Recovery of Temperate-Stream Fish Communities from Disturbance: A Review of Case Studies and Synthesis of Theory

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ABSTRACT / To evaluate the relative effect of autecologic factors, site-specific factors, disturbance characteristics, and community structure on the recovery of temperate-stream fish communities, we reviewed case histories for 49 sites and recorded data on 411 recovery end points. Most data were derived from studies of low-gradient third- or fourth-order temperate streams located in forested or agricultural watersheds. Species composition, species richness, and total density all recovered within one year for over 70% of systems studied. Lotic fish communities were not resilient to press disturbances (e.g., mining, logging, channelization) in the absence of mitigation efforts (recovery time >5 to >52 yr) and in these cases recovery was limited by habitat quality. Following pulse disturbances, autecological factors, site-specific factors, and disturbance-specific factors all affected rates of recovery. Centrarchids and minnows were most resilient to disturbance, while salmonid populations were least resilient of all families considered. Species within rock-substrate/nest-spawning guilds required significantly longer time periods to either recolonize or reestablish predisturbance population densities than did species within other reproductive guilds. Recovery was enhanced by the presence of refugia but was delayed by barriers to migration, especially when source populations for recolonization were relatively distant. Median population recovery times for systems in which disturbances occurred during or immediately prior to spawning were significantly less than median recovery times for systems in which disturbances occurred immediately after spawning. There was little evidence for the influence of biotic interactions on recovery rates.

While studies of the effect of natural and anthropogenic disturbances on fish populations are common, relatively few studies examine the recovery of fish populations and communities (Niemi and others 1990). Data on recovery rates of aquatic communities are necessary not only for establishing exceedance criteria for water quality standards (Plafkin 1988), but also for testing current ecological theory (Resh and others 1988, Yount and Niemi 1990). Theories concerning the role of biotic versus abiotic control of fish communities (Schoener 1987), the role of succession in streams (Fisher 1983), island biogeography theory (Minshall and others 1983), life history strategies, zoogeographical constraints, the effects of environmental variability, and the effect of food web complexity on the stability of fish communities (Horwitz 1978, DeAngelis and others 1989, Poff and Ward 1990, Reice and others 1990) are all relevant to the study of recovery processes. In this study, we review case histories containing data on fish recovery rates in temperate streams and explore the

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application of theories of community ecology to these data.

Early studies of the recovery process in streams considered only features of individual organisms (autoecological factors) that influenced recovery rates, rather than inherent properties of communities or ecosystems. Shelford (1911) suggested that succession in stream fish communities progressed through stages, each stage typified by a range of environmental conditions and by fish with similar physiologic tolerances, behaviors, feeding habits, and habitat preferences. Thompson and Hunt (1930) examined behavioral and feeding habits affecting the persistence of warmwater fish species in small streams of Champaign County, Illinois. Species that had disappeared from one or more drainage basins between the time of earlier surveys (1882–1901) and 1930 tended to be small nonvagile trophic specialists. In contrast, of the 14 species common within areas of chronic pollution, seven of these were typical headwater species, which tended to be more vagile and less specialized in feeding habits.

More recent studies have demonstrated that autecological factors alone are inadequate for explaining recovery rates, but disturbance- and site-specific factors must be considered as well. Berra and Gunning (1970)

measured rapid recovery of both sunfish and sucker populations (<1 yr) following removal, in spite of the limited home range of individual centrarchids (30–40 m) relative to that of suckers. They suggested that lack of predation and relaxation of competition during early colonization phases were responsible for increased rates of movement among the centrarchids following disturbance. Recolonization following drought in an intermittent midwest stream was influenced not only by the tolerance and vagility of fish species present, but also by the magnitude and spatial extent of the disturbance, and by the presence of barriers to migration (Larimore and others 1959).

Interest in fish community ecology (Heins and Matthews 1987) and its application to recolonization phenomena accelerated between 1975 and the present. Sheldon (1987) applied species-area or species-discharge curves to predict local extinctions (i.e., nonrecovery) of fish species in response to disturbances that fragment drainage systems. Resh and others (1988) examined the interaction between disturbance and natural environmental variability in structuring lotic fish communities.

Controversies concerning the stochastic versus deterministic nature of constraints on fish communities and the degree of abiotic versus biotic control (Schoener 1987) are central to the study of the recovery process. The persistence or stability of fish communities subject only to natural environmental variability (e.g., fluctuations in flow, temperature, dissolved oxygen) influences our ability to detect both the response (resistance) of fish communities and also the time required for communities to recover to within an expected range of variation (resilience). Grossman and colleagues (1982) have argued that stream fish communities are normally stochastic, but Matthews (1986) demonstrated a high degree of year-to-year persistence and stability of fish communities over a 10 yr period that included a 100 yr flood. Within each year, seasonal variability in species abundance and composition can be relatively high (e.g., Binns 1967, Hall 1972), thus limiting the resolution of recovery time estimates.

The debate concerning the role of abiotic versus biotic control has been resolved in part by ranking fish stream communities along an abiotic–biotic continuum based on (1) a decrease in relative environmental variability as stream order increases (Horwitz 1978); (2) regional variations in the harshness of flow, temperature, and dissolved oxygen extremes (Resh and others 1988); and (3) the influence of channel morphology (pool–riffle ratio) on predator–prey interactions (Schlosser 1982). Thus, the role of natural disturbance in struc-

turing communities and the degree to which different populations of fish are adapted to stressors is expected to vary according to stream order and geographic region.

Succession also may influence the recovery process, but classical theories developed for terrestrial communities must be modified to reflect the unique nature of spatial and temporal heterogeneity in stream ecosystems (Fisher 1990). Stochastic seasonal events (e.g., spring floods) should influence succession more strongly in aquatic systems than in terrestrial systems, because succession is likely faster in aquatic systems. Secondly, because pools or upstream reaches can be seasonally isolated, succession can proceed in a deterministic fashion on the scale of small pools, yet in a stochastic fashion over a basin-wide scale (e.g., Gray and Fisher 1981).

In this review, we have summarized available data on recovery rates for both individual fish species and community-level parameters following acute or chronic disturbances. We have tested the effect of autecologic factors, site-specific factors, disturbance characteristics, and community structure on observed recovery rates. Finally, we have summarized the limitations of the available data base for testing current ecological theory and presented the regulatory implications of our current state of knowledge.

Methods

Details on the selection of case studies and encoding of data have been described by Niemi and others (1990). Case studies were identified through automated and manual searches of bibliographies of the aquatic science literature. Briefly, case studies were selected based on three criteria:

1. Availability of predisturbance data, reference system data, an investigator's assurance of recovery, or data indicating return to a stable population density, species richness, or biomass following a disturbance;
2. Availability of repeated post-disturbance sampling data; and
3. Ability to pinpoint a time when the physical activity that initiated the stressor ended.

We used the definition of disturbance described by Pickett and White (1985): "a disturbance is any rela-

tively discrete event in time that disrupts ecosystem, community, or population structure, and that changes resources, availability of substratrum, or the physical environment." Thus, both studies of chemical stressors and studies of physical disturbances that temporarily or permanently modified habitat were included. Studies of recovery following eutrophication were excluded because it was difficult to say when eutrophication (or nutrient input) had abated. Rehabilitation efforts generally were excluded because we were primarily concerned with natural recovery in the absence of artificial enhancement.

Our definition of recovery is by necessity a working definition because of the limitations of available data sets. Our working definition of recovery is more consistent with an equilibrium view of stream fish communities than with the intermediate disturbance hypothesis or dynamic equilibrium views (Resh and others 1988), i.e., it assumes that steady-state conditions did exist. Unfortunately, the paucity of data on both mean and variance of predisturbance conditions precluded us from considering the natural level of variability in a system when assessing recovery. For fish communities exhibiting high intra- or interannual variation, our working definition should yield a conservative estimate of recovery times for species composition and population densities.

We use the term end point to identify the time required for biological attributes to recover. Time to recovery was measured from the point at which either pulse inputs or the physical activity that caused the disturbance had ended. End points consisted of: (1) time required for a species to reappear; (2) time for recovery of total fish density, species richness (at least 80% of predisturbance taxa), or biomass; and (3) the time for recovery of the density, biomass, or average size of individual species. When recovery had not occurred by the end of a study, or when recovery had occurred well before sampling was started, recovery times were recorded as >x years or <x years, respectively.

