Effects of seasonality and fish movement on tropical river food webs

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Tropical rivers and their associated floodplain habitats are dynamic habitat mosaics to which fishes are challenged to respond in an adaptive manner. Migratory fishes create linkages among food webs that are partitioned along a nested hierarchy of spatial scales. Such linkages are examined across a hierarchy of spatio-temporal scales, ranging from small streams to entire drainage basins, for rivers in South America and Africa. Migratory herbivorous fishes originating from eutrophic, productive ecosystems may subsidize resident predators of oligotrophic river ecosystems, which may result in cascading direct and indirect effects on other species in local food webs. Successful management of many of the most important stocks of tropical river fishes requires conceptual models of how fish movement influences food web structure and dynamics. © 1998 The Fisheries Society of the British Isles

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INTRODUCTION

Future management of tropical fish stocks and the aquatic ecosystems that support them will require greater knowledge of foodweb ecology. For example, commercial exploitation of marine fish stocks has changed foodweb structure and dominant species in many regions of the world (Parsons, 1996). Likewise, the introduction of exotic piscivores into tropical Lake Gatun in Panama (Zaret & Paine, 1973) and Lake Victoria in Africa (Kaufman, 1992; Goldschmidt, 1996) was followed by altered foodweb structure and important features of aquatic and terrestrial ecosystems. A variety of approaches have been used to increase our understanding of the influence of foodweb structure on ecological processes in aquatic and marine systems. In the temperate zone, whole-lake manipulations of predatory fishes have demonstrated how predation can influence population densities at several different trophic levels and how this affects water quality indirectly (Carpenter *et al.*, 1987; Schindler *et al.*, 1997). Production and the flow of energy and matter through food webs has been simulated for several estuarine systems, including Chesapeake Bay in North America (Baird & Ulanowicz, 1989). Relatively little research has been directed at the influence of ecological processes, such as natural succession or migration, on foodweb structure (Polis *et al.*, 1996).

Leaving aside potential influences of methodology, a variety of ecological factors can influence the structure of aquatic food webs. Species life-history strategies influence recruitment dynamics, population size structure, and population density. Habitat spatial heterogeneity and patch dynamics, at

different scales, strongly influence predator–prey interactions. Physical habitat disturbance and seasonal changes in habitat quality and quantity influence both population dynamics and species interactions. Physical transport of nutrients, detritus, or food between habitats or larger landscape units, as well as animal movement between habitat patches or ecosystems, can greatly influence productivity, material cycling, and predator–prey interactions (Polis et al., 1996). The importance of animal movement in structuring local food webs and in linking food webs of different landscape units has been appreciated only recently (Vanni, 1996; Polis et al., 1997). This paper uses information from our own research on tropical river fishes to examine the ways that movement by fishes at a range of spatial scales can influence the structure of aquatic food webs. A firm grasp of the importance of such influences will be critical for research that seeks to understand how foodweb structure affects ecological processes at the community and ecosystem levels.

FISH MOVEMENT FROM LOCAL TO REGIONAL

At the local scale, many fishes move frequently between habitat patches. Some ambush predators maximize their foraging success by positioning themselves at the interface between two different habitats, one patch being relatively more productive or safe than the other. For example, piscivorous fishes often feed at the edge of shallow riffles, shorelines or beds of submerged macrophytes, habitats that serve as prey refuges. Prey species may exhibit risk-sensitive foraging, in which the animal must integrate the potential costs and benefits of leaving a refuge to forage on higher quality or more abundant resources in a more dangerous habitat (Fraser & Cerri, 1982; Fraser & Gilliam, 1987; Power, 1987; Turner & Mittelbach, 1990). Fish movement on the local scale can be a response to changing gradients of resource availability, such as shelter or food, or abiotic conditions, such as salinity, current velocity or dissolved oxygen. Local movements associated with ontogeny are a major feature of the life histories of many freshwater, estuarine, and marine fishes worldwide.

At the regional scale, fish movement between ecosystems can be a response to major changes in abiotic conditions or resource availability. Some fishes increase the probability that their eggs and larvae will survive and grow by taking advantage of differences in productivity or predator densities in marine and freshwater ecosystems (Gross et al., 1988). Spawning migrations may cover hundreds of kilometres in some cases (e.g. anadromous salmonids, catadromous eels). Floodplain rivers provide another clear example of how fishes migrate to exploit ecological opportunities. Many fishes move into newly flooded riparian zones to feed and/or reproduce. The occupation of the flooded Amazon forest by river fishes is a well-documented phenomenon (Lowe–McConnell, 1975; Goulding, 1980). Most evidence indicates that flooding of lowland rivers is important for recruitment of many fishes throughout the world (Sparks, 1995).

TROPICAL RIVERS

Tropical rivers have large spatial heterogeneity across a continuum of spatial scales that range from microhabitats to landscapes. At the local scale, small forest and savanna streams often show longitudinal successions of pool and riffle

habitats with a variety of substrates, depths, and current velocities within and among each. Lowland floodplain habitats of eutrophic landscapes typically present a patchwork of densely vegetated and open-water habitats. Moving up to a broader spatial scale, floodplains contain a greater variety of aquatic habitats, including ephemeral pools, permanent lagoons, and secondary channels. Even within a restricted area of the same floodplain, these habitats can be associated with very different hydrologies, soils, water qualities, and vegetation (Wissmar et al., 1981; Day & Davies, 1986). The lateral gradient of floodplain rivers presents fishes with a tremendous diversity of options for habitat selection. Scaling up still further, the longitudinal axis of rivers presents a gradient of habitats that span different landscape topographies, soils, productivities, and disturbance regimes (Junk et al., 1989). This large-scale, longitudinal and lateral variation is exploited by several groups of migratory fishes of the Neotropics, most notably the prochilodontids (Bayley, 1973; Goulding, 1980; Bonetto et al., 1981; Ribeiro & Petrere, 1990; Vazzoler & Amadio, 1990; Agostinho et al., 1993).

