J. N. Am. Benthol. Soc., 2001, 20(2):255–265

Life in the fast lane: fish and foodweb structure in the main channel of large rivers

JOHN M. DETTMERS[1,5], DAVID H. WAHL[2], DANIEL A. SOLUK[3], AND STEVE GUTREUTER[4]

[1]*Lake Michigan Biological Station, Illinois Natural History Survey, 400 17th Street, Zion, Illinois 60099 USA*
[2]*Kaskaskia Biological Station, Illinois Natural History Survey, RR1, Box 157, Sullivan, Illinois 61951 USA*
[3]*Center for Aquatic Ecology, Illinois Natural History Survey, 607 E. Peabody Drive, Champaign, Illinois 61820 USA*
[4]*US Geological Survey, Upper Midwest Environmental Sciences Center, 2630 Fanta Reed Road, La Crosse, Wisconsin 54603 USA*
[5]*Email address: dettmers@mail.inhs.uiuc.edu*

Abstract. We studied the main channel of the lower Illinois River and of the Mississippi River just upstream and downstream of its confluence with the Illinois River to describe the abundance, composition, and/or seasonal appearance of components of the main-channel community. Abundance of fishes in the main channel was high, especially adults. Most adult fishes were present in the main channel for either 3 or 4 seasons/y, indicating that fishes regularly reside in the main channel. We documented abundant zooplankton and benthic invertebrates in the main channel, and the presence of these food types in the diets of channel catfish and freshwater drum. All trophic levels were well represented in the main channel, indicating that the main channel supports a unique food web. The main channel also serves as an important energetic link with other riverine habitats (e.g., floodplains, secondary channels, backwater lakes) because of the mobility of resident fishes and because of the varied energy sources supplying this food web. It may be more realistic to view energy flow in large-river systems as a combination of 3 existing concepts, the river continuum concept (downstream transport), the flood pulse concept (lateral transport to the floodplain), and the riverine productivity model (autochthonous production). We urge additional research to quantify the links between the main channel and other habitat types in large rivers because of the apparent importance of main-channel processes in the overall structure and function of large-river ecosystems.

Key words: foodweb structure, large rivers, main channel, fish community.

Large-river–floodplain ecosystems are extremely diverse, exhibiting extensive spatial and temporal variability across habitats (Sparks 1995). These systems are very productive (Bayley 1991) and support a high diversity of organisms (Sparks 1995), many of which are adapted to the particular habitats within these ecosystems. Because of the high habitat diversity, physical complexity, and number of species present in large rivers, a coordinated and comprehensive understanding of processes occurring in large rivers has been slow to develop (Johnson et al. 1995). Although ecologists lack a thorough understanding of how large rivers operate, several hypotheses have been developed to describe elements of large-river structure and function.

The river continuum concept (RCC) describes the expected longitudinal changes that occur from headwater streams to large rivers, and predicts that biotic diversity should be highest in rivers of intermediate order (4–6) because these rivers typically exhibit greater diversity in food resources and physical conditions than rivers of other sizes (Vannote et al. 1980). However, the RCC does not specifically address structure and function of large rivers (>6th order), nor does it explicitly predict patterns in diversity and abundance for fishes in these systems.

Perhaps the most comprehensive perspective on how large-river–floodplain ecosystems operate is presented by the flood pulse concept (FPC, Junk et al. 1989), which contends that much of the high productivity in these systems results from the seasonal use of floodplains by fishes and invertebrates during annual flooding (Junk et al. 1989, Bayley 1991). However, the FPC asserts that most fishes use the main channel only as a migration corridor to reach other, more suitable habitats (Junk et al. 1989). When fishes do persist in the main channel, this concept predicts that fishes derive most of their energy from the productivity associated with floodplains, rather than from the main channel (Junk et al. 1989).

The riverine productivity model (RPM) predicts that substantial amounts of energy in large rivers are derived from local sources of autochthonous production and coarse particulate organic matter (CPOM) associated with riparian zones away from the main body of flowing water (Thorp and Delong 1994). This concept was developed in the Ohio River, a system unlike most other large lowland rivers because it lacks an extensive floodplain. Like the RCC, the RPM does not specifically address patterns for fish in large rivers.

The RCC, FPC, and RPM have produced a greater understanding of the structure and function of large-river ecosystems, but none offers a complete perspective on how communities function across habitats within these systems. Each concept may apply in a single river, but all tend to exclude potentially important habitats or groups of organisms from their analysis. For example, perhaps the single largest habitat type present in large rivers during the nonflood season is the main channel (Leopold et al. 1964). Although the main channel carries most of the river's water during most of the year, it is frequently considered to be of relatively minor biological importance compared to other habitats, especially for fishes and invertebrates (e.g., Hynes 1970, Junk et al. 1989). In part, this perception has arisen because the main channel is difficult to sample. Main-channel work on fishes has typically focused on the movement of a single species (e.g., shovelnose sturgeon *Scaphirhynchus platorynchus*, Curtis et al. 1997) or on the distribution of larval fish (e.g., Holland and Sylvester 1983). The functional relationships of fish in the main channel of temperate rivers are virtually unexplored (but see Winemiller and Jepsen 1998 for an example in tropical rivers).

In contrast, the importance of off-channel habitats for fishes has been documented conceptually by the FPC (Junk et al. 1989) and by Ward and Stanford (1995). In tropical rivers, these off-channel habitats are frequently important for maintaining multispecies fisheries because off-channel habitats provide extensive habitat diversity and abundant food (Welcomme 1985). Off-channel habitats also serve as important spawning areas for many fishes in large rivers (Scheaffer and Nickum 1986, Copp and Penaz 1988).