The following parameters on disturbance characteristics were recorded when available: disturbance type, frequency, and duration; time of year; distance of source populations for recolonization; and magnitude of disturbance impact as measured by species persistence. Data on system characteristics (latitude, longitude, watershed size, stream order, gradient, mean and range of discharge, and land use) were obtained from USGS topographic maps (1:25,000), peer-reviewed literature, U.S.G.S. discharge records, or directly from state agencies. Discharge records were summarized for the period of disturbance studies only. Autecological

characteristics that were encoded included: family, trophic guild, reproductive guild, size and age at first reproduction, season of spawning, number of spawns per year, native vs. introduced status, anadromy, and vagility (Winn 1958, Breder and Rosen 1966, Carlander 1969, Pfleiger 1971, Scott and Crossman 1973, Eddy and Underhill 1974, Balon 1975, 1984, Manooch 1984). Based on a knowledge of home ranges and distances traveled during spawning migrations, the vagility of different species was classified as none, moderate, or high (Gunning and Berra 1969, Berra and Gunning 1970, Padgett 1975). Information on reproductive traits was derived from references pertinent to the geographic regions in which disturbances occurred.

To accommodate the use of less than or greater than recovery time values, we used median rather than mean time to compare community recovery rates. By using system median recovery times rather than individual end points to compare the effects of disturbance and site characteristics, we avoided biases that would have been created by giving more weight to systems with numerous end points recorded. Where possible, effects of site characteristics, disturbance characteristics, or organism traits on median recovery times were tested statistically. Effects of continuous variables were tested first through simple correlation analysis. Effects of categorical variables (e.g. fish family, disturbance type) were analyzed using a Kruskal-Wallis test followed by Tukey's multiple comparison of mean ranks to differentiate among groups. In cases where many recovery end points were recorded as less than or greater than values, we could only compare simple frequency distributions among categories using the chi-square test. Use of a chi-square test is not advised if many cell frequencies are less than 5; thus when the number of recorded end points was limited, only semiquantitative generalizations could be made.

Review of Case Studies

System and Disturbance Characteristics

The data discussed below do not represent a random sample of recovery information for fish in temperate lotic systems, but were limited to those systems for which case histories were available for review. Forty-nine lotic systems were identified for which data were available on recovery from disturbance. The majority of these systems were located in the continental United States (Appendix A). Most systems were low-gradient

Table 1. Median values for characteristics of study sites

Parameter	N	Median across Systems	Median across End points	Range
End points (N/system)	49	3	—	1–54
Latitude (°N)	49	42	40	30–58
Longitude (°)	49	89	90	3–153
Watershed area (ha)	35	9046	7290	71–3,910,000
Stream order (N)	46	3	3	1–6
Elevation (m)	43	244	280	0–2160
Discharge				
Mean (m³/sec)	27	1.1	5.1	0.04–154
Minimum (m³/sec)	19	0.2	0.7	0–5.4
Maximum (m³/sec)	19	23	88	1–710
Max:min	17	44	44	3–2536
Gradient (%)	40	0.6	0.2	0.01–14
Agriculture (% area)	13	47	79	0–100
Forest (% area)	13	21	5	0–100
Grassland (% area)	13	0	13	0–47
Urban (% area)	13	0	1	0–55

(<1% slope) third- or fourth-order streams, with a baseflow <0.5 m³/sec and peak flow <100 m³/sec (Table 1). Two-thirds of streams for which adequate flow data were reported had relatively stable flow, with discharge ratios (maximum:minimum) of <150. Most of the systems studied were in predominantly forested or agricultural watersheds (Appendix A). Few data were available for recovery of fish communities in large (≥5th order) or urban lotic systems.

Results are potentially biased by the distribution of end points among systems. Studies contained a median of three end points per system, although some studies contained as many as 54 end points per system. For most system characteristics, median values calculated across all systems (N = 49) were similar to median values calculated for all end points (N = 411; Table 1). Thus, the few systems with many end points should not bias the results of our comparisons among different taxa or guilds.

Recovery of fish communities from a wide range of natural (flooding, drought) and anthropogenic stressors has been studied. Anthropogenic stressors studied include chemical inputs (e.g., DDT, rotenone), habitat manipulation (instream habitat development, nonchemical organism removal), and watershed-level disturbances (mining, timber harvesting, channelization).

A total of 411 end points were recorded for fish recovery, the majority of which represent recovery times for individual taxa: recovery of fish populations to predisturbance densities (48%), time to first appear-

ance (34%), or recovery of average size (6%). Data were reported for 15 different families, although most end points (87%) represented fish species within five common families: Catostomidae, Centrarchidae, Cyprinidae, Salmonidae, and Percidae. Fewer data were available on recovery of community-level parameters (total fish biomass, density, productivity, or species richness), i.e., 27 case studies representing only 12% of all end points.

Sensitivity of Different Measures of Recovery

Most species and community parameters were relatively resilient, recovering within 2 years of disturbance. Within two years following acute disturbance events (e.g. chemical spills, rotenone treatment), half of the species in a system had reappeared in 67% of the cases and half of the species population densities had recovered to pre-disturbance levels in 52% of the systems (Figures 1A,B). Recovery of community parameters occurred more rapidly; the majority of systems studied (71%–75%) had recovered to former levels of species richness or total density with 2 yr. During the first year following disturbance, total biomass recovered more slowly than other community-level parameters recorded; only 29% of systems recovered within 1 yr, but 71% of systems had recovered within 2 yr.

Recovery of all individual species-population densities within each system was much slower than recovery
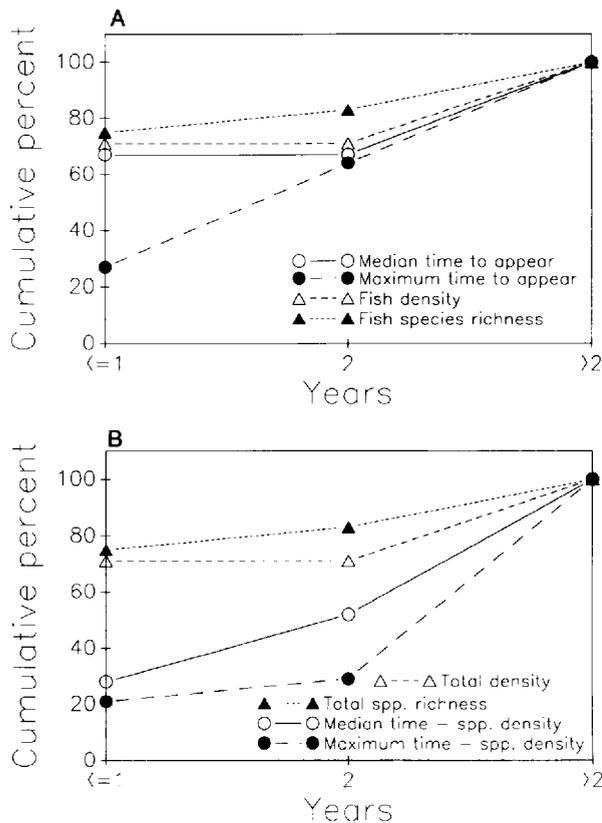
Figure 1. (A) Cumulative recovery of systems according to median (open circles) and maximum time (closed circles) to reappearance of fish species and time to recover fish species richness (closed triangles) or fish density (open triangles). (B) Cumulative recovery of systems according to median (open circles) and maximum time (closed circles) to recovery of pre-disturbance population density and time to recover total density (open triangles) or species richness (closed triangles).


Figure 2. Cumulative recovery curves by press: channelization (open circles), or pulse disturbance type: DDT (closed circles), flooding (open triangles), or other chemicals (closed triangles).

of community parameters such as species richness or total density (Figure 1B). Within 2 yr following a disturbance, densities of the least resilient species had recovered in less than 30% of the systems studied (N = 24).

Press vs. Pulse Disturbances

The single most important factor affecting fish recovery rates was the nature of the disturbance. As defined by Bender and others (1984), press disturbances are chronic, with a duration longer than the life-span of the longest-lived species in a community. We have extended the definition for press disturbances from that of planned disturbances (treatments) in laboratory ex-

periments to include "unplanned" disturbances as observed in the field. As defined by Niemi and others (1990), the term press disturbance is used for those events that involve significant (long-term) modifications of instream habitat and that may affect the surrounding watershed as well. Press disturbances included in studies reviewed here were channelization, habitat enhancement, mining, and timber harvesting. In the extreme, press disturbances can be considered as a shift to an alternate state because the magnitude of critical driving forces (e.g., nutrient inputs and volume of watershed runoff, inputs of particulate organic matter and large woody debris) or the transformation of energy inputs (e.g., the absorption of radiant energy by an overhead canopy, the balance between deposition and erosion as influenced by channel morphology) for these systems has been drastically altered.