Most regions of the tropics experience strongly seasonal precipitation that produces seasonal patterns of river discharge. A variety of physicochemical attributes vary in relation to seasonal hydrologic variation in tropical rivers. During extended wet periods, water temperatures and conductivities tend to be lower, and water depths, velocities, and dissolved oxygen concentrations tend to be greater. Organic nutrients in sediments are mineralized and inorganic nutrients are leached into flood waters which produces an increase in primary production within a greatly expanded aquatic habitat (Sioli, 1984; Carignan & Neiff, 1992; Camargo & Esteves, 1995). Aquatic macrophytes of floodplain lakes assimilate inorganic nutrients from the advancing floodwater, and return them to the water column and sediments via decomposition during the isolation and falling-water phases. Flooding brings fishes into contact with a greater abundance and diversity of allochthonous food resources, especially within forested watersheds (Goulding, 1980; Henderson, 1990). In small tropical streams, flash floods scour substrates and reduce the availability of benthic food resources such as periphyton (Pringle & Hamazaki, 1997). The gradual drying of tropical river floodplains causes fish densities (per unit surface area) to increase and species interactions to intensify as habitat and resource availability decline. Some fishes become stranded in isolated pools where they compete for limited resources, often are exposed to deteriorating water quality, and risk being preyed upon by piscivorous fishes, birds and other vertebrates. Many fishes perish in pools that dry completely.

Fishes are conspicuous, important components of tropical river food webs. The degree of trophic diversification in tropical river fish assemblages is greater than that of fish assemblages in similar habitats of temperate regions that contain less species (Winemiller, 1991a). Compared to temperate river fishes, tropical fishes show proportionally more herbivorous, detritivorous, and omnivorous feeding behaviours (Winemiller, 1990, 1991a; Wootton & Oemke, 1992). Invertebrate feeders and piscivores also show greater niche specialization in the tropics, and some tropical feeding niches are entirely absent in temperate fish assemblages (e.g. among piscivores: mucus feeding, fin nipping, scale feeding and blood feeding). This diversification of feeding niches results in fishes playing

significant roles in perhaps the majority of the food chains of aquatic food webs (Winemiller, 1990). Fishes function as conduits of matter and energy, as well as predators that potentially affect the population dynamics of their prey, and prey that potentially influence the foraging success and fitness of their predators. Therefore, the manner in which fishes move about on landscapes influences strongly the structure and function of aquatic food webs.

MATERIALS AND METHODS

This paper presents an overview and synthesis of selected literature relevant to the thesis that movement by tropical fishes on a range of spatial scales influences tropical river food webs. Most of the cited literature is from the past 15 years, and we draw heavily on examples from our own research from the Río Orinoco Basin in Venezuela and Zambezi River Basin in Zambia. In attempts to illustrate specific mechanisms that affect aquatic food webs, we present new analyses of fish population and trophic data obtained during prior field research. Our ultimate goal was to present a synthesis of ideas supported by evidence in order to arrive at a heuristic model of how fish movement influences river food webs in the tropics.

The following aspects of fish movement are examined: risk-sensitive foraging, the importance of habitat interfaces for predators, responses associated with gradients of resource availability or abiotic conditions, movements associated with reproduction, and movements associated with ontogeny/recruitment. Some of these aspects will apply to large-scale spatial variation (lateral and longitudinal river gradients), and others will apply to spatial variation on a smaller scale (stream pools *v.* riffles, vegetation *v.* open-water habitats, the heterogeneity of dynamic floodplain habitats). Seasonal precipitation is a master driving variable that influences hydrology, primary and secondary production, habitat availability, anoxic conditions, and cover at all spatial scales.

RESULTS AND DISCUSSION

LOCAL MOVEMENTS IN STREAMS

Tropical fishes inhabiting small forest and savanna streams can select microhabitats for refuge, foraging, and reproduction based on a variety of well-studied physical, chemical, and biotic attributes of the stream channel (Angermeier & Karr, 1983). Substrate-type influences prey taxa and availability and may select for specific foraging behavioural patterns (e.g. digging and sifting burrowing invertebrates from sand, or algae scraping on rocks). Most fish species are found within restricted ranges of water depth and current velocity, often yielding patterns of characteristic pool and riffle sub-assemblages.

The food web of Caño Volcán, a small stream of the forested lower piedmont of the Andes Mountain range in western Venezuela, was studied over 12 consecutive months during 1984 (Winemiller, 1990). The stream contains a series of alternating pools with sand bottoms and shallow riffle or run habitats with coarse sand and cobble substrates. Leaf litter is also abundant in both mesohabitats. Of the 20 fish species that occurred in the study reach, five occurred exclusively or were much more common in riffle and run habitats than in pool habitats (*Lebiasina erythrinoides* (Valenciennes, 1849), plus the species listed in Table I). When these species were present in pools, they always occupied shallow areas near the pool head, tail, or margins. Juveniles of several other species were restricted largely to shallow riffle and run habitats that separated deeper pool habitats. The top aquatic predator in the food web of

TABLE I. Numbers and percent volumes of characteristic pool fishes and riffle/run fishes consumed by *Hoplias malabaricus* at Caño Volcán, Venezuela based on examination of stomach contents of 150 specimens

Pool species	Number	% volume	Riffle, run species	Number	% volume
Astyanax bimaculatus (Linnaeus, 1758)	1	1	*Ancistrus triradiatus*	1	12
Bryconamericus beta Eigenmann, 1914	4	3	*Creagrutus melasma*	1	<1
Corynopoma riisei Gill, 1858	1	1	*Poecilia reticulata*	17	3
Crenicichla geayi Pellegrin, 1903	1	10	*Synbranchus marmoratus* Bloch, 1795	1	5
Hoplias malabaricus	3	7			
*Hypostomus argus**	2	<1			
Roeboides dayi	2	6			
Rhamdia sp.*	2	36			
Total	16	64·5		20	20·5

*Juveniles generally inhabit riffle and run habitats.

Caño Volcán was the erythrinid *Hoplias malabaricus* (Bloch, 1794) (Winemiller, 1990). Adult *Hoplias* occurred in pool habitats, whereas small juveniles (<5 cm standard length, L_S) inhabited leaf packs in shallow riffles and runs and root masses in undercut stream banks.

