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Recovery of a temperate riverine fish assemblage from a major diesel oil spill

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SUMMARY

1. Biological resilience is of heightened concern in increasingly anthropogenic landscapes. Quantification of faunal resilience across a wide range of spatial scales and geographical areas is necessary to understand factors influencing the rate and degree of recovery, especially in fragmented ecosystems.

2. We evaluated the recovery of a riverine fish assemblage from a major diesel oil pipeline spill and associated fish kill in 37 km of the Reedy River, South Carolina, U.S.A. The fish assemblage was monitored at four disturbed sites within the fish kill zone and one upstream, undisturbed reference site over a 112-month (9.3-year) period following the disturbance. We used non-metric multidimensional scaling (NMS) ordination to evaluate change in fish assemblage structure among sites and to determine the degree of recovery in assemblage structure.

3. NMS ordination of species relative abundance in two dimensions represented 93% of the total variation in fish assemblage structure among samples and illustrated recovery of the fish assemblage. Initial dissimilarity in assemblage structure was evident between the disturbed sites and the reference site, reflecting high mortality from the oil spill. The disturbed sites as a group increased in similarity to the reference assemblage with time, while the reference assemblage remained relatively stable. Strongest similarity in assemblage structure between the disturbed group and the reference group was achieved by October 2000 (52 months post-disturbance), indicating recovery from the oil spill. Remaining variation in assemblage structure was consistent with longitudinal site position and comparable to that of an undisturbed reference river, attributable to inherent longitudinal variation along the 37-kilometre river section.

4. Recovery rate among sites varied in relation to proximity and connectivity to recolonisation sources on a landscape scale. Recovery of the uppermost disturbed site was faster than the other disturbed sites because of its proximity to the undisturbed main stem fish assemblage, whereas the three most downstream sites were slower to recover largely because of isolation by anthropogenic barriers. These observations illustrate the influence of fragmentation on fish assemblage resilience at large spatial scales.

Keywords: colonisation, disturbance, fragmentation, resilience, streams

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Introduction

The recovery of aquatic biota from anthropogenic disturbance is a fundamental concern of ecological risk assessment and conservation in freshwaters (Baker, 1995; Leuven & Poudevigne, 2002). Disturbances to aquatic ecosystems can be broadly categorised according to temporal and physical characteristics, ranging from discrete, 'pulse' events (e.g. floods, pollutant spills) to long-term, 'press' disturbances with changes to the catchment or stream channel (e.g. channelisation, sedimentation; Bender, Case & Gilpin, 1984; Niemi *et al.*, 1990). Chronic, widespread anthropogenic disturbances such as habitat alteration clearly represent the overarching threat to aquatic biodiversity (Allan & Flecker, 1993; Scott, 2006; Jelks *et al.*, 2008). However, discrete disturbance events may also cause prolonged impacts on aquatic species and assemblages at local scales (Niemi *et al.*, 1990; e.g. Ensign *et al.*, 1997; Albanese, Angermeier & Peterson, 2009), contributing to overall decline especially in altered landscapes and in range-restricted species. Resilience in aquatic assemblages is largely a function of adaptation to environmental variability (Resh *et al.*, 1988; Schlosser, 1990), yet anthropogenic factors may disrupt the natural zoogeographic mechanisms by which recovery occurs (Poff & Ward, 1990).

Fish assemblages in smaller stream reaches have shown rapid recovery in assemblage structure from pulse disturbances in a wide range of settings, including the southern Atlantic coastal plain (Meffe & Sheldon, 1990; Sheldon & Meffe, 1995), midwestern interior valleys (Peterson & Bayley, 1993), Ouachita Mountains (Lonzarich, Warren & Lonzarich, 1998) and southern Appalachians (Albanese *et al.*, 2009). In these cases, recovery to a similar pre-disturbance assemblage structure occurred within days to months of experimental removal from reaches spanning 4–426 m. At the assemblage level, recovery of fishes in short, contiguous stream reaches may reflect near-maximal rates of recolonisation (Sheldon & Meffe, 1995), contrary to the conditions under which many anthropogenic disturbances are likely to occur. Fragmentation of aquatic ecosystems, by both habitat degradation and erection of physical barriers to movement, can reduce recolonisation rates of aquatic organisms following disturbance (Niemi *et al.*, 1990; Pringle, 2003). Furthermore, the cumulative influence of repeated or underlying press disturbances can prolong or prevent the recovery of fishes from discrete events (Niemi *et al.*, 1990; Detenbeck *et al.*, 1992). Because many stream fish populations fulfil life history processes and use refugia at scales of 1–100 km (Schlosser, 1991; Fausch *et al.*, 2002; Magoulick & Kobza, 2003), connectivity may be particularly important in facilitating recovery from disturbances of this extent.

At larger scales, fishes can recolonise extensive areas following natural disturbances including floods (e.g. Matthews, 1986; Roghair & Dolloff, 2005) and drought (Larimore, Childers & Heckrotte, 1959; Matthews & Marsh-Matthews, 2003; Adams & Warren, 2005). Similar observations have accompanied large-scale anthropogenic events, provided fishes have access to the disturbed areas. Fish species richness had largely recovered within about 3 months of a 1.6-km pesticide-induced complete fish kill in a diverse Arkansas stream (Olmsted & Cloutman, 1974). No differences were found in fish abundance, species richness and Index of Biotic Integrity scores between fish kill and reference sites 7.7 months after a manure spill in 22.3 km of a large Missouri stream (Meade, 2004). Recolonisation in these cases occurred rapidly; however, more time may be required for assemblage structure to recover if the anthropogenic disturbance is extensive or occurs in fragmented systems (Niemi *et al.*, 1990; Detenbeck *et al.*, 1992; e.g. Ensign *et al.*, 1997).

In one of the largest inland oil spills in United States history, a petroleum pipeline ruptured and released 22 800 barrels (3 624 910 L) of No. 2 fuel oil (diesel fuel) into the Reedy River near Fork Shoals, South Carolina, on 26 June 1996. Early July 1996 surveys confirmed near-complete fish and macroinvertebrate extirpation for 37 km downstream to the headwaters of Boyd Mill Pond, a 74-ha impoundment on the Reedy River (Rankin, Geddings & Hayes, 1996; Glover, 1996; Fig. 1). About 94% of the oil was recovered within 12 days of the incident with the remainder primarily infiltrating the ground water near the spill site (National Transportation Safety Board, 1998). Therefore, the event represented a pulse disturbance in that structural habitat was not altered and the stressor was relatively short-lived.

