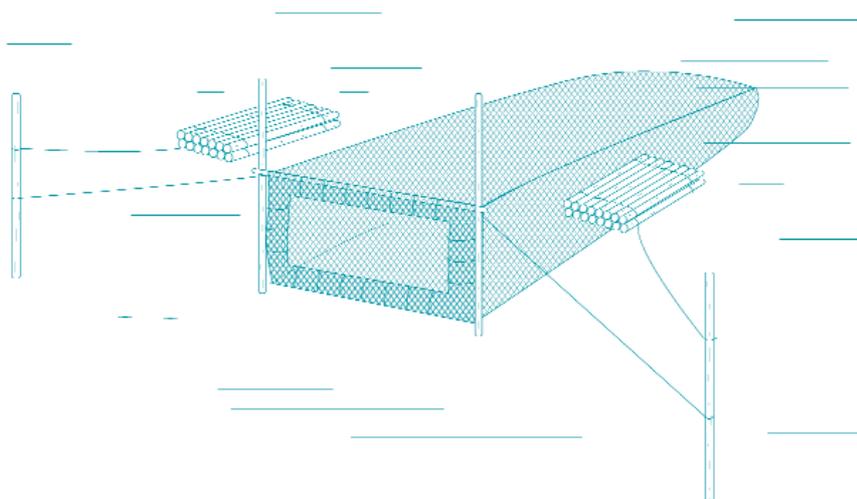


FLOODPLAIN RIVER FOOD WEBS: GENERALIZATIONS AND IMPLICATIONS FOR FISHERIES MANAGEMENT

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► ABSTRACT

Based on the relationship between temperature variation and flood dynamics, three types of floodplain rivers can be identified: temperate stochastic, temperate seasonal and tropical seasonal. The degree to which flooding occurs in phase with warm temperatures and enhanced system productivity influences selection for alternative life history strategies in aquatic organisms. In addition, regional geochemistry and temporal dynamics of disturbance and recovery of local habitats within the landscape mosaic favour different life history strategies, sources of production and feeding pathways. In most habitats, algae seem to provide the most important source of primary production entering

Keywords: connectivity, detritus, migration, primary production, species interaction, trophic position

the grazer web. Large fractions of periphyton and aquatic macrophyte production enter aquatic foodwebs in the form of detritus and detrital consumption is greater during low-water phases. Even in species-rich tropical rivers, most of the material transfer in food webs involves relatively few species and short food chains (3-4 levels, 2-3 links). Longer food chains that involve small or rare species are common and increase ecological complexity, but probably have minor effects on total primary and secondary production. In the tropics, fishes appear to perform many ecological functions performed by aquatic insects in temperate rivers. Oftentimes, a small number of common species disproportionately influences benthic ecosystem structure, productivity and dynamics. Similarly, a relatively small number of predatory species may exert a disproportionately large influence on prey populations, even in species-rich tropical systems. Under seasonal flood-pulse regimes, species have the opportunity to evolve adaptations to exploit predictable resources. Under aseasonal flood-pulse regimes, species are more challenged to respond appropriately to relatively unpredictable patterns of resource variation and access to floodplain habitats, while nonessential for most species, usually enhances recruitment. Seasonal rivers in nutrient-rich landscapes can sustain greater harvest than aseasonal rivers or seasonal rivers in nutrient-poor landscapes. Loss of habitat connectivity and overharvest of dominant species can have unpredictable effects on food web dynamics and community structure. Maintenance of natural flood regimes is important for biodiversity conservation and sustainable harvest of fishes, especially in strongly seasonal systems.

IMPORTANCE OF RIVER-FLOODPLAIN SYSTEMS

River-floodplain systems, especially in the tropics, support high biological diversity and important fisheries (Welcomme 1985; 1990; Lowe-McConnell 1987). High biological diversity, both taxonomic and functional, is associated with high spatial complexity and the dynamic nature of aquatic, terrestrial and ecotonal habitats (Schiemer 1999; Ward, Tockner and Schiemer 1999; Robinson, Tockner and Ward 2002). River networks are ubiquitous features of landscapes that have provided many opportunities for allopatric speciation of aquatic taxa and also serve as reservoirs that accumulate species over evolutionary time. The high habitat heterogeneity and ecotonal nature of river-floodplain landscapes also fosters high richness of terrestrial taxa.

The nutrient-rich alluvial soils often associated with lowland floodplains have always been targets for intensive agriculture. Use of floodplains for agriculture has resulted in construction of levee systems to control flooding. Levees sever aquatic connections between the river channel and aquatic habitats of the floodplain (Sparks 1995; Ward *et al.* 1999). In addition to direct impacts from agriculture and other land uses that destroy natural terrestrial, wetland and aquatic habitats, lowland rivers are impacted by pollution, including nutrient loading, from locations anywhere within their catchments. The natural hydrology of most large rivers in developed nations and increasingly in developing nations has been severely altered by dams, levees, channelization and landscape changes. In spite of their great ecological, economic and cultural importance, large rivers remain one of the most poorly studied among major ecosystems (Thorp and Delong 1994). Recent years have witnessed an increase in research on large rivers, especially in Europe, Australia and the Americas. Even as we begin to understand the ecology of large river ecosystems, with each passing year fewer relatively un-impacted large rivers remain as models for future restoration.

The purpose of this paper is to briefly review food web structure and dynamics in lowland river-floodplain systems and to explore management implications of this body of ecological knowledge. The food web paradigm provides an approach that allows us to model complex communities and ecosystems with the

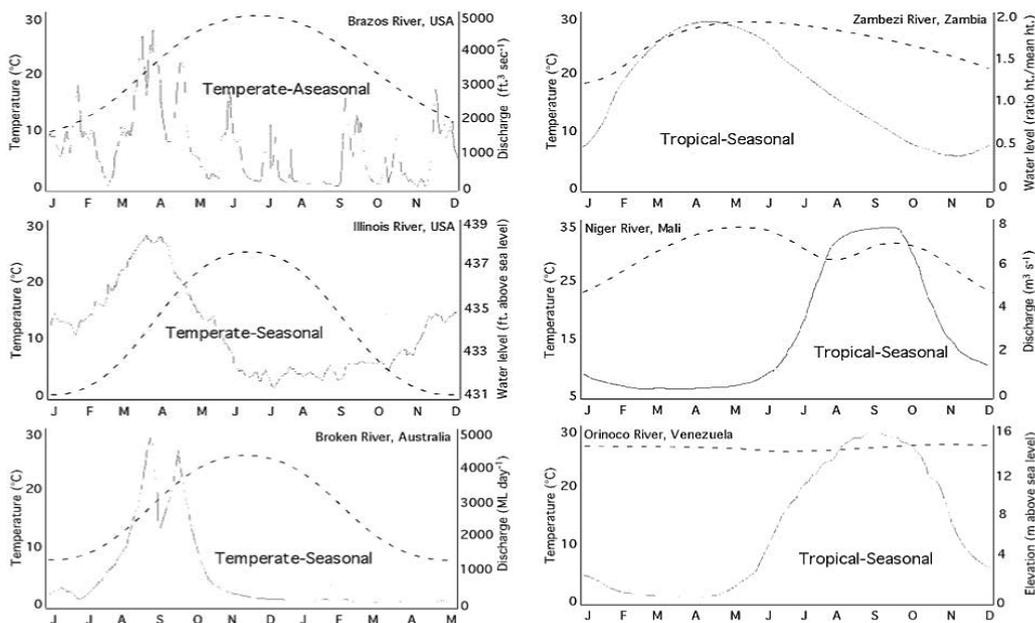
ultimate aim of understanding relationships and predicting dynamics. The historic development of the food web paradigm has been reviewed previously (Hall and Raffaelli 1993; Polis and Winemiller 1996). Woodward and Hildrew (2002) recently reviewed food web structure in rivers, with a strong focus on theories and evidence associated with system stability. Their review emphasized evidence from streams, since comparatively little food web research has been conducted on large rivers. The present review seeks to summarize recent findings and perspectives from large lowland rivers. Additionally, the features of lowland rivers from tropical and temperate regions will be compared and generalizations sought for application to conservation of biodiversity, fisheries and ecosystem integrity and productivity.