At Caño Volcán, fishes from riffles and runs comprised 20% of the diet of pool-dwelling *Hoplias* by volume and over half of all individual fish prey that could be identified to species (mostly *Poecilia reticulata* Peters, 1859) (Table I). If shallow riffle and run mesohabitats provided refuge from predation by *Hoplias*, riffle species must have been captured at riffle-pool interfaces, or they were attacked when they ventured into pools in search of foraging opportunities or for dispersal. *Lebiasina erythrinoides* was the only riffle/run species not detected in the sample of 150 *Hoplias* stomachs.

During the dry season, a thin layer of attached algae (diatoms and filamentous green algae) developed over the sand substrate of pools at Caño Volcán. In the larger pools that contained adult *Prochilodus mariae* (Eigenmann, 1922) and *Hypostomus argus* (Fowler, 1943), this algal layer was restricted to the shallow stream margins (covering from 10 to 20% of the wetted stream bottom). These algivores apparently were effective at cropping algae from deeper areas, and they were too large (>20 cm L_S) to be vulnerable to predation by *Hoplias* (*Prochilodus* tended to be even larger at this site, and *Hypostomus* has large pectoral and dorsal spines). The pool margins may have been too shallow to allow foraging by these larger species, or alternatively, the threat of predation by larger avian predators, such as herons and egrets, may have restricted their use of shallow marginal habitats. The latter situation was demonstrated for the Río Frijoles in Panama, where three species of loricariid catfishes were shown to avoid shallow pool margins due to predation threat from avian predators (Power, 1984).

Experiments in which fishes were starved for 8 days showed that these loricariids would move into water as shallow as 20 cm in order to access standing stocks of attached algae (Power *et al.*, 1989).

Caño Volcán in Venezuela differed from the Río Frijoles in Panama in that shallow riffle and run habitats of the former tended to be depleted of attached algae during the dry season. In the Río Rijoles, loricariid densities in shallow riffles and runs were considered insufficient to deplete algae (Power *et al.*, 1989). In contrast, adult and juvenile *Ancistrus triradiatus* Schultz, 1944 and juvenile *H. argus* appeared to deplete attached algae from hard substrates (rocks and woody debris) of riffles and runs, and the abundant *Creagrutus melasma* Vari, 1994 and *P. reticulata* (first and third most abundant fishes in samples) fed on attached algae and associated microfauna over sand in these shallow mesohabitats (Winemiller, 1990).

Evidence from South and Central American streams suggests that risk-sensitive foraging by algivorous fishes may be a general phenomenon that influences food web dynamics at small spatial scales in tropical streams. Large algivores can deplete attached algae in deeper pools where these fishes are not vulnerable to large avian predators. Depletion of attached algae can have effects on benthic community composition and ecosystem processes (Power, 1990*a*,*b*; Gelwick & Matthews, 1992). Experimental exclusion of *P. mariae* in a Venezuelan piedmont river resulted in significant changes in standing stocks of attached algae and changes in benthic fauna and water quality due to lack of substrate suspension (Flecker, 1992, 1996). In Venezuelan streams, small algivorous fishes appear to be restricted largely to shallow mesohabitats by the threat of predation from pool-dwelling, piscivorous fishes. In contrast to findings in Panama, most of the shallow riffle and run habitats of Caño Volcán contained little conspicuous attached algae, which suggests that densities of small algivores, especially fishes, were high enough to deplete algae. Attached algae were most conspicuous in shallow marginal areas of pools, areas where small algivorous fishes presumably are vulnerable to attack by *Hoplias*.

Herbivore predation mortality (Power, 1990*a*) and the risk of predation (Power *et al.*, 1985; Gelwick *et al.*, 1997) can influence the dynamics of algal growth in streams and produce patchy distributions of benthic primary production that support food webs. Fish movement, viewed at this small scale, should influence the spatial distributions and levels of primary production at the base of stream food webs. The threat of predation by avian piscivores can result in higher algal stocks and productivity in shallow areas along pool margins, whereas the threat of predation by pool-dwelling piscivores, such as *H. malabaricus*, can result in reduced algal stocks in shallow riffle and run habitats due to the use of these habitats as refuges by small algivorous fishes. Fish movements between mesohabitats that are resource-depleted refuges and those that are dangerous but resource-rich will affect the functional and numerical predation responses, and hence foodweb dynamics in tropical streams. It could be argued logically that trophic dynamics involving small-scale, risk-sensitive movement among such patches should have a stabilizing effect on community dynamics, because resource populations would have spatial refuges that reduce the probability that their densities would crash periodically due to predation pressure.

LOCAL MOVEMENTS IN SEASONAL FLOODPLAIN WETLANDS

The tremendous heterogeneity of floodplain aquatic habitats presents fishes with a diverse array of abiotic and biotic environments in which they can seek refuge, feed, and reproduce. This study examines briefly two ways in which fish movement influences food webs at the local scale by reviewing findings from research on Caño Maraca, a floodplain aquatic habitat in the Venezuelan llanos. First, the influence of the seasonal cycle of flooding on fish movement, reproduction and feeding in response to the changing physical environment is examined. Second, the role of habitat heterogeneity (i.e. dense macrophyte beds) on predator–prey interactions is investigated.