Emerging evidence suggests that the main channel also may be an important component of the spatially complex suite of habitats within large-river ecosystems. For instance, production of benthic invertebrates in the main channel, although comparatively low on a per-square-meter basis (Benke et al. 1984), can potentially be large with respect to the whole system (Soluk 1985), especially during low-flow periods. This apparent contradiction occurs because the main channel is the single largest habitat type (Leopold et al. 1964). In some systems, main-channel crustacean zooplankton densities regularly exceed 100/L (Pace et al. 1992) and can serve as an important food source for young-of-year anadromous fishes. However, little is known about the importance of zooplankton to resident riverine fishes in the main channel.

A recent classification of the fish assemblages of 7 large rivers in North America and Europe revealed that 38 to 58% of native fishes depend on channel habitat for ≥1 of their primary life functions (Galat and Zweimüller 2001). Thus, many fishes may depend on main-channel habitat to a greater degree than previously thought. The Galat and Zweimüller (2001) classification also revealed that an alarmingly high % of endangered or threatened species require channel habitat for at least 1 of their life stages, so the main-channel is a critical habitat for the preservation of these rare species.

We present data on seasonal abundance and composition of larval and adult fishes in the main channel of portions of the Mississippi and Illinois rivers. We provide literature-based and empirical diet information for fish in these rivers, as well as zooplankton and benthic invertebrate abundances to explore the resources actually consumed by fishes. These data lead to a revised framework describing 1) the importance of the main channel to maintaining fish populations, and 2) the function of river–floodplain ecosystems. We also describe a main-channel food web, present evidence that many fishes regularly use the main channel, and discuss the links between the main channel and other riverine habitats.

Methods

Study site

We sampled the main channel of the lower 32 km of the Illinois River and ~65 km in Reach 26 of the Upper Mississippi River, between navigation locks and dams located at River Mile 201 and River Mile 240. Within Reach 26, the upper 32 km of the main channel are relatively unaffected by impounding, with surface flow rates consistently ≥0.8 m/s and main-channel depth rarely >7 m. The middle 6 km of Reach 26 are characterized by lower flow rates and a deepening main channel, with depths reaching 10 m. The lower 23 km of Reach 26 are heavily influenced by Lock and Dam 26, which impounds water for navigation purposes during the nonflood season, creating main channel depths ≥15 m but surface flow rates <0.4 m/s. The confluence of the Illinois River with the Mississippi River occurs about halfway down Reach 26, at River Mile 218. The Mississippi River displays relatively high flow rates, lower turbidity, and a steep gradient compared to the Illinois River (Butzer 1977, Sparks et al. 1990). Within this stretch of the 2 rivers, the Mississippi has a more complex river bed, with relatively extensive side-channel area. Both river floodplains have substantial levees to protect residential and agricultural holdings. Natural backwater habitat is present primarily in the lower Illinois River within the study reach, although most backwaters are surrounded by low-head levees.

Fish sampling

We used a rockhopper bottom trawl (10.2 m headrope, 8.0 m footrope with 2.54 cm stretch mesh cod end, Dettmers et al. 2001) to sample adult fish, (>10 cm total length [TL]), in the main channel. We sampled during August to December 1996 and March to October 1997, as equipment, weather, and flow rates permitted. We regularly sampled 8 sites on the Mississippi River and 4 sites on the Illinois River. All fishes collected were identified, measured, weighed, and immediately released.

For analyses with adult fishes, we defined spring as March and April, summer as June to August, autumn as September and October, and winter as November and December. We could not sample during January and February because of heavy ice cover.

Because trawling data are discrete and instantaneous measures through time, they alone cannot conclusively determine that fish reside in the main channel. Therefore, we used Gittinger's (1999) determinations of hourly time budgets for schools of adult fish present in the main channel of the Mississippi and Illinois rivers as a more direct measure of fish persistence. Ten sites were sampled from July to September 1997 using a phased array hydroacoustic unit suitable for determining the locations of fish in the main channel or main-channel border (Gittinger 1999). Sampling was conducted 5 d/wk for 4 h/d such that each of 4 time strata (early morning, late morning, early afternoon, and late afternoon) were sampled 8 times for 1 h between 0700 and 1900.

We collected larval fishes every 2 wk from May to July 1996 at up to 10 main-channel sites on the Mississippi River and 4 sites on the Illinois River. During 1997, we sampled 4 main-channel sites and 2 backwater sites along the Illinois River to compare larval fish assemblage composition in these 2 habitats. We sampled in an upstream direction with paired 1-m diameter, 500-μm mesh ichthyoplankton nets mounted to the bow of a boat, and pushed near the surface of the water at 1.0 to 1.5 m/s. Each push lasted 8 to 10 min, after which larval fishes and drifting debris were preserved in 95% ethanol. All fishes were identified to the lowest practical taxonomic category and enumerated in the laboratory.

Fish-food sampling

To evaluate the availability of food resources for all life stages of main-channel fishes, zooplankton were collected every 2 wk from March to September 1997 from 4 main channel sites and from 2 backwater lake sites in the Illinois River. All samples were collected with a hand-operated peristaltic pump, contained 30 L of water, and were vertically integrated by raising and lowering the intake tube at a constant rate through the water column. All samples were immediately preserved in buffered Lugol's solution. Zooplankton were identified as either calanoid or cyclopoid copepods, copepod nauplii, or rotifers; cladocerans were identified to genus.

