cope)	Bluebreast darter	Substratum Chooser – Lithophil
Etheostoma flabellare Rafinesque	Fantail darter	Nest Spawner – Speleophil
Etheostoma nigrum Rafinesque	Johnny darter	Nest Spawner – Speleophil
Etheostoma tippecanoe Jordan & Evermann	Tippecanoe darter	Substratum Chooser – Lithophil
Etheostoma variatum Kirtland	Variegate darter	Substratum Chooser – Lithophil
Etheostoma zonale (Cope)	Banded darter	Substratum Chooser – Phytophil
Perca flavescens (Mitchill)	Yellow perch	Open Substratum – Phytolithophil
Percina caprodes (Rafinesque)	Logperch darter	Brood Hider – Lithophil
Percina copelandi (Jordan)	Channel darter	Brood Hider – Lithophil
Percina evides (Jordan & Copeland)	Gilt darter	Brood Hider – Lithophil
Percina macrocephala (Cope)	Longhead darter	Brood Hider – Lithophil
Sander vitreus (Mitchill)	Walleye	Open Substratum – Lithopelagophil
Scianidae		
Aplodinotus grunniens Rafinesque	Freshwater drum	Open Substratum – Pelagophil

^{15}N-depletion (lower trophic level) at 180°. We defined the origin as being the site with the least anthropogenic disturbances (undredged), while the distal end of the vector represents the impacted site (dredged). 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 ($P < 0.05$) to test whether the distribution of vectors was random or uniform, and thus whether there was a consistent shift in resource use (δ^{13}C and δ^{15}N signatures) across species between undredged and dredged sites.

Results

Fish abundance and diversity

In 90 trawls, we captured 5942 fishes comprising at least 32 species (Table 1). There was a negative correlation between total catch and depth ($P < 0.05$), but there was no

Table 2 Mixed-model likelihood ratio tests (LRTs) comparing full and reduced models that exclude the fixed effects (depth or dredging)

Response	Reduced model	LRT	d.f.	P
Total catch	Excluding depth	19.08	1	<0.01
	Excluding dredged	0.11	1	0.74
Species richness	Excluding depth	25.44	1	<0.01
	Excluding dredged	11.32	1	<0.01
Brillouin's diversity	Excluding depth	21.24	1	<0.01
	Excluding dredged	19.55	1	<0.01
Proportion of lithophils	Excluding depth	0.85	1	0.36
	Excluding dredged	9.92	1	<0.01

P-values <0.05 indicate that depth or dredging has a significant effect on that response variable for benthic fish communities in the Allegheny River, Pennsylvania, U.S.A.

significant relationship between dredging and total catch (*P* > 0.05; Table 2 and Fig. 2). Species richness and Brillouin diversity each declined with depth (both *P* < 0.05) and were both lower at dredged sites (both *P* < 0.05). The proportion of lithophils was also significantly lower at dredged sites (*P* < 0.05), but there was no relationship between proportion of lithophils and depth (*P* > 0.5; Table 2 and Fig. 2). Deeper trawls thus caught fewer fishes and species, contributing to lower taxonomic diversity in these samples. Regardless of depth, the

relative absence of lithophilic species, such as most darters, and selected minnow species such as streamline chub, *Erimystax dissimilis*, seems to be driving lower species richness and diversity at dredged sites. Total catch at dredged sites appears to be compensated by an increase in tolerant species such as catfishes (channel catfish, *Ictalurus punctatus*, and flathead catfish, *Pylodictus olivaris*), freshwater drum, *Aplodinotus grunniens*, and Johnny darter, *Etheostoma nigrum*.