The food web of Caño Maraca, a seasonal wetland in the floodplain of a savanna creek in the llanos of western Venezuela, was studied over 12 consecutive months during 1984 (Winemiller, 1990). Precipitation is strongly seasonal with most rain falling from late May to August (wet season). Seasonal flooding causes large seasonal variation in community structure, with some fish species being common only during a particular period (Winemiller, 1996a). Some species have seasonal migrations and exit during the onset of harsh dry season conditions (January–April). These migrations are mostly local, and fishes return later from channel areas downstream to spawn and feed in the newly flooded wetland. Examples include the redbelly piranha *Pygocentrus cariba* Valenciennes, 1849, the tube-snouted knifefish *Rhamphichthys marmoratus*, Castelnau 1855, and headstander *Leporinus friderici* (Bloch, 1794). Other species remain at the site throughout the year, but suffer high mortality during the dry season. The small darter characin *Characidium* sp., the guppy *P. reticulata* and corydoras catfishes *Corydoras aeneus* (Gill, 1858), *C. habrosus* Weitzman, 1961 and *C. septentrionalis* Gosline, 1940 are among the resident populations that decline during the dry season and rebound during the wet season. A few species are present at the site year-round, and show some evidence of successful reproduction even during the dry season [e.g. the characid, *Roeboides dayi* (Steindachner, 1778), and the cichlid, *Caquetaia kraussii* (Steindachner, 1878)]. Fish abundance and diversity are associated with water depth and dissolved oxygen (DO) in a non-linear fashion (Fig. 1). The greatest fish abundance and diversity occur during the transition, or falling water season (September–December) when water depth and DO are declining from their wet-season maxima. Given the predictable influence of emigration and high mortality from hypoxia and predation, lowest abundances and species richness are associated with low water and low DO during the peak dry months.

Life-history strategies influence population dynamics of fishes at Caño Maraca greatly (Winemiller, 1989). The wet-season food web is dominated by fishes with divergent tactics: species that remain throughout the dry season and survive harsh conditions and predation owing to special adaptations like aerial respiration and armour, and that tend to reproduce aseasonally with relatively small broods and parental care (the equilibrium strategists of Winemiller, 1992; Winemiller & Rose, 1992); species that remain during the dry season but their population densities are reduced by hypoxic conditions or predation, and whose numbers recover quickly due to high fecundity and pulsed spawning after the first floods (periodic strategists), or to early maturation and multiple spawning of small clutches (opportunistic strategists); and species that exit during the dry
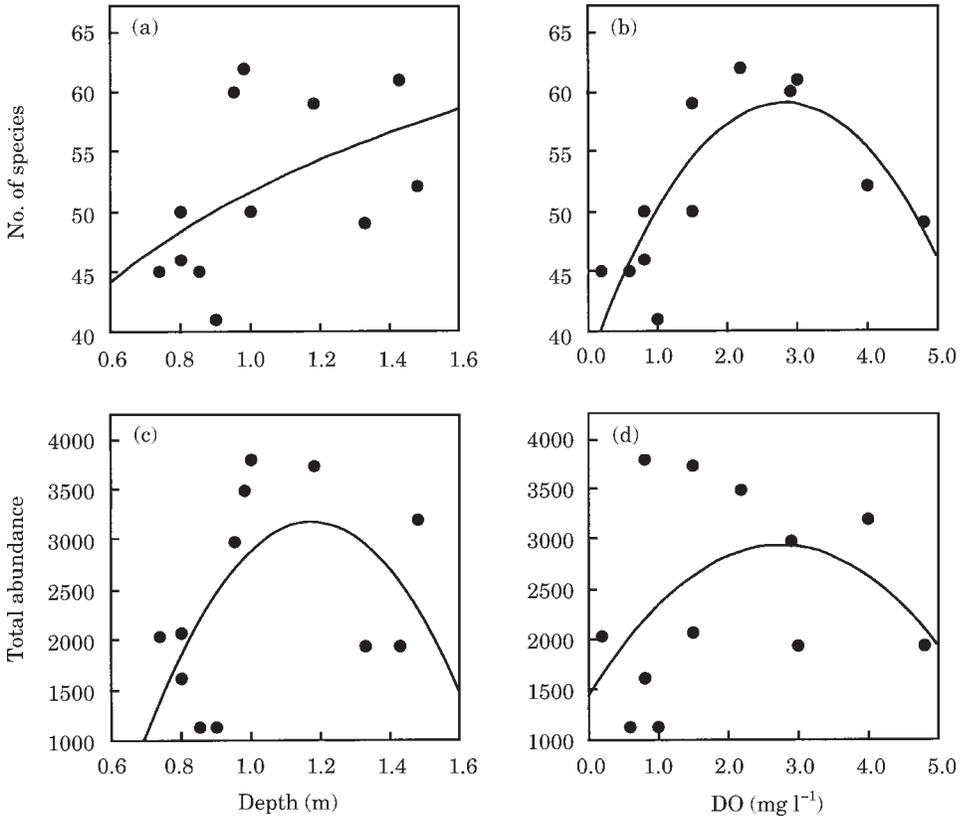
FIG. 1. Biplots showing relationships between water depth (maximum), dissolved oxygen (DO), species richness and total fish abundance based on monthly samples taken at Caño Maraca, a swamp in the western llanos of Venezuela (from Winemiller, 1996a). (a) $y = 51 \cdot 53 + 33 \cdot 93 \log (x)$, $r^2 = 0 \cdot 24$; (b) $y = 37 \cdot 4 + 15 \cdot 4x - 2 \cdot 7x^2$, $r^2 = 0 \cdot 67$; (c) $y = 9823 \cdot 4 + 0 \cdot 0002x - 9379x^2$, $r^2 = 0 \cdot 30$; (d) $y = 1431 \cdot 7 + 1088 \cdot 2x - 197 \cdot 6x^2$, $r^2 = 0 \cdot 17$.

season but return with the rains to spawn large numbers of eggs (periodic strategists). Despite large seasonal changes in the local fish assemblages, a large, complex food web is present throughout the year (Winemiller, 1990). Representatives of three basic trophic groups (herbivore/detritivores, omnivore/invertivores and piscivores) were surveyed during each month of the field study (Table II).