Benthic invertebrates were sampled from the main channel of the Mississippi River to determine the potential importance of these organ-

TABLE 1. Seasonal catch (total number of individuals) of the most frequently encountered adult fishes in the main-channel Mississippi and Illinois rivers, 1996 and 1997. Sp = spring, Su = summer, Au = Autumn, Wi = winter. ND = the river was not sampled.

	1996			1997			
Species	Su	Au	Wi	Sp	Su	Au	Wi
Illinois River							
Channel catfish (*Ictalurus punctatus*)	0	77	110	ND	40	19	3
Common carp (*Cyprinus carpio*)	1	16	11	ND	6	26	0
Freshwater drum (*Aplodinotus grunniens*)	2	643	575	ND	280	270	46
Gizzard shad (*Dorosoma cepedianum*)	1	21	14	ND	1	21	355
Smallmouth buffalo (*Ictiobus bubalus*)	0	29	24	ND	44	50	0
Mississippi River							
Channel catfish	50	167	62	14	47	102	ND
Common carp	0	111	3	0	0	12	ND
Freshwater drum	13	716	50	2	96	475	ND
Gizzard shad	0	998	20	22	3	52	ND
Mooneye (*Hiodon tergisus*)	0	136	14	0	3	25	ND
Shovelnose sturgeon (*Scaphirhynchus platorynchus*)	26	18	83	14	63	30	ND
Smallmouth buffalo	19	253	8	3	28	159	ND

isms in diets of main-channel fishes. Samples from the shifting sand substrate in the main channel were obtained using a core-freezer modified from Soluk (1985), with the addition of lead weights, 2 extra core barrels, and pressure relief valves so that the sampler could be used in depths >2 m. Frozen cores were thawed and the organic material separated from sand grains by elutriation (63-μm sieve). Organisms were sorted under a dissecting microscope at 12X magnification, and identified to genus.

To determine if main-channel fishes consumed food that was present in the main channel, we classified collected adult fishes as piscivores, zooplanktivores, insectivores, and omnivores based on descriptions in Becker (1983). Fish were classified as omnivores if they consumed a combination of zooplankton, organic material, benthic invertebrates, and/or fish (Becker 1983). To empirically examine if fishes actually consumed prey organisms from the main channel, we also examined diets of age-0 channel catfish (*Ictalurus punctatus*) and freshwater drum (*Aplodinotus grunniens*) collected from the Mississippi and Illinois rivers during August to November 1996 and June to October 1997. These species and life stages were sufficiently abundant to allow reasonable sample sizes for diet information. Fish were immediately preserved in 95% ethanol. Individual fish were measured in the laboratory (mm, TL) and weighed (nearest g). Stomachs were removed, and diet items were identified to genus and counted.

Results

Fish collected

We collected a total of 26 species of fish in both rivers. This total is ~30% of the fish species collected over 11 y by a long-term monitoring program that included most habitat types in our study area (E. Ratcliff, Great Rivers Field Station, Illinois Natural History Survey, personal communication). Monthly catch per unit effort (CPUE) for adult fishes ranged from 15 to 375 fish/h in the main channel of the Mississippi River and from ~4 to >1000 fish/h in the Illinois River, from August 1996 to October 1997.

Freshwater drum was the most frequently collected species in both years in both rivers (Table 1). Gizzard shad (*Dorosoma cepedianum*) and channel catfish also were abundant in both rivers, whereas smallmouth buffalo (*Ictiobus bubalus*) and shovelnose sturgeon were abundant only in the Mississippi River. At least 18 species of adult fishes were collected from the main channel during summer, autumn, and winter but only 8 species were collected during spring (Fig. 1A). Over half (58%) of the fish species we collected were present in the main chan-

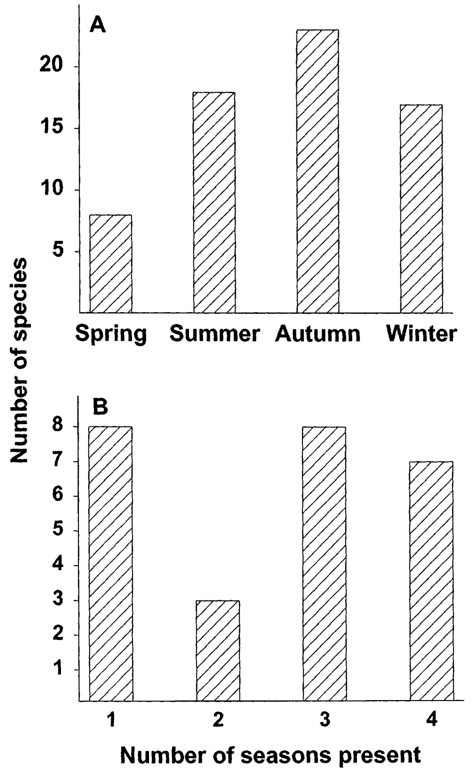

FIG. 1. Number of fish species present in the main channel of Reach 26 of the Mississippi River during each season (A), and number of fish species present in the main channel of Reach 26 of the Mississippi River during ≥1 seasons (B).

nel during either 3 or 4 seasons, whereas only 31% (8 species) were collected during a single season (Fig. 1B).

During 1-h sampling bouts, hydroacoustic data indicated that schools of fish moved very little (on the scale of meters) unless disturbed by objects such as commercial towboats and barges (Gittinger 1999). Short-term hydroacoustic data revealed that individual schools of fish spent >50 min/h in the main channel.