TYOLOGY OF RIVER-FLOODPLAIN ABIOTIC DYNAMICS

The degree to which flooding occurs in phase with warm temperatures and enhanced system productivity influences selection for alternative life history strategies in aquatic organisms. Rivers display at least three general patterns: temperate with aseasonal (seemingly random) flood pulses, temperate with seasonal flood pulses and tropical with seasonal flood pulses. The ramifications of these patterns for ecological dynamics, food web dynamics in particular, are the

focus of this paper. Photoperiod and temperature are key environmental drivers of ecological dynamics in fluvial systems. Longer photoperiods during summer support increased primary production. Warmer temperatures increase rates of microbial metabolism, nutrient cycling, primary production and feeding by ectotherms. At high latitudes and elevations, spring warming also is associated with snowmelt and increased water availability. The effect of flooding on feeding, growth and survival of aquatic organisms can be particularly strong in lowland floodplain river systems. Floods stimulate remineralization of nutrients as well as primary and secondary production in floodplain habitats (Welcomme 1985; Junk, Bayley and Sparks 1989).

In temperate regions, temperature varies in a predictable seasonal pattern, with the magnitude of variation greater at higher latitudes and elevations. Regions having fairly unpredictable rainfall and lacking significant runoff from snowmelt display unpredictable, aseasonal flood pulses. Examples of temperate-aseasonal rivers are found along the northwestern Gulf of Mexico coast of North America and in certain regions within Australia's Murray-Darling Basin. In Texas, the Brazos River shows unpredictable hydrology, both within and between-years (Winemiller 1996a, Figure 1). High discharge events vary greatly in



■ **Figure 1.** Examples of lowland floodplain rivers with temperate-aseasonal (Brazos River- from US Geological Survey database), temperate-seasonal (Illinois River- from Sparks 1995; Broken River- from Humphries *et al.* 2002) and tropical-seasonal (Zambezi River- from Handlos and Williams 1985; Niger River- from Quensiene *et al.* 1994; Orinoco River- from Hamilton and Lewis 1990) abiotic regimes.

magnitude and most are of short duration. Floods that top riverbanks and enter oxbow lakes are infrequent and can occur any time of the year (Winemiller *et al.* 2000). The unpredictable nature of flood pulses and river-floodplain connections pose challenges for species that exploit ephemeral or dynamic ecotonal aquatic habitats.

Many temperate regions have cyclic patterns of precipitation and/or springtime melting of ice and snow that yield seasonal flood pulses. Local flooding may derive from local precipitation and thawing (e.g. Broken River, Australia; Illinois River, United States, Figure 1), precipitation and/or snowmelt in headwater areas (e.g. lower Colorado River, United States), or some combination of local and upstream factors. Seasonal flooding in the temperate rivers also can be strongly influenced by evapotranspiration as a function of seasonal temperature regimes (Benke *et al.* 2000). The magnitude of flooding in most temperate rivers is highly variable between years (e.g. Ogeechee River, south eastern United States, Benke *et al.* 2000) and in some systems floods may not occur at all during some years (e.g. Broken River, Australia, Humphries, Luciano and King 2002). Thus, whereas temperate-seasonal rivers provide a relatively predictable temporal regime to which organisms may respond adaptively (Resh *et al.* 1994), stochastic between-year variation may seriously challenge adaptive responses to seasonal environmental periodicity. In most cases, seasonal flooding in the temperate zone coincides with springtime warming, which selects for reproduction during this period. Recruitment is enhanced when early life stages occur in appropriate habitats when warm temperatures stimulate ecosystem productivity, metabolism and growth.

In tropical continental regions, the flood pulse of lowland rivers is almost universally driven by strongly seasonal precipitation. In some cases, local flooding coincides with local precipitation (Upper Orinoco, Upper Paraná, Upper Zambezi and Fly Rivers), whereas in others the seasonal flood pulse is most strongly influenced by rainfall in distant headwaters (e.g. lower Niger, Congo and Solimões-Amazon Rivers). Because temperature varies relatively little in tropical lowland regions, the hydrological regime is the major factor that drives ecological dynamics and natural selection in response to environmental varia-

tion. The tropical-seasonal model has dominated thinking about the ecology of river-floodplain systems (e.g. the flood-pulse model, Junk *et al.* 1989), but global generality of this pattern and its consequences has scarcely been discussed (but see below, also Thorp and Delong 1994, 2002; Humphries, King and Koehn 1999; Humphries *et al.* 2002).

PRIMARY PRODUCTION SOURCES FOR LOWLAND RIVER FOOD WEBS

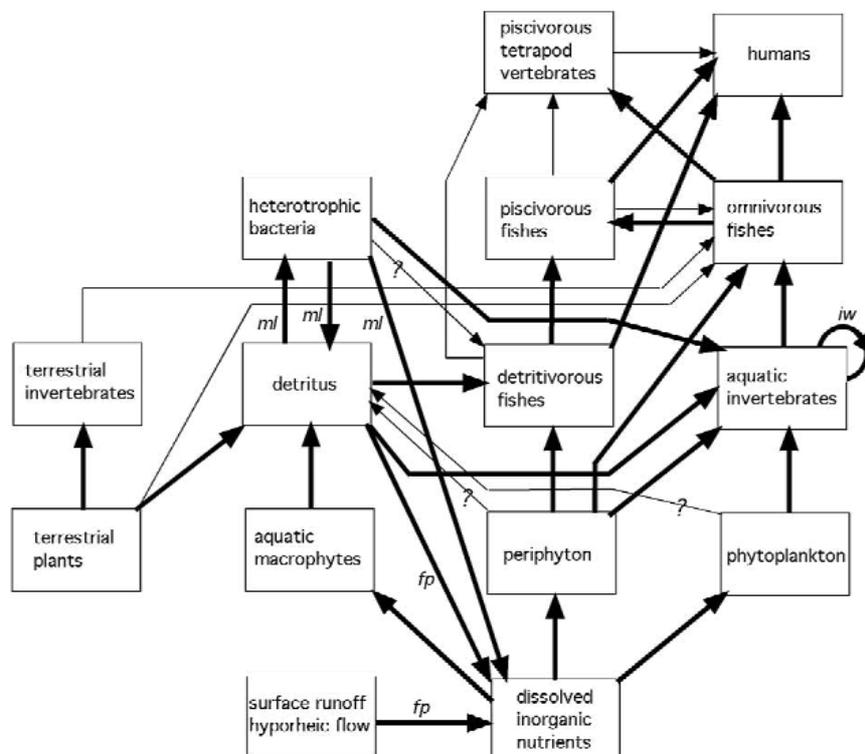
A fundamental aspect of any food web is the source of primary production that supports consumer populations. Geology and landscape features influence nutrient and flood dynamics that affect production rates of different primary producers (Rai and Hill 1984). Primary production has high spatiotemporal variation within most river-floodplain systems. In the central Amazon Basin, primary productivity ranges from 50 to 3 500 mg C m⁻² d⁻¹ (Rai and Hill 1984) according to location and flood stage. Macrophytes, both terrestrial and aquatic, appear to be the major producers in floodplains (Bayley 1989; Melack *et al.* 1999; Lewis *et al.* 2001). Analysis of stable isotopes indicates that dominant production sources for higher consumers in river-floodplain food webs appear to be phytoplankton, periphyton and fine particulate organic matter derived from algae (Araujo-Lima *et al.* 1986; Hamilton, Lewis and Sippel 1992; Forsberg *et al.* 1993; Thorp and Delong 1994, 2002; Thorp *et al.* 1998; Benedito-Cecilio *et al.* 2000; Lewis *et al.* 2001; Leite *et al.* 2002). Even in highly turbid floodplain lakes of arid central Australia, benthic filamentous algae in the shallow littoral zone are the major production source supporting higher consumers (Bunn, Davies and Winning 2003).

Both algae and aquatic macrophytes appear to enter aquatic food webs mostly in the form of detritus (fine and coarse particulate organic matter), some being transported in the water column and some settling onto substrates. Direct consumption of aquatic macrophytes is rare, but aquatic macrophytes are consumed by a few fish genera from South America (*Schizodon* [Anostomidae] and *Pterodoras* [Doradidae]) and Africa (*Tilapia* [Cichlidae]). Detritivory is extremely common in river communities, both among invertebrates and fishes. In seasonal

floodplain habitats of the Orinoco and Zambezi rivers, consumption of detritus by fishes was greater during low-water phases (Winemiller 1990, 1996a). As determined from analysis of stomach contents, fishes consumed large fractions of both fine and coarse particulate material. In these systems, coarse detritus is derived almost entirely from aquatic macrophytes. The origin of fine particulate matter in diets could not be determined from microscopic analysis, but isotopic studies suggest mixtures of algae and macrophytes that use the C3 photosynthetic pathway (Jepsen and Winemiller 2002).