The annual cycle of flooding and desiccation affects the lower food web at Caño Maraca dramatically (Winemiller, 1990, 1996b). Aquatic plants and invertebrates display an impressive burst of production during the earliest phase of wet-season flooding. Aquatic macrophytes, algae, and various microcrustacea pass through the dry season as resting seeds, eggs (zygotes), or rhizomes. The annual killifish *Rachovia maculipinnis* (Radda, 1964), an abundant fish during the wet season, is virtually eliminated by predators by the beginning of the transition season (September–December). During the wet season, the wetland covers an area of several hundred ha blanketed with emergent and aquatic macrophytes. Few invertebrates or fishes feed directly on these plants, but many herbivores consume periphyton that grow on the submerged macrophytes. During the wet

TABLE II. Relative percentages of herbivore/detritivores, piscivores, and other trophic groups (omnivores and invertebrate feeders) among fishes in monthly samples from Caño Maraca, Venezuela

Trophic group	Dry				Wet					Transition		
	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Herbivore	17	32	25	26	41	30	19	22	17	16	13	26
Piscivore	5	12	7	8	3	9	16	22	12	10	15	11
Others	77	56	67	65	56	61	65	56	71	74	72	63
Total fish sample	2059	1139	1611	2028	1132	1934	3181	1925	3729	3801	2976	3489

season, algal production is transferred to top predators, such as *H. malabaricus* and *P. cariba,* via food chains involving invertebrates and juvenile fishes (Winemiller, 1996b). During the transition season, the accumulated macrophyte biomass dies and decomposes. Decomposition of plant biomass and the drainage of water into ever smaller pools and channels yield aquatic hypoxia. Yet many fishes, including many without any apparent accessory respiration capabilities, continue to feed under hypoxic conditions. Detritus derived from aquatic macrophytes is the primary source of basal production during the late transition and dry seasons. These basal inputs flow upward through the food web *via* microbes, protozoa, invertebrates, and fishes (Winemiller, 1990, 1996b).

Upon initial inspection, the great magnitude of the seasonal restructuring of the food web at Caño Maraca may seem unusual, yet undoubtedly this is the norm for river floodplain ecosystems throughout the tropics. Fish movement in response to changing water levels and dissolved oxygen concentrations has been documented for a variety of tropical river floodplains, including the Amazon (Lowe-McConnell, 1964; Fittkau, 1973; Fernandez, 1997), Orinoco (Mago-Leccia, 1970); Kafue (Lagler *et al.*, 1971), and Okavango (Merron & Bruton, 1988) rivers (see Welcomme, 1985 for a review of additional case studies). In each case, seasonal changes in sources of primary production and fish movement in response to changing habitat conditions resulted in massive restructuring of local assemblages, hence, food webs. Newly inundated floodplains are associated with high dissolved oxygen concentrations, low fish densities, dense growth of aquatic macrophytes and high primary and secondary production, conditions conducive to successful feeding, growth and reproduction. As waters recede slowly from floodplains, these optimal conditions begin to deteriorate which motivate adult and young-of-the-year (YOY) fishes to seek more favourable habitats. What is perceived as more favourable depends on the shifting conditions within the mosaic of floodplain habitats, as well as the suite of physiological and ecological attributes possessed by a given species. Some resistant species may move little, less-resistant species may move from ephemeral habitats to floodplain channels or lagoons, and intolerant species may leave the floodplain and enter primary river channels. These local movements within the floodplain ultimately yield food web patterns at the larger, regional scale.

TROPHIC INTERACTIONS IN RELATION TO AQUATIC MACROPHYTES

Dense beds of aquatic macrophytes provide structured habitats that serve as refuges from predators and substrates for production of periphyton and invertebrates such as microcrustacea and aquatic insect larvae. Aquatic vegetation of tropical floodplains provides an important nursery habitat for a great number, perhaps the great majority, of the fish species of lowland rivers (Junk, 1973; Howard-Williams & Junk, 1977; Sazima & Zamprogno, 1985; Araujo-Lima *et al.*, 1986; Machado-Allison, 1990). Many of these fishes eventually leave dense vegetation for more open-water habitats of the floodplain. Others, such as the knifefish *Gymnotus carapo* Linnaeus, 1758 and the cichlid *Apistogramma hoignei* Meinken, 1965, are associated with patches of dense vegetation throughout their life cycles. Much like the pool and riffle mesohabitats in small streams, patches of open-water and dense vegetation in floodplains influence fish predator–prey interactions and the spatial distribution of primary production on

a local scale. A quantitative analysis of the Caño Maraca food web failed to identify significant compartmentalization in relation to dense vegetation *v.* open-water habitats during any season. Moreover, the frequency of trophic interactions involving species categorized as being more common in vegetation or in open-water was greater than would be predicted at random. This result indicates that the interface between vegetation and open water is a particularly active zone for feeding interactions at all trophic levels.

At Caño Maraca, several herbivorous and omnivorous characiform fishes were most commonly captured from open-water habitats, yet they appeared to forage most intensely at the edges of dense beds of aquatic macrophytes (see Winemiller, 1990 for a description of dominant plant species). Among these fishes were the macrophyte-feeder *Schizodon isognathus* (Kner) 1859, the algivore/detritivore *Steindachnerina argenteus* (Gill, 1858) (the most abundant fish at the site), and the omnivores *Cheirodon pulcher* (Gill, 1858) and *Ctenobrycon spilurus* (Cuvier & Valenciennes, 1848). This feeding behaviour by herbivores and omnivores brings them into contact with vegetation-dwelling piscivores such as *G. carapo*. Based on analysis of stomach contents of 298 *Gymnotus*, 64% of individual fish prey were open-water species, with *C. spilurus* dominant.

Two of the dominant piscivores, *H. malabaricus* and the cichlid *C. kraussii*, were captured frequently near the edge of dense macrophyte beds (juveniles of both species were almost always captured from within macrophyte beds). Stomach contents of 383 *H. malabaricus* were examined, and the numbers of characteristic vegetation-dwelling and open-water fishes in the diet are compared (Table III). Equal numbers of individual vegetation and open-water prey were consumed, but the latter comprised three times the volumetric percentage of the former. The difference in volumetric percentages was due to the consumption of two large open-water fishes [*Hoplosternum littorale* (Hancock, 1829) and *P. mariae*]. Because it brings them into contact with both vegetation-dwelling prey as well as open-water prey that feed on or near vegetation, the edge of macrophyte beds seems to be a particularly profitable foraging area for relatively inactive, ambush predators, such as *Hoplias* and *Caquetaia*. More actively swimming, open-water predators, such as *P. cariba*, fed more frequently on open-water species. Based on contents from 204 stomachs, *Pygocentrus* consumed 97·5% open-water prey and 2·5% vegetation-dwelling prey at Caño Maraca. Yet, such within-habitat feeding was more the exception than the rule, because the number of cross-habitat trophic interactions exceeded random expectations for each of three seasonal webs (Winemiller, 1990).