Peak densities of larval fishes in the main channel ranged from ~1.5/m^3 in the Mississippi River to ~2.5/m^3 in the Illinois River; densities were consistently >0.8 larvae/m^3 in both rivers from mid-May to mid-July. Larval composition in the main channel was similar in both rivers, consisting primarily of common carp (*Cyprinus carpio*), gizzard shad, and freshwater drum, with some catostomid larvae also present in May (Fig. 2). In the Illinois River, freshwater drum occurred almost exclusively in the main channel, whereas centrarchids and cyprinodontids occurred almost exclusively in off-channel habitats (Table 2). Larval cyprinids and *Dorosoma* spp. occurred in both main-channel and off-channel habitats with approximately equal frequency.

Fish-food organisms collected

Zooplankton were present in the main channel of the Illinois River from March through September. Main-channel densities were consistently >80/L and peaked at ~640/L by late May; zooplankton in backwaters did not peak until July. Mean density (±1 SE) of zooplankton in the main channel from March to September was 224/L (±39/L), and 297/L (±50/L) in backwaters. Rotifers were numerically dominant in the main channel, whereas copepods were dominant in backwaters (Table 3). Cladocerans were a minor component of the zooplankton in both habitats.

Benthic invertebrates also were abundant in the main channel of the Mississippi River. Organisms in the sediments consisted primarily of a few specialized larval chironomids (primarily *Robackia* and *Rheosmittia*), nematodes, and sand-dwelling oligochaetes (*Barbidrilus* spp.). Mean density of invertebrates in the upper, free-flowing portions of sampling reaches was >80,000/m^2 in the main channel of the Mississippi River (Fig. 3).

Based on prior published knowledge of fish diets for species we collected, omnivores composed 54% (14 species) of the 26 species collected, whereas insectivores composed 42% (11 species) of the total. Only 1 of the 26 species (4%) was primarily piscivorous. Empirical analysis of diets of age-0 freshwater drum and channel catfish revealed that these fish consumed primarily benthic invertebrates and/or zooplankton in both rivers. Channel catfish (mean TL 137.3 mm, range 47–200 mm) consumed primarily benthic invertebrates in both years (>80% by number), whereas freshwater drum (mean TL 134.9 mm, range 62–197 mm) fed more on zooplankton (Fig. 4). Channel catfish also consumed a small number of other prey types, including fishes, zebra mussels, and native mussels (Fig. 4). For zooplankton, fish in both rivers consumed copepods almost exclusively, although several freshwater drum consumed *Moina* and *Daphnia* in the Illinois River. For ben-

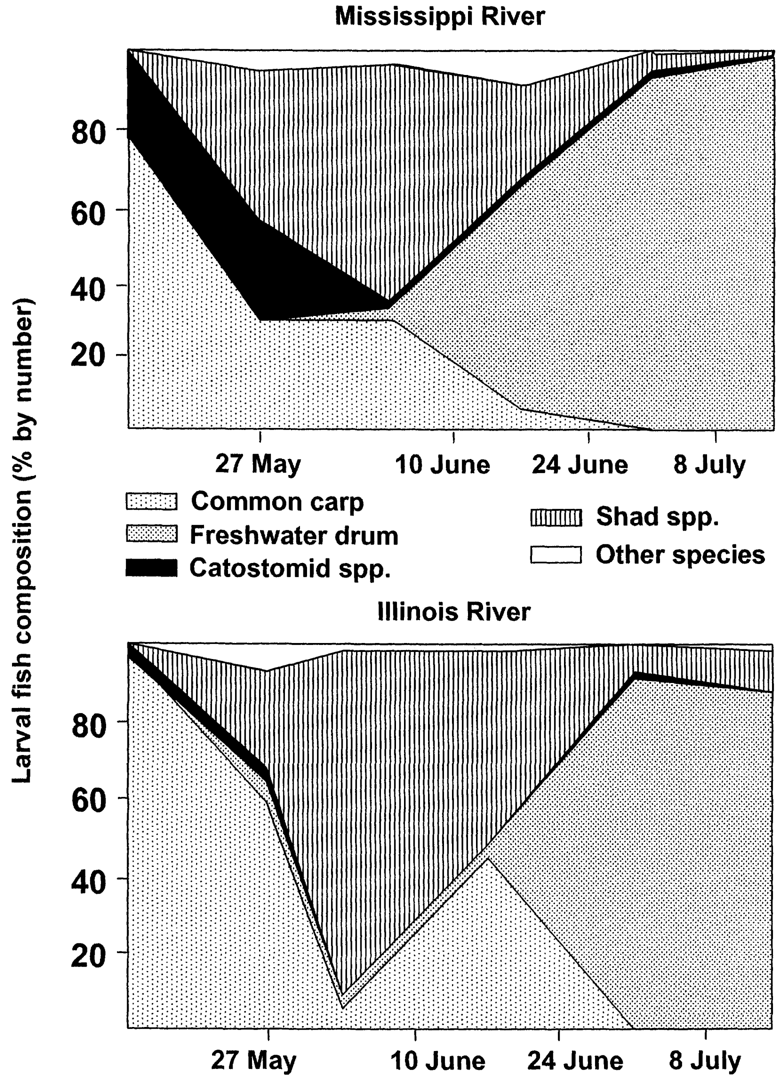

FIG. 2. Proportion of larval common carp, shad spp., catostomids, freshwater drum, and other taxa in the main channel of the Mississippi and Illinois rivers, mid-May through mid-July 1996.

thic invertebrates, fish in the Mississippi River consumed almost exclusively hydropsychid caddisflies (85–92% of all benthic invertebrates consumed), whereas fish in the Illinois River consumed chironomid larvae and pupae (26–43%) and hydropsychids (10–55%). Of the 106 stomachs we examined (49 channel catfish, 57 freshwater drum), only 1 was empty.

