Recovery of riverine fish assemblages after anthropogenic disturbances

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Abstract. Disturbances within many communities are common, but the recovery of riverine fish assemblages from anthropogenic fish kills is often not well documented. Quantification of fish community recovery is needed to assess how rapidly or whether recovery occurs without mitigation. To address this need, we evaluated the temporal dynamics of six streams located in central Illinois, including systems impacted by fish kills and an undisturbed reference system. We found species richness and the index of biotic integrity experienced dramatic shifts within the first year after the disturbance event, while fish density varied less within most streams. Interestingly, local extinctions following a kill event were not limited to only rare species, with some dominant components of the local community also lost. Some impacted streams experienced small compositional changes, similar to those within the reference system, while other streams experienced large and continued compositional shifts following disturbance. The rate of compositional change decreased significantly with time since disturbance in all locations, especially within the first year. Most metrics of recovery reached a level of relative stasis three years after the disturbance event. Based on this, we recommend disturbed streams should be monitored for at least three years to fully document recovery dynamics and to determine whether active restoration efforts are warranted. Streams which do not recover during this time frame will likely require direct intervention to achieve recovery. Our results also highlight the importance of regular stream monitoring to document a stream’s baseline composition and dynamics if a disturbance were to occur.

Key words: anthropogenic disturbance; fish community dynamics; fish kills; passive restoration; recovery dynamics.

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INTRODUCTION

Aquatic systems are subjected to natural and anthropogenic disturbance from various sources (Bash and Ryan 2002) that may impact fish assemblages (Peterson and Bayley 1993, Ensign et al. 1997, Zamor et al. 2014). Overexploitation, pollution, and habitat modification have resulted in declines in freshwater biodiversity, with a greater impact in lotic rather than lentic systems (Thompson et al. 2018). These disturbances result in changes to population dynamics, species interactions, and community structure (Martin et al. 2012), which may result in altered resource availability and opportunities for newly colonizing species (Zamor et al. 2014). Natural or anthropogenic disturbances commonly result in compositional shifts to a dramatically new community
or a variation of the pre-disturbance community (Matthews 1986, Kinsolving and Bain 1993, Broadway et al. 2015). Initially, less abundant species may recolonize following the perturbation, at least temporarily escaping the predatory or competitive processes that had limited their populations (Lamy et al. 2015).

Anthropogenic perturbations to aquatic systems are often caused by acute industrial, municipal, or agricultural discharge events. These pulse perturbations can rapidly impact fish communities and are discrete events that occur on timescales shorter than the maximum lifespan of the longest-lived species in the affected area (Schulz and Costa 2015). Recovery of the fish community may be rapid (happening in months) or take many years depending on type, scale, and timing of the disturbance (Matthews 1986, Matthews et al. 2013, Murry and Farrell 2014, Piller and Geheber 2015). Changes to fish assemblage structure may alter critical ecosystem services including productivity, nutrient cycling, and resistance to invasion (McIntyre et al. 2008, Martin et al. 2012). Alteration to these ecosystem services could result in impairment of the stream system, highlighting the necessity of understanding natural processes of recovery.

Recovery is the ability of an assemblage to repopulate following a disturbance and involves the accelerated production of new individuals within a disturbed site and/or recolonization of the disturbed area from surrounding fish populations (Ross 2013). The effects of disturbance events on community dynamics and recovery are commonly studied in terrestrial systems (Pickett and White 1985, White and Jentsch 2001). Despite the commonness of aquatic disturbances (Kubach et al. 2011), these potentially critical forces receive much less attention than their terrestrial counterparts (Phillips and Johnston 2004). Aquatic system recovery can be difficult to understand due to limited availability of pre-disturbance data for impacted streams (Piller and Geheber 2015), high variability in recovery dynamics (Verdonschot et al. 2013), and the spatial and temporal variability that characterize these systems (Grossman et al. 1982, Taylor and Warren 2001, Albanese et al. 2009, Martin et al. 2012). Furthermore, many external pressures may act on an aquatic ecosystem simultaneously, which makes isolating disturbance effects difficult (Kruk et al. 2017). Quantification of fish assemblage recovery represents invaluable information that can directly improve the assessment of ecosystem recovery and management (Lamy et al. 2015). This type of information is increasingly sought out for its usefulness in interpreting and predicting stream dynamics (Burdon et al. 2016).