Reproductive guild composition of fish assemblages differed between undredged and dredged sites (MANOVA; *F* = 9.05, *P* < 0.05; Table 3). Brood hider lithophils, substratum chooser lithophils and substratum chooser phytophils reproductive guilds were significantly more abundant at undredged sites (all *P* < 0.05; Table 3) and were associated with principal component 1 axis (PC1), which accounted for 24.5% of the variation (Table 3 and Fig. 3). Principal component 2 axis (PC2; 16.6% of variation) did not reveal such strong differences between dredged and undredged sites, although nest spawner speleophils and open substratum lithophils and phytophils were associated with dredged sites (all *P* < 0.05; Table 3). Although MANOVA and PCA gave similar results, PC1 and PC2 accounted for just 41.1% of variation in reproductive guilds, and so inference solely from PCA may be limited. None of the other reproductive guilds were significantly different between undredged and dredged sites (all *P* > 0.05; Table 3).
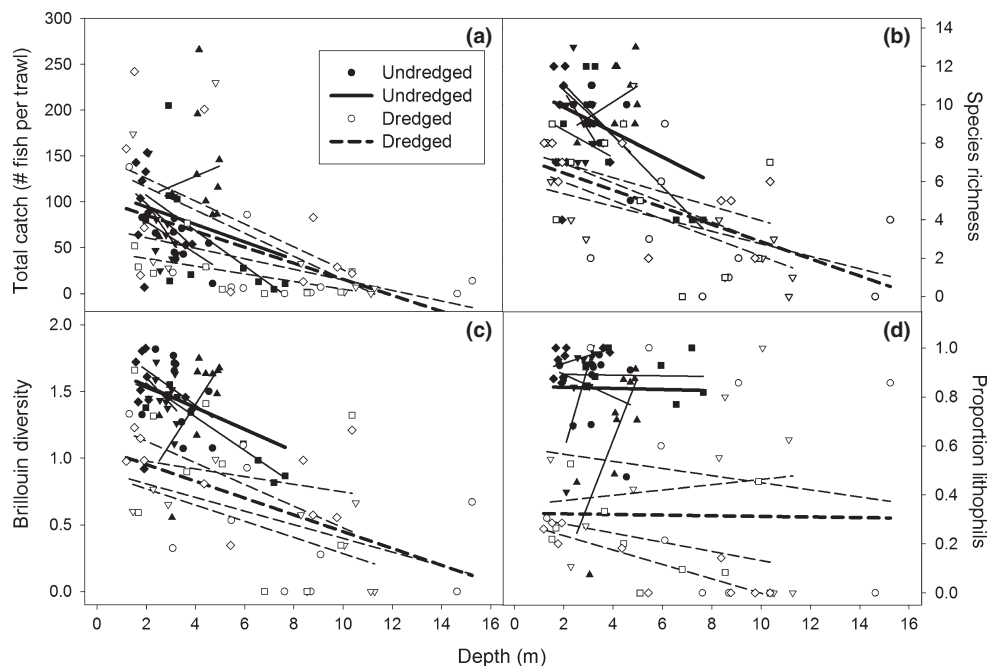

Fig. 2 (a) total catch per trawl, (b) number of species per trawl, (c) Brillouin Index diversity per trawl, (d) Proportion of total catch per trawl consisting of lithophilic substratum choosers and brood hiders, at five undredged (closed symbols and solid lines) and four dredged sites (open symbols and dashed lines) in the Allegheny River, Pennsylvania, U.S.A. Each data point represents one trawl sample, and each light regression line represents one site; solid and dashed bold lines represent means of all undredged and dredged sites, respectively.

Table 3 Results from principal components analysis and MANOVA of distribution of common fish reproductive guilds at undredged and dredged sites in the Allegheny River, Pennsylvania, U.S.A.

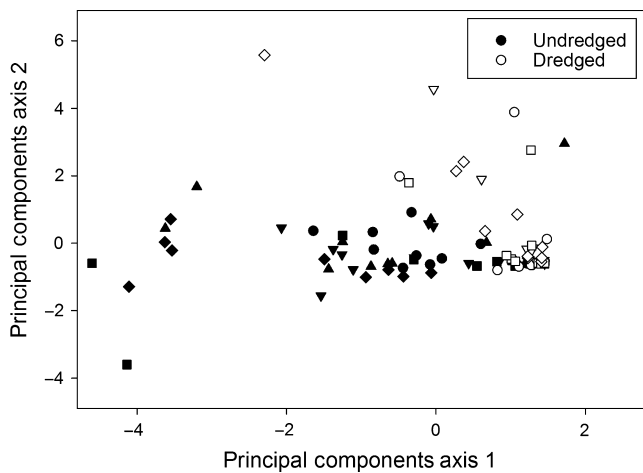| Reproductive guild	Principal components		MANOVA	
	PC1	PC2	*F*	*P*
Nest spawner polyphil	−0.17	0.32	1.06	0.31
Nest spawner speleophil	−0.04	0.62	8.17	<0.01
Open substratum lithopelagophil	−0.26	−0.20	0.02	0.89
Open substratum lithophil	−0.27	0.41	10.89	<0.01
Open substratum pelagophil	−0.18	−0.23	0.04	0.84
Open substratum phytolithophil	0.09	0.26	2.37	0.13
Open substratum phytophil	0.05	0.37	5.77	<0.05
Brood hider lithophil	−0.57	0.13	14.31	<0.01
Substratum chooser lithophil	−0.50	−0.10	19.64	<0.01
Substratum chooser phytophil	−0.46	−0.17	15.87	<0.01
% Variation	24.5	16.6		
Cumulative % variation	24.5	41.1		