The Reedy River oil spill provided an opportunity to assess fish assemblage recovery from a severe and extensive anthropogenic disturbance. Our aim here is to evaluate change in the Reedy River fish assemblage

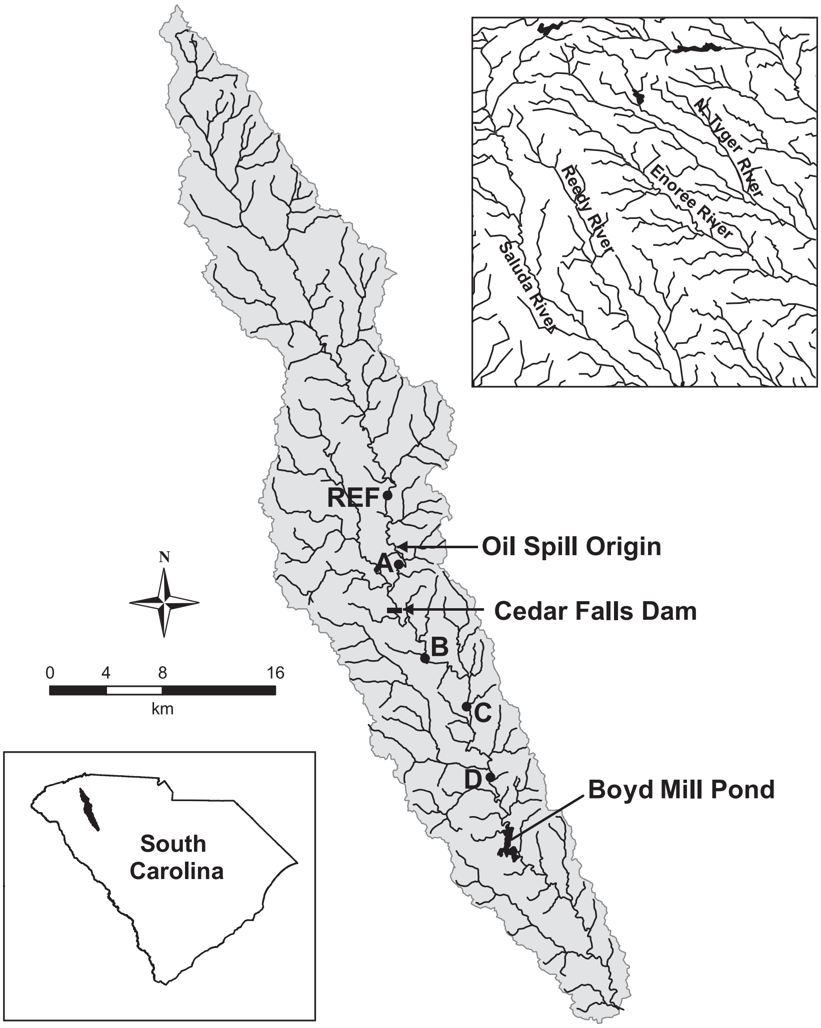

Fig. 1 Location of the Reedy River catchment and the reference (REF) and disturbed (A–D) study sites in relation to the oil spill origin.

following the disturbance and to estimate the rate of recovery in fish assemblage structure within the disturbed section.

Methods

Study system

The Reedy River drains a narrow catchment of about 651 km^2 within the Southern Inner and Outer Piedmont ecoregions of the upper Santee River basin in northwestern South Carolina (Griffith *et al.*, 2002; Fig. 1). Land cover within the Reedy River catchment is about 42% forest, 28% urban, 18% agriculture, 8% grassland/shrubland and 3% wetland (Homer *et al.*, 2004), ranging from widespread urban land use in the upper catchment to moderately forested and agricultural land in the lower catchment. The lower Reedy River supports at least 33 fish species (two introduced), predominantly cyprinids, centrarchids and ictalurids (Table 1). Drainage area to the oil spill site is 269 km^2 with a mean annual discharge of about 6.4 m^3 s^{-1} (base flow 4.7 m^3 s^{-1}; USGS Fork Shoals gauge station 02164110).

By all indications, the 1996 oil spill caused a near-complete fish kill in the Reedy River main stem from the spill site downstream to Boyd Mill Pond (Fig. 1; Rankin *et al.*, 1996). For the purpose of measuring assemblage recovery, it was assumed that all points began the recovery process from the same original level of disturbance. Unfortunately, the hazardous nature of the oil spill and rapid decomposition of fish prevented collection and identification of many of the dead fishes, particularly smaller species. Therefore, these fish kill data could not be used to quantify pre-disturbance fish assemblage structure.

Table 1 Fish species collected from the Reedy River study sites (August 1996–October 2005) and earliest date of collection in the disturbed river section (sites in parentheses) following the 26 June 1996 oil spill

			Kendall's tau	
Scientific name	Common name	Earliest collection	Axis 1	Axis 2
Cyprinidae				
Cyprinella chloristia (Jordan & Brayton)	Greenfin shiner	October 1996 (D)	0.016	−0.249
Cyprinella nivea (Cope)	Whitefin shiner	August 1996 (D)		
Cyprinus carpio Linnaeus	Common carp	August 1996 (B)		
Hybopsis rubrifrons (Jordan)	Rosyface chub	2005 (B)		
Nocomis leptocephalus (Girard)	Bluehead chub	August 1996 (BC)	−0.496	0.466
Notemigonus crysoleucas (Mitchill)	Golden shiner	October 1996 (A)	−0.131	0.174
Notropis hudsonius (Clinton)	Spottail shiner	October 1996 (CD)	−0.282	−0.188
Notropis lutipinnis (Jordan & Brayton)	Yellowfin shiner	October 1996 (ABD)	−0.205	0.185
Notropis scepticus (Jordan & Gilbert)	Sandbar shiner	2000 (D)		
Centrarchidae				
Centrarchus macropterus (Lacepede)	Flier	August 1996 (D)	0.269	0.021
Lepomis auritus (Linnaeus)	Redbreast sunfish	August 1996 (CD)	−0.483	−0.163
Lepomis cyanellus Rafinesque	Green sunfish	August 1996 (B)	0.068	−0.038
Lepomis gibbosus (Linnaeus)	Pumpkinseed	August 1996 (D)	0.495	−0.394
Lepomis gulosus (Cuvier)	Warmouth	August 1996 (C)	0.172	−0.135
Lepomis macrochirus Rafinesque	Bluegill	August 1996 (BCD)	0.936	−0.163
Lepomis microlophus (Gunther)	Redear sunfish	1997 (ABD)	0.070	−0.305
Micropterus salmoides (Lacepede)	Largemouth bass	August 1996 (CD)	−0.296	0.192
Pomoxis nigromaculatus (Lesueur)	Black crappie	1997 (BC)	−0.016	−0.165
Ictaluridae				
Ameiurus brunneus Jordan	Snail bullhead	October 1996 (A)	−0.041	−0.421
Ameiurus catus (Linnaeus)	White catfish	October 1996 (AD)	−0.029	−0.044
Ameiurus natalis (Lesueur)	Yellow bullhead	October 1996 (A)	−0.372	0.305
Ameiurus nebulosus (Lesueur)	Brown bullhead	1997 (B)		
Ameiurus platycephalus (Girard)	Flat bullhead	August 1996 (CD)	−0.655	0.408
Ictalurus punctatus (Rafinesque)	Channel catfish	August 1996 (CD)	0.221	−0.544
Noturus insignis (Richardson)	Margined madtom	1997 (D)	0.154	−0.289
Catostomidae				
Catostomus commersoni (Lacepede)	White sucker	2005 (A)		
Erimyzon oblongus (Mitchill)	Creek chubsucker	August 1996 (C)		
Hypentelium nigricans (Lesueur)	Northern hogsucker	August 1996 (D)	−0.384	−0.038
Moxostoma rupiscartes (Jordan & Jenkins)	Striped jumprock	1998 (B)		
Poeciliidae				
Gambusia holbrooki Girard	Eastern mosquitofish	August 1996 (C)		
Percidae				
Etheostoma thalassinum (Jordan & Brayton)	Seagreen darter	2005 (D)		
Clupeidae				
Dorosoma cepedianum (Lesueur)	Gizzard shad	August 1996 (D)	0.398	−0.277
Esocidae				
Esox americanus Gmelin	Redfin pickerel	October 1996 (C)		

Site A was not sampled in August 1996. Correlation coefficients (Kendall's tau) for ordination axes are provided for species included in non-metric multidimensional scaling (see Fig. 3). Scientific names follow Rohde *et al.* (2009).