SEASONAL LATERAL MOVEMENTS FROM FLOODPLAINS TO RIVERS

Eventually, fish production from ephemeral, densely-vegetated habitats of savanna floodplains moves back to more permanent bodies of water as floodplains gradually dry. As noted above, fishes move out of ephemeral floodplain habitats to different degrees at different rates depending on body size and the degree of resistance to harsh abiotic conditions and predation. Some tropical fishes remain in permanent water bodies on floodplains, such as creeks and lagoons (oxbow lakes). Other fishes are consumed by predators before they reach primary river channels. Others migrate to primary river channels and

TABLE III. Numbers and percent volumes of characteristic vegetation-dwelling fishes and open-water fishes consumed by *Hoplias malabaricus* at Caño Maraca, Venezuela based on examination of stomach contents of 383 specimens

Vegetation species	Number	% volume	Open-water species*	Number	% volume
Aequidens pulcher (Gill, 1858)	9	1	*Astyanax bimaculatus*	6	4
Apistogramma hoignei	1	<1	*Cheirodon pulcher*	2	<1
Astronotus ocellatus (Spix, 1829)	1	4	*Ctenobrycon spilurus*	8	4
Caquetaia kraussii	5	1	*Gephyrocharax valenciae* Eigenmann, 1920	1	1
Cichlasoma orinocense Kullander, 1983	6	1	*Hemigrammus* sp.	17	<1
Gymnotus carapo	1	<1	*Hoplosternum littorale*	1	23
Hoplias malabaricus—juv	6	2	*Loricariichthys platymetopon* Isbrücker & Nijssen, 1979	2	<1
Poecilia reticulata	4	<1	*Markiana geayi* (Pellegrin, 1908)	2	2
Pyrrhulina lugubris Eigenmann, 1922	2	<1	*Prochilodus mariae*	1	24
Rachovia maculipinnis	4	<1	*Thoracocharax stellatus* (Kner, 1859)	1	<1
Rineloricaria caracasensis (Bleeker, 1862)	1	6			
Synbranchus marmoratus	1	2			
Total	41	19·5		41	60·0

*Small juveniles of all 10 species tend to occur in densely vegetated habitats.

remain in the same region, but some are migrants that disperse long distances upstream or downstream (this latter group is discussed below). As adult and YOY fishes move from productive, ephemeral habitats of floodplains toward the primary river channel, they move through a nested hierarchy of habitats (Johnson *et al.*, 1995). Within this nested hierarchy, patterns and processes at smaller scales create other patterns and processes at larger scales. On the temporarily flooded terrain, dense beds of aquatic macrophytes support periphyton production and a complex food web containing invertebrates, juvenile fishes, and a variety of vegetation-dwelling, adult fishes. As described above, the interface between vegetation beds and open-water habitats is a very active region for trophic interactions. Production moves gradually from densely-vegetated patches to open-water patches and eventually to ever deeper and more stable aquatic habitats containing smaller patches of aquatic vegetation. The combined effects of trophic interactions and fish movement result in the ultimate transfer of a significant fraction of the annual production of seasonal floodplain habitats to the food web of the primary river channel. At the landscape scale, fish migration within the river channel can transfer secondary and tertiary production great distances along the longitudinal axis of the river.

The Upper Zambezi River in western Zambia has a broad, grassland floodplain and a seasonal cycle of flooding. Based on field research conducted during 1989 (Winemiller, 1991*b*; Winemiller & Kelso-Winemiller, 1994, 1996), Winemiller (1996*b*) created a composite, annual food web for this system based on fish diets estimated from stomach content analyses. Most of the basal production (aquatic macrophytes, periphyton, detritus from aquatic plants) originated on the floodplain during high water (January–April). Virtually all fish species appeared to use the floodplain as a nursery habitat. For the most part, basal production was transferred to higher trophic levels within the aquatic habitats of the floodplain (ephemeral pools, lagoons, sloughs, canals). During the falling-water period (May–August), floodplain fishes moved to secondary channels and some arrived at the main river channel. During the low-water period (September–December), top predators of floodplain habitats [e.g. African pike, *Hepsetus odoe* (Bloch, 1794) and silver catfish, *Schilbe intermedius* Rüppell, 1832] inhabited lagoons, but some occupied edge habitats of the river channel. Many of these channel-dwelling piscivores were preyed upon by the African tigerfish, *Hydrocynus vittatus* Castelnau, 1861 (=*H. forskahlii* in Winemiller & Kelso-Winemiller, 1994). Except for small juveniles, tigerfish seemed to be virtually restricted to the primary channel of the Zambezi River, yet a minimum of 40% of its prey (by volume) were species that were primarily floodplain inhabitants (Fig. 2). Some *Hydrocynus* species from other African rivers are also restricted largely to main channels (Daget, 1954, cited in Welcomme, 1985).

Jackson (1961) proposed that tigerfish restrict occupancy of the main river channel by a great many of the fish species of Africa. He postulated that the life histories and patterns of migration of many African river fishes represent ecological and/or evolutionary responses to the threat of predation by tigerfish in the river channels. Jackson's hypothesis is supported by the observation that most of the fish diversity of the Upper Zambezi consists of species associated primarily with floodplain habitats or upland tributaries. In addition, many of
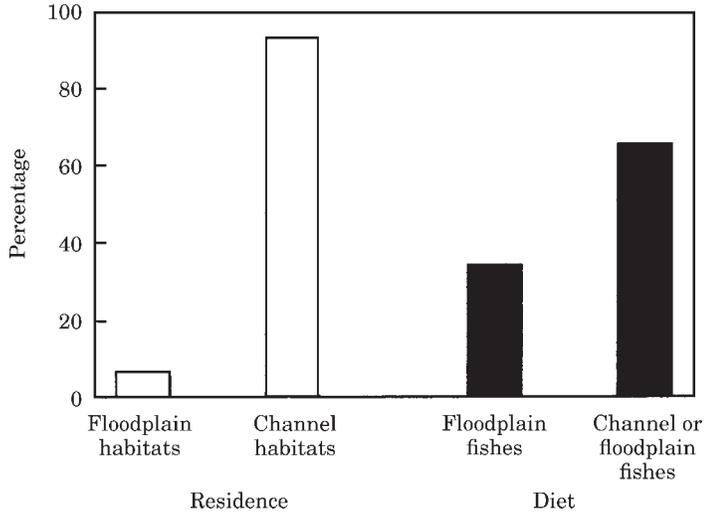
F IG . 2. Percentages of African tigerfish collected from floodplain and river channel habitats of the Upper
Zambezi, and volumetric percentages of floodplain *v.* channel–floodplain fishes in the diet of
tigerfish (from Winemiller & Kelso-Winemiller, 1994).