Discussion

We demonstrated that substantial densities of zooplankton, benthic invertebrates, and fish occur in the main channel, a habitat previously thought to be relatively depauperate and used primarily as a corridor for migration (Junk et al. 1989). In fact, we collected larval, age-0 and adult life stages of freshwater drum, gizzard shad, and channel catfish, as well as age-0 and adult stages of shovelnose sturgeon in the main channel (J. M. Dettmers and coworkers, unpublished data). Our data also confirm the predictions of Galat and Zweimüller (2001) that the main channel is an important, and overlooked, habitat for river fishes.

TABLE 2. Percent of all fish larvae collected in either main-channel or backwater habitats of the lower Illinois River, May to July 1997.

	Habitat type	
Larval taxon	Backwater	Main channel
Aplodinotus grunniens	2	92
Morone spp.	15	85
Dorosoma spp.	56	44
Cyprinidae	62	38
Centrarchidae	98	2
Cyprinodontidae	100	0

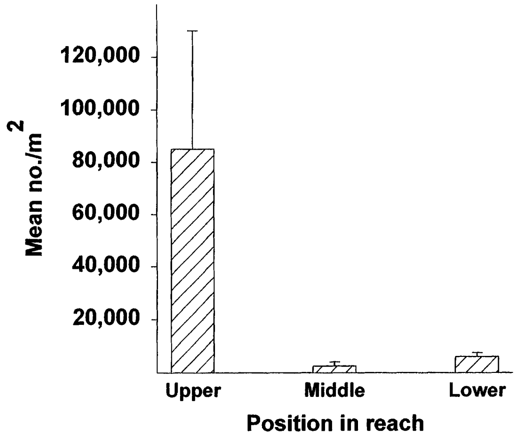

FIG. 3. Mean (+1 SD) number/m² of river bottom of sand-dwelling invertebrates in the main channel of Reach 24 of the Mississippi River. Position in the reach refers to the position relative to the navigation lock-and-dam. Upper is the most remote and most riverine, whereas lower is closest and has the lowest flow rates.

Fish populations

The % of fishes that we observed using the main channel of the Mississippi River (30%) was very close to the 38 to 58% of native fishes that rely on channel habitat in other North American and European rivers (Galat and Zweimüller 2001). Furthermore, our trawling revealed that fishes were present during all seasons in both the Mississippi and Illinois rivers. This information, coupled with our hydroacoustic data demonstrating minimal fish movement, indicates that many fishes are residing, and not simply present, in the main channel during much of the year. We infer from this behavior that fish hold their position in the water column and feed on material drifting to them. Although we do not know the species of fishes observed by hydroacoustics, we believe that they are a subset of the pelagic fishes commonly caught in our bottom trawls (gizzard shad, goldeye [*Hiodon alosoides*], mooneye [*H. tergisus*], skipjack herring [*Alosa chrysochloris*], and white bass [*Morone chrysops*]) because these species are pelagic and travel in schools (Becker 1983). Gizzard shad and white bass are common in this portion of the upper Mississippi River, with mooneye and

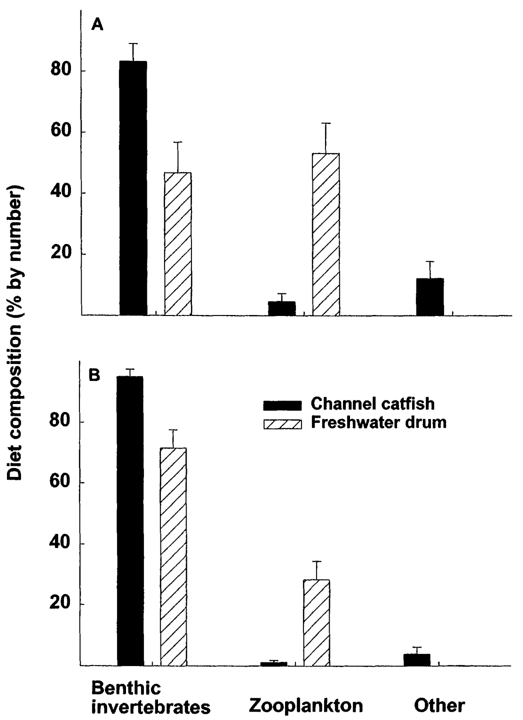

FIG. 4. Mean composition of the diet (% by number +1 SE) of channel catfish and freshwater drum collected from August to November 1996 and June to October 1997 from the Illinois (A) and Mississippi (B) rivers.

TABLE 3. Percent composition of the zooplankton in main-channel and backwater habitats of the Illinois River, March to September 1997.

	Habitat type	
Zooplankton taxon	Backwater	Main channel
Rotifers	27	58
Copepods	66	31
Cladocerans	7	11

goldeye exhibiting occasionally high concentrations (Fremling et al. 1989).

The larval fish assemblage in the Illinois River was very different from the assemblage present in backwater lakes. Although some taxa (e.g., *Dorosoma* spp. and cyprinids) were common in both habitat types, *A. grunniens* and *Morone* larvae were found predominantly in the main channel, whereas centrarchids and cyprinodontids occurred primarily in backwater lakes. This divergence in habitat use by larval fishes suggests that at least some fish taxa are suited for the unique physical conditions encountered in the main channel. Although much recent work has focused on describing differences between larval and juvenile fish distributions in off-channel areas (Copp 1992, 1993, Copp et al. 1994), our research indicates that larvae in the main channel appear consistently and broadly distributed throughout our study area in both the Illinois and Mississippi rivers, as do the adults of these taxa.