Although the disturbed reach was open to the adjacent upstream undisturbed river section, two major barriers existed within the fish kill reach. Cedar Falls Dam is located about 7 km downstream of the oil spill origin (Fig. 1). This former mill dam (height = 4.6 m) represented a physical and behavioural barrier to fish movement, although some downstream drift of ichthyoplankton was possible. In addition to Cedar Falls Dam, Boyd Mill Pond and dam marked the downstream end of the fish kill and represented a barrier to fish movement between the downstream, undisturbed section of the Reedy River main stem and the fish kill section (Fig. 1). Thus, the fish kill section essentially consisted of a 7-km upper reach open to upstream colonists and a 30-km downstream reach isolated from main stem colonists by two dams (Fig. 1). The fish kill assessment indicated that fish mortality in Boyd Mill Pond was primarily in the headwater region of the reservoir and surviving fishes were mainly lentic species including centrarchids and *Dorosoma cepedianum*.

At least 15 tributaries ranging from <4 to 92 km^2 in catchment area enter the Reedy River within or near the fish kill section. Although tributaries were not sampled during the initial recovery period, samples taken in 2004–2005 from the five primary tributaries of this section showed fish assemblages of 10–18 species dominated by *Nocomis leptocephalus*, *Notropis lutipinnis*, *Lepomis macrochirus*, *Lepomis auritus* and *Hypentelium nigricans*, in order of average relative abundance.

Sampling design

Following the June 1996 fish kill, a longitudinal sampling design was initiated to evaluate the fish assemblage in the disturbed section. Given logistical constraints in available personnel and the urgency to document conditions as soon as possible after the spill, sample sites were selected based on accessibility and to maximise coverage of the disturbed section. In the absence of pre-disturbance fish assemblage data, one site 5.4 km upstream of the spill origin was selected to represent undisturbed assemblage conditions in the context of the oil spill and is hereafter referred to as the ‘reference’ site (Fig. 1). Four sites located 1.8, 14.2, 20.6, and 29.5 km downstream of the spill and within the 37-km fish kill zone were selected as ‘disturbed’ sites and are hereafter termed A, B, C and D, respectively (Fig. 1). Elevation ranged from 171 to 225 m over the 34.9-km span of the five study sites (0.15% slope). The study section consisted predominantly of sand/gravel runs and pools with scattered large woody debris and occasional boulder/bedrock shoals. Wetted width among sample sites averaged 16.3 m (range 12.8–17.7) under low-flow conditions.

Because of safety restrictions and clean-up efforts following the spill, access to the study section was not permitted until August 1996. Each site was sampled once in August 1996 and during low annual flows in October 1996, 1997, 1998, 2000 and September–October 2005, or about 1.5, 4, 16, 28, 52 and 112 months post-disturbance. Gaps in sampling (1999, 2001–2004) were because of high flows during target sample periods or project limitations. Site A was not sampled in August 1996; 29 samples were conducted altogether. Fish sampling consisted of three-pass depletion electrofishing by 12–15 persons using backpack and barge-mounted electrofishers (Smith-Root Inc., Vancouver, WA, U.S.A.; Halltech Aquatic Research Inc., Guelph, ON, Canada). The entire wetted channel including all submerged cover was sampled in an upstream direction over a reach length of 150 m to obtain a representative sample of the fish assemblage. All fish were collected with dip nets (4.8-mm mesh), identified and enumerated after each pass and released after the third pass. Questionable specimens were preserved in 70% ethanol and returned to the laboratory for identification. To standardise sampling effort and area, sample sections were precisely marked and electrofishing was conducted only when discharge was ≤3.7 m^3 s^{-1} at Fork Shoals (≤86% of mean October discharge). The same crew and equipment configuration was employed during all sampling. Abundance of each species was summed across electrofishing passes for each sample prior to analysis.

To evaluate the degree of inherent longitudinal variation in fish assemblage structure, and given the large spatial span of the sample sites (35 km) and lack of pre-disturbance data, we compared the Reedy River study section to a similar river section that had not suffered an oil spill (Sheldon, 1968; Vannote *et al.*, 1980). The North Tyger River was selected as the most comparable system within the upper Santee River basin containing sites approximating the elevation range of the Reedy River study section (Fig. 1). Four sites spanning 25.1 km and ranging from 183–233 m in elevation (0.20% slope) were selected to assess longitudinal variation in the North Tyger River. Sites were sampled once each between 5 October and 17 November 2005 in identical fashion to the Reedy River as described earlier.

Data analysis

Fish assemblage recovery was evaluated as a function of relative compositional similarity among sites through time with the hypothesis that the disturbed sites would initially be dissimilar to the reference site and become collectively more similar to the reference site with time. The lack of pre-disturbance data meant that recovery could not be measured as a return to some level of pre-disturbance assemblage structure.

However, since the disturbance did not physically alter stream habitat, we expected assemblage structure to return towards that represented by the undisturbed reference site. Recovery of the Reedy River fish assemblage was therefore anticipated to coincide with stabilisation in assemblage structure of the disturbed sites relative to the expectedly stable reference site (Matthews, Cashner & Gelwick, 1988). We use the term 'recovery' with acknowledgement that pre-disturbance assemblage structure was unknown.

We used non-metric multidimensional scaling (NMS) ordination to extract spatiotemporal patterns in fish assemblage structure (Kruskal, 1964a,b; Mather, 1976; Kruskal & Wish, 1978). NMS is a general ordination procedure recommended for non-normal or questionably distributed data and calculates ranked ecological distances (Clarke, 1993; McCune & Grace, 2002), providing a relative measure of proportional similarity in fish assemblage structure. NMS was conducted using PC-ORD version 4 (McCune & Mefford, 1999) with a random starting configuration and 40 runs with real data. Sorensen distance was selected as the similarity measure (Bray & Curtis, 1957). The probability of obtaining by chance a stress less than or equal to that observed in the real data was assessed with a Monte Carlo test (50 runs, $\alpha = 0.05$).