Inter-specific variation in the colonization rates of stream fishes is expected to lead to variable rates of population recovery and may generate temporal dynamics within disturbed areas (Kinsolving and Bain 1993, Albanese et al. 2009, Kubach et al. 2011). Understanding the dynamics of fish community recovery can provide guidelines for fisheries management, establish criteria for water quality standards, and help to evaluate the successfulness of restoration efforts (Adams et al. 2005, Albanese et al. 2009, Stanford et al. 2018). Management of streams after an anthropogenic disturbance is a combination of passive (allowing natural recovery) or active (habitat improvement) restoration efforts (McCrackin et al. 2017, Meli et al. 2017). Unfortunately, active restoration is expensive, protocols are not always effective or successful (Sundermann et al. 2011, Haase et al. 2013), and natural recovery may not be sufficient. Many studies focus on recovery following the implementation of restoration efforts, without incorporating the natural resilience and resistance of the fish assemblage to disturbance (Thomas et al. 2015, Höckendorff et al. 2017, McCrackin et al. 2017, Nuttle et al. 2017, Thompson et al. 2018). Active restoration efforts may not be needed if the fish assemblage naturally returns to a pre-disturbance state relatively quickly after a disturbance.

The focus of this study was to assess natural recovery of riverine assemblages exposed to acute anthropogenic disturbances (fish kills) and to compare the dynamics of disturbed systems to an undisturbed reference stream. Specifically, we determined (1) the magnitude of disturbance effects on fish community composition and structure, (2) the degree and timing of fish community recovery, and (3) the impacts of disturbance on individual fish species. We use this information to determine an adequate time period to allow recovery to occur in order to assess whether active restoration efforts will be necessary.
METHODS

Study sites and sampling

The fish assemblages of six streams in Illinois were sampled for this study: Beaver Creek (BC), Hooper Branch (HB), Kickapoo Creek (KC), Lone Tree Creek (LT), Riley Creek (RC), and Hurricane Creek (HC; Table 1; Appendix S1: Fig. S1, Table S1). All streams, except HC (the reference site), experienced at least one anthropogenic fish kill (disturbance) resulting from a variety of material releases (Table 1). With no recorded disturbances, HC should portray fish assemblage changes responding to regional and climatic variation only. As fish kill events are by nature unplanned and often accompanied by legal action, details available on each are restricted to the IDNR assessments of their impacts. No other fish kill events were reported for these streams during the time period studied.

We studied a total of seven fish kills in the five disturbed streams. RC experienced sequential fish kills at the same site that occurred in different years (RC1 and RC2). LT experienced the same perturbation (dairy farm effluent) in three different years (2003, 2004, and 2010) at two different sites in the same stream (LT1 and LT2; 8.17 km apart). Here, we only analyze recovery following the 2010 kill for LT, as sufficient pre-disturbance data were not available for the earlier events. The remaining streams experienced only a single disturbance event.

For each disturbance event, pre-disturbance fish assemblage data were available as a part of normal stream monitoring efforts. Pre- and post-disturbance data available varied across streams, with post-kill sampling typically beginning two months after the fish kill event and conducted annually after that. When there were multiple samples available prior to the disturbance event, compositional data were averaged for the site to generate a single reference condition (Table 1). Pre-disturbance data were straightforward in structure for most streams that had single disturbance events. For LT1 and LT2, we used data from a 2008 sampling event as the pre-kill reference for both sites. RC1 and RC2 experienced a kill in 2001 and 2003, respectively. By the sampling event in September 2003, the fish assemblage appeared to have reached relatively stable conditions and was used as the pre-kill reference data for the RC2 fish kill that occurred later in the year as the best measure available. To standardize data sets, we report all time as months after the kill event.

Fish sampling was done using Illinois Department of Natural Resources standard protocols as determined by stream size and accessibility. All

| Stream                     | Sampling ranges          | Date of kill | Type of kill            | No. fish | Kill distance (km) |
|----------------------------|--------------------------|--------------|-------------------------|----------|-------------------|
| Hurricane Creek            | July 1996–July 2011      | ...†         | ...                     | ...      | ...               |
| Beaver Creek               | Pre: August 1994–August 2010 Post: November 2012–October 2015 | November 2012 | Swine waste discharge  | 148,283  | 32.94             |
| Hooper Branch              | Pre: September 2003 Post: November 2012–October 2015 | November 2012 | Swine waste discharge  | 148,283  | 32.94             |
| Beaver Creek and Hooper Branch |                         | November 2012 | Swine waste discharge  | 148,283  | 32.94             |
| Kickapoo Creek             | Pre: July 1996–July 2000 Post: August 2001–July 2011 | June 2001    | Furfural (solvent)     | 259,220  | 14.48             |
| Riley Creek 1              | Pre: July 1996 Post: July 2001–September 2003 | October 2003 | Waste water effluent   | 7173     | 2.57              |
| Kickapoo Creek and Riley Creek 1 |                         | October 2003 | Waste water effluent   | 7173     | 2.57              |
| Riley Creek 2              | Pre: July 2003 Post: June 2004–July 2011 | September 2010 | Dairy farm effluent   | 40,044   | 18.54             |
| Lone Tree Creek 1 and 2    | Pre: August 2008 Post: October 2010–October 2015 | September 2010 | Dairy farm effluent   | 40,044   | 18.54             |