Fish-food populations

Some of the highest zooplankton densities we observed occurred during the peak of the spring flood, clearly indicating that zooplankton persist in the main channel even during very turbulent and turbid conditions associated with high discharge. Moreover, conditions in the main channel of the Illinois River appeared favorable for reproduction because zooplankton egg production occurred from March to September (Goodrich 1999). Rotifers were the numerically dominant zooplankton in the main channel of the Illinois River, consistent with zooplankton assemblages reported from Europe (Rossaro 1988, Ferrari et al. 1989), South America (Saunders and Lewis 1988), and North America (Thorp et al. 1994, Basu et al. 2000). Conversely, copepods dominated off-channel habitats throughout the year.

The density of zooplankton in the Illinois River main channel (seasonal mean, 224/L) was much higher than the seasonal mean of 4 to 14/L observed in the main channel of the Ohio River (Thorp et al. 1994). Our estimates compared favorably with the annual mean zooplankton density of 138/L observed in the Apure River, Venezuela (Saunders and Lewis 1988), but were much lower than the density of zooplankton observed in a tidal portion of the Hudson River, New York, and in the St. Lawrence River, USA–Canada (>1000/L, Pace et al. 1992, Basu et al. 2000).

Benthic chironomids are often abundant in the main channel of rivers from Alabama (e.g., Ogeechee River, Benke 1998) to Canada (e.g., Sand River, Soluk 1985), as are mayflies and caddisflies (Benke and Jacobi 1994, Benke and Wallace 1997), although most benthic production in medium-sized rivers occurs on snags or in the floodplain (Benke 2001). Secondary production of macroinvertebrates from shifting sands in riverine habitats is comparatively low, especially if expressed on a per-square-meter basis (Soluk 1985), although production from sand substrates could be significant at larger scales (e.g., reaches or river segments) because this habitat can cover >90% of the river bed in large lowland rivers (Soluk 1985).

Functional relationships

Based on our dietary classification, most adult fishes in the main channel were either omnivorous or insectivorous. Strict piscivores or zooplanktivores were uncommon, likely because of a wide variety of prey types available. Our dietary data for freshwater drum and channel catfish also supported this pattern, with both of these species feeding as omnivores. These observations are consistent with previous assessments of feeding habits of freshwater drum, which eat more insects in large rivers than in lakes (Wahl et al. 1988). However, our observations run contrary to the predictions of the RCC, which posits that piscivores and some planktivores should be common in medium- to large-sized rivers (Vannote et al. 1980). Although many fishes consume zooplankton and fish as part of their diet, few of the species we collected could be considered specialists on these prey types.

We did not directly examine the diets of larval fishes, but appropriate sizes and densities of zooplankton are critical to growth and survival of many larval fish species (Miller et al. 1988, Dettmers and Stein 1992, Bremigan and Stein 1997, Mayer and Wahl 1997). In fact, larval fishes will starve without sufficient zooplankton within a few days after hatching (Miller et al. 1988). Because larvae of freshwater drum and white bass were found primarily in the main channel (as are older life stages of these fishes), we believe that their larvae feed on riverine zooplankton. Indeed, the density of zooplankton we observed in the Illinois River was sufficient to support growth and survival of larval fishes, based on similar zooplankton densities linked with strong larval fish survival in other environments (Werner and Blaxter 1980, Eldridge et al. 1981, Li and Mathias 1982).

The high abundance and diversity of zooplankton and benthic invertebrates we observed in the main channel strongly suggest that sufficient energy at these and lower trophic levels may be present in the main channel to support a functional food web. We hypothesize that the sources of energy to support these higher trophic levels result from both autochthonous production within the main channel (Thorp et al. 1994) as well as from allochthonous sources either from floodplain or upriver sources (Junk et al. 1989). We also hypothesize that the diverse fish assemblage that feeds on multiple prey types in the main channel indicates that large-river–floodplain ecosystems do not strictly operate according to the RCC, the FPC, or the RPM. Rather, elements of each concept likely apply to energy flow and the trophic links among organisms residing in the main-channel food web. Downstream transport likely provides the sources of fine particulate organic matter, according to the RCC (Vannote et al. 1980). However, it is clear that much energy used in the main channel does not come from upriver sources. The floodplain also is an important energy contributor to the main-channel food web through local input of CPOM and through the movement of fishes between the 2 habitat types (FPC, Junk et al. 1989). Similarly, instream autochthonous production supports zooplankton, according to the RPM.

However, even the combination of these 3 river concepts may fail to provide an adequate basis for understanding and management of these systems because they do not explicitly address biotic compensatory processes and top-down processes that may exist. The existing paradigms of large-river science assume that abiotic physical and chemical forces drive the dynamics of biota and shape community structure. Where investigations have been broadened to include biotic interactions, evidence for top-down effects is apparent (Power 1990, Thorp et al. 1998). In fact, some manifestations of the FPC (Bayley 1988, Gutreuter et al. 1999) can be explained alternatively as density dependence because floods quickly increase aquatic area, whereas fish population abundance responds more slowly. Therefore, a broader and more integrative perspective, including melding of the RCC, FPC, and RPM into a broader framework that considers life-history theory, food-web dynamics, and metapopulation dynamics, will be necessary to advance our understanding of large-river ecosystems and provide a basis for adaptive ecosystem management.