Preliminary analysis of the full dataset of 33 species revealed an inordinate influence of several rare species on the ordination (Lohr & Fausch, 1997). Ten species whose abundances represented ≤0.1% of the grand total across samples were identified as strongly influencing variation based on rarity alone, with little spatiotemporal association in the context of fish assemblage recovery. Seven of these species had grand totals of ≤3 individuals occurring in ≤2 of 29 samples: *Cyprinella nivea*, *Cyprinus carpio*, *Hybopsis rubrifrons*, *Ameiurus nebulosus*, *Catostomus commersoni*, *Erimyzon oblongus* and *Etheostoma thalassinum*. Therefore, we excluded these 10 rare species from ordination (e.g. Lonzarich *et al*., 1998; Wang, Seelbach & Lyons, 2006; Table 1). We also detected a strong influence of *Gambusia holbrooki* based on its extreme variability in abundance. Relative abundance of *G. holbrooki* was initially low at all sites in August and October 1996 (mean 1 and 9%, respectively) then increased substantially at all sites including the reference site in 1997 (mean 43%; range 28–69%) before decreasing sharply in 1998. Although we acknowledge these dynamics as they may relate to colonisation, the variability of this species masked the underlying fish assemblage dynamics and it was thus excluded from NMS (e.g. Lohr & Fausch, 1997). Abundances of the 22 remaining species were standardised by sample totals to produce relative abundance, thereby reducing the potential effects of minor differences in sampled area among sites. The final data matrix was processed with NMS, producing a single output of all samples in species space. Correlation coefficients (Kendall's tau) were generated to provide a rank measure of axis association for each species (McCune & Grace, 2002). For the longitudinal analysis, a separate NMS was performed on the North Tyger River + Reedy River dataset (2005 only), providing a relative comparison of variation in assemblage structure within both systems. Eight rare (i.e. <0.20% of grand total combined catch) species and *G. holbrooki* were excluded from this analysis for reasons described earlier.

From the NMS output, 95% confidence ellipses were constructed about the mean axis scores (centroids) for the reference site (across all time periods) and disturbed sites (within time periods), characterising the variation within and similarity between groups during each of the six sample periods. The reference site samples were grouped across time periods because we expected this site to chiefly reflect natural assemblage dynamics and therefore show relative stability (i.e. remain relatively localised in ordination space) when compared to the disturbed assemblages (Matthews *et al*., 1988). Grouping across time periods would effectively represent this natural variability and provide a target condition towards which assemblage structure of the disturbed sites would be expected to shift as recovery occurred. Because of the aforementioned likelihood of natural longitudinal variation, we did not necessarily expect the disturbed sites to approach 100% similarity to the reference site nor to one another, but rather to show a net shift towards the reference condition.

To test for differences in assemblage structure between disturbed sites and the reference site over time, multi-response permutation procedure (MRPP; Mielke, 1984) was performed using PC-ORD version 4 (McCune & Mefford, 1999). MRPP is a nonparametric procedure that tests the null hypothesis of no difference among groups by comparing observed weighted average within-group homogeneity with that obtained by chance (McCune & Grace, 2002). Groups were defined as the reference group (across sample periods; $n = 6$ samples) and the disturbed groups (within sample periods; $n = 3$ samples in August 1996; $n = 4$ samples in all other periods). MRPP was performed using rank transformation of the Sorensen distance matrix, with relative abundance as described earlier to complement NMS ($\alpha = 0.05$; McCune & Grace, 2002). Post hoc pairwise comparisons were performed to test for differences in assemblage structure between reference and disturbed groups within each of the six sample periods (i.e. with time). The experiment-wise Type I error rate for $\alpha = 0.05$ was controlled by applying a Bonferroni correction in which groups were significantly different if $P < 0.0083$ (=0.05/6 comparisons).

Results

Abundance and species richness

A total of 8454 fish representing 33 species were collected in the Reedy River (Table 1). Total catch by sample ranged from 14 to 768 and species richness from 4 to 22 (Fig. 2). Both fish species richness and abundance at disturbed sites were markedly low in August 1996 (1.5 months post-disturbance) compared with the reference site (Fig. 2). However, as many as 10 species (mean 7.7) were present at the disturbed sites by this time (Fig. 2a). Abundance in the disturbed reach remained low for 4 months after the disturbance then increased substantially among all sites by 16 months post-disturbance (Fig. 2b). Fish abundance at disturbed sites subsequently decreased from October 1997 to October 1998 (16–28 months post-disturbance) but increased gradually over the remainder of the study. Reference abundance decreased from 1998–2000 but returned to a maximum in 2005. Unlike abundance, species richness at disturbed sites in general increased substantially over the first 4 months, with two sites (A, D) exceeding reference species richness by October 1996 (Fig. 2a). Species richness among disturbed sites for the most part had stabilised at higher levels than the reference site by October 1997 (16 months post-disturbance).

At least 16 fish species were present in the disturbed reach in August 1996 (1.5 months post-disturbance; Table 1). *Lepomis macrochirus* numerically dominated the disturbed reach at this time, accounting for 77% of all individuals collected. Relative abundance of *L. macrochirus* at disturbed sites in August 1996 averaged 66% (range 55%–85%), compared with 12% at the reference site. *Lepomis macrochirus* relative abundance was particularly high at Site D (85%). No other species yielded more than five individuals or a relative abundance of greater than 21% (*N. leptocephalus*, B) at any of the disturbed sites in August 1996, although the species composition of Site A was not determined at this time.

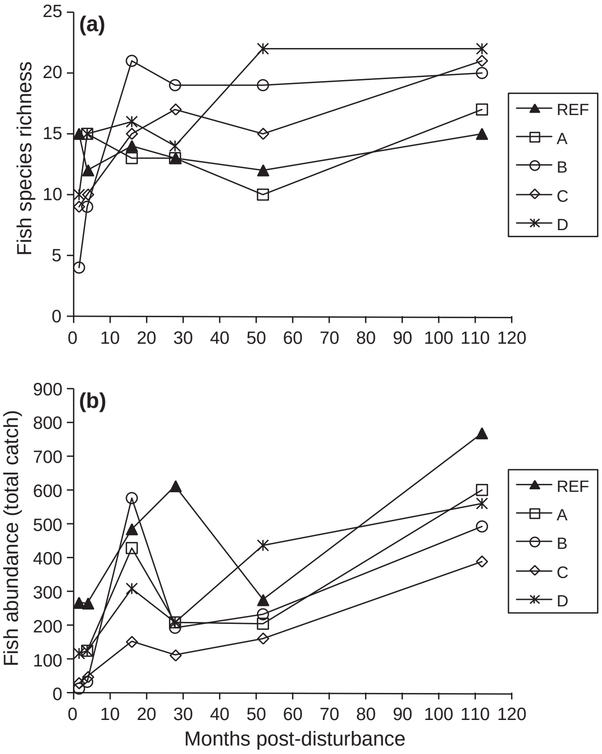

Fig. 2 Recovery of fish species richness (a) and abundance (b) at the Reedy River reference (REF) and disturbed (A–D) sites following the June 1996 oil spill.

Eight species were first collected in the disturbed reach in October 1996 (4 months post-disturbance; Table 1). *Lepomis macrochirus* again accounted for the greatest relative abundance among disturbed sites in October 1996, averaging 48% (range 28–66%) compared with 11% at the reference site. Nine species were not collected in the disturbed reach until October 1997 or later (≥16 months post-disturbance; Table 1).