Fig. 3 Principal components analysis of relative composition of reproductive guilds (see Table 3) from benthic trawl samples of five undredged (closed symbols) and four dredged (open symbols) sites in the Allegheny River, Pennsylvania, U.S.A. Each site is represented by a unique symbol.

Trends in stable isotope signatures

Most fish species from dredged sites had ^{13}C-depleted signatures relative to undredged sites, consistent with higher reliance on pelagic and deep-derived nutrients rather than on shallow or benthic-derived nutrients (Figs 4 & 5). The fish assemblages from undredged sites included a wider range of δ^{13}C consistent with being supported by a range of nutrient sources, while those from dredged sites were more heavily influenced by pelagic and deep-derived nutrients (Fig. 4). Shifts in δ^{13}C were not consistent, although fish species trended
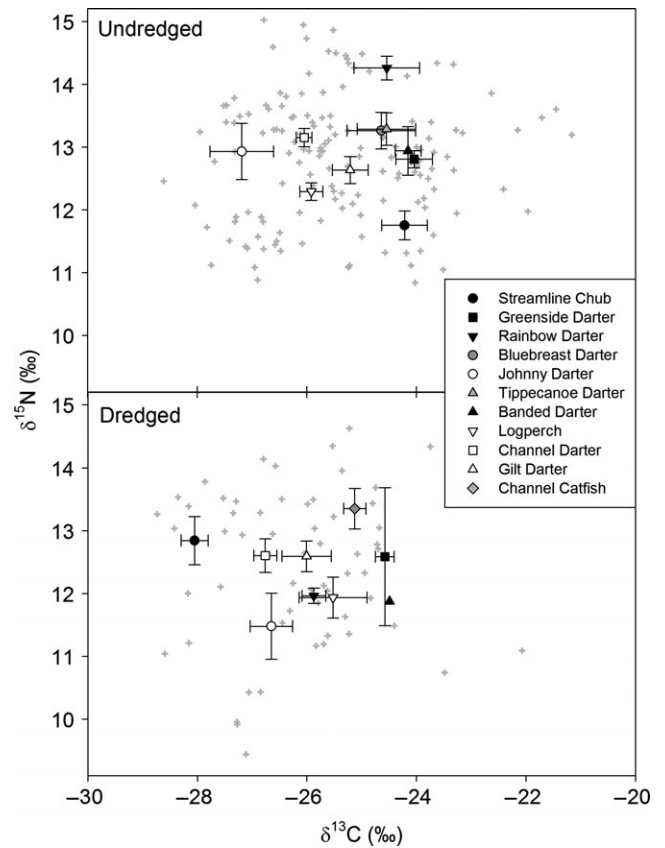

Fig. 4 Stable isotope cross-plots of δ^{13}C and δ^{15}N for benthic fishes at three dredged and three undredged sites in the Allegheny River, Pennsylvania, U.S.A. Symbols indicate mean stable isotope values for fish species pooled across three replicate sites, and error bars indicate 1 standard error; grey crosses represent stable isotope values of individual fish.