Based on isotopic evidence and the fact that coarse particulate matter derived from macrophytes is refractory and of poor nutritional value, Thorp and Delong (1994, 2002) made a case for a dominant role of algae in river food webs. In tropical-seasonal rivers, macrophytes generally produce well over half of the primary production on floodplains, yet only contribute small fractions of the total carbon assimilated by fishes (Forsberg *et al.* 1993; Lewis *et al.* 2001). Macrophyte production is high during the period of floodplain inundation (Rai and Hill 1984; Welcomme

1985; Junk *et al.* 1989). As floodwaters recede, aquatic macrophytes die and produce massive amounts of coarse detritus, only a minor fraction of which is probably consumed in any form by aquatic macrofauna. Most of the labile dissolved organic carbon leaches from this material and is quickly consumed by microbes. Most of the remaining refractory material seems to be consumed by microbes (the microbial loop), without direct entry into the upper food web (Figure 2). The fraction of microbial carbon that makes its way to the upper web is unknown for virtually all rivers, but assumed to be small based on available isotopic evidence (e.g. Bunn *et al.* 2003). In eutrophic floodplains, huge stocks of water hyacinths, grasses, or other macrophytes build up during the flood phase. As water levels drop, microbial metabolism of dead macrophyte tissues can deplete dissolved oxygen within shrinking aquatic habitats (Winemiller 1996b). In many savanna floodplains, such as the Kafue flats of the Zambezi system, submergence of terrestrial grasses during the rising-water phase leads to plant death, decay and aquatic hypoxia over large areas (Junk *et al.* 1989).



■ **Figure 2.** Generalized food web for floodplain-river ecosystems. Boxes are aggregate material pools and vectors represent consumer-resource interactions with thick arrows representing dominant pathways (ml= microbial loop path, fp = nutrient pathways enhanced by flood pulses, iw = invertebrate web having complex trophic structure involving invertebrates and ? = poorly quantified pathways).

In tropical systems, terrestrial sources of primary and secondary production are directly consumed by diverse fish taxa. In the central Amazon, several abundant fish species consume seeds, fruits, arthropods and other forms of allochthonous resources (e.g. Goulding 1980; Goulding, Carvallo and Ferreira 1988). Some characiform fishes (e.g. *Brycon*, *Colossoma*, *Piaractus* and *Myleus* spp.) are morphologically and physiologically specialized to feed on fruits and seeds. Goulding (1980) described large amounts of fruit and seeds in diets of many Amazonian catfishes (Siluriformes). Terrestrial invertebrates and vertebrates also enter the aquatic food webs. The aruana (*Osteoglossum bicirrhosum* Spix and Agassiz) is able to leap several meters above the water surface to feed on arthropods, reptiles, birds and bats. Accounts of direct consumption of allochthonous resources in the flooded forests of the Amazon had a large influence on the development of the flood pulse concept for large rivers. Yet when the aquatic food web is viewed as a whole (i.e. major biomass components) allochthonous carbon sources appear to be less important for macrofaunal populations than autochthonous sources of primary production. The greatest fraction of terrestrial vegetation that enters river-floodplain food webs appears to do so as detritus (leaf litter and woody debris), most of which is highly refractory and processed via the microbial loop.

FOOD WEB STRUCTURE

River food webs are extremely complex and dynamic (Winemiller 1990). Yet one of the most striking features of river communities is the domination of standing biomass by a relatively small number of species. This pattern appears to be true both in low-diversity temperate systems, but more surprisingly the pattern holds also for taxonomically diverse biotic assemblages in tropical rivers. Fishery yields from almost every major floodplain-river system in the world are strongly skewed in favour of a handful of dominant species (e.g. see summaries in Welcomme 1985). In terms of standing biomass, the Orinoco and Amazon river mainstems are dominated by a few species of *Prochilodus*, *Semaprochilodus*, *Mylossoma*, *Hydrolycus*, *Brycon*, *Pseudoplatystoma*, *Pinirampus*,

and *Brachyplatystoma*. Obviously, much biomass may be represented by small fishes of little or no commercial value, however, even these small fish assemblages are strongly skewed with few abundant and many uncommon species (e.g. Winemiller 1996b, Arrington and Winemiller 2003). Thus, it is reasonable to assume that matter and energy moving through a local food web are doing so via a comparatively small subset of the total pathways represented in the trophic network. This was indeed the pattern demonstrated for the aquatic food webs in four tropical freshwater systems, including a creek-floodplain system in the Venezuelan llanos and Atlantic coastal plain of Costa Rica (Winemiller 1990). When the magnitude of trophic links was estimated as the volumetric proportion of resource categories in consumer diets, the distribution of link magnitudes was strongly skewed in every instance. In terms of biomass, relatively few dominant producer and consumer taxa and a limited number of major trophic pathways dominate river food webs.

Aquatic and terrestrial macrophytes usually are dominant sources of primary production in floodplains (Rai and Hill 1984) and most of this material is consumed by microbes that ultimately return nutrients to the inorganic pool (Figure 2). However, not all detritus is recycled within the microbial loop, with variable fractions consumed directly by a variety of invertebrate and fish taxa, some of which are dominant food web elements. Important components of aquatic meio- and macro-invertebrate faunas are detritivores (Schmid-Araya and Schmid 2000; Benke *et al.* 1984; Benke *et al.* 2001). Although the standing biomass of these taxa is generally low, they have high rates of population growth and turnover and represent important pathways in river food webs. Much more research is needed to elucidate the functional significance of aquatic invertebrates, particularly meiofauna, in large river food webs.

Detritivorous fishes are always abundant in river-floodplain systems and routinely dominate fishery catches (Welcomme 1985). Although some detritivorous fishes consume coarse vegetative detritus, most of the material classified as detritus in gut

contents is fine amorphous material of undetermined origin. Detritivorous fishes are important prey for large piscivores. In the Cinaruco River of Venezuela, *Semaprochilodus kneri* (Pellegrin) were estimated to contribute about 45 percent of the diet of large *Cichla temensis* Humboldt during the falling-water period (Jepsen, Winemiller and Taphorn 1997; Winemiller and Jepsen 2002). Detritivorous fishes form major portions of the diets of piscivorous catfishes in large South American rivers (Barthem and Goulding 1997; Barbarino and Winemiller unpublished). Tigerfish (*Hydrocynus vittatus* Castelnau) and African pike (*Hepsetus odoe* (Bloch) of the Upper Zambezi River consume large numbers of detritivorous tilapines and

cyprinids, respectively. Yet isotopic evidence indicates that comparatively little carbon from macrophytes, especially grasses using the C4 photosynthetic pathway, makes its way to higher consumers (Hamilton *et al.* 1992; Lewis *et al.* 2001; Jepsen and Winemiller 2002). Information currently available from research in large rivers in North and South America indicates that much of the fine particulate organic matter assimilated by detritivorous fishes is derived from algae, even in systems in which aquatic macrophytes dominate aquatic primary production (Araujo-Lima *et al.* 1986, Hamilton *et al.* 1992; Forsberg *et al.* 1993; Winemiller and Akin unpublished).

Table 1: Estimated trophic positions of dominant piscivores in floodplain river ecosystems and estuaries (References are 1- Winemiller 1990, 2- Peterson 1997, 3- Jepsen & Winemiller 2002, 4-Winemiller 1996a, 5- Akin 2001, 6- Winemiller & Akin unpublished data).