Assemblage structure

A distinctive spatiotemporal pattern of recovery in fish assemblage structure emerged from the ordina-

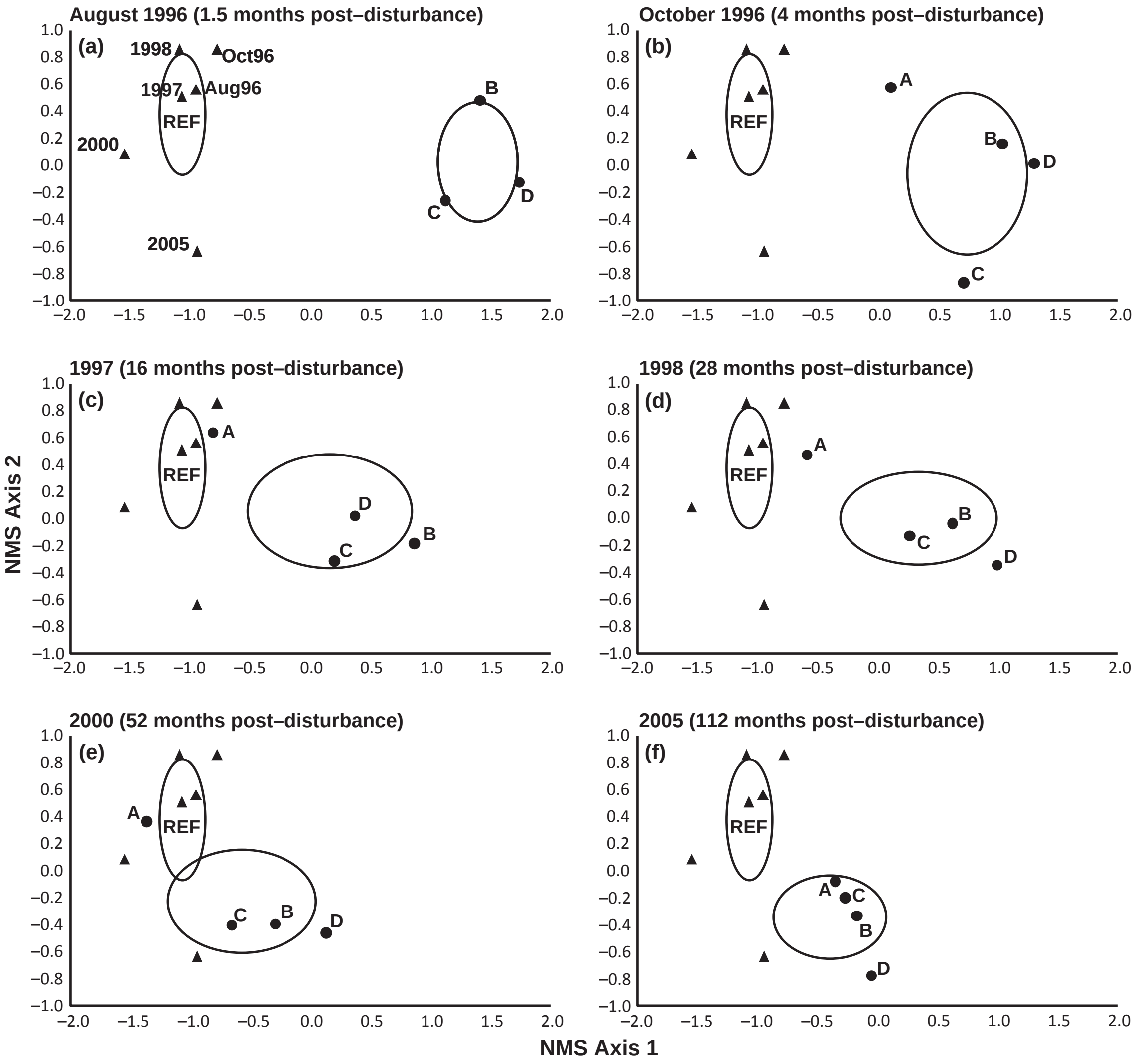

Fig. 3 Recovery of fish assemblage structure in the Reedy River following the June 1996 oil spill as illustrated in non-metric multi-dimensional scaling ordination plots by sample period. Ellipses show 95% confidence intervals about the centroid position for the reference site (▲, REF; across samples from all time periods) and disturbed sites (●, A–D; within sample periods). Sample labels for the reference site are shown in (a) and removed from the remaining panels for clarity (Aug96, August 1996; Oct96, October 1996). Axis 1 represents the majority (79%) of variation among samples; Axis 2 = 14%. Site A was not sampled in August 1996.

tion (Fig. 3). About 93% of the total variation in fish assemblage structure among samples was represented by two dimensions in NMS (Monte Carlo test, $P < 0.02$; final stress = 10.97; Fig. 3). Axis 1 accounted for the majority of variation (79%) and clearly characterised the primary temporal component of variation among samples. Axis 2 represented about 14% of the variance among samples and reflected a less apparent pattern stemming from other sources of variation.

Recovery in fish assemblage structure was clearly illustrated by the position of sites through time on Axis 1 (Fig. 3). The reference site showed relatively little variability along Axis 1 and occupied a localised area towards the negative end of this axis, indicating relative stability in assemblage structure (Fig. 3a). In August 1996, a marked difference in Axis 1 position existed between the disturbed sites and the reference condition, reflecting strong dissimilarity in assemblage structure about 1.5 months after the oil spill (Fig. 3a). Sites B–D shifted slightly along Axis 1 towards the reference condition from August to October 1996 (1.5–4 months post-disturbance) with Site A showing greater similarity than the other disturbed sites to the reference site by the time it was first sampled in October 1996 (Fig. 3b). From 1996 to 1997 (4–16 months post-disturbance), the disturbed sites further increased in similarity to the reference assemblage on Axis 1 (Fig. 3c). Site A exhibited strong similarity to the reference assemblage by 1997 (Fig. 3c). Little overall change in assemblage structure was apparent in the disturbed sites from 1997 to 1998 (16–28 months post-disturbance; Fig. 3d). By 2000 (52 months post-disturbance), the disturbed sites had further increased in similarity to the reference site with considerable overlap in assemblage variation (95% confidence intervals) between reference and disturbed groups on Axis 1 (Fig. 3e). The disturbed sites maintained a similar level of overall similarity to the reference condition in 2005 (112 months post-disturbance) with additional convergence in assemblage structure among disturbed sites as evident by a tighter ellipse (Fig. 3f). This convergence was mainly driven by a shift in Site A concurrent with the reference site (Fig. 3f, note position of 2005 reference point in Fig. 3a). In all, assemblage structure at the disturbed sites began in a state of dissimilarity to the reference site and shifted towards the reference condition with time, largely stabilising in assemblage structure as a group by 2000 (52 months post-disturbance).

We rejected the null hypothesis of no difference in assemblage structure among reference (across sample periods) and disturbed (within sample periods) groups through time (MRPP, $A = 0.349$; $P = 0.00007$). Pairwise comparisons of the reference group versus the disturbed group within sample periods were significantly different for August and October 1996 then were not different in 1997 (Bonferroni-corrected $\alpha = 0.0083$; Table 2). Pairwise differences subsequently alternated between significant (1998, 2005) and not significant (2000; Table 2). Differences appeared to be driven primarily by the aforementioned fluctuations in Site A and a general lack of complete convergence in assemblage structure among groups (Fig. 3). Despite these statistical fluctuations, sites had generally stabilised in ordination position by 2000 (Fig. 3).