towards increased reliance on pelagic nutrients. Minnows (streamline chub, vector length 3.99 and shiner species, mean vector length 1.82; Table 4) had strong shifts towards ^{13}C-depleted nutrients and slight increases in trophic position at dredged relative to undredged sites. The relative magnitude of these shifts suggests that these minnows are feeding on pelagic or profundal resources in deep areas at dredged sites. Both large and small (vector lengths 0.94 and 0.23, respectively; Table 4) logperch, *Percina caprodes*, had more reliance on shallow nutrients at dredged than at undredged sites with only slight decreases in trophic position, suggesting that they may have moved inshore to feed. Rainbow darter, *Etheostoma caeruleum* (vector length 2.66), and young-of-year smallmouth bass, *Micropterus dolomieu*, and bluegill, *Lepomis macrochirus* (vector lengths 1.58 and 0.86, respectively; Table 4), were similar to the mean. There was a negative trend in fish species δ^{15}N from undredged to dredged sites (Figs 4 & 5); fish species (mean vector length: 0.53,
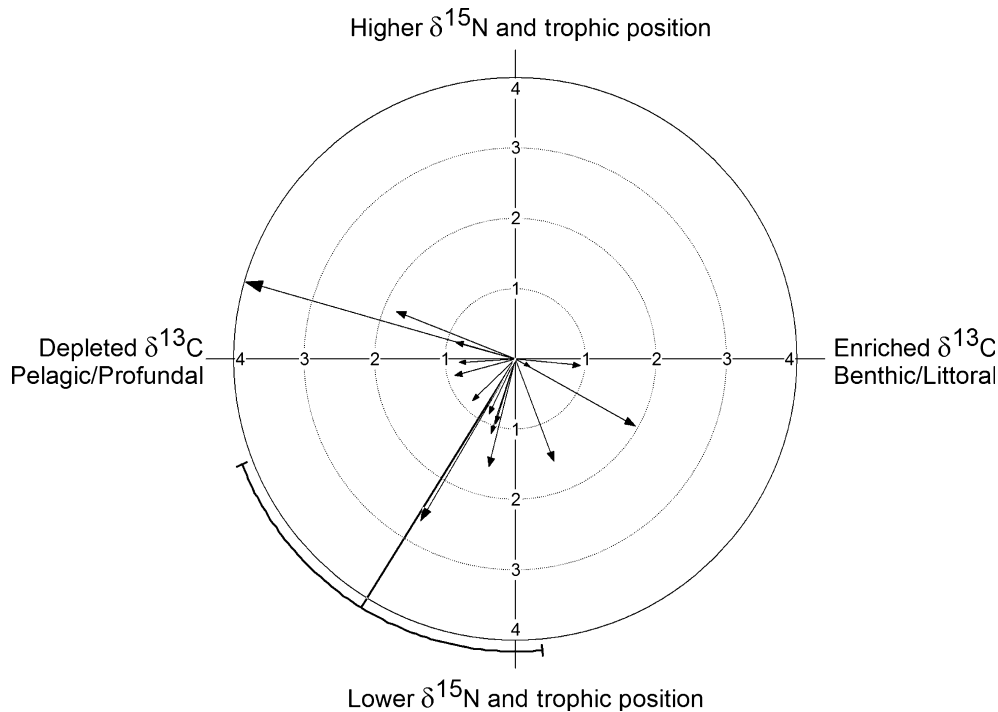
Fig. 5 Circular distribution plot of directional food-web changes of fish species from undredged to dredged sites in the Allegheny River, Pennsylvania, U.S.A. Each vector represents a fish species or size-class pooled across three replicate undredged and dredged sites (Table 4); the arrows indicate the direction in trophic niche space that the species or size-class moved, while the lengths indicate the relative magnitude of directionality from undredged to dredged sites. Vector directionality towards the top of the plot represent higher δ^{15}N (higher trophic position), while the bottom of the graph represents lower δ^{15}N (lower trophic position), and to the left and right are depleted and enriched δ^{13}C (pelagic/profundal and benthic/littoral carbon sources), respectively. The line at the circumference of the plot represents the 95% confidence interval around the mean.

mean vector angle: 211.8°, Rayleigh's test, $P < 0.05$) had significantly lower mean δ^{15}N values at dredged relative to undredged sites (Table 4, Fig. 5).

Discussion

There were declines in both species richness and diversity of benthic fishes at dredged sites. This could potentially be due to the lack of suitable spawning habitat, or decreased food availability or foraging efficiency (Harvey, 1986; Berkman & Rabeni, 1987; Kanehl & Lyons, 1992; Paukert *et al.*, 2008). While in the short term gravel dredging can increase sedimentation rates (Rivier & Seguier, 1985), longer-term consequences can be significant. Macroinvertebrate assemblages in dredged streams were significantly different from reference streams (lower abundance, biomass and community evenness), even >50 years later (Milner & Piorkowski, 2004). Restoration of gravel bars used by salmonids as spawning substratum has benefits to macroinvertebrate communities, with restored sites equalling and even surpassing unenhanced sites within

Table 4 Changes (vector angles) and magnitude of change (vector lengths) in stable isotope signatures representing resource use of fish species between undredged and dredged sites in the Allegheny River, Pennsylvania, U.S.A., from circular statistics analysis of stable isotope data in Fig. 5 (0°: higher trophic position; 90°: benthic/littoral nutrients; 180°: lower trophic position; 270°: pelagic/profundal nutrients)