the common channel-dwelling species are either large [e.g. large catfishes, *Clarias
gariepinus* (Burchell, 1822) and *C. ngamensis* Castelnau, 1861, and cichlids,
Serranochromis robustus (Günther, 1864) and *S. giardi* Pellegrin, 1903] or possess
special antipredation morphological adaptations, such as long, stout dorsal and
pectoral spines (e.g. catfishes of the mochokid genus *Synodontis*). A few small
fishes were primarily channel inhabitants, but these tended to be located in very
shallow water below sand bars (e.g. *Micralestes acutidens* Peters, 1852). Most of
the small fishes collected from the river channel tended to occupy dense masses
of submerged sedges fringing the shoreline, and these species were always more
common in floodplain habitats [e.g. the mormyrid *Petrocephalus catostoma*
(Günther, 1866) and anabantid *Ctenopoma intermedium* (Pellegrin, 1920)].

During the falling-water period, a variety of predators, including humans,
exploit the seasonal movement of fish production from floodplains to river
channels. During this time, fishermen of the Upper Zambezi floodplain con-
struct low grass or earthen dams (called ' maalelos ' in the local Lozi language)
along the margin of secondary channels. The dams have openings in which reed
fences are placed in order to channel fishes into traps. A great quantity and
diversity of YOY and adult fishes are obtained in this manner (Kelley, 1968;
Winemiller, 1991*b*). Where secondary channels drain into the main river channel
of the Zambezi, large flocks of cormorants feed on dense aggregations of YOY
Synodontis catfishes (Winemiller, pers. obs.). During the falling-water period of
the Okavango swamps located south of the Upper Zambezi, schools of
C. gariepinus and *C. ngamensis* rove along the vegetated shoreline of the river
channel where they feed on the great influx of small fishes, especially mormyrids
(Merron, 1993).

The phenomenon of piscivores intercepting fishes as they move from drying
floodplains to permanent channels seems to occur in most other major tropical
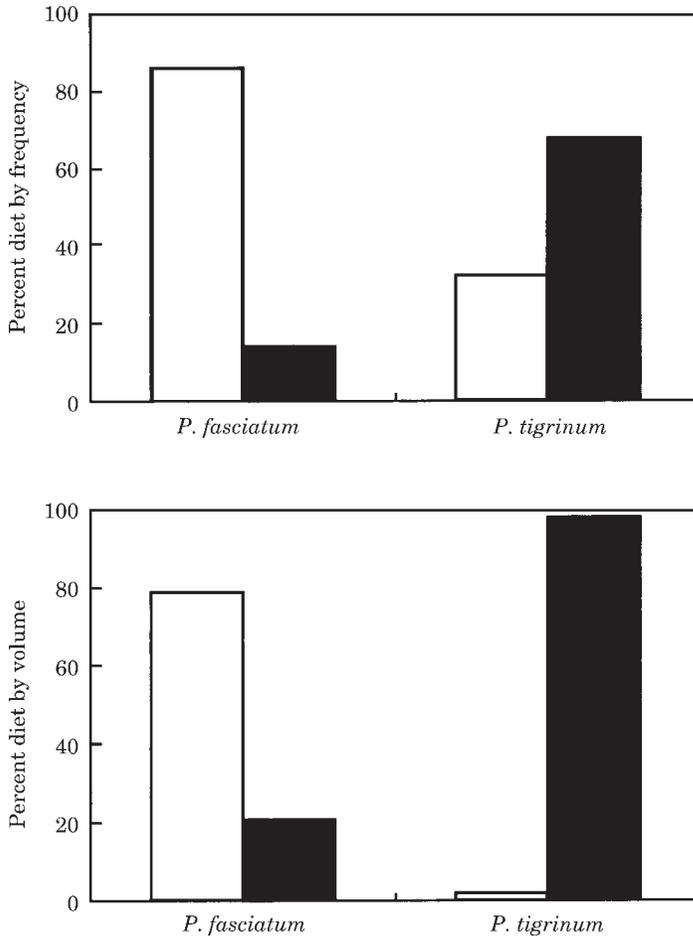floodplain ecosystems. In the Río Orinoco Basin, commercial fishermen target

FIG. 3. Per cent diet composition of floodplain fishes (□) *v.* floodplain–channel fishes (■) by frequency (top) and volume (bottom) for two species of predatory catfishes (*Pseudoplatystoma* spp.) from the Río Apure, Venezuela (based on data from Reid, 1983).

large piscivores where tributary creeks enter larger rivers during the falling-water period. We have observed fishermen of San Fernando de Apure (the largest inland fishery in the Orinoco Basin) capturing pimelodid catfishes from the muddy waters of the Río Apure using harpoons. When hurling their harpoons, the fishermen cannot see the catfishes, but they know they are concentrated near the mouths of creeks and lagoons, from which abundant prey fishes enter the river channel. The ecology of the two most important catfishes of the Apure fishery, *Pseudoplatystoma fasciatum* (Linnaeus, 1766) and *P. tigrinum* (Valenciennes, 1840) was studied by Reid (1983). Both species feed on a variety of fishes. *Pseudoplatystoma fasciatum* (*n* stomachs examined = 389) fed mostly on species that typically are associated with floodplain habitats (Fig. 3). A greater fraction of the diet of *P. tigrinum* (*n* = 428) consisted of species that are common in both floodplain and channel habitats or more common in channel habitats, especially when percentages were based on prey volume (Fig. 3). *Pseudoplatystoma fasciatum* was captured from more structured habitats,

especially near the edge of aquatic macrophyte beds, and *P. tigrinum* was captured more frequently from open-water habitats. Reid believed that both catfishes moved longitudinally within the river channel in pursuit of migrating schools of *P. mariae*, however, he did not perceive such movements by the catfishes to be spawning migrations, and they did not seem to include all individuals of the populations.