Species varied widely in strength of association with the ordination axes (Kendall's tau; Table 1). The four strongest positive Axis 1 correlations were *L. macrochirus*, *L. gibbosus*, *D. cepedianum* and *Centrarchus macropterus* (Table 1). The strongest negative Axis 1 values were those of *Ameiurus platycephalus*, *N. leptocephalus*, *L. auritus* and *H. nigricans* (Table 1). Plotting relative abundance against time for the two most polar species on Axis 1, *L. macrochirus* and *A. platycephalus*, showed a representative contrast of species responses (Fig. 4). *Lepomis macrochirus* relative abundance was initially high at disturbed sites and decreased with time, whereas relative abundance of *A. platycephalus* was at or near zero at most of the disturbed sites in August 1996 (1.5 months post-disturbance) and more slowly increased to relatively stable levels (Fig. 4). *Ameiurus platycephalus* actually exhibited a gradual decrease in relative abundance at the reference site and at Site A from 1998 to 2005 (28–112 months post-disturbance).

Table 2 MRPP test statistics for pairwise comparisons between the reference site (grouped across sample periods) versus disturbed sites (grouped within sample periods) by sample period

Reference versus disturbed comparison	Months post-disturbance	T	A	*P*
August 1996	1.5	−4.71	0.40	0.0017*
October 1996	4	−4.79	0.36	0.0022*
1997	16	−3.01	0.21	0.0143
1998	28	−3.57	0.25	0.0079*
2000	52	−2.22	0.17	0.0346
2005	112	−4.34	0.34	0.0041*

Groups are significantly different if $P < 0.0083$ (Bonferroni correction for 0.05/6 comparisons) and are marked with an asterisk. MRPP, multi-response permutation procedure.

Longitudinal variation

The Reedy River and North Tyger River sites in 2005 produced a combined total of 5440 fishes from 36 species. Three dimensions in NMS characterised over 91% of the total variation in assemblage structure among samples (Monte Carlo test, $P < 0.02$). The first and third dimensions represented about 62% and 20% of this variation, respectively (Fig. 5). The second dimension accounted for about 9% of the variation and did not reflect any interpretable sources of variation.

Two major patterns of variation in fish assemblage structure were apparent among the concurrent Reedy River and North Tyger River samples (Fig. 5). A difference in assemblage composition between rivers was evident along Axis 1 and represented the majority of variation among samples (62%). Strongest

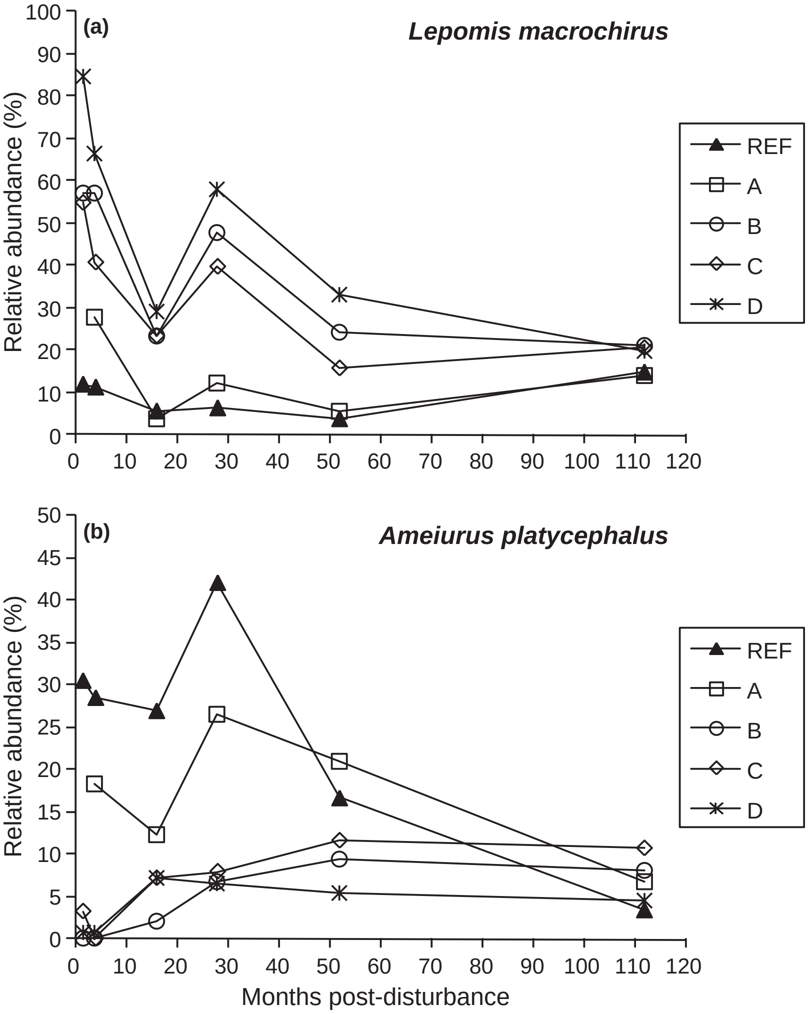

Fig. 4 Contrasting relationships between relative abundance and time for two fish species in the Reedy River following the June 1996 oil spill: *Lepomis macrochirus* (a) and *Ameiurus platycephalus* (b).

associations (Kendall's tau) for the Reedy River were *Lepomis cyanellus* (−0.667), *H. nigricans* (−0.609), *Ameiurus catus* (−0.609) and *Ameiurus natalis* (−0.559). The North Tyger River was characterised most strongly by *Etheostoma olmstedi* Storer (0.618), *E. thalassinum* (0.588), *Cyprinella zanema* (Jordan & Brayton; 0.523) and *N. leptocephalus* (0.500). *Etheostoma olmstedi* and *C. zanema* only occurred in the North Tyger River, contributing to the differences between rivers.

The second and more noteworthy pattern in assemblage structure occurred among sites within systems, following a distinct upstream–downstream longitudinal gradient from positive to negative along Axis 3 (Fig. 5). Longitudinal variation was more pronounced in the North Tyger River despite its shorter reach length. Species common to both rivers and exhibiting the strongest upstream distribution (Kendall's tau) were *Notropis lutipinnis* (0.551), *L. cyanellus* (0.444), *A. natalis* (0.387) and *Notropis hudsonius* (0.222; Fig. 5). Those most strongly associated with downstream habitats were *Cyprinella chloristia* (−0.841), *Notropis scepticus* (−0.609), *C. nivea* (−0.471) and *E. thalassinum* (−0.458). *Lepomis macrochirus* was neutral in longitudinal association (0.000).

Discussion

Given the severity, extent and timing of the Reedy River fish kill, it is not surprising that the disturbed sites were dissimilar to the reference site in fish assemblage structure during the first two sample periods at 1.5 and 4 months post-disturbance. Although many species were present in the disturbed section by October 1996 (4 months post-disturbance), total fish abundance was still low at the disturbed sites compared with the reference site (Fig. 2).