In contrast to press disturbances, pulse disturbances are relatively discrete events, with a duration shorter than the life-span of longest-lived individuals, and typically involve point-source inputs or short-lived hydrologic events. Pulse disturbances covered in the review of studies here were chemical spills or treatments (e.g., rotenone), floods or droughts, construction activity, and nonchemical organism removal. Population recovery times following pulse disturbances varied between 0.08 and 6 yr, while recovery times following press disturbances varied between 5 and >52 yr (Figure 2). A significantly greater proportion of recovery times were >20 yr for channelization (the predominant press disturbance studied) than for pulse disturbances (flooding, DDT, other chemicals; chi-square test, $P <$ 0.0001).

Characteristics of Press Disturbances Affecting Recovery Rates

Press disturbance typically cause large-scale modification of instream and riparian habitat, which prolongs the recovery process. With the exception of cases of habitat development, the lowest recovery times observed following press disturbances were 6 or 7 yr following cessation of mining or timber harvesting, respectively. In these cases, no direct habitat modification had occurred. Channelization, which greatly degrades and simplifies instream habitat, required recovery periods greater than 52 yr (Bayless and Smith 1964, Congdon 1971, Arner and others 1976, Lund 1976, Moyle 1976, Edwards and others 1984, Portt and others 1986). In cases where effective habitat mitigation occurred, leading to decreased siltation and increased pool volume, recovery occurred within 5 yr (Hunt 1976, Edwards and others 1984).

Recovery in channelized systems was mediated by organism-specific food requirements and habitat preferences. In the Olentangy River, Ohio, USA, bottom-dwelling detritus feeders (catostomids, cyprinids) or species such as channel catfish (*Ictalurus punctatus*) common to productive backwater refugia persisted (Arner and others 1976, Edwards and others 1984). In the Luxapalila River, Mississippi, USA, only migratory fish (*Minytrema melanops, Ictiobus bubalus*) were dominant in a newly channelized section (Arner and others 1976), while nonmigratory bottom-dwellers were scarce (Padgett 1975). Following mitigation in the Olentangy River, levels of invertebrate drift increased, and populations of deepwater sight-feeders (sunfish, crappies, bass, and catfish) increased (Edwards and others 1984).

In two coldwater systems studied, recovery was related to habitat preferences of fish species and to habitat quality. In Rush Creek, California, USA, riffle dwellers (e.g., speckled dace (*Rhinichthys osculus*) and pit sculpin (*Cottus pitensis*)) that are adapted to fast current dominated channelized sections. Following mitigation within the St. Regis River, Montana, USA, recovery of trout populations was related to the availability of pool habitats (Lund 1976).

Characteristics of Pulse Disturbances Affecting Recovery Rates

Within the category of pulse disturbances, recovery times were greatest following DDT treatments, in part because of bioaccumulation. DDT was found at abnor-
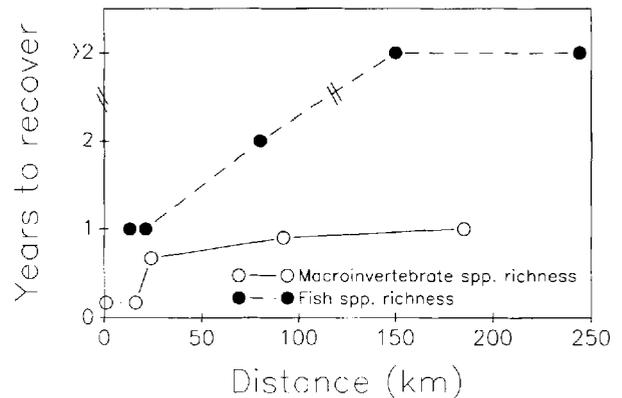
Figure 3. Recovery time for fish species richness (closed circles) or macroinvertebrate species richness (open circles) as a function of distance from recolonization source in Green River, Wyoming.

mally high levels in brook trout tissue 3–16 months following treatment (Warner and Fenderson 1962, Graham and Scott 1958) and may have been responsible for delayed mortality observed in the fall and early winter when it was remobilized during metabolism of fat reserves (Graham 1958).

The spatial extent of pulse disturbances affected recovery times by increasing the distance source populations must migrate to recolonize disturbed areas. A 715-km section of the Green River, Wyoming, USA, and its tributaries was treated with rotenone above the site of the Flaming Gorge Dam to allow the establishment of a sports fishery (Binns 1967). Times to reappearance were significantly greater for stations distant from upstream recolonizing sources (150–244 km) than for those stations relatively close to undisturbed stretches (13–21 km; chi-square test $P < 0.001$). Fish species richness recovered within 1 yr at sample stations 13 or 21 km from untreated headwater populations, but required more than 2 yr to recover at sites 150 or 244 km downstream from refugia (Figure 3).

According to island biogeography theory, equilibrium species number is determined by the intersection of immigration and extinction curves, i.e., $I = E$ (MacArthur and Wilson 1967). Here immigration is defined as the rate at which new species appear; extinction is defined as the localized disappearance of species from a given station. Immigration rates decrease with time (or as species number increases) while extinction rates increase due to competitive exclusion (Figure 4A). In the Green River, however, final species richness levels were influenced by immigration rates only and not by competitive exclusions. Average immigration rates were
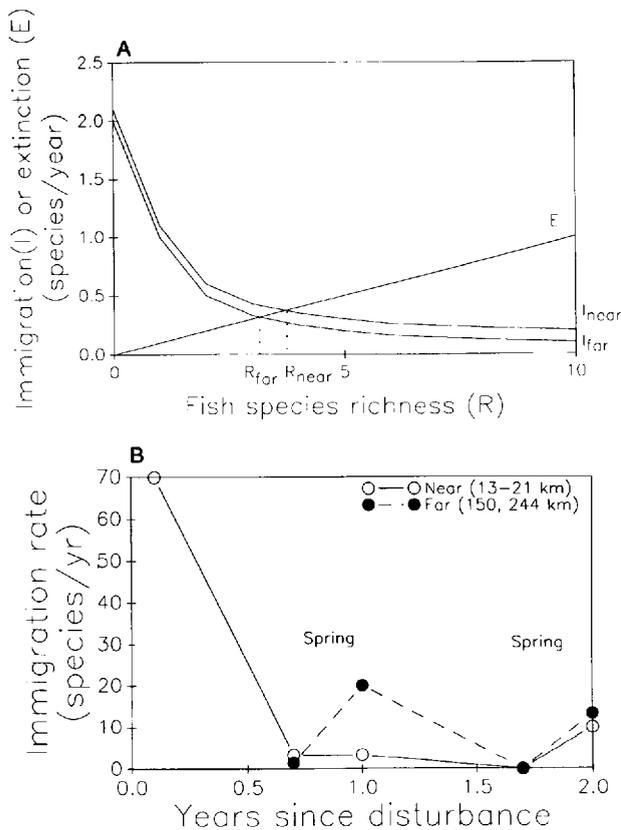
Figure 4. (A) Theoretical rates of fish immigration and extinction as a function of species richness (MacArthur and Wilson 1967). (B) Immigration rate of fish species in Green River as a function of time and distance from recolonization source. Near stations (open circles) were 13–21 km and far stations (closed circles) were 150 or 244 km from the colonization source.


Figure 5. Effect of disturbance timing on recovery time of fish species population densities: disturbance during or prior to spawning (closed circles) vs. disturbance after spawning (open circles).

lower far from recolonization sources (150–240 km). For proximal stations, immigration rates decreased with time following disturbance (Figure 4B). At distant stations, immigration rates varied more with season; a temporary increase in immigration occurred between spring and summer sampling periods (0.7–1.0 yr, 1.7–2.0 yr). In another temperate system studied, fish movement rates varied as much as tenfold among seasons, with the greatest number of migratory individuals occurring during spring months (Hall 1972).