The seasonal movement of fishes in floodplain habitats ('várzea') of the central Amazon River was described by Lowe-McConnell (1975); Goulding (1980); Junk (1984); Fernandez & de Merona (1988) and Fernandez (1997). Based on data obtained from both experimental and commercial fishing in a large floodplain lagoon, Fernandez & de Merona (1988) identified two general patterns. The first group of fishes contained mostly herbivorous and detritivorous species that entered and exited the lagoon in two pulses, corresponding to the rising and falling-water periods, respectively. The curimatid *Potamorhina latior* (Spix in Agassiz, 1829), the most common fish in their study, represented this group. The second group, represented by the clupeid *Pellona flavipinnis*, contained mostly predatory species that entered and exited the lagoon with roughly equal frequencies throughout the year.

In the central Amazon, many fishes enter seasonally flooded forests to feed on fruits, seeds, and other terrestrial, allochthonous resources (Goulding, 1980; Hamilton & Lewis, 1987; Goulding *et al.*, 1988). Many fishes also reproduce in the flooded forest, and others spawn in the river channel and their buoyant eggs and larvae enter the flooded forest and floodplain lagoons with the advancing floodwaters. Even livebearing tropical fishes enter flooded forests to feed and reproduce. In Costa Rica, three poeciliid fishes showed greater reproductive effort during the wet season, the period when most individuals migrated from streams to the flooded forest (Winemiller, 1993). The flooded forest had lower densities of potential neonate predators, abundant invertebrate prey, but lower abundance of algae for adults of two algivorous poeciliids.

When fishes enter flooded riparian zones to feed, the resultant local communities, hence food webs, can be rearranged randomly from place to place and from year to year. Bonetto *et al.* (1969) investigated the temporal dynamics of floodplain lagoons of the Middle Río Paraná in Argentina, and determined that both between-pool variation and within-pool seasonal variation were very large. Because no significant correlations were found between fish assemblage composition and pool attributes, such as vegetation type or cover, they concluded that assemblages were essentially random. This view has dominated the tropical fish literature (e.g. Goulding *et al.*, 1988), however, Rodriguez & Lewis (1994) determined recently that fish assemblages within Orinoco floodplain lakes were to a large extent predictable from year to year. They also showed how water clarity influenced assemblage composition and inferred that predation was the likely mechanism (i.e. sight-feeding predators were more efficient foragers in clearer lakes, nocturnal predators using olfactory cues and electroreception dominated turbid lakes). Similarly, the fish assemblage of the Caño Maraca swamp in Venezuela showed regular patterns of seasonal variation in the fish assemblage over a 10-year period (Winemiller, 1996*a*). An 8-year study of fish assemblages from a variety of channel and floodplain habitats of the Upper Río Paraná in Brazil revealed that assemblages varied in relation to habitat type, and

that total fish abundances varied between-years in relation to the height of the annual floods (Agostinho *et al.*, 1997).

SEASONAL LONG-DISTANCE MIGRATIONS

The important role of fish movement (diadromy) as a nutrient transport system and its effect on local food webs have been addressed recently in arctic and temperate ecosystems (Kline *et al.*, 1990; Hesslein *et al.*, 1991; Deegan, 1993; Schuldt & Hershey, 1995; Willson & Halupka, 1995; Bilby *et al.*, 1996). This important issue never has been addressed in the tropics, where massive, long-distance, fish migrations are commonplace (Ribeiro & Petrere, 1990; Barthem *et al.*, 1991). The most conspicuous of the long-distance migrants are the prochilodontid fishes of the genera *Prochilodus* (' coporo ' in northern South America, ' sábalo ' in the south, and ' curimbatá ' in Brazil) and *Semaprochilodus* (' bocachico ' or ' sapuara ' in Spanish and ' jaraqui ' in Portuguese). These abundant, characiform fishes have complex feeding and spawning migrations that coincide with seasonal changes in water levels. Prochilodontids feed on detritus, algae, and associated micro-organisms (Bowen, 1983; Bowen *et al.*, 1984) and are important prey for piscivores. Because they transfer energy and biomass from basal production directly to species higher in the food web, these fishes should increase the ecological efficiency of piscivore production *via* short food chains (Winemiller, 1996*b*). Moreover, foraging by *Prochilodus* can have strong effects on benthic community structure and species interactions (Flecker, 1992, 1996). Prochilodontids are the primary species in some of the most important commercial and subsistence fisheries throughout South America (Welcomme, 1990).

The direction and extent of longitudinal migration varies by species among the prochilodontids. During the early wet season in the western Orinoco Basin, adult *Prochilodus* migrate from Andean piedmont tributary rivers to their wet-season spawning and feeding habitats in channels and floodplains of the lowlands (Lilyestrom, 1983). Migrating, prespawning males and courting males emit a low-pitched, drumming sound that presumably attracts ripe females. Fertilized eggs, embryos and larvae drift downstream with the river current and eventually enter floodplain habitats where juveniles feed on rich invertebrate and algal production. During the falling-water period, massive schools of coporos (the ' ribazón ') migrate upstream and disperse among the tributary rivers draining the Andes. On many of these rivers, dams now block migration (Winemiller *et al.*, 1996; Barbarino Duque *et al.*, 1998).

A similar but somewhat more complex situation is observed for *Prochilodus* inhabiting tributaries of the Amazon Basin. During the flood phase of the Río Madeira, schools of *Prochilodus* and *Semaprochilodus* migrate downstream from nutrient-poor