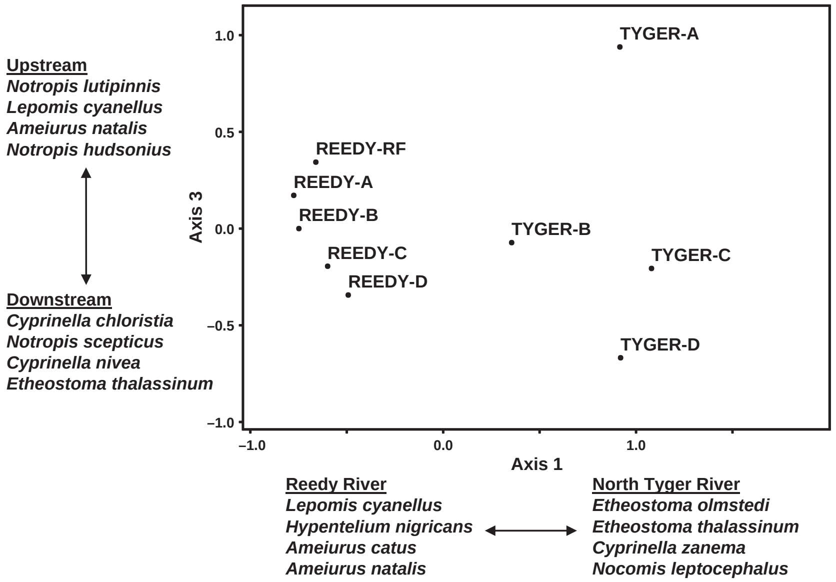

Fig. 5 Non-metric multidimensional scaling plot showing variation in fish assemblage structure between (Axis 1; 62% of variation explained) and within (Axis 3; 20%) the Reedy River (REEDY) and North Tyger River (TYGER) study sections in 2005. Assemblage structure follows a longitudinal pattern along Axis 3 from upstream (positive) to downstream (negative). The four species most strongly associated with each axis direction are shown. Total section length on Reedy River = 34.9 km and North Tyger River = 25.1 km.

Consequently, fish assemblage structure was relatively dissimilar between the disturbed sites and the reference site (Fig. 3). The rapid increase in species richness observed between August and October 1996 prior to increase in abundance has similarly characterised the recovery process after other natural and experimental disturbances (Detenbeck *et al.*, 1992; Lonzarich *et al.*, 1998; Adams & Warren, 2005).

As in many other studies (Niemi *et al.*, 1990; Detenbeck *et al.*, 1992; Sheldon & Meffe, 1995; Lonzarich *et al.*, 1998; Davey & Kelly, 2007), variation in assemblage recovery rate among sites was consistent with proximity and connectivity to recolonisation sources. By the time it was first sampled in October 1996 (4 months post-disturbance), the fish assemblage of Site A was notably more similar to the reference condition than were those of the other disturbed sites (Fig. 3). Site A subsequently became highly similar to the reference site in 1997 (16 months post-disturbance) and maintained a relatively high degree of similarity to the reference condition over the remainder of the study, with slight fluctuations probably owing to natural variability, whereas the other disturbed sites were slower to increase their similarity to the reference condition.

The early similarity of Site A to the reference condition can be attributed to two factors. First, Site A was only 1.8 km downstream of the undisturbed main stem fish assemblage, affording rapid immigration of colonists from upstream. Proximity to a source of colonists predictably influences fish population and assemblage recovery rates from a wide range of disturbances, both natural and anthropogenic (Olmsted & Cloutman, 1974; Detenbeck *et al.*, 1992; Bayley & Osborne, 1993; Sheldon & Meffe, 1995; Magoulick & Kobza, 2003). In a chemically defaunated 715-km section above a dam on the Green River, Wyoming, fishes reappeared significantly later at sites 150–244 km away from upstream sources of colonists than at sites within 13–21 km (Detenbeck *et al.*, 1992 citing Binns, 1967). Fish density was inversely related to distance from permanent water sources in sites resuming flow after seasonal drought along 45 km of a New Zealand river (Davey & Kelly, 2007). Second, the apparently rapid recovery of Site A may in part reflect a natural similarity to the reference site because of longitudinal proximity and lack of barriers between these sites (Sheldon, 1968; Vannote *et al.*, 1980; Taylor, 1997). Based on longitudinal position, these two sites should be more similar to one another at any point in time than the reference site to any of the other disturbed sites (Fig. 1). However, recovery rates were clearly influenced by differential access to recolonisation sources.

Barriers in the form of both anthropogenic structures and natural channel features can slow or prevent fish recolonisation along stream courses (Niemi *et al.*, 1990; Detenbeck *et al.*, 1992; Lonzarich *et al.*, 1998). Fishes in a site with partial barriers (cascades, culverts) recovered more slowly from experimental removal than those in a lower gradient site lacking barriers in the same Virginia mountain stream system (Albanese *et al.*, 2009). In the Reedy River, we observed a delay in fish assemblage recovery consistent with the positions of two major barriers within the study section (Fig. 1). Sites B–D occurred within the section isolated by dams and exhibited a slower rate of increase in similarity than Site A to the reference condition. The isolation from main stem colonists suggests that initial recolonisation of this lower section was accomplished primarily by immigration from smaller tributary sources (e.g. Olmsted & Cloutman, 1974; Angermeier & Schlosser, 1989; Osborne & Wiley, 1992). Hence, it appeared that the lower disturbed section (B–D) experienced a slower rate of recovery than the upper section (A), which was near the larger main stem river assemblage as well as tributaries. Although we assume that *in situ* reproduction played an increasing role in assemblage recovery in the Reedy River over time (e.g. Larimore *et al.*, 1959; Bayley & Osborne, 1993; Adams & Warren, 2005), our observations suggest that differences in the proximity, connectivity and size of recolonisation sources strongly influenced recovery rates among sites in the early stages.

Despite some constraints to recolonisation along the Reedy River, the ultimate stabilisation of assemblage structure across sites leads us to conclude that recovery did occur during the study. Sites B–D collectively showed little change in ordination position from 2000 to 2005 (52–112 months post-disturbance) in spite of the relatively long time between these samples. The concurrent shift in assemblage structure of the reference site and Site A from 2000 to 2005 appears to reflect increases in the abundance of *N. hudsonius*, *H. nigricans*, *L. macrochirus* and *L. cyanellus* at these two sites and may be owing to a shift from relatively dry (2000) to wet (2005) hydrological conditions. We attribute the lack of complete convergence in assemblage structure among sites to longitudinal variation (Sheldon, 1968; Vannote *et al.*, 1980); the sites were as similar to one another as could be expected because of natural upstream–downstream variability. Longitudinal variation also may explain the statistical difference between groups in the pairwise comparison for 2005 (Table 2), as groups were defined *a priori* under the assumption of similar assemblage structure. We thus place the time of section-wide recovery in fish assemblage structure by the 2000 sample period, at 52 months or 4.3 years post-disturbance, the earliest time at which collective stabilisation among disturbed sites was observed. Estimated site-specific recovery rates ranged from ≤16 months (A) to ≤52 months (B–D).