Common name	Vector angle	Vector length
Streamline chub	286.0	3.99
Shiner species	291.6	1.82
Brook silverside	119.3	1.96
Bluegill	205.4	0.86
Smallmouth bass	194.0	1.58
Greenside darter <40 mm	196.9	0.96
Greenside darter >40 mm	285.1	0.88
Rainbow darter	210.2	2.66
Johnny darter	159.6	1.55
Banded darter	197. 8	1.11
Logperch <50 mm	118.8	0.23
Logperch >50 mm	96.1	0.94
Channel darter <30 mm	225.5	0.86
Channel darter >30 mm	254.4	0.89
Gilt darter	267.1	0.80
Mean vector	211.8	0.53

weeks (Merz & Ochikubo Chan, 2005), although it should be noted that this study dealt with habitat augmentation rather than removal.

We found declines in fish species richness and diversity with increasing depth that were likely driven by sharp declines in substratum chooser and brood hiding species, while at dredged sites there was a higher relative proportion of open substratum and nest spawning species. Substratum choosers, including many darters, lay and guard eggs in or on specific substrata, such as gravel and rocks or macrophytes; brood hiders are similar, but do not have parental care (Simon, 1998). Open substratum spawners broadcast ova and sperm over the substrata and have no parental care of either the eggs or young; these reproductive guilds include many sucker species as well as freshwater drum and were more abundant at dredged sites. Nest spawners such as catfishes and Johnny darter that build and guard nests and have parental care were more abundant at dredged sites, possibly due to softer substratum (such as detritus and leaf litter) that would be easier to excavate. Rivier & Seguier (1985) found three stages of changes in fish assemblages due to stream dredging: (i) reduction in lotic species, and an increase in lentic species; (ii) reduction in lithophilic species; (iii) decline in overall diversity, with a fish assemblage dominated by eurytopic (able to tolerate a range of environmental conditions) generalist, silt-tolerant and deeper-water species. Lower abundance and diversity of lithophilic species were also found in stream fishes in Missouri and were largely attributed to increased siltation (Berkman & Rabeni, 1987).

During SCUBA surveys, we found thick layers of fine sediments and organic detritus at dredged sites (J. A. Freedman, J. R. Stauffer, pers. obs.). Given that sedimentation has detrimental effects on the survival of fish eggs and larvae in coarse gravel (Cordone & Kelly, 1961; Newcombe & Macdonald, 1991; Kondolf, 2000), the loss of suitable habitat for reproduction likely reduced the proportion of lithophils, and thus fish diversity, at dredged sites. Shallow trawl samples near the banks at dredged sites had lower species richness and diversity than equivalent depths at undredged sites. Because dredging is restricted from near-shore areas, we did not expect to see direct effects of dredging on these habitats. Since the near-bank sites at dredged and undredged sites comprise similar shallow habitats, lower diversity may best be explained by changes in water flow and subsequent effects on nutrient dynamics and sediment flow as it is channelled into the centre of the river away from the banks (Kondolf, 1997; Rinaldi *et al.*, 2005; Rempel & Church, 2009).

We caught fewer fish in deeper waters than in shallow waters; however, it is important to consider whether this could be the result of sampling bias if benthic trawls were less effective or altered detection probability in deeper water. We used longer tow lines while sampling deeper habitats (*per* Herzog *et al.*, 2005), and during all trawl samples, researchers monitored the tow-ropes to ensure that they were feeling 'tugs' and 'bumps' indicative of dragging along the river bottom. Many of our benthic trawls across all depths contained substratum material and/or benthic macroinvertebrates, indicating that the trawls were indeed sampling benthic habitats. If the trawl was twisted upon retrieval, or may not have been dragging the bottom, we discounted it and redeployed the trawl. We attempted to verify our trawl data by conducting video transects by SCUBA divers at all sites; however, this proved impossible at dredged sites where visibility was <10 cm below 8 m depth due to turbidity; however, at shallow sites, we did observe the same fish species that were present in the trawl samples (J. A. Freedman, J. R. Stauffer, pers. obs). To test whether false absences, or non-detection of species that are actually present, could have affected our results, we simulated the effects of the detection of additional species on our data. Detection of either one or two additional species increased Brillouin diversity at each site by an average of 0.08 (SD ±0.07) and 0.15 (±0.13), respectively. Average observed Brillouin diversity was 1.43 (±0.28) for undredged sites and 0.68 (±0.47) for dredged sites so, even if there was differential detection probability between dredged and undredged sites, false absences are unlikely to have significantly altered our results.