Timing of disturbance events relative to spawning season were unrelated with time to first appearance of fish species but were related with time to recovery of fish densities (Binns 1967, Engstrom-Heg and Loeb 1971, Olmsted and Cloutman 1974). Median population recovery times for systems in which disturbances

occurred during or immediately prior to spawning were significantly less (median = 1 yr) than median recovery times of systems in which disturbances occurred immediately after spawning (median = 2 yr; $P < 0.05$, Kruskal-Wallis test; Figure 5). Disturbances occurring in the season following spawning were likely to decimate young-of-the-year (YOY) fishes, and subsequent recovery fish density would be delayed by a year until spawning runs occurred again. If disturbances occurred in the season prior to spawning, population densities could be restored through spawning migrations (e.g., brown trout in the Green River; Binns 1967), through subsequent reproduction by persistent species as in Mud Creek, Arizona, USA (Olmsted and Cloutman 1974), or through migration of YOY from nearby unaffected areas as in Mud Creek and Ten Mile River, New York, USA (Engstrom-Heg and Loeb 1971). Disturbances occurring during the spawning season decimate spawning individuals, but the remaining eggs could be more tolerant of pulse disturbances than adults. For example, one month following the extensive rotenone treatment of the Green River, flannelmouth sucker fry (*Catostomus latipinnus*) appeared in backwater channels in the absence of any adults, apparently reestablished from eggs present at the time of treatment (Binns 1967).

Effect of Site-Specific Factors on Recovery from Pulse Disturbances

When data for members of all fish taxa were combined, none of the site characteristics examined (lati-

Table 2. Effect of recolonization source on median system recovery time

Known recolonization source	Frequency of median population recovery time		
	<1 yr	1–2 yr	>2 yr
Upstream source	8	9	3
Downstream source, no upstream source	4	4	2
No downstream or upstream source	1	5	3

Table 3. Description of selected reproductive guilds according to Balon (1975)

Parental investment	Substrate[a]
Open substratum spawners	Pelagophils
	Lithopelagophils
	Lithophils
	Phytolithophils
	Phytophils
	Psammophils
Brood hiders	Lithophils
Substratum choosers	Lithophils
	Phytophils
Nest spawners	Lithophils
	Phytophils
	Speleophils

[a]Pelago = open water; litho = rock or gravel; phyto = vegetation; psammo = sand; speleo = natural cavities.

tude, longitude, watershed size, stream order, channel gradient, mean, minimum, or maximum discharge) were significantly correlated with recovery times (P > 0.05). Within fish families however, some trends were significant. For centrarchids, (log) recovery time for population density was negatively correlated with channel gradient:

$$Log(TIME) = 0.24 - 1.2(GRADIENT)$$
$$(Adj. r^2 = 0.31, P < 0.01)$$

Within the family Cyprinidae, recovery time to first appearance or to predisturbance densities was greater for fifth-order streams (≥2 yr for all three cases) than for second- to fourth-order streams (Kruskal-Wallis, first appearance, $P < 0.001$; density, $P < 0.01$). The trend for increased resilience of cyprinid populations in low-order streams is consistent with Matthews' (1987) finding that individuals of cyprinid species from headwater streams were more tolerant of dissolved oxygen and temperature stress than those resident in higher-order streams. Likewise, Schlosser (1990) has argued that upstream fish communities should exhibit more rapid recovery from disturbance because species characteristic of upstream communities have a shorter generation time and smaller body size than do species characteristic of downstream communities.

Recovery rates within specific case studies were significantly affected by the location of disturbances relative to barriers to migration and by the presence of refugia upstream or downstream of the disturbance event (chi-square test, $P < 0.025$). Over one-third of those systems with recolonization sources upstream or downstream from a site had median recovery times to first reappearance of ≤1 yr (Table 2). In contrast, only one of nine sites without known recolonization sources upstream or downstream had a median recovery time of ≤1 yr, and species within this system had persisted

throughout the disturbance period. Following rotenone treatment of the Green River, squawfish did not reappear within 2 yr because the treated section of the river represented the upper limit of their range and migration from downstream reaches was prevented by the Flaming Gorge Dam (Binns 1967).

The presence of barriers to migration prolonged, but did not necessarily prevent, recovery. In Seas Branch, Wisconsin, USA, a fish barrier installed in the middle of the study section prior to antimycin A treatment significantly delayed the time to species reappearance (chi-square test, $P < 0.001$; Avery 1978). Above the fish barrier, only eight of 13 original species had reappeared within 3.5 yr of treatment, while below the barrier all species present before treatment reappeared within 1 yr. Recolonization events above the fish barrier were linked to stochastic events. Immediately following a spring flood, individuals of smaller species (brook stickleback, *Culaea inconstans*, and fathead minnow, *Pimephales promelas*) and fish of young age classes appeared above the barrier. An increase in flow can trigger upstream migrations by selected species (Hynes 1970).

Organism-Specific Factors Affecting Recovery from Pulse Disturbances

Data on recovery of age and/or size structure of fish populations were not adequate to assess effects of organism-specific factors. Thus, the discussion that follows focuses on recovery of species composition and/or population densities following pulse disturbances. Recovery rates differed according to fish taxon or repro-
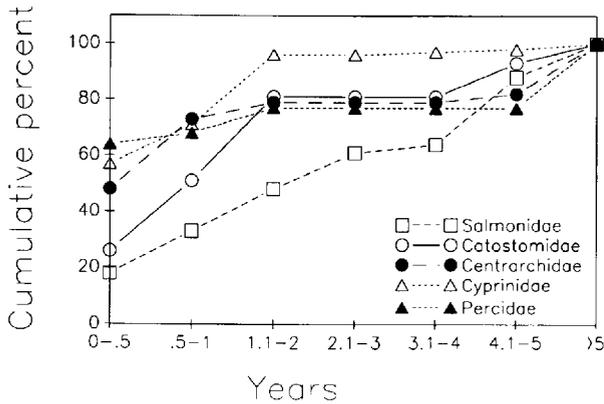
Figure 6. Cumulative recovery curves by fish family: Salmonidae (open squares), Catostomidae (open circles), Centrarchidae (closed circles), Cyprinidae (open triangles), and Percidae (closed triangles).

ductive guild (Table 3, Appendix B; see also Balon 1975, 1984). Recovery times for population densities were shortest for the Centrarchidae or Percidae and longest for the Salmonidae (Kruskal-Wallis, $P < 0.001$; Tukey's multiple comparison of mean ranks, $P < 0.05$; Figure 6).

Times for reappearance or recovery of population density following pulse disturbances did not differ significantly among members of different trophic guilds (benthic insectivores, omnivores, generalized insectivores, herbivore–detrivores, insectivore–piscivores; Kruskal-Wallis, $P > 0.05$). Fish species commonly switch to alternative prey items during initial phases of recovery (Kingsbury and Kreutzweiser 1987, Warner and Fenderson 1962), and subsequent recolonization by macroinvertebrates is relatively rapid following pulse disturbances (Niemi and others 1990).

Reproductive guilds vary by substrate type used for spawning, level of parental investment, degree of development of respiratory organs or adaptation to low dissolved oxygen levels in larval fish, and time of spawning (Table 3) (Balon 1975, 1984). Recovery times of species reappearance or population densities varied significantly among the most common reproductive guilds represented in available data (Kruskal-Wallis, $P < 0.05$; see Figure 7A). Recovery times varied as follows (Tukey's multiple comparison of mean ranks, $P < 0.05$):

For time to first reappearance: open-substrate/rock spawners < nest-building/rock spawners.