Note: Data acquired from the Illinois Department of Natural Resources Division of Fisheries’ internal report of the pollution that caused each fish kill.
† An ellipsis indicates “none” as Hurricane Creek is the reference stream.
sites were at least 100 m in length and contained at least one pool/riffle sequence. Block nets were placed at the upper and lower limits of each site for those sampled with electric seines or backpack electrofishing. Most streams (HC, KC, RC, and LT1) were sampled by electric seine (Angermeier et al. 1991). BC was sampled by 3000-watt AC boat electrofishing; HB and LT2 were sampled by backpack electrofishing. As all comparisons are made within streams, and sampling methodology was held consistent within streams, variation in gear types should not alter the dynamics observed. During sampling, all fish over 100 mm were identified, measured in mm, and weighed to the tenth of a gram in the field and released alive. Many of the smaller individuals, especially cryptic minnow and darter species, were preserved in 10% formalin for laboratory analysis, including species identification and physical metrics.

From the fish collected, proportional composition, total catch, and index of biotic integrity (IBI) were determined. Index of biotic integrity is a metric designed to quantitatively assess the overall quality of the fish assemblage relative to regional reference conditions (Smogor 2000). Catch per unit effort (CPUE, as fish per hour) was used to standardize for variation in effort with relative abundances used for compositional data. Community metrics were expressed as a proportional change from their pre-disturbance conditions (i.e., a baseline of zero) to standardize across sites. As the streams were monitored for varying lengths of time, we disregarded any sampling events after 60 months post-disturbance in this analysis, allowing more comparable results across all studies. Beyond 60 months, most streams experienced only minor compositional changes. For the undisturbed HC site, the entire span of data was presented (July 1996–July 2011), using the midpoint as the baseline.

Data analysis
To determine compositional shifts within sites, non-metric multidimensional scaling (NMS) ordination was conducted in two dimensions on log10 + 1 transformed data and Sorensen’s distance using PC-ORD (McCune and Grace 2002) for the entire dataset. This dimensionality was determined to be optimal in comparison with analyses of randomized data. Species that occurred fewer than four times across all sampling events were removed from this analysis as uninformative. To assess changes in the rate of compositional turnover, Euclidean distances between NMS coordinates for adjacent times were determined for each site.

To directly assess recovery of individual species, log10 + 1 transformed CPUE data for all species were correlated between pre- and post-disturbance data (last sampling event prior to disturbance and the sampling event closest to 36 months post-disturbance) using Pearson correlation for each site. Because preliminary visualizations of community metrics revealed the apparent achievement of stasis by 36 months post-disturbance, we chose that time to assess compositional recovery. We also plotted the post-kill abundance (log10 + 1 transformed CPUE) as a function of pre-kill abundance for each species. Data points above the 1:1 line represent an increase in a species’ abundance and any data point below the line represents a decrease following the fish kill. In this display, data points on the y-axis line indicate a new species colonization and data points on the x-axis line represent an extinction event of a species present before the disturbance. A similar analysis was conducted on the reference stream for comparison, using a randomly selected 36-month interval. Although this stream was not sampled in all years, other 36-month intervals within HC were qualitatively similar in community metrics overall to justify this random selection.

RESULTS

Community metrics
All sites experienced large depressions in species richness immediately following disturbance (Fig. 1). Following this initial change, there were large fluctuations in richness after the kill, followed by relative stasis after approximately 36 months. Streams which had experienced previous perturbations (RC2, LT1, and LT2) recovered to richness values substantially below pre-disturbance conditions. Additionally, both LT locations experienced the greatest percent decrease (61.8%) in species richness of all sites from pre-kill data to the last post-kill sampling event. These changes were larger than those observed in the undisturbed reference stream (Fig. 2).
After an initial depression immediately after the disturbance, fish density (CPUE) recovered and remained relatively consistent post-disturbance in most sites (Fig. 1). RC1 experienced a substantially larger increase in CPUE compared with other streams, but still appeared to stabilize 17 months after the kill at levels well above pre-disturbance conditions. Most streams reached relative stasis in CPUE by approximately 36 months after the fish kill. RC1, which was only sampled 27 months after the disturbance also had dampened changes by that time. Disturbance-related changes in CPUE were overall larger than those seen in the undisturbed reference stream, HC (Fig. 2).