Piscivore	Trophic position	Site	Analysis method	Reference
<i>Pygocentrus cariba</i> Valenciennes	3.4	Caño Maraca, Venezuela	diet	1
<i>Hoplias malabaricus</i> (Bloch)	3.4	Caño Maraca, Venezuela	diet	1
<i>Caquetaia kraussii</i> (Steindachner)	3.5	Caño Maraca, Venezuela	diet	1
<i>Cichla orinocensis</i> Humboldt	4.0	Morichal Charcote, Venezuela	diet	2
<i>Hoplias malabaricus</i>	4.0	Morichal Charcote, Venezuela	diet	2
<i>Cichla orinocensis</i>	3.5	Cinaruco River, Venezuela	isotopes	3
<i>Cichla temensis</i>	3.6	Cinaruco River, Venezuela	isotopes	3
<i>Cichla temensis</i>	4.8	Pasimoni River, Venezuela	isotopes	3
<i>Serrasalmus manueli</i> Fernandez-Yepez & Ramírez	3.8	Cinaruco River, Venezuela	isotopes	3
<i>Pygocentrus cariba</i>	3.8	Apure River, Venezuela	isotopes	3
<i>Hoplias malabaricus</i>	3.6	Apure River, Venezuela	isotopes	3
<i>Hoplias malabaricus</i>	4.0	Aguaro River, Venezuela	isotopes	3
<i>Hydrolycus armatus</i> (Schomburgk)	3.6	Apure River, Venezuela	isotopes	3
<i>Hydrolycus armatus</i>	4.2	Aguaro River, Venezuela	isotopes	3
<i>Hydrolycus armatus</i>	3.7	Cinaruco River, Venezuela	isotopes	3
<i>Pseudoplatystoma fasciatum</i> (L.)	3.5	Apure River, Venezuela	isotopes	3
<i>Pseudoplatystoma fasciatum</i>	4.4	Pasimoni River, Venezuela	isotopes	3
<i>Nandopsis dovii</i> (Günther)	3.3	Tortuguero River, Costa Rica	diet	1
<i>Gobiomorus dormitor</i> (Lacepede)	3.3	Tortuguero River, Costa Rica	diet	1
<i>Hepsetus odoe</i>	4.3	Zambezi River, Zambia	diet	4
<i>Hydrocynus vittatus</i>	4.6	Zambezi River, Zambia	diet	4
<i>Serranochromis robustus</i> (Günther)	3.7	Zambezi River, Zambia	diet	4
<i>Lepisosteus osseus</i> (L.)	3.6	Brazos River, Texas	diet	4
<i>Lepisosteus oculatus</i> (Winchell)	3.3	Brazos River, Texas	diet	4
<i>Lepisosteus oculatus</i>	3.3	Mad Island Marsh, Texas	diet	5
<i>Lepisosteus oculatus</i>	3.1	Mad Island Marsh, Texas	isotopes	6
<i>Sciaenops ocellatus</i> (L.)	3.4	Mad Island Marsh, Texas	diet	5
<i>Sciaenops ocellatus</i>	3.3	Mad Island Marsh, Texas	isotopes	6
Mean	3.7			

Descriptions of food web structure in river-floodplain ecosystems based on analysis of both diets and stable isotopes reveal short food chains. In terms of biomass, the most important pathways connect detritus to detritivorous fishes (and to a lesser extent invertebrates) and to piscivorous fishes. Consumer trophic positions can be estimated as a continuum using algorithms applied to dietary or isotopic data. In river-floodplain systems, large abundant piscivores almost invariably occupy positions between the third and fourth trophic levels (Table 1). This pattern arises because piscivore diets are dominated by detritivores and other fishes feeding near the second trophic level. In Caño Maraca, a creek-floodplain ecosystem in the Venezuelan llanos, the most abundant species in the fish assemblage, *Steindachnerina argentea* (Gill), also was the dominant prey of abundant red-belly piranhas (*Pygocentrus cariba*) and guavinas (*Hoplias malabaricus*) (Winemiller 1990). In the Cinaruco River, detritivorous and algivorous hemiodid and prochilodontid fishes dominate the diet of abundant *Cichla temensis* (Jepsen *et al.* 1997). In the Apure River, detritivorous *Prochilodus mariae* Eigenmann dominate the diet of the two most abundant large catfishes, *Pseudoplatystoma fasciatum* and *P. tigrinum* (Valenciennes) (Barbarino and Winemiller unpublished). Clearly, most matter and energy passes from the base to the top of the aquatic food web via food chains that are short (2-3 links and 3-4 levels). Isotopic analysis of fishes in a Pantanal lake indicated 3-4 trophic levels, with consumers arranged along a trophic continuum rather than discrete levels (Wantzen, Machado, Voss *et al.* 2002). Lewis *et al.* (2001) noted that short food chains facilitate efficient transfer of energy from algae to fishes and may explain why large fish stocks in tropical floodplains can be supported by the minor algal component of system primary production.

Given the dominant role of a relatively small number of short food chains, the high complexity of river-floodplain food webs is derived from numerous weak links among diverse species of both common and rare taxa. The most numerically abundant species (e.g. algae, invertebrates, fishes) are small-bodied with low

to moderate standing stocks of biomass. Given high rates of population turnover, many of these taxa probably have greater functional significance in food webs than their low abundance implies. Although average food chain length leading to top piscivores is short, this does not imply that all food chains are short. Longer chains involving small or rare species can be identified. Small fishes that consume scales, fins, mucus, or blood of other fishes occur in most large rivers of South America. These fishes represent insignificant components of system biomass, but they contribute to high species diversity and high food web complexity. Thus, longer food chains that involve small or rare species are common and increase ecological complexity, but probably have very minor effects on primary and secondary production. In terms of biomass, tropical river food webs appear to consist of dominant (foundation, or core) species connected by short food chains, plus a much richer assemblage of small (subordinate, or interstitial) species, many of them uncommon, that greatly increase food web complexity while having relatively little influence on material and energy flow with the ecosystem. Of course these species could have important ecological functions that have not yet been identified (e.g. seed dispersal for riparian plants, Goulding 1980).

SPECIES FUNCTIONAL DIVERSITY IN LARGE RIVER FOOD WEBS

The tropics are widely recognized to harbour higher taxonomic and ecological diversity than temperate regions and large river systems provide no exception to this rule. Globally, fish species richness is strongly related to basin size (Welcomme 1985; Oberdorff, Guegan and Hugueny 1995). However, fishes show greater taxonomic and ecological diversity in lowland continental rivers of tropics relative to comparable rivers of temperate regions (Winemiller 1991a). Whereas the core feeding groups are represented in both temperate and tropical regions (i.e. algivores, detritivores, omnivores, invertivores and piscivores), the relative proportions differ. Fish assemblages of large tropical rivers contain greater fractions of detritivorous, herbivorous and omnivorous fishes relative to temperate fish assemblages (Winemiller

1991a). In this regard, tropical river fishes appear to occupy niche space occupied by invertebrates in temperate rivers.

Although no formal comparisons appear to have been made, macroinvertebrate species richness in large rivers does not seem to reveal a latitudinal gradient as steep as that of fishes. Bivalve mollusks actually have greater species richness in temperate rivers of the Western Hemisphere and the abundance and functional diversity of aquatic insects in lowland rivers does not appear to be much greater in tropical than temperate rivers. In tropical blackwater rivers (high concentrations of dissolved organic compounds, low PH and conductivity, low concentrations of nutrients and suspended solids), aquatic insect abundance is low with most species and biomass concentrated in leaf litter and woody debris. Shrimp are abundant in most lowland tropical rivers, with various taxa feeding on detritus, algae and microfauna. Even oligotrophic tropical blackwater rivers can support large populations of atyid and palaemonid shrimp. Leaf litter and woody debris seem to provide particularly important habitats in blackwater rivers (Benke *et al.* 1984). In tropical whitewater rivers (high concentrations of nutrients and suspended sediments in flowing channels, high conductivity, neutral pH), the root zone of floating aquatic macrophytes, such as *Paspalum repens* and *Eichhornia* spp., support high biomass of aquatic macroinvertebrates. Macroinvertebrates in channel habitats are concentrated in patchy, structurally complex habitats, such as woody debris (Benke *et al.* 2001). Clay nodules at the bottom of deep channel areas of Neotropical whitewater rivers support mayfly populations that consume detritus and provide a major food resource for weakly-electric gymnotiform fishes (Marrero 1987). Gymnotiforms also feed heavily on planktonic microcrustacea that feed on phytoplankton (Lundberg *et al.* 1987).