For time to recover population density: nest-building/cavity, brood-hiding/rock spawners < nest-building/ rock spawners. When substrate type alone was con-
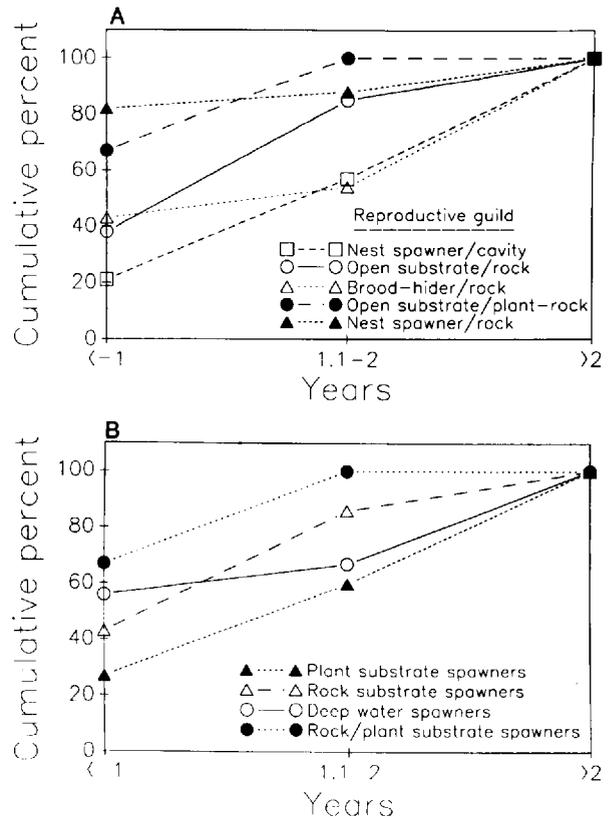
Figure 7. (A) Cumulative recovery rate by reproductive guild: nest-spawner speleophils (open squares), open-substrate spawner lithophils (open circles), brood-hider lithophils (open triangles), open-substrate spawner phytolithophils (closed circles), and nest spawner lithophils (closed triangles). See Table 3 for description of reproductive guilds. (B) Cumulative recovery rate by preferred spawning substrate: phytophils (closed triangles), lithophils (open triangles), pelagophils (open circles), phytolithophils (closed circles). See Table 3 for description of reproductive guilds.

sidered, rock-substrate spawners reappeared more quickly than do open water spawners ($P < 0.05$, Figure 7B).

Reproductive guilds can be expected to recover at different rates depending on tolerance to stress, fecundity, and the degree of protection offered by microhabitats in which eggs are laid and in which larval fish develop. Nest-guarder/rock spawners produce larval fish with moderately well-developed respiratory organs, so recovery of fish within these guilds is probably not limited by scarcity of high-quality sites with respect to dissolved oxygen (Balon 1975). However, rock substrates are likely to be in moderate to high flow areas, which would also be sites of high exposure to stress (toxicants),

Table 4. Organismic traits associated with short or long population recovery times

Rapid recovery	Delayed recovery
Centrarchids or percids	Salmonids
Small size at reproduction (≤20 cm)	Large size at reproduction (>20 cm)
Generalized spawning habitat: pelagophils (open-water)	Specialized spawning habitat: lithophils (rock-substrate) Anadromy or limited home range
Presence in natural refugia, e.g., off-channel brood ponds	

scouring during floods, and desiccation during droughts. With respect to choice of spawning substrate, the open water spawners are the least specialized, and thus are least likely to be limited by availability of suitable substrate.

Size of fish at reproduction also was related to species-specific population recovery rates. Minnows (≤20 cm at reproduction) had significantly shorter recovery times (median = 1.5 yr, range = 0.1–2.75 yr) than did larger fish (median > 2 yr, range = 1–6 yr; $P < 0.01$, Wilcoxon test). Minnows tend to be more vagile and to have shorter generation times than larger fish, so that both immigration and population growth rates would be optimal for recovery.

For cases in which large areas are affected by disturbance and source populations are limited, the normal range of fish movement can affect time to first reappearance. Anadromous fish present an extreme example of migratory controls on recovery. Following aerial spraying of DDT onto watersheds in Aroostook County, Maine, USA, recovery of brook trout populations to predisturbance densities required 4–5 yr (Warner and Fenderson 1962). The only source for repopulation of younger age classes was spawning of adult fish which require 4+ yr to mature. Because brook trout exhibit homing behavior to the specific streams in which they originally hatched, the source of recolonizing organisms for a given stream was limited.

Nonanadromous species migrate as well, either to reach suitable habitat for spawning, to alleviate population pressures, or to escape seasonally unfavorable temperature and dissolved oxygen conditions in headwater reaches (Hynes 1970). Cumulative recovery of fish presence or population density did not vary significantly with species vagility (Kruskal-Wallis, $P > 0.05$),

possibly because vagility increases following disturbance (Gunning and Berra 1969, Berra and Gunning 1970).

In summary, a variety of organism-specific factors influenced species-specific recovery rates (Table 4). Population recovery times varied significantly among fish families and among reproductive guilds. Minnows (highly vagile, ≤20 cm at first reproduction) recovered more quickly than did larger (less vagile) species.

Community-Level Parameters

Among the 12 systems that were extensively sampled, neither species richness nor trophic guild richness was significantly correlated with median or maximum recovery time for fish species densities within a system ($P > 0.05$). Within specific case studies, there was little evidence for the influence of facilitative or inhibitory biotic interactions on recovery from pulse disturbances. Rather, the rarity of local invasion and subsequent extinctions during recolonization suggest that competition and predation pressures are relaxed during recovery.

Limitations of Available Data Set

The nature of data available probably has led us to overestimate the overall resilience of lotic fish communities for at least three reasons. First, the systems reviewed here consist of predominantly low (second to fourth) order streams. Life-history characteristics of fish species vary with stream size. Schlosser (1990) determined that maximum life-span, maximum body size, and age at sexual maturity differed for species associated with different order reaches of the Illinois River system. Species found in high-order streams or rivers tended to be larger, longer-lived, and to have a greater age at sexual maturity. These are traits associated with longer recovery times and are not well represented in the published studies on recovery.

Second, our data set also was limited in the type and frequency of end points recorded. Few data on recovery of age- or size-class structure were available. For long-lived species, recovery of age- or size-class structure should lag behind that of total fish density, species richness, or median time for recovery of individual fish population densities. Fish species richness can actually increase in response to intermediate levels of human disturbance, as in the case of exotic species invasions to streams tributary to San Francisco Bay (Leidy and Feidler 1985). Virtually no data were available on re-

covery end points for sublethal effects of stressors, e.g., changes in health, growth rate, or feeding behavior of fish.

Finally, our data set focused on recovery from discrete pulse disturbances rather than multiple events. Multiple disturbances could have cumulative effects greater than the sum of individual events, particularly for long-lived species that require several years to mature. In the Rhone River in France and in New Brunswick, Canada, streams, repeated pulse inputs of chemicals wiped out entire age classes of fish, thereby delaying recovery (Roux 1984, Elson 1967).

Measures for Assessing Recovery

While recovery at the population level is straighforward to assess, the question of when a community has recovered has not been assessed adequately. Commonly measured community-level parameters such as overall species richness were relatively resilient to disturbance, while the reappearance of more sensitive indicator species was not. In particular, reappearance of larger species, salmonids, and nest-building/rock substrate reproductive guilds was delayed. An alternative metric to species richness such as the index of biotic integrity (Karr and others 1986) would be sensitive to both general community composition and the presence or absence of indicator species. In contrast to individual population densities, which may show high interannual variation, measurements of the IBI varies little within and between years in unperturbed systems (Steedman 1988). However, data on reference systems are needed to calculate an index of biotic integrity, and these are not readily available for most of the case studies considered.

Measurement of recovery following press disturbances is even more problematical. In the absence of mitigation, none of the lotic systems exposed to press disturbances had a known recovery time of less than 6 or 7 yr for species richness or population density, respectively. Rather, the evidence suggests that these systems shift to an alternate state. Thus, the pertinent questions become not how fast these systems will recover, i.e. how often can lotic systems be disturbed without being permanently altered?, but rather: To what degree are these systems altered? How many species will become extinct? What degree of habitat modification or mitigation is necessary to restore x% of the original species present in a given drainage system?

The development of predictive relationships between species richness and watershed area (e.g., Karr and others 1986, Eadie and others 1986) or habitat het-

erogeneity should provide useful tools for these latter questions. Relationships between habitat heterogeneity and species diversity have been developed successfully for lakes (Eadie and Keast 1984), but only recently have these relationships been formally expressed for streams (e.g., Rankin 1988). Meffe and Sheldon (1990) suggested that the rapid recovery of fish community structure following experimental defaunation of 37 southeastern stream reaches supported the role of habitat in structuring fish communities. Unfortunately, their data did not allow a sufficient test of alternative hypotheses, i.e., that community assemblages were the result of rapid immigration from surrounding reaches or that assemblages were formed as the result of biotic interactions.