Index of biotic integrity changed dramatically in the first few months following disturbance, similar to the response of species richness, persisting up to about a year after the kill, followed by an extended period of relative stasis in stream fish quality after 36 months (Fig. 1). Surprisingly, IBI values for HB and KC initially increased past original values within the first 12 months after the kill and maintained values above pre-kill conditions. Most disturbance events (4/7 kills) ultimately attained IBI values equal to or greater than before the disturbance about two years after the fish kill. The exceptions were RC1, LT1, and LT2, which remained below pre-kill values in almost all subsequent sampling events.

Individual species recovery

The pre- and post-disturbance abundances of individual species were significantly and positively correlated \((P < 0.005)\) for most sites except HB, RC1, and LT2 (Fig. 3). As expected, the undisturbed HC site experienced minimal compositional shifts over time (a randomly selected 3-yr interval as described previously in the methods; \(R = 0.83\)), with the majority of the data points reasonably close to the 1:1 line and only four species extinctions and two colonizations. Other time periods were qualitatively similar for this stream.
The greatest recovery occurred in KC ($R = 0.85$) with most species relatively close to the 1:1 line, similar to the undisturbed HC site. Many species in this stream were more abundant following the disturbance; however, their relative abundances remained fairly similar. All remaining streams experienced much larger shifts in composition following disturbance ($R$ values between 0.74 and 0.10), including both large decreases and increases in species abundance. Furthermore, there was a substantial number of species that went locally extinct (species on the $x$-axis), especially for LT2, and new species colonizations (species on the $y$-axis; Appendix S1: Table S2). Interestingly, species extinction was not restricted to the rarest members of the species.

Fig. 3. Recovery of individual species’ abundance 36 months after the kill as a function of pre-disturbance abundance. Data are catch per unit effort (CPUE) values (+1) for each sampling period and are plotted on a log10 scale. The 1:1 line plotted represents complete CPUE recovery, values above indicate an increase, and values below this line indicate a decrease in abundance.
community, and some of the new colonists became local dominants, especially in RC1. Streams, which ultimately recovered to pre-disturbance conditions, averaged much larger correlations with pre-disturbance species abundances at year 3 (average $R = 0.59$) whereas sites which did not (HB, LT1, LT2) exhibited much lower values (average $R = 0.36$).

**Compositional recovery**

There was marked variation in recovery across the rivers/disturbances as visualized with a NMS ordination (Fig. 4). As would be predicted for an undisturbed system, HC had very minor compositional shifts over the 15 yr of observation, indicating compositional stability of fish in the region. Similar to the reference stream, there were only slight compositional changes in BC, RC1, RC2, and KC; remaining compositionally similar to their pre-disturbed conditions after their initial perturbation. In contrast, HB, LT1, and LT2 had the greatest compositional shifts following disturbance and did not return to their respective pre-disturbed composition after five years.

The rate of compositional recovery also varied dramatically among disturbed streams (Fig. 5). The undisturbed reference site HC behaved as

![Fig. 4. Compositional changes over time as illustrated with a two-dimensional non-metric multidimensional scaling (NMS) of fish assemblage composition (2D stress of 0.123) across all streams (disturbed and reference). For clarity, streams are separated into different panels. Hurricane Creek (upper left) is the undisturbed reference stream. To show directionality, pre-kill composition is indicated with a square and all subsequent samples connected with a line.](image-url)
expected showing a minimal rate of change over time. BC, HB, KC, and RC2 also had consistently low rates of compositional change during the first two years. In contrast, RC1, LT1, and LT2 had high rates of change initially after the disturbance that were double or triple those of the other streams. These higher rates of change dramatically decreased over time to relatively low levels by approximately two years post-disturbance and maintained a relative level of stasis after about 36 months. After a period of relative stasis, compositional change in the two LT sites increased toward the end of sampling.

**DISCUSSION**

The undisturbed system used as a reference site remained remarkably unchanged and stable throughout the 15-yr monitoring period, although some temporal variation was evident (Grossman et al. 1982, Taylor and Warren 2001). Compositional shifts and loss and gain of species were minimal in HC and would reflect the natural fluctuations that represent the baseline for comparisons with the streams that experienced disturbance. The average number of colonizations in the undisturbed stream within a three-year period was 4.50 and 4.67 for extinctions and was generally limited to species in low abundance. The dynamics within the undisturbed HC system indicate the natural scale of fish assemblage fluctuations that occurred in regional stream systems. Temporal variation in species abundances resulted in relatively consistent composition of HC over time rather than accumulating directional changes (Matthews et al. 2013).