As noted above, a relatively small fraction of the total species in a community appear to have large roles in the flow of matter and energy in floodplain river food webs. Yet species affect ecosystem properties via mechanisms besides consumer-resource inter-

actions. Some of the most dominant species of large lowland rivers have been shown to have strong effects on ecosystem structure and processes. A few benthivorous fish species have been shown to disproportionately influence sediments of channel or floodplain habitats. Using field experiments, Flecker (1996) showed how benthivorous *Prochilodus mariae* remove organic-rich sediments and change the structure of benthic algae and insect assemblages in a whitewater river of the Andean piedmont in Venezuela. *Semaprochilodus kneri* have similar effects in clearwater and blackwater rivers in Venezuela (Winemiller unpublished). North American gizzard shad (*Dorosoma cepedianum* (Lesueur)) feed on detritus and move nutrients from sediments to the water column in reservoirs (Vanni 1996). The gizzard shad is a common detritivore and periphyton grazer of lowland rivers in North America and could significantly affect ecosystem dynamics. Benthic feeding by large omnivorous cypriniform fishes (e.g. *Ictiobus* spp., *Cyprinus carpio* L.) can increase sediment suspension in the water column (Drenner, Smith and Threlkeld 1996). Other grazing taxa have been shown to affect standing stocks of algae and organic sediments in tropical and temperate rivers. Field manipulations have shown grazer effects on standing stocks of algae and organic sediments in upland tropical and temperate rivers, including studies involving shrimp (Cowl *et al.* 2001), tadpoles (Flecker, Feifarek and Taylor 1999) and aquatic insect larvae (Power 1990, 1992).

In tropical lowland rivers, a few predatory species may disproportionately influence the distribution or abundance of prey populations. Jackson (1961) proposed that tigerfish (*Hydrocynus* spp.) restrict use of main channels of African rivers to a subset of the fish fauna that possess morphological features that inhibit predation (e.g. deep body, dorsal and pectoral spines). In South American rivers, piranhas appear to restrict the use of open-water off-shore areas by many fishes (Winemiller 1989a). Experimental exclusion of *Cichla* species and other large piscivores significantly affected the abundance and size distribution of fishes in the Cinaruco River, Venezuela (Layman and Winemiller unpublished).

FOOD WEB DYNAMICS IN RESPONSE TO FLOOD PULSES

EFFECT OF THE FLOOD PULSE ON PRODUCTION DYNAMICS

The temporal dynamics of disturbance and recovery of local habitats in the river-floodplain habitat mosaic drive spatiotemporal variation in primary production sources and favour alternative life history strategies. According to the flood-pulse model, flood conditions should be associated with greater nutrient availability, aquatic primary production (dominated by macrophytes), allochthonous inputs and secondary production, especially among juvenile fishes, in floodplain habitats. Low-water conditions result in contraction of marginal aquatic habitats, death and decay of aquatic macrophytes and higher densities of aquatic organisms, including phytoplankton and zooplankton in floodplain lagoons (Rai and Hill 1984; Putz and Junk 1997). Because overall productivity is lower during low-water conditions and densities of consumer taxa are high, there is a strong advantage for spawning during flood pulses, but only if these pulses endure long enough to yield sufficient survival and growth of early life stages prior to flood subsidence.

In a strongly seasonal environmental regime, species have the opportunity to evolve adaptations to exploit relatively predictable habitats and resources (Southwood 1977, Winemiller and Rose 1992, Resh *et al.* 1994). Under this regime, a periodic life history strategy is favoured (i.e. seasonal spawning, high fecundity, small eggs and larvae, little parental care). In tropical-seasonal systems, temperature is relatively constant and periodic flooding is the primary factor driving ecological dynamics. Access to floodplain habitats is important for successful recruitment by many fish species in tropical-seasonal rivers. Inter-annual variation in fish recruitment generally is more strongly associated with flood duration than flood magnitude. In the Upper Paraná floodplain-river system, years with higher and longer duration floods were associated with increases in condition, growth and recruitment of *Prochilodus scrofa* Steindachner (Gomes and Agostinho 1997). In tropical northern Australia, fish abundance in billabongs (oxbows) was

positively correlated with duration of the annual flood (Madsen and Shine 2000). Even so, a range of successful life-history strategies is observed among fish species of tropical lowland rivers (Winemiller 1989b, 1996a, 1996b). Small opportunistic species with high reproductive effort protracted spawning periods and short-life spans are common in shallow marginal habitats that are constantly shifting across the river-floodplain landscape as water level rises and falls. The most extreme examples of the opportunistic strategy are observed among annual killifishes (Aplocheilidae) that inhabit shallow ephemeral pools. Many equilibrium strategists (relatively low fecundity with well-developed parental care) spawn just prior to the annual flood pulse and then move into newly flooded areas to brood. Based on growth variation, this seasonal spawning pattern seems to apply to *Cichla* species in Venezuela (Jepsen *et al.* 1999) and *Serranochromis* species in the Upper Zambezi River (Winemiller 1991b). Fishes with the equilibrium strategy may have higher reproductive success when water fluctuation is low. Some of the brood-guarding species of the upper Paraná River have greater abundance during years with low floods (Agostinho *et al.* 2000).

In temperate-seasonal rivers, access to flooded habitats may be non-essential, beneficial but non-essential, or detrimental to recruitment. Flooding enhances nutrient concentrations; particle loads and phytoplankton biomass in connected floodplain habitats (Hein *et al.* 1999), but can reduce densities of crustacean zooplankton (Baranyi *et al.* 2002). In temperate regions, temperature may have an influence on reproductive strategies that is equal to or greater than flooding. When warming temperatures coincide with a reliable annual flood pulse, selection should favour a periodic strategy just as in the tropics. Indeed, contracted spawning of large batches of small eggs is the dominant pattern observed in temperate-seasonal river fish faunas. Greater availability of floodplain habitats enhances fish recruitment and species diversity in lowland rivers in Europe (Copp 1989; Schiemer *et al.* 2001a) and North America (Sparks 1995). As in tropical systems, other life history strategies succeed in temperate-seasonal systems (e.g. sunfishes with rela-

tive equilibrium strategies and small cyprinids and poeciliids with opportunistic strategies). Humphries, King, and Koehn (1999); Humphries *et al.* 2002) identified three fish life-history strategies (gradient similar to model of Winemiller and Rose 1992) among fishes of Australia's Murray-Darling system. Flood regimes of many rivers of this region are regulated. Unregulated rivers display a temperate-seasonal pattern (Figure 1) but with large inter-annual variation in the magnitude of the seasonal flood-pulse. Humphries and co-workers discovered that virtually all fish species spawn each year with variable recruitment success depending on flow and temperature conditions. Because large floods do not occur each year, many species are able to recruit successfully by spawning and completing their life cycle entirely within main-channel habitats (the "low flow recruitment hypothesis"). Their studies demonstrate the potential importance of marginal channel habitats with low current velocity and abundant benthic micro-invertebrates that support fish early life stages.

In aseasonal flood-pulse regimes, aquatic organisms are more challenged to respond appropriately to relatively unpredictable patterns of resource variation. As in the Murray-Darling system, spatiotemporal connectivity of habitats and access to floodplain habitats is nonessential for most species, but greatly enhances recruitment for many, if not most, species in temperate-aseasonal rivers. Winemiller *et al.* (2000) discovered that certain fish species dominated oxbow lakes and others were more common in the active channel of the Brazos River, Texas. Opportunistic species numerically dominated the river channel and shallow oxbow lakes with high rates of disturbance and periodic strategists dominated deeper oxbow lakes with irregular but periodic flood connections to the river (Winemiller 1996a). When flooding occurs during springtime, recruitment by periodic strategists, such as gizzard shad, buffalo (*Ictiobus bubalus* (Rafinesque)) and crappie (*Pomoxis annularis* Rafinesque) is high. Yet springtime floods only occur during some years, so that spawning during most years is associated with low recruitment success (Winemiller unpublished data). Interspecific differences in respons-

es to hydrologic regimes in habitats across the lateral floodplain gradient have been shown for other taxonomic groups in other regions, including trees (Junk 1989), phytoplankton (van den Brink *et al.* 1993) and benthic macroinvertebrates (Marchese and Ezcurra de Drago 1992).

EFFECT OF THE FLOOD PULSE ON CONSUMPTION DYNAMICS

The expansion and contraction of aquatic habitats in response to flooding has a major influence on consumer-resource interactions. Newly expanded floodplain habitats provide an immediate influx of allochthonous detritus and invertebrates and, with time, greater nutrient availability and aquatic primary production. Densities of aquatic organisms are low initially and increase over time as new individuals recruit under productive flood conditions. Fish growth rate and condition are high in flooded habitats (Welcomme 1985). In the central Amazon, juveniles of omnivorous species, but not detritivorous species, grew faster during the rising-water period (Bayley 1988). Growth of omnivores was positively associated with flood magnitude and in all cases growth appeared to be density-independent.