Not surprisingly, these recovery rates are slower than those reported for fish faunas in smaller and less fragmented stream reaches (4–426 m), which range from days to months (Meffe & Sheldon, 1990; Peterson & Bayley, 1993; Sheldon & Meffe, 1995; Lonzarich *et al.*, 1998; Albanese *et al.*, 2009). On a larger scale, Meade (2004) found that index of biotic integrity scores in 22.3 km of a large Missouri stream had recovered to reference levels by about 7.7 months after a major fish kill, showing relatively rapid recovery in a measure of assemblage structure.

The rate of recovery in species richness is comparable to that observed following other large-scale fish kills. In the Reedy River, fish species richness among disturbed sites generally approached maximum levels by 16 months after the 37-km fish kill (Fig. 2a). This rate is in line with times of about 3 months for 1.6 km of an Arkansas stream (Olmsted & Cloutman, 1974) and 7.7 months for 22.3 km of a large Missouri stream (Meade, 2004). Twenty-four of 29 resident fish species were observed within 3 months of flow resumption in an Illinois stream recovering from drought, with many occurring up to 10.1 km upstream of the recolonisation source (Larimore *et al.*, 1959).

Recovery of fishes in the Reedy River was probably also influenced by the substantial mortality of macroinvertebrates from the oil spill (Glover, 1996). The loss of forage invertebrates would be expected to delay the recovery of fishes compared with cases in which only fishes are removed (e.g. experimental removal) or where invertebrates may persist to some degree in the substrate and hyporheic habitats (e.g. drought). Macroinvertebrate assemblage characteristics in the Reedy River had recovered to historic and upstream control levels by July 1997 (12 months post-disturbance; J. B. Glover, unpubl. data), preceding fish assemblage recovery by more than 3 years as reported here. In another study, Meade (2004) observed numerical improvement in invertebrates at some sites within 22 weeks (5.1 months) following an effluent-induced fish and invertebrate kill of 31.4 km in a Missouri stream; fish abundance and species richness had recovered by 33 weeks (7.7 months).

Although our analysis focused on the recovery of fishes at the assemblage level, certain species stand out in the recovery process. *Lepomis macrochirus* was relatively abundant at all disturbed sites (including A) in August and October 1996 (1.5–4 months post-disturbance; Fig. 4) and was neutral in longitudinal association, indicating recolonisation from sources located throughout the disturbed section rather than a single primary source such as Boyd Mill Pond at the downstream end of the section. Tributary mouths and backwater areas probably provided refugia and sources of recolonisation (Detenbeck *et al.*, 1992). Juvenile *L. macrochirus* were collected in the early samples, suggesting some reproduction in or near the disturbed section (e.g. Olmsted & Cloutman, 1974). The presence of other centrarchid species in low abundance in 1996 but that subsequently increased in relative abundance (e.g. *L. auritus*) suggests that the high relative abundance of *L. macrochirus* was not simply a product of electrofishing selectivity towards shoreline-associated fish (Reynolds, 1983). *Lepomis macrochirus* demonstrated a high immigration probability in Mississippi upper coastal plain streams resuming flow following drought (Adams & Warren, 2005) but has also shown low immigration tendency in Arkansas stream fish assemblages (Taylor & Warren, 2001). In other large-scale fish kills, *L. macrochirus* took 7 weeks to reappear in an Arkansas stream (14th of 26 species; Olmsted & Cloutman, 1974) and did not increase in abundance until 22–33 weeks (5.5–7.7 months) after a similar Missouri event (Meade, 2004).

Species with relatively neutral longitudinal association and most strongly characterising the reference end of the recovery axis (i.e. negative tau for Axis 1, Fig. 3) were *A. platycephalus*, *N. leptocephalus*, *L. auritus* and *H. nigricans*. *Nocomis leptocephalus* had generally reached its maximum relative abundance among disturbed sites by October 1996 (4 months post-disturbance), showing high resilience as reported in other studies (Ensign *et al.*, 1997; Albanese *et al.*, 2009). *Lepomis auritus* increased sharply from August to October 1996 (1.5–4 months) at certain sites (B, C), but otherwise steadily increased with time until 2000.

Relative abundance patterns in *A. platycephalus* and *H. nigricans* were indicative of slower recovery (i.e. lower resilience), especially in the lower section (Sites B–D; Fig. 4b). These two species exhibit certain life history traits that can translate into lower resilience, such as relatively slow growth and longer time to reproductive maturity (Schlosser, 1990; Detenbeck *et al.*, 1992). Resilience of ictalurids and catostomids varied in other studies. Olmsted & Cloutman (1974) indicated apparent recovery of *Ameiurus melas* (Rafinesque) but not *A. natalis* within 1 year of a 1.6-km fish kill in Arkansas. Certain catostomid populations have been slower to recover than other fishes after pulse disturbances (e.g. *Moxostoma duquesnei* (Lesueur) in Olmsted & Cloutman, 1974; *Moxostoma cervinum* (Cope) in Ensign *et al.*, 1997; *Thoburnia rhothoeca* (Thoburn) in Ensign *et al.*, 1997; Albanese *et al.*, 2009). Conversely, *H. nigricans* was nearly twice as abundant about 3 months after flow resumption in a previously dry Illinois stream than in a pre-drought sample of the same area and time of year, whereas other catostomids were far less abundant post-drought (Larimore *et al.*, 1959).

Low abundance or mobility may place species at greater risk of extirpation in increasingly disturbed and fragmented river systems (Albanese *et al.*, 2009). *Catostomus commersoni* was the only species collected at the reference site or Site A (upstream of the barriers) that was not also collected at Site B, C or D (between the barriers) at any time during the study. This species was represented by only two individuals during the study (reference site, 2000 and Site A, 2005), suggesting that it normally occurs in low numbers in this section of the river. The long time between samples and distance between sites could have reduced our ability to detect such rare or sporadically occurring species; however, we cannot rule out the possibility that *Ca. commersoni* was extirpated from the Reedy River between Cedar Falls Dam and Boyd Mill Pond as a result of the oil spill. Olmsted & Cloutman (1974) similarly failed to collect *Ca. commersoni* despite frequent sampling for 1 year following a 1.6-km fish kill in an Arkansas stream; its pre-disturbance abundance was also low in their study.

Our study demonstrates biological recovery from a severe and extensive disturbance, yet the recovery process highlights the influence of anthropogenic factors on resilience. Especially given the barriers to fish movement along the Reedy River main stem, recovery of the fish assemblage was in large part dependent on the integrity of tributaries in supporting adequate sources of colonists and pathways for dispersal. However, like many other areas in the south-eastern United States, the Reedy River catchment is currently experiencing unprecedented human population growth and associated conversion of forested and agricultural landscapes into those dominated by urban settings and impervious surfaces (Campbell, Allen & Lu, 2007). Resulting cumulative degradation of aquatic resources in this and other catchments is increasingly documented and includes reductions in stream water quality, altered geomorphic properties and loss of biological integrity (Sciera *et al.*, 2008). Such degradation represents the principal long-term threat to aquatic biodiversity and may also confound the recovery of aquatic ecosystems from acute disturbances.

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