In marked contrast to the reference stream, there were much larger changes in all impacted streams. The average number of colonizations over the first three years post-disturbance was 4.3, similar in magnitude to the reference stream. In contrast, disturbed streams averaged a much higher 7.3 extinctions than seen in the reference stream. Disturbed streams also experienced much greater changes in composition than the reference stream. These differences between unimpacted and disturbed systems strongly suggest that the changes seen were not generated by regional climatic or temporal variation. Because of this, assemblage responses in the disturbed streams appear to be a direct response to the fish kill events.

Our current understanding of stream recovery dynamics stems largely from studies monitoring one system experiencing one disturbance or one type of disturbance (e.g., effects of a single pollution disturbance in one river over a 10-yr period; Schulz and Costa 2015 or responses to several areas of active channel modification; Favata et al. 2018). Based on the dynamics observed in this study, it is clear that some stream fish assemblages have the ability to recover or even exceed pre-disturbance conditions and to maintain that recovery with no active remediation (Matthews 1986). These disturbances may reset the system and may ultimately increase diversity by presenting the new fish assemblage with an environment that might not have the original biological constraints such as competition or predation (Adámek et al. 2016).

In this study, it appeared that some fish assemblages recovered almost immediately after the

![Fig. 5. Changes in the rate of compositional change over time for disturbed (upper) and undisturbed reference (lower) streams. Data plotted are Euclidean distances between sampling events in the non-metric multidimensional scaling ordination (Fig. 4) as a function of time since the disturbance event or time of monitoring (reference stream).](image-url)
disturbance, within 1–2 yr reaching or exceeding pre-disturbance conditions followed by relative stasis. If recovery was not achieved, relative compositional and structural stasis still occurred, but appeared to represent a new and persistent community structure. Frequent anthropogenic disturbances also appeared to decrease fish assemblage resilience, resulting in increased vulnerability to compositional shifts (Broadway et al. 2015). All streams that experienced only one perturbation recovered community metrics (IBI, species richness, fish density) to values equal to or exceeding pre-disturbance conditions. Conversely, in those systems perturbed multiple times, as with Lone Tree Creek and Riley Creek sites, community metrics were dramatically and persistently altered.

We were unable to identify definitive patterns between size of disturbance (fish/km killed) and the magnitude of compositional shifts, suggesting something other than magnitude is controlling the level of recovery. For example, KC had the greatest damage, with 17,902 fish killed/km and the LT sites had a much lower 2160 fish killed/km. Even though the damage to KC was greater, both LT sites experienced compositional shifts that were dramatically greater than those of KC. These streams experienced different types of effluent (furfural vs. dairy farm runoff) and likely differed in the fish populations adjacent to the kills. Data compiling replicated disturbance types (e.g., natural, agricultural discharge, and industrial effluent), and the landscape context of fish assemblages would be necessary to fully understand the landscape and disturbance characteristics that allow fish communities to recover.

Management recommendations
Pre-disturbance data were critical to assessing the level of fish assemblage recovery, illustrating the necessity of regular stream monitoring to provide reasonable benchmarks for assessment (Buckwalter et al. 2018). Without valid pre-disturbance data, there would be no knowledge of the original system’s structure or dynamics. Across all metrics, 36 months appears to be when post-disturbance compositional shifts reached a level of relative stasis. Therefore, we recommend stream monitoring for at least three years following a disturbance at regular intervals to ensure a clear recovery trajectory. If, after three years, the system has not achieved sufficient recovery, it should be targeted for active remediation efforts. Additionally, attention should be directed toward streams that have experienced a greater frequency of disturbance, as they appear less able to recover.

There are no clear criteria for determining recovery of a system (Adams et al. 2005), but the measures used here are similar to those used in other studies (Kubach et al. 2011, Favata et al. 2018). Knowledge of streams natural recovery dynamics will provide necessary insight on how to handle a disturbance event most appropriately. If streams are regularly monitored before and after perturbations, we can refine metrics to assess recovery dynamics (Pedley and Dolman 2014, Thomas et al. 2015), and inform restoration practices (Hanna et al. 2018). Further, assessing similar metrics in any subsequent restoration will provide fisheries managers with the ability to evaluate the success of implemented restoration efforts, ensuring that time and resources are not wasted.

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**Supporting Information**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3459/full