Our data describe a functioning community living in one of the physically harshest habitats present in large-river–floodplain ecosystems. The main-channel riverine community, although deriving much of its energy from adjacent or upstream habitat, is a viable organizational unit in its own right. We conclude that most fishes collected in the main channel use it as a seasonal or permanent residence, rather than as a migration route, and that abundant zooplankton and benthic invertebrates provide a ready food source for riverine fishes. As a result, we recommend more careful attention to the role the main channel plays in supporting fishes and as a link between other habitat types in large floodplain rivers.

Acknowledgments

We thank Randy Claramunt, Chad Dolan, Lisa Einfalt, Eric Gittinger, Jodi Goodrich, Brian Herwig, Jory Jonas, Eric Larsen, John Rader, and Frank Wadda for their efforts in the field, lab, and for analytical support. Comments from B. Ickes, B. Johnson, and 2 anonymous reviewers substantially improved an earlier version of the manuscript. Funding for this work was provided in part by the US Army Corps of Engineers under a subcontract through Cooperative Agreement 1434-HQ-97-AG-01771 between the US Geological Survey and the Illinois Natural History Survey. Additional support was provided by the Department of Natural Resources and Environmental Sciences and the Biology Program at the University of Illinois, and by the Illinois Natural History Survey.

Literature Cited

BASU, B. K., J. KALFF, AND B. PINEL-ALLOUL. 2000. Midsummer plankton development along a large temperate river: the St. Lawrence River. Canadian

Journal of Fisheries and Aquatic Sciences 57(Supplement 1):7–15.

BAYLEY, P. B. 1988. Factors affecting growth rates of young tropical floodplain fishes: seasonality and density-dependence. Environmental Biology of Fishes 21:127–142.

BAYLEY, P. B. 1991. The flood pulse advantage and the restoration of river-floodplain systems. Regulated Rivers: Research and Management 6:75–86.

BECKER, G. C. 1983. The fishes of Wisconsin. University of Wisconsin Press, Madison, Wisconsin.

BENKE, A. C. 1998. Production dynamics of riverine chironomids: extremely high biomass turnover rates of primary consumers. Ecology 79:899–910.

BENKE, A. C. 2001. Importance of flood regime to invertebrate habitat in an unregulated river–floodplain ecosystem. Journal of the North American Benthological Society 20:225–240.

BENKE, A. C., AND D. I. JACOBI. 1994. Production dynamics and resource utilization of snag dwelling mayflies in a blackwater river. Ecology 75:1219–1232.

BENKE, A. C., T. C. VAN ARSDALL, D. M. GILLESPIE, AND F. K. PARRISH. 1984. Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. Ecological Monographs 54:25–63.

BENKE, A. C., AND J. B. WALLACE. 1997. Trophic basis of production among riverine caddisflies: implications for food web analysis. Ecology 78:1132–1145.

BREMIGAN, M. T., AND R. A. STEIN. 1997. Experimental assessment of the influence of zooplankton size and density on gizzard shad recruitment. Transactions of the American Fisheries Society 126:622–637.

BUTZER, K. W. 1977. Geomorphology of the lower Illinois Valley as a spatial-temporal context for the Koster archaic site. Reports of Investigations No. 34. Illinois State Museum, Springfield, Illinois.

COPP, G. H. 1992. An empirical model for predicting microhabitat of 0+ juvenile fishes in a lowland river catchment. Oecologia (Berlin) 91:338–345.

COPP, G. H. 1993. Microhabitat use of fish larvae and 0+ juveniles in a small abandoned channel of the Upper Rhone, France. Folia Zoologica 42:153–164.

COPP, G. H., G. GUTI, B. ROVNÝ, AND J. ČERNÝ. 1994. Hierarchical analysis of habitat use by 0+ juvenile fish in Hungarian/Slovak flood plain of the Danube River. Environmental Biology of Fishes 40: 329–348.

COPP, G. H., AND M. PENAZ. 1988. Ecology of fish spawning and nursery zones in the flood-plain, using a new sampling approach. Hydrobiologia 169:209–224.

CURTIS, G. L., J. S. RAMSEY, AND D. L. SCARNECCHIA. 1997. Habitat use and movements of shovelnose sturgeon in Pool 13 of the upper Mississippi River during extreme low flow conditions. Environmental Biology of Fishes 50:175–182.

DETTMERS, J. M., S. GUTREUTER, D. H. WAHL, AND D. A. SOLUK. 2001. Patterns of abundance of fishes in main channels of the upper Mississippi River system. Canadian Journal of Fisheries and Aquatic Sciences 58:933–942.

DETTMERS, J. M., AND R. A. STEIN. 1992. Food consumption by larval gizzard shad: zooplankton effects and its implications for reservoir communities. Transactions of the American Fisheries Society 121:494–507.

ELDRIDGE, M. B., J. A. WHIPPLE, D. ENG, M. J. BOWERS, AND B. M. JARVIS. 1981. Effects of food and feeding factors on laboratory-reared striped bass larvae. Transactions of the American Fisheries Society 110:111–120.

FERRARI, I., A. FARABEGOLI, AND R. MAZZONI. 1989. Abundance and diversity of planktonic rotifers in the Po River. Hydrobiologia 186/187:201–208.

FREMLING, C. R., J. L. RASMUSSEN, R. E. SPARKS, S. P. COBB, C. F. BRYAN, AND T. O. CLAFLIN. 1989. Mississippi River fisheries: a case history. Pages 309–351 *in* D. P. Dodge (editor). Proceedings of the International Large River Symposium (LARS). Canadian Special Publication of Fisheries and Aquatic Sciences 106.