Highest fish abundance and per-unit-area densities typically occur as floodwaters recede. As dictated by the functional response, the falling-water period is when predator-prey interactions are most intense. This is also the period when resource limitation may occur for species that exploit algae and aquatic and terrestrial invertebrates. Bayley (1988) found that juveniles of only 2 of 8 omnivorous species in the central Amazon showed significant evidence of density-dependent growth during the falling water period. For piscivores, the falling-water period represents a time of resource abundance, as fishes become increasingly concentrated in aquatic habitats of reduced volume. Piscivore feeding rates increase during the falling water period and piscivore growth and body condition increase (Jepsen *et al.* 1999). If piscivores deplete prey populations during the falling-water period, they may eventually become resource limited for several months during the lowest water stages. For size-selective

(gape-limited) piscivores, optimal prey sizes become depleted first and piscivores shift to increasingly smaller prey as water levels continue to fall. Jepsen *et al.* (1997) described a decline in mean prey size consumed by *Cichla* species in the Cinaruco River during the 6-month falling water period. This shift in the average size of consumed prey size almost exactly matches the shift in the mode for the size distribution of fishes in the littoral zone (Layman and Winemiller unpublished data).

The scope of seasonal changes in population densities and predator-prey interactions obviously depends on the timing, magnitude and duration of flooding. The scope of these changes will be smaller in temperate-aseasonal rivers and greater in seasonal rivers with floras and faunas well adapted to take advantage of periodic changes in habitat and resource quality and availability. As a result, seasonal rivers can sustain greater fish harvest than aseasonal rivers in landscapes with comparable geomorphology and nutrient availability. Power *et al.* (1995) created a simple simulation model that linked floodplain river hydrology to food web dynamics based on the Lotka-Volterra algorithms. They examined four scenarios: a river with connection to its floodplain and seasonal (sinusoidal) discharge, a river confined by levees with sinusoidal discharge and regulated rivers with low and average discharge that never lead to flooding. Only the connected river with seasonal discharge produced stable populations of predators and grazers. The leveed river yielded unstable predator-prey dynamics as a result of channel confinement and regulated rivers resulted in low or oscillating grazer populations that ultimately were unable to sustain viable predator populations. Whereas this model represents a gross oversimplification of natural food webs, the findings highlight the influence of discharge dynamics and channel-floodplain connections on community dynamics.

EFFECTS OF THE FLOOD PULSE ON MIGRATION

In addition to its effects on population dynamics and consumer-resource interactions, flooding also influences movement of materials and organisms. Movement in response to flooding may be essentially

longitudinal or lateral and passive or active. Seasonal succession and food web dynamics are influenced by all of these forms of movement. The initial stages of a flood pulse submerge terrain which results in inputs of dissolved inorganic nutrients from terrestrial vegetation, both living and dead (Junk *et al.* 1989). Surface runoff and floodwater recession carries these nutrients into channel areas where aquatic production may be stimulated (Rai and Hill 1984; Putz and Junk 1997; Lewis *et al.* 2000). Likewise, phytoplankton, zooplankton, floating macrophytes and terrestrial allochthonous resources are washed into flowing channels as well as deeper permanent floodplain lagoons. Based on a mass-balance approach, Lewis *et al.* (2000) concluded that the floodplain of the lower Orinoco River exports no organic carbon to the river channel. They concluded that this hydrologically open system behaves like a closed system with respect to organic carbon balance. They observed that the natural levee of the floodplain restricts water movement to a direction parallel to the longitudinal axis of the river channel. Thus, passive export of organic carbon is low because only a minor fraction of water actually passes from the floodplain to the channel. Presumably then, floodplains internally recycle organic carbon captured from surrounding uplands.

The Lewis *et al.* (2000) carbon-balance model does not consider active movement by aquatic organisms. Fishes, in particular, migrate between channel and floodplain locations in response to seasonal changes in the relative benefits and costs associated with conditions in each area (Welcomme 1985). Flooding provides fishes with almost unlimited access to a range of habitats. In tropical-seasonal rivers, fish movements from river channels into floodplain habitats are particularly regular (Goulding 1980; Welcomme 1985; Fernandes 1997; Hocutt and Johnson 2001). In temperate-seasonal and temperate-aseasonal rivers, these fish movements are common, but apparently less predictable. Depending on the taxon and region, tropical river fishes may migrate locally (1-100 km) or regionally (>100 km). In the llanos region of the Orinoco Basin, many and probably most, fishes perform local migrations into seasonally

inundated savannas for reproduction. These seasonal habitats are highly productive and serve as classic nursery areas that enhance juvenile growth and survival (Winemiller 1989b, 1996b). When water levels drop, these areas become hypoxic and fishes that fail to migrate downstream to deeper channels risk death from hypoxia or stranding in drying pools (Lowe-McConnell 1964). Even though many floodplain fishes possess special adaptations for dealing with aquatic hypoxia (Kramer *et al.* 1978), a great deal of aquatic biomass moves out of floodplain habitats into deeper creeks and rivers. During the annual falling-water period, piscivores in mainstem rivers feed heavily on fishes that migrate out of tributaries draining the floodplains (Winemiller 1996a; Winemiller and Jepsen 1998). Thus, if we add these higher food web components to Lewis *et al.* (2000) calculation of organic carbon mass-balance, floodplains export large amounts of organic carbon to river channels.

Some river fishes undergo regular seasonal migrations on regional scales. Welcomme (1985) summarized evidence of longitudinal and lateral migrations by South American and African fishes. Highly migratory fishes can be extremely abundant with strong effects on local food webs. In rivers of the North Pacific region, the decaying carcasses of anadromous salmon import significant amounts of limiting nutrients that can enhance ecosystem productivity during summer (Kline *et al.* 1990; Willson, Gende and Marston 1998; Cederholm *et al.* 1999). In South American rivers, prochilodontid and other characiform fishes perform seasonal migrations of hundreds of kilometres (Bayley 1973; Vazzoler, Amadio and Daraciolo-Malta 1989; Ribeiro and Petrere 1990). Immigration of these abundant fishes during the falling-water period produces large effects on local food webs. First, prochilodontids have large effects on sediments and ecological dynamics in benthic communities (discussed above). Thus, prochilodontids are both ecosystem engineers as well as strong interactors with benthic elements of the food web (Flecker 1996). Second, immigrating prochilodontids provide an abundant food resource for resident piscivores (discussed above), which can be particularly significant for olig-

otrophic systems that receive young migrants from more productive systems. In this capacity, prochilodontids provide a spatial food web subsidy (Polis, Anderson and Holt 1997), in which material from a more productive ecosystem (floodplain wetlands) enters the food web in a less productive ecosystem (flowing channel). Food web subsidies can have major effects on food web dynamics, including induction of trophic cascades (Polis *et al.* 1997; Winemiller and Jepsen 2002) and stabilization of complex systems (Huxel and McCann 1998).

Some large predatory fishes of floodplain rivers also undergo long-distance regional migrations. Barthem and Goulding (1997) described migrations by large pimelodid catfishes that span almost the entire Amazon Basin. African tigerfish (*Hydrocynus* spp.), *Alestes* and *Labeo* species migrate longitudinally according to seasonal hydrological regime (Jackson 1961; Welcomme 1985). Predatory ariid, centropomid and eleotrid fishes of Australia, Southeast Asia, the East and West Indies and tropical Americas habitually migrate between rivers and coastal marine waters. The food web implications of these "reverse subsidies" have scarcely been explored. If the effects of exotic piscivores on lake communities (Zaret and Paine 1973; Kaufman 1992) provide any indication, the effects of immigrant piscivores on fish populations in local fluvial habitats are potentially great. Likewise, removal of resident piscivores can affect local populations. Negative impacts of commercial fishing on large piscivores in floodplain lagoons of the Cinaruco River had a significant effect on local assemblage structure of small prey fishes (Layman and Winemiller unpublished).