Predictive Power: Autecology vs. Community or Systems Approach

Both stochastic factors (season of disturbance, distance of source populations, barriers to migration, type of disturbance) and autecological factors (fish taxon, reproductive guild, size at reproduction) significantly affected recovery rates of fish populations. In contrast, community characteristics (species richness, trophic guild richness) and system parameters (latitude, longitude, watershed size, stream order, mean discharge) had no significant effect on rates of species reappearance or recovery of population densities, although our conclusions are limited by the range of system characteristics of the available data set.

The utility of current theories of community ecology in explaining variation in stream recovery rates may be limited because these theories (succession, island biogeography) were developed for terrestrial or insular systems (Fisher 1990), and assume stable communities exist in the absence of disturbance. Instead, species diversity could be maintained by an intermediate level of disturbance throughout a system or by temporally or spatially patchy disturbances within a system (Resh and others 1988). For example, a reduction in variability of flow can actually lead to species extinctions due to shifts in competitive advantage (Minckley and Meffe 1987). The colonization process is very different in streams than in terrestrial systems. Recolonization in streams cannot occur from an infinite number of directions as in the terrestrial landscape, but is severely constrained by the geometry of drainage systems. The composition of fish communities available for recolonization is not random but is likely a product of local geological history (Gilbert 1980), the history of competitive exclusions

within a region, i.e., the "ghost of competition past" (Connell 1980), and the history of exotic species introductions. Furthermore, the probability of recolonization is not constant but varies with time due to seasonal migration patterns and stochastic flow events on a scale concordant with that of the recovery process.

Regulatory Implications

Current water-quality criteria are based on knowledge of the resistance of fish and other aquatic species to toxins, but these criteria do not guarantee recovery of fish communities once an impact has occurred. Recent guidelines suggest that water-quality criteria should not be exceeded more frequently than once every three years on the average (US EPA 1985). Our data suggest that the majority of species within each system will be protected by this guideline but that certain classes of species will not. In particular, larger species, salmonids, and rock-substrate/nest-building reproductive guilds require longer recovery periods.

A single limit on the frequency with which water-quality criteria can be exceeded will not be adequate to protect lotic fish communities. Regional criteria would be more appropriate; these should be based on both site-specific factors (the presence of temporal or spatial barriers to migration, presence of isolated populations and of refugia such as off-channel brood ponds) and characteristics of species typically found in a given region. For example, salmonids (especially anadromous populations) or fish within sensitive reproductive guilds will require more rigorous criteria for protection.

The basic assumptions of models of community and systems ecology will need to be modified to fit the unique characteristics of lotic fish communities if they are to be useful in providing a conceptual framework for predicting recovery. Currently, the known disturbance-, site-, and organism-specific factors affecting recovery should be integrated into a set of guidelines (or an expert system) to predict relative resilience of different communities under varied disturbance scenarios (e.g., Marshall and others 1988).

Summary

Lotic fish communities were not resilient to press disturbances (e.g., mining, logging) in the absence of mitigation efforts. Recovery times varied from >5 to >52 yr. Because most studies did not last long enough to document full recovery, the factors affecting recovery rates in these systems could not be investigated.

Estimates of the recovery of fish communities following pulse disturbances vary with the parameter used to assess recovery. At least 70% of systems studied recovered within 1 yr with respect to species richness, total density, or reappearance of half of the resident species. However, recovery of population densities of the least resilient species required more than 2 yr for 70% of the cases examined. Our review of recovery times was limited and potentially biased by the availability of data. Relatively few data were available for high-order streams or for end points potentially less resilient (e.g., age or size structure of fish populations).

Given our present state of knowledge, recovery times following pulse disturbances cannot be accurately predicted; rather they are a complex function of disturbance-, site-, and organism-specific factors. Recovery was affected by the degree of isolation of affected species from nonstressed populations and by the timing of disturbance events with respect to spawning season. The only site characteristic related to overall recovery of fish communities was the presence of barriers to migration or of refugia. Organism-specific factors affecting recovery rates included: family, reproductive guild, and size at first reproduction.

Appendix A. Site characteristics

| Study area | Lat. | Long. | Elevation (m) | Size of watershed (ha) | Stream order | Mean discharge (m^3/sec) | Annual range in discharge (m^3/sec) | Gradient (%) | Land use characteristics | | | |
									Agriculture (%)	Forest (%)	Grass (%)	Urban (%)
Afon Hirnant, North Wales	53,00N	3,30W			2							
Alexander Brook, Maine	46,55N	68,15W	220	2,710	2			0.91				
Armstrong Brook, Maine	47,05N	68,11W	232	2,725	3			1.04				
Bayou Lacombe (1), Louisiana	30,30N	90,05W	10		2	0.178		0.06				
Bayou Lacombe (2), Louisiana	30,15N	89,50W	2		3	0.252		0.02				
Big Kitoi Creek, Alaska	58,10N	153,00W	8		1	1.340	0.40–4.30	2.30	0	100	0	0
Chariton River, Missouri	40,15N	92,45W	240	47,140	3	0.420	0.28–710.00	0.04	47	5	47	1
Gardner Brook, Maine	46,48N	68,17W	197	3,782	3			0.83				
Green River (1), Wyoming	42,40N	109,58W	2105	520,000	3		2.00–87.70	0.24				
Green River (3), Wyoming	42,07N	110,11W	1990	1200,000	4	39.700	5.36–223.60	0.16				

Appendix A. *Continued.*

Study area	Lat.	Long.	Elevation (m)	Size of watershed (ha)	Stream order	Mean discharge (m³/sec)	Annual range in discharge (m³/sec)	Gradient (%)	Land use characteristics			
									Agriculture (%)	Forest (%)	Grass (%)	Urban (%)
Green River (4), Wyoming	41,31N	109,27W	1810	3910,000	5	7.800	5.36–263.20	0.09				
Jacquet River, New Brunswick	47,45N	66,00W			4							
Lawrence Creek, Louisiana	30,50N	90,10W	245		5	0.405		0.65				
Lawrence Creek, Wisconsin	43,40N	89,30W	282	1,660	2	0.450	0.53	0.28	30	70	0	0
Little Armstrong Brook, Maine	47,05N	68,08W	197	1,200	1			0.69				
Little Auglaize River, Ohio	41,00N	84,20W	235	105,700	3	2.040	0.10–4.54	0.04	100	0	0	0
Luxapalila River, Mississippi	33,37N	88,00W	105	207,717	4	5.100	.65–280.00	0.08				
Miramichi River, New Brunswick	47,00N	66,00W			4							
Mud Brook, Maine	47,07N	68,07W	206	3,472	2			0.57	0	100	0	0
Mud Creek, Arkansas	36,00N	94,10W	360	650	3			1.55				
Mud Creek, Ontario	43,08N	80,54W			3							
Mussellshell River, Montana	46,30N	109,00W	1100									
Needle Branch, Oregon	44,30N	124,00W	174	71	2	0.368	0.05–1.27	1.40				
New Fork River, Wyoming	42,34N	109,56W	2160	319,000	4		0.85–141.50	0.15				
New River Drainage, Tennessee	36,30N	83,55W	333	98,900		18.000	0.23–150.00	14.00	0	95	0	5
North Carolina Stream, North Carolina	35,30N	77, 0W	0				0.00–1.40					
North Fork River, Kentucky	38,30N	83,40W	253		3	153.900		0.11				
Olentangy River, Ohio	40,10N	83,00W	280	139,000	4	13.000	0.72–31.93	0.10	30	7	7	55
Olentangy River, Ohio	40,10N	83,00W	280	139,000	4	13.000	0.72–31.93	0.10				
Pine Creek, Tennessee	35,55N	85,45W	280	7,290	2		0.18–0.50	0.61				
Piney Creek, Arkansas	36,10N	92,03W	190	45,000	6			0.35				
Restigouche River, New Brunswick	47,30N	67,40W			4							
Rush Creek, California	41,30N	120,30W	1652	9,046	2	2.970	0.20	4.31	95	5	0	0
Salmon Brook, Maine	46,48N	68,10W	198	5,900	4			0.85				
Seas Branch Creek (1), Wisconsin	43,30N	90,40W	244	3,603	3	0.170		0.95	79	21	0	0
Seas Branch Creek (2), Wisconsin	43,30N	90,40W	244	3,603	3	0.200		0.95	79	21	0	0
Sheep Creek, Montana	44,46N	110,49W	1780	14,100	4	1.100	0.19–7.90					
Smiths Branch, Illinois	40,00N	88,00W	195	5,200	3			0.12	97	2	0	1
South Willow Creek, Utah	40,25N	112,30W	1827	5,200	2	0.085	0.07–0.74	4.70	0	100	0	0
St. Regis River, Montana	47,20N	115,30W	1256	78,500	4	15.900		1.43				
St. Regis River, Montana	47,20N	115,30W	1256	78,500	4	15.900		1.43				
Talisheek Creek, Louisiana	30,30N	89,55W	18	4,356	3	0.173		0.01				
Ten Mile River, New York	41,30N	75,00W	290	11,700	4	1.770	0.12–23.00	0.74				
Tobique River, New Brunswick	47,00N	67,20W			4							
Trail Creek, Montana	45,30N	110,30W	1600	18,500	3	0.850	0.17–20.10	0.60				
Valley Creek, Minnesota	44,55N	92,50W	226	2,660	3	0.140		0.59				
Warner Creek, Louisiana	30,40N	90,10W	57	2,533	4	0.040		0.36				
Whippoorwill Creek, Kentucky	36,40N	87,15W	163		4			0.03	55	0	40	5
Whitley Creek, Illinois	39,30N	88,30W	183	13,750	3			0.03				