Stable isotope data suggest that fishes at dredged sites generally consumed more pelagic-derived nutrients, while their conspecifics at undredged sites relied more on benthic-derived nutrients. Exceptions included littoral taxa such as young-of-year smallmouth bass and bluegill that we expected would be less influenced by dredging than benthic species. It is therefore not surprising that their $\delta^{13}C$ did not shift much, while their decline in trophic position may be indicative of short food chain length even in the littoral of dredged sites. Rainbow darters may also be living and foraging primarily in littoral areas and thus show similar signatures. These changes in food-web structure suggest a more limited nutrient pool and shifts in resources and habitat use by fishes at dredged sites in the Allegheny River.

This apparent nutrient limitation is consistent with our hypothesis that dredging reduces benthic productivity, mediated by lower light penetration due to the interaction of increased depth with turbidity, and a decrease in

suitable habitat for periphyton to colonise. Site surveys by SCUBA diving revealed that there was zero light penetration beyond 8–10 m depth, with thick layers of fine sediment and detritus covering the substratum at dredged sites; undredged sites had light penetration to the river bottom and relatively low embeddedness (J. A. Freedman, J. R. Stauffer, pers. Obs.). Highly embedded substrata alter invertebrate community compositions from vulnerable prey to invulnerable burrowing taxa, with related declines in fish growth and condition (Suttle *et al.*, 2004). Rivier & Seguier (1985) reported 54–94% declines in diatom populations and reduced densities of algae and plants as a result of dredging in the Doubs River in France, and attributed these changes to increased turbidity and sedimentation, decreased light penetration and changes to the substratum. These results are similar to shifts from benthic-driven primary production (e.g. periphyton) to pelagic-derived primary 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).

Fish $\delta^{15}N$ was generally lower at dredged sites relative to undredged sites. Enriched $\delta^{15}N$ is correlated with depth in lakes (Vander Zanden & Rasmussen, 1999); if fishes in the Allegheny River were feeding at a consistent trophic level (e.g. secondary consumers), they would therefore be expected to show a similar trend. Since fishes at dredged sites have lower relative $\delta^{15}N$, we can extrapolate that they are feeding at lower trophic levels at these sites. In effect, there is a simpler food web present within the dredged sites than within the undredged and free-flowing sites. Lower $\delta^{15}N$ at dredged sites is correlated with a decrease in species diversity and overall fish abundance and may be indicative of simpler food-web structure and reduced food chain length.

Macroinvertebrates of scraper–grazer feeding groups (Gastropoda: Bithyniidae) were only collected from undredged sites and were significantly enriched in ^{13}C (−20.97 ‰) relative to collector gatherers, which were similar from both dredged (−25.12 ‰) and undredged (−24.80 ‰) sites (Freedman, 2010). Filter-feeding bivalves (invasive *Corbicula fluminea* and *Dresisenna polymorpha*) had more negative $\delta^{13}C$ at dredged sites (−28.36 ‰) than at undredged sites (−26.02 ‰; Freedman, 2010). This may be due to increased consumption of suspended FPOM at the deep dredged sites or to differences in zooplankton isotopic

composition. $\delta^{13}C$ of terrestrial C4 leaves from the banks (*Salix* sp., −29.77 ‰ and *Acer* sp., −27.38 ‰) were more depleted in ^{13}C than that of detritus in the Allegheny River (−24.65 ‰; J. A. Freedman, unpubl. data), consistent with other studies that found terrestrial plants undergo significant enrichment in ^{13}C during decomposition (Finlay, 2001).

Stable isotopes revealed the differences in trophic structure between dredged and undredged sites. This is the first time stable isotope analysis has been used to determine the effects of dredging on lotic food webs, and is therefore supported as a valuable tool for assessing the impacts of such large-scale and long-term disturbances on fish assemblages. Furthermore, the significant patterns in fish stable isotope between dredged and undredged sites are evidence that these fish tend to feed within a site or habitat type. If fishes were frequently moving and feeding among habitats, we would expect a higher degree of homogenisation in stable isotope signatures among sites rather than the consistent directional changes that we observed (Fig. 5). While the proximate effects seen in this study were likely caused by turbidity and sedimentation, the ultimate cause of these patterns in fish diversity and food webs, and primary result of dredging, is increased depth. Prior studies of the effects of dredging have generally been conducted in shallower rivers, in part due to limitations of sampling gear for sampling small fishes in deeper habitats.