MANAGEMENT IMPLICATIONS OF FOOD WEB ECOLOGY

Floodplains of lowland rivers provide important ecosystem services (i.e. nutrient cycling, flood mitigation) and renewable natural resources (e.g. fishery and forest products). Human impacts on river-floodplain systems have been described repeatedly (Welcomme 1985; Ward and Stanford 1989; Bayley 1995; Sparks 1995; Dudgeon 2000; Pringle, Freeman

and Freeman 2000), but the focus of discussion here will be the interaction between food web ecology, human impacts and sustainable fisheries.

HABITAT CONNECTIVITY

Dams obviously fragment rivers in the longitudinal dimension. Many important river fishes undergo seasonal longitudinal migrations that make them highly vulnerable to impacts from not only dams, but also other channel obstructions such as weirs and gillnets. As discussed above, some of these fishes have large ecosystem effects (e.g. salmon affecting nutrients). In addition to affecting sediments and benthic biota, migratory prochilodontids also provide nutritional subsidies to piscivores that likely affect food web dynamics in the receiving communities.

A major human impact on large rivers is levee construction for the purpose of preventing floodplain inundation or draining of wetlands for agriculture and other land uses. Levees obviously disrupt important connections between river channels and floodplains, which cuts off exchanges of material and organisms among dynamic habitats critical for completion of species life cycles (Ward *et al.* 1999; Amoros and Bornette 2002) and ecosystem dynamics (Junk *et al.* 1989; Aspetsberger *et al.* 2002). Disconnecting the river channel from its floodplain has obvious negative impacts on nutrient cycling (Tockner *et al.* 1999), system productivity (Bayley 1989; Junk *et al.* 1989; Agostinho and Zalewski 1994) and biodiversity (Schiemer *et al.* 2001a; Robinson *et al.* 2002). Magnitudes of these impacts should be greater for tropical- and temperate-seasonal rivers than for temperate-aseasonal rivers. For example, recruitment by fishes in temperate-aseasonal rivers usually is more dependent on temperature regime than flood regime. Reproductive timing and recruitment by fishes in tropical floodplain rivers are strongly correlated with dynamics of the annual flood pulse. Large cichlids in South America (*Cichla*, *Hoplarthus*, *Heros* spp.) and Africa (*Serranochromis*, *Oreochromis* spp.) exhibit protracted spawning periods in reservoirs, but seasonal, contracted spawning periods in rivers (Winemiller personal observation). Evidence from temperate rivers

indicates that many fish species complete their entire life cycle within the main channel (Galat and Zweimüller 2001; Dettmers *et al.* 2001) although even these species are strongly dependent on natural flood regimes (Schiemer *et al.* 2001b). Early life stages of these lotic-adapted species frequently depend on nearshore channel habitats with relatively lentic conditions. The inshore retention of fish larvae and their food resources is a critical feature influenced by river geomorphology and hydrology (Schiemer *et al.* 2001b).

Human impacts that reduce habitat connections in river-floodplain landscapes also can affect biodiversity and food webs by inhibiting patch colonization and community succession (Sedell *et al.* 1990). Recent research on the Cinaruco River in Venezuela indicates that fishes and macroinvertebrate communities of the littoral zone are significantly structured in relation to substrate type (Arrington and Winemiller unpublished). Habitat patches are colonized and abandoned in sequence as they are submerged and exposed by the moving littoral zone. Field experiments demonstrated that artificial habitat patches undergo community succession that is accompanied by increasing degrees of non-random assemblage structure (Winemiller *et al.* unpublished). The littoral food web appears to conform to Holt's (1996) spatial model of food web dynamics. In this model, taxa at lower trophic levels are restricted to the smallest habitat patches, with larger, more mobile consumers at higher trophic levels feeding across multiple patches. This pattern continues in a trophic hierarchy that ultimately yields a sink web defined by food chains terminating with a single large, mobile top predator. River channelization, levee construction and wetland drainage disrupt not only community dynamics in the littoral zone, but also restrict access by predators to habitat patches containing prey (Toth *et al.* 1998). Disruption of both factors (community assembly and predation by large mobile fishes) is certain to affect biodiversity.

Fishes are not the only vertebrates that depend on dynamic connections between channel and floodplain aquatic habitats. Dynamic habitats of river-flood-

plain systems enhance species diversity of aquatic insects (Smock 1994), mussels (Tucker, Theiling and Camerer 1996), turtles (Bodie and Semlitsch 2000), birds (Remsen and Parker 1983) and mammals (Sheppe and Osborne 1971).

FLOW REGIMES

Regulation of river hydrology changes natural flood regimes that determine elemental cycles, system productivity, reproduction and population dynamics of aquatic organisms and consumer-resource interactions. Clearly, significant alteration of the natural flood-regime in temperate- and tropical-seasonal rivers will have detrimental effects for native fish species that time reproduction to maximize recruitment success under predictable patterns of spatio-temporal environmental variation. High primary production and inputs of allochthonous resources that accompany flood-pulses tend to enhance fish recruitment success, but some species are less responsive than others. Many species achieve low to moderate recruitment even under no-flow conditions (Humphries *et al.* 2002). Consequently, community dynamics are partially a function of the timing and magnitude of flooding and this is bound to have large effects on food web dynamics that in turn influence dynamics of exploitable fish stocks. For example, years in which the Upper Paraná River, Brazil experiences higher, longer duration floods produce greater abundance of age-0 *Prochilodus scrofa*, the most important commercial fish of the region (Gomes and Agostinho 1997). *Prochilodus* is a principal prey for *Salminus maxillosus* Valenciennes, *Plagioscion squamosissimus* (Heckel) and other large piscivores that are important in the local fishery (Hahn *et al.* 1997). Thus, flood pulses affect these large predators both directly, in terms of their own recruitment success, as well as indirectly via food chain interactions. Management of multispecies fisheries in large rivers requires a food web perspective. Stock dynamics are influenced both by bottom-up factors related to ecosystem productivity and by top-down factors influenced by relative densities of predator and prey populations.

Flood dynamics affect both bottom-up and top-down effects in food webs. In large tropical rivers, flooding occurs predictably over large areas, which results in a pulse of primary production (Junk *et al.* 1989). This, in turn, is efficiently transferred to higher trophic levels due to species life history strategies that maximize fitness (i.e. population rate of increase) under predictable regimes of environmental variation. Harvest rates increase as fish populations become vulnerable to fishing when flood subsidence increases their per-unit-area densities (i.e. a functional response). The world's most productive river fisheries are associated with seasonal flood-pulse dynamics in tropical areas. Holding all other factors equal, nutrient-rich landscapes in the tropics (e.g. Mekong, Niger, Zambezi, middle Orinoco and lower Amazon rivers) produce greater fish yields than nutrient-poor regions (Rio Negro and other rivers draining South America's Guyana Shield region). In temperate regions, lower temperatures result in lower annual productivity. On geologic-evolutionary time scales, temperate regions have experienced more recent and frequent climatic disturbances that have inhibited biological diversification and ecological specialization within regional fish faunas. Currently, there is much interest in the potential positive relationship between biodiversity and community productivity (e.g. Tilman 1999) and this relationship could contribute to the greater productivity of seasonal tropical-seasonal river fish assemblages relative to those of temperate-seasonal rivers.

Fish production should be lowest in temperate-aseasonal rivers for three reasons. The timing of floods often will not coincide with periods with highest temperatures. Additionally, the timing of floods often will not synchronize with the spawning periods innately cued to photoperiodicity and seasonal temperature variation. Finally, temperate faunas are less likely to have evolved life history strategies and ecological adaptations designed to capitalize on flood pulse conditions, because these conditions are unpredictable on both intra- and inter-annual time scales. All other factors being equal, temperate-aseasonal rivers are less resistant to intense sustained harvest, of the kind practiced for generations in many tropical regions.

Direct consumption of allochthonous resources by fishes is particularly important in forested lowland regions of the Amazon Basin, with some species notably adapted for consuming fruits and seeds (Goulding 1980; Loubens and Panfili 2001). Reduced flood frequency, in addition to deforestation, will negatively impact direct entry of allochthonous resources into aquatic food webs, to the detriment of yields of several commercially important stocks (Goulding 1980; Reinert and Winter 2001).