Acknowledgments

Appendix B.   Fish life history classifications[a]

Fish species	Fish family	State	Mobility	First reprod. (yr)	Season of spawn
Ambloplites rupestris	Centrarchidae	Illinois		2.0	1
		Tennessee		2.0	1
Ammocrypta asprella	Percidae	Mississippi	2		
Anguilla rostrata	Anguillidae	New York		7.0	2
Aphredoderus sayanus	Aphredoderidae	Mississippi	1		1
Campostoma anomalum	Cyprinidae	Arkansas	3	3.0	1
		Illinois	3	3.0	1
		Tennessee	3	3.0	1
		Wisconsin	3	3.0	2
Carassius auratus	Cyprinidae	Ohio		3.0	5
		Tennessee		3.0	5
Carpiodes cyprinus	Catostomidae	Illinois			1
		Ohio			1
Catostomus ardens	Catostomidae	Wyoming		3.0	1
Catostomus commersoni	Catostomidae	Illinois		6.0	1
		Kentucky		6.0	1
		New York		6.0	1
		Wisconsin		6.0	1
Catostomus latipinnis	Catostomidae	Wyoming			
Catostomus sp.	Catostomidae	Wyoming		3.0	1
Clinostomus funduloides	Cyprinidae	Tennessee			
Coregonus sp.	Salmonidae	Wyoming		4.0	3
Cottus aleuticus	Cottidae	Alaska			1
Cottus carolinae	Cottidae	Tennessee		2.0	1
Cottus cognatus	Cottidae	Wisconsin			2
Cottus sp.	Cottidae	Montana		3.0	1
		Wyoming		3.0	1
Culaea inconstans	Gasterosteidae	Wisconsin		1.0	1
Cyprinidae	Cyprinidae	Kentucky		2.0	1
Cyprinus carpio	Cyprinidae	Kentucky		3.0	1
		Wyoming		3.0	1
Dionda nubila	Cyprinidae	Arkansas			1
Dorosoma cepedianum	Clupeidae	Kentucky		2.0	1
Ericymba buccata	Cyprinidae	Illinois			1
Erimyzon oblongus	Catostomidae	Illinois			1
Esox americanus americanus	Esocidae	Louisiana		2.0	1
Esox niger	Esocidae	Mississippi	3	1.0	1
Etheostoma blennioides	Percidae	Illinois	1	1.0	1
		Tennessee	1	1.0	1
Etheostoma caeruleum	Percidae	Illinois	1	2.0	1
Etheostoma flabellare	Percidae	Illinois	1		1
		Wisconsin	1		1
Etheostoma nigrum	Percidae	Illinois	1	2.0	1
		Wisconsin	1	2.0	1
Etheostoma proeliare	Percidae	Mississippi	1		
Etheostoma simoterum	Percidae	Tennessee	1		
Etheostoma sp.	Percidae	Kentucky	1		1
Etheostoma spectabile	Percidae	Arkansas	1	2.0	1
		Illinois	1	2.0	1
Fundulus olivaceus	Cyprinodontida	Arkansas	3		
		Mississippi	3		
Gila atraria	Cyprinidae	Wyoming		4.0	2
Gila cypha	Cyprinidae	Wyoming			
Hybognathus hayi	Cyprinidae	Mississippi	2		
Hypentelium nigricans	Catostomidae	Ohio			1
		Tennessee			1
		Wisconsin			1
Hypentelium sp.	Catostomidae	Illinois		3.0	1
	Catostomidae	Kentucky		3.0	1
Ictalurus melas	Ictaluridae	Arkansas		3.0	1
		Illinois		3.0	1
		Kentucky		3.0	1
		Tennessee		3.0	1

Anadromous	Native distrib.	Size first reprod. (cm)	Functional group	Spawns per (N/yr)	Guarder	Parental investment	Substrate type
2	1	9	6	1	b	2	1
2	1	9	6	1	b	2	1
	1						
3	1	76	6	1	a	1	1
	1		6	1	a	2	1
2	1	18	1	1	a	2	1
2	1	18	1	1	a	2	1
2	1	18	1	1	a	2	1
2	1	18	1	1	a	2	1
2	2	14	2	1			
2	2	14	2	1			
1	1		5	1	a	1	6
2	1		5	1	a	1	6
2	1	21	1	1			
2	1	38	5	1	a	1	3
2	1	38	5	1	a	1	3
2	1	38	5	1	a	1	3
2	1	38	5	1	a	1	3
	1						
1	1	33	5	1			
			5				
2	2	30	7	1	a	1	
2	1		5	1	b	2	5
2	1	6	6	1			
2	1		6	1	b	2	5
2	1	7	6	1			
2	1	7	6	1			
2	1		6	1	b	2	7
2	1		2	1			
1	1	47	2	1			
1	1	47	2	1			
2	1						
2	1	13	2	1	a	1	2
2	1		5	1			
2	1		3	1			
2	1	14	6	1	a	1	5
2	1	20	6	1	a	1	5
1	1	8	5	1	a	1	5
1	1	8	5	1	a	1	5
2	1	6	6	1	a	2	1
2	1	4	5	1	b	2	5
2	1	4	5	1	b	2	5
2	1	4	5	1	b	2	5
2	1	4	5	1	b	2	5
			5				
2	1		5	1			
2	1	4	5	1	a	2	1
2	1	4	5	1	a	2	1
	1						
	1						
2	1	20	3	1			
			3				
	1						
2	1	13	5	1	a	1	3
2	1	13	5	1	a	1	3
2	1	13	5	1	a	1	3
2	1	17	5	1			
2	1	17	5	1			
2	1	18	5	1	b	2	1
2	1	18	5	1	b	2	1
2	1	18	5	1	b	2	1
2	1	18	5	1	b	2	1