Benthic trawls capture different fish communities than boat electrofishing or gill nets, and have been used to replace or supplement these gears in large rivers (Koryak *et al.*, 2008; Freedman, 2010; Argent & Kimmel, 2011). Given that dredging is most likely to affect benthic, channel-dwelling species, the use of benthic trawls, and particularly electrified trawls, for determining the effects of dredging across all depths is therefore highly supported. Fish community response to sand dredging in the Kansas River showed higher fish diversity at sites that had been dredged 26 years earlier than at undredged sites, although most of this diversity was due to an increased prevalence of non-native and lentic species at the disturbed sites, while native lotic species declined (Paukert *et al.*, 2008). Fish community compositions in the undredged (control) sites were thus more similar over time than were the dredged sites. Irizarry (1969) found that areas on the Salmon River in Idaho, dredged 30 years earlier, produced 97% less biomass of trout and whitefish than undredged areas. Head-cutting and erosion of the sides of dredged holes and the bank may help to replenish the holes (Davis *et al.*, 2000), but only at the expense of shallow benthic habitat in the surrounding areas. In a study of gravel mining in Spain, Rovira *et al.* (2005) found that between 1956 and 1987

gravel was mined at 14 times the rate of replenishment. They calculated that, at the current rate of deposition, it would take up to 420 years for the river to recover to the pre-extraction bed level. Even as dredged areas are replenished, dams limit the transport of larger sediment such as gravel (Kondolf, 1997). This is consistent with the findings of Rinaldi *et al.* (2005) who found that the effects of gravel mining are especially difficult to reverse when the rate of gravel extraction greatly exceeds the rate of replenishment, and is compounded by other human activities reducing sediment delivery. Rinaldi *et al.* (2005) concluded by recommending that in-stream mining should be prohibited except in rivers with exceptionally high rates of replenishment.

Our study found lower diversity and abundance of small, benthic fish species at dredged sites. Ecological traits such as small body size (Angermeier, 1995; Maitland, 1995; Burkhead *et al.*, 1997) and benthic habits (Angermeier, 1995; Burkhead *et al.*, 1997) are commonly associated with imperilment of fish species. While freshwater fishes may be the most globally threatened group of vertebrates after amphibians, pearly mussels (Bivalvia: Unionidae) are considered the most imperilled group of animals in North America, primarily as a result of habitat loss (Strayer *et al.*, 2004). Lower diversity of both benthic fishes (present study) and pearly mussels (Smith & Meyer, 2010) was found in deep, dredged sections of the Allegheny River; shallow areas, for instance under bridges and downstream of navigation dams where dredging is not permitted, had higher diversity of both taxa. Freshwater protected areas (FPAs) are increasingly being used as a management tool for conserving imperilled species, habitats and ecosystems (Saunders, Meeuwig & Vincent, 2002; Suski & Cooke, 2007). While dredging in the Allegheny River occurs exclusively in dam-influenced reaches, designation of undredged sections of the dam-influenced river as FPAs may be justified in order to protect the high fish and mussel diversity in this system, and should be considered in other systems where in-stream dredging and mining threaten species of concern.

Our study was conducted during summer and early autumn; it is important to note that there may be seasonal shifts in habitat and resource use. In particular, fishes may move to deeper water during colder months and many species undergo ontogenetic habitat and dietary shifts throughout the year. Our sampling was logistically constrained, but future studies examining seasonal habitat use by fishes in dredged rivers would further add to our knowledge of this issue. We should also note that our fish community sampling occurred 2 years after the stable isotope sampling. We had previously sampled these sites

using Missouri benthic trawls, but while similar species were caught using both trawls, we believe that the higher capture efficiency of the PSU trawl (Freedman *et al.*, 2009) provides a more robust and representative sample of the fish assemblages at these sites. Future studies, both in the Allegheny River and in other dredging-impacted rivers, should include long-term environmental monitoring programmes, including pre- and post-dredging sampling using targeted methodologies such as benthic trawling. Used in conjunction with fish community metrics, techniques such as stable isotope analysis provide complementary data and therefore should also be considered for determining factors influencing fish diversity and trophic dynamics in relation to dredging and other large-scale anthropogenic impacts.

Acknowledgments

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