On geological time scales, flood regimes maintain physical habitat heterogeneity by alternately eroding and depositing sediments on the landscape (Kellerhals and Church 1989). On shorter time scales, erosion and deposition of sediments are disturbances to vegetation communities. Natural hydrological processes create new substrates for community succession. The result is a rich mosaic of habitat patches with different degrees of structural complexity, exposure to natural disturbances and community composition (Shiel, Green and Neilsen 1998). Thus, chronic absence of flooding results in altered disturbance regimes and ultimately lowers habitat heterogeneity and species diversity (Schiemer *et al.* 2001a).

Flow regimes, in concert with soils and landscape geomorphology, also influence suspended sediment loads. Turbidity influences predatory-prey interactions and community composition and dynamics. Highly turbid systems often are dominated by siluriform fishes and, in Africa and South America respectively, weakly electric fishes (mormyriforms and gymnotiforms). Predators that rely on vision, such as cichlids and many characiform and cypriniform fishes, tend to be scarce in turbid whitewater rivers. In turbid river-floodplain systems, visually orienting fishes are most abundant in clear tributaries creeks and lacustrine habitats of floodplains where sediments settle out. Turbidity varies among floodplain lagoons as a function of local soils and other landscape features. During the dry season, water transparency is associated with a fairly consistent pattern of fish assemblage composition in Orinoco River floodplain lagoons, with turbid lagoons having more siluriforms and gymnotiforms

and clear lagoons having more characids (Rodríguez and Lewis 1997). Wet-season flooding mixes water and allows organisms to move freely across the landscape, which presumably homogenizes these lagoon fish assemblages. The effect of turbidity on river food web structure and dynamics has not been investigated.

FISHERIES HARVEST

Fisheries obviously impact river food webs in many different ways. Overfishing changes consumer-resource dynamics and the distribution of interaction strengths in the food web. If affected populations are species with large functional importance to the community or ecosystem, the effect of their depletion may be large and immediate. For example, overharvest of benthivorous prochilodontids would fundamentally alter the sediment dynamics and benthic ecology in Andean piedmont rivers. There is some evidence that this is already occurring in Venezuela where extensive gillnetting removes large numbers of *Prochilodus mariae* during their upstream migrations (Barbarino-Duque, Taphorn and Winemiller 1998). With reduced densities of *Prochilodus* that consume and resuspend fine sediments, river channels accumulate a thick layer of soft sediments that inhibit development of a benthic community dominated by diatoms and grazing insects (Flecker 1996). Because benthic primary production is the principal energy source in this system, the entire food web undoubtedly changes with unknown consequences for biodiversity and secondary production. Similar effects of prochilodontids on benthic processes have been demonstrated experimentally in channel and lagoon habitats of the Cinaruco River (Winemiller *et al.* unpublished data).

In North America and Europe, commercial fishing in rivers is relatively insignificant. In cold-water regions, salmonids, esocids and percids are heavily targeted by sportfishers, sometimes with negative impacts on stocks. Tropical river fisheries provide a major source of animal protein for people of developing countries. Fishing effort in African and Asian rivers is generally more intense than in South American rivers, the latter having fisheries that continue to be dominated by a relatively small number of

large and economically valuable species (Welcomme 1990). Yet some regions of South America have extremely high fishing effort (Welcomme 1990) and effort is generally increasing everywhere, in some cases rapidly. Size overfishing is pervasive in large rivers worldwide (e.g. Mekong River fisheries discussed during LARS 2). In Venezuela, maximum and average sizes of *Cichla temensis* has declined markedly in rivers over the past 20 years and *C. temensis* abundance declined precipitously in the Rio Aguaro with commencement of commercial netting in the 1970s. The migratory characid *Salminus hillari Valenciennes* was a popular sportfish in rivers of the Andean piedmont of Venezuela until the early 1960s. The species is now extremely rare due to dam construction and gillnetting (Winemiller, Marrero and Taphorn 1996). *Salminus* was once the principal predator of *Prochilodus mariae* that migrated *en mass* into piedmont rivers during the dry season. Although *Prochilodus* also have declined in piedmont rivers (Barbarino-Duque *et al.* 1998), this species, unlike *Salminus*, has a broad dry season distribution with large populations maintained in lowland rivers.

Large piscivores often are among the first fishes to be targeted by river fisheries. The phenomenon of "fishing down food webs" was described for marine systems globally (Pauly *et al.* 1998). This pattern may apply equally to river fisheries. In the Amazon, the abundance and size of pirarucu (*Arapaima gigas* (Cuvier) and pimelodid catfishes has declined steadily in most regions. Although less well documented, a similar pattern is observed for pimelodid catfishes and payaras (*Hydrolycus* spp.) of the Orinoco, *Salminus maxillosus* of the Paraná and *Lates niloticus* (L.) and *Hydrocynus* spp. of the Niger, Ome and other West African rivers. As stocks of these large piscivores become depleted, fish markets become even more strongly dominated by less valuable but more numerous detritivorous and omnivorous species, such as prochilodontids, *Mylossoma* and *Brycon* species in South America and tilapiine cichlids and *Barbus* species in Africa. Some of the major predatory fishes inhabiting large warmwater rivers of North America are nocturnal catfishes (siluriforms) and lepisosteid gars, the

latter having no commercial value and generating little sportfishing interest. Because commercial river fisheries are insignificant in North America and Europe and sportfisheries essentially target predatory species, the fishing-down-food-webs phenomenon has not been observed in rivers of these regions.

Overharvest of fish stocks changes population abundance and the structure and dynamics of river food webs. The elimination of top predators could yield top-down effects in food chains, but in many cases prey populations are targeted just as intensely. Virtually no information is available from any large river to enable even modest predictions regarding fishing effects on food web dynamics. In tropical rivers, fish communities are species rich and food webs are complex. Even when top predators feed on a similar broad array of prey taxa, fisheries that exploit multiple predator species can yield chaotic dynamics of individual populations (Wilson *et al.* 1991). Fisheries harvest also can change population size structure, which in turn affects population dynamics via effects on life history strategies (e.g. reduction in size at maturity) and size-dependent predator-prey interactions. These effects have been demonstrated in fish populations from streams, lakes and marine systems, but so far little information has been gathered from large rivers. Strong sustained harvest of the largest individuals selects for earlier age and smaller size of maturation (Conover and Munch 2002). The combined effects of overharvest of the largest size classes and the evolution of smaller size at maturation should profoundly influence both predator and prey populations when predation is size-limited. Smaller predators will result in smaller average and maximum size of consumed prey. If large piscivores are targeted more intensely than their prey, as is frequently the case, this could lead to a negative feedback that affects predator populations negatively, with potential positive effects on prey abundance. The study of predator-prey dynamics in large-river food webs remains in its infancy and a great deal of research is needed before we can even begin to construct predictive models.

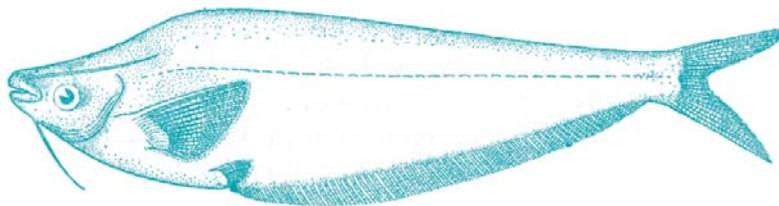
CONCLUSION

The study of food web ecology in river-floodplain systems remains in its infancy. This review has highlighted only a few of the most basic issues, most of which are largely unresolved. For example, the influence of flood regimes on population dynamics of aquatic organisms with different life history strategies and regional/evolutionary histories is highly variable. Therefore, it may be erroneous to assume that regular flood pulses, of the sort that occur in large tropical rivers, are required for maintenance of high biodiversity in every instance. The flood pulse concept of Junk *et al.* (1989) probably overestimates the role of floodplains for river biota in systems with flood regimes that are naturally unpredictable or out of phase with spring-summer. Certainly at some scale of spatial and temporal resolution, flood pulses are essential for biodiversity in any river ecosystem. The challenge is to identify the biological responses to variation at multiple scales. Food webs are complex and influenced by many abiotic and biotic factors. Although several of the most important and obvious factors were discussed here, many more must be examined. For example, exotic species sometimes dominate river communities (e.g. European carp in rivers of North America and Australia), usually with undetermined effects on food

web dynamics and ecosystem processes. Given the important ecosystem services provided by floodplain rivers, the high value of river fisheries, especially in the tropics, as well as the multiple human impacts on river-floodplain systems, vastly greater research investment is warranted.

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