Appendix B. *Continued.*

Fish species	Fish family	State	Mobility	First reprod. (yr)	Season of spawn
		Wyoming		3.0	1
Ictalurus natalis	Ictaluridae	Arkansas		3.0	1
		Illinois		3.0	1
		Kentucky		3.0	1
		Ohio		3.0	1
Ictalurus punctatus	Ictaluridae	Kentucky		4.0	2
		Mississippi	0	4.0	2
		Wyoming	0	4.0	2
Ictiobus bubalus	Catostomidae				
Ictiobus cyprinellus	Catostomidae	Kentucky		3.0	1
Labidesthes sicculus	Atherinidae	Arkansas	3	1.0	1
Lepomis cyanellus	Centrarchidae	Arkansas	2	2.0	5
		Illinois	2	2.0	5
		Kentucky	2	2.0	5
		Tennessee	2	2.0	5
Lepomis gulosus	Centrarchidae	Kentucky		1.0	2
		Louisiana		1.0	2
Lepomis macrochirus	Centrarchidae	Arkansas	0	2.0	3
		Louisiana	0	2.0	3
		Mississippi	0	2.0	3
		Ohio	0	2.0	3
		Tennessee	0	2.0	3
Lepomis megalotis	Centrarchidae	Arkansas	0	2.0	5
		Illinois	0	2.0	5
		Louisiana	0	2.0	5
		Ohio	0	2.0	5
Micropterus dolomieui	Centrarchidae	Illinois		4.0	1
		Ohio		4.0	1
Micropterus notius	Centrarchidae	Kentucky		2.0	1
Micropterus salmoides	Centrarchidae	Arkansas	3	3.0	1
		Mississippi	3	3.0	1
		Ohio	3	3.0	1
		Tennessee	3	3.0	1
Minytrema melanops	Catostomidae	Arkansas	2		1
		Kentucky	2		1
		Mississippi	2		1
Moxostoma anisurum	Catostomidae	Ohio		5.0	1
Moxostoma duquesnei	Catostomidae	Arkansas		5.0	1
		Ohio		5.0	1
Moxostoma erythrurum	Catostomidae	Illinois		3.0	1
Moxostoma sp.	Catostomidae	Kentucky		3.0	1
Nocomis biguttatus	Cyprinidae	Wisconsin			1
Notemigonus crysoleucas	Cyprinidae	Illinois		2.0	5
		Illinois	2		
Notropis boops	Cyprinidae	Arkansas		3.0	1
Notropis cornutus	Cyprinidae	Illinois		3.0	1
		New York		3.0	5
Notropis sp.	Cyprinidae	Illinois	0	2.0	1
Notropis spilopterus	Cyprinidae	Illinois		1.0	2
Notropis umbratilis	Cyprinidae	Illinois			1
Oncorhynchus clarki	Salmonidae	Montana		5.0	3
		Oregon		5.0	1
Oncorhynchus mykiss	Salmonidae	California		3.0	1
		Montana		3.0	1
Percina caprodes	Percidae	Mississippi		2.0	1
		Ohio		2.0	1
		Ohio	1		
Percina maculata	Percidae	Illinois	1		1
		New York	1		1
Percina sciera	Percidae	Mississippi	1		
Phenacobius mirabilis	Cyprinidae	Illinois		1.0	1
Phoxinus erythrogaster	Cyprinidae	Tennessee			1

Anadromous	Native distrib.	Size first reprod. (cm)	Functional group	Spawns per (N/yr)	Guarder	Parental investment	Substrate type
2	2	18	5	1	b	2	1
2	1	26	5	1	b	2	5
2	1	26	5	1	b	2	5
2	1	26	5	1	b	2	5
2	1	26	5	1	b	2	5
2	1	35	2	1	b	2	5
2	1	35	2	1	b	2	5
2	1	35	2	1	b	2	5
					a	1	5
1	1	40	3	1			
2	1	8	6	1	a	1	4
2	1	6	6	3	b	2	1
2	1	6	6	3	b	2	1
2	1	6	6	3	b	2	1
2	1	6	6	3	b	2	1
2	1	9	6	3			
2	1	9	6	3			
2	1	10	5	3	b	2	1
2	1	10	5	3	b	2	1
2	1	10	5	3	b	2	1
2	1	10	5	3	b	2	1
2	1	11	6	2	b	2	1
2	1	11	6	2	b	2	1
2	1	11	6	2	b	2	1
2	1	11	6	2	b	2	1
2	1	28	6	1	b	2	1
2	1	28	6	1	b	2	1
2	1	25	6	1			
2	1	26	6	1	b	2	2
2	1	26	6	1	b	2	2
2	1	26	6	1	b	2	2
2	1	26	6	1	b	2	2
2	1		5	1	a	1	3
2	1		5	1	a	1	3
2	1		5	1	a	1	3
2	1	39	2	1	a	1	3
2	1	24	5	1	a	1	3
2	1	24	5	1	a	1	3
1	1	26	5	1	a	1	3
2	1	25	5	1			
2	1		3	1	a	2	1
2	1	8	3	1			
					a	1	5
2	1	5	4	1			
2	1	7	3	1	b	2	1
2	2	14	2	1	b	2	1
2	1	7	4	1			
2	1	7	4	1	a	1	4
	1		1	1			
1	1	40	6	1	a	2	1
1	1	40	6	1	a	2	1
1	1	30	6	1	a	2	1
1	1	30	6	1	a	2	1
2	1	6	4	1	a	1	6
2	1	6	4	1	a	1	6
2	1		5	1	a	2	1
2	1		5	1	a	2	1
2	1	6	4	1			
2	1	5	1	1	a	1	3
2	1	5	1	1	a	1	3
2	1	5	2	1	b	2	5

Appendix B. *Continued.*

Fish species	Fish family	State	Mobility	First reprod. (yr)	Season of spawn
		Wisconsin			1
Pimephales notatus	Cyprinidae	Arkansas	2	2.0	1
		Illinois	2	2.0	1
		Mississippi	2	2.0	1
		Wisconsin	2	2.0	2
Pimephales promelas	Cyprinidae	Wisconsin		1.0	5
		Wyoming		1.0	5
Pomoxis annularis	Centrarchidae	Ohio	3	2.0	1
Prosopium williamsoni	Salmonidae	Montana		3.0	3
Ptychocheilus lucius	Cyprinidae	Wyoming		6.0	5
Pylodictis olivaris	Ictaluridae	Kentucky		4.0	2
		Mississippi		4.0	2
Rhinichthys atratulus	Cyprinidae	New York		2.7	2
		Tennessee		2.7	1
		Wisconsin		2.7	2
Rhinichthys cataractae	Cyprinidae	New York			1
		Wisconsin			1
Rhinichthys osculus	Cyprinidae	Wyoming			2
Richardsonius balteatus	Cyprinidae	Wisconsin		3.0	1
		Wyoming		3.0	1
Salmo salar	Salmonidae	New Brunswick		5.0	3
Salmo trutta	Salmonidae	California		3.0	3
		Montana		3.0	3
		New York		3.0	3
		Wisconsin		3.0	3
		Wyoming		3.0	3
Salvelinus fontinalis	Salmonidae	Maine		1.5	3
		Minnesota		1.5	3
		Montana		1.5	3
		Tennessee		1.5	3
		Wisconsin		1.5	3
Semotilus atromaculatus	Cyprinidae	Illinois		4.0	1
		Kentucky		4.0	1
		Tennessee		4.0	1
	Cyprinidae	Wisconsin		4.0	1
Xyrauchen texanus	Catostomidae	Wyoming			1

[a]Mobility: 1 = low; 2 = medium; 3 = high vagility. Season of spawning: 1 = spring; 2 = summer; 3 = fall; 4 = winter; 5 = spring and winter. Anadromous: 1 = anadromous; 2 = nonmigratory; 3 = catadromous. Native distribution: 1 = native; 2 = nonnative; 3 = stocked. Functional group: 1 = herbivore/detritivore; 2 = omnivore; 3 = generalized insectivore; 4 = surface and water column insectivore; 5 = benthic insectivore; 6 = insectivore-piscivore; 7 = planktivore. Guarder: a = nonguarders; b = guarders. Parental investment: 1 = open substrate spawner; 2 = brood hider; 3 = substratum spawner; 4 = nest spawner. Substrate type: 1 = pelagophils; 2 = lithopelagophils; 3 = lithophils; 4 = phytolithophils; 5 = phytophils; 6 = psammophils.

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Anadromous	Native distrib.	Size first reprod. (cm)	Functional group	Spawns per (N/yr)	Guarder	Parental investment	Substrate type
2	1	5	2	1	b	2	5
2	1	5	2	1	b	2	5
2	1	5	2	1	b	2	5
2	1	5	2	1	b	2	5
2	1	4	3	3	b	2	5
2	1	4	3	3	b	2	5
2	1	19	6	1	b	1	2
2	1	24	2	1			
2	1	30	6	1			
2	1	32	6	1			
2	1	32	6	1			
2	1	7	3	1	a	1	3
2	1	7	3	1	a	1	3
2	1	7	3	1	a	1	3
2	1		5	1	a	1	3
2	1		5	1	a	1	3
2	1		5	1	a	1	3
2	2	8	3	1	a	1	4
2	2	8	3	1	a	1	4
1	1	35	6	1	a	2	1
1	3	40	6	1	a	2	1
1	1	40	6	1	a	2	1
1	1	40	6	1	a	2	1
1	3	40	6	1	a	2	1
1	1	25	6	1	a	2	1
1	1	25	6	1	a	2	1
1	1	25	6	1	a	2	1
1	1	25	6	1	a	2	1
1	1	25	6	1	a	2	1
2	1	13	3	1	a	2	1
2	1	13	3	1	a	2	1
2	1	13	3	1	a	2	1
2	1	13	3	1	a	2	1
2	1		1	1			

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