GALAT, D. L., AND I. ZWEIMÜLLER. 2001. Conserving large-river fishes: is the *highway analogy* an appropriate paradigm? Journal of the North American Benthological Society 20:266–279.

GITTINGER, E. J. 1999. Fish movement patterns in the main channel of large floodplain rivers. MSc Thesis, University of Illinois, Champaign-Urbana, Illinois.

GOODRICH, J. L. 1999. Exploring zooplankton and larval fish dynamics within three habitats of the Illinois River. MSc Thesis, University of Illinois, Champaign-Urbana, Illinois.

GUTREUTER, S., A. D. BARTELS, K. IRONS, AND M. B. SANDHEINRICH. 1999. Evaluation of the flood-pulse concept based on statistical models of growth of selected fishes of the Upper Mississippi River system. Canadian Journal of Fisheries and Aquatic Sciences 56:2282–2291.

HOLLAND, L. E., AND J. R. SYLVESTER. 1983. Distribution of larval fishes related to potential navigation impacts on the Upper Mississippi River, Pool 7. Transactions of the American Fisheries Society 113:293–301.

HYNES, H. B. N. 1970. The ecology of running waters. University of Toronto Press, Toronto, Ontario.

JOHNSON, B. L., W. B. RICHARDSON, AND T. J. NAIMO. 1995. Past, present, and future concepts in large river ecology. BioScience 45:134–141.

JUNK, W. J., P. B. BAYLEY, AND R. E. SPARKS. 1989. The flood pulse concept in river–floodplain systems. Pages 110–127 *in* D. P. Dodge (editor). Proceedings of the International Large River Symposium (LARS). Canadian Special Publication of Fisheries and Aquatic Sciences 106.

LEOPOLD, L. B., M. G. WOLMAN, AND J. P. MILLER. 1964. Fluvial processes in geomorphology. W. H. Freeman and Company, San Francisco, California.

LI, S., AND J. A. MATHIAS. 1982. Causes of high mortality among cultured larval walleyes. Transactions of the American Fisheries Society 111:710–721.

MAYER, C. M., AND D. H. WAHL. 1997. The relationship between prey selectivity and growth and survival in a larval fish. Canadian Journal of Fisheries and Aquatic Sciences 54:1504–1512.

MILLER, T. J., L. B. CROWDER, J. A. RICE, AND E. A. MARSCHALL. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Canadian Journal of Fisheries and Aquatic Sciences 45:1657–1670.

PACE, M. L., S. E. G. FINDLAY, AND D. LINTS. 1992. Zooplankton in advective environments: the Hudson River community and a comparative analysis. Canadian Journal of Fisheries and Aquatic Sciences 49:1060–1069.

POWER, M. E. 1990. Effects of fish in river food webs. Science 250:411–415.

ROSSARO, B. 1988. Mid-Po River zooplankton. Hydrobiologia 160:97–105.

SAUNDERS, J. F., AND W. M. LEWIS. 1988. Zooplankton abundance and transport in a tropical white-water river. Hydrobiologia 162:147–155.

SHEAFFER, W. A., AND J. B. NICKUM. 1986. Backwater areas as nursery habitats for fishes in Pool 13 of the upper Mississippi River. Hydrobiologia 136: 131–140.

SOLUK, D. A. 1985. Macroinvertebrate abundance and production of psammophilous Chironomidae in shifting sand areas of a lowland river. Canadian Journal of Fisheries and Aquatic Sciences 42:1296–1302.

SPARKS, R. E. 1995. Need for ecosystem management of large rivers and their floodplains. BioScience 45:168–182.

SPARKS, R. E., P. B. BAYLEY, S. L. KOHLER, AND L. W. OSBORNE. 1990. Disturbance and recovery of large floodplain rivers. Environmental Management 14: 699–709.

THORP, J. H., A. R. BLACK, K. H. HAAG, AND J. D. WEHR. 1994. Zooplankton assemblages in the Ohio River: seasonal, tributary, and navigation dam effects. Canadian Journal of Fisheries and Aquatic Sciences 51:1634–1643.

THORP, J. H., AND M. D. DELONG. 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large rivers. Oikos 70:305–308.

THORP, J. H., M. D. DELONG, AND A. F. CASPER. 1998. *In situ* experiments on predatory regulation of a bivalve mollusc (*Dreissena polymorpha*) in the Mississippi and Ohio Rivers. Freshwater Biology 39: 649–661.

VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

WAHL, D. H., K. BRUNNER, AND L. A. NIELSEN. 1988. Trophic ecology of freshwater drum in large rivers. Journal of Freshwater Ecology 4:483–491.

WARD, J. V., AND J. A. STANFORD. 1995. The serial discontinuity concept: extending the model to floodplain rivers. Regulated Rivers: Research and Management 10:159–168.

WELCOMME, R. L. 1985. River fisheries. Fisheries Technical Paper 262. Food and Agriculture Organization of the United Nations, Rome, Italy.

WERNER, R. G., AND J. H. S. BLAXTER. 1980. Growth and survival of larval herring, *Clupea harengus*, in relation to fry density. Canadian Journal of Fisheries and Aquatic Sciences 37:1063–1069.

WINEMILLER, K. O., AND D. B. JEPSEN. 1998. Effects of seasonality and fish movement on tropical food webs. Journal of Fish Biology 53(Supplement A): 267–296.

Received: 2 May 2000
Accepted: 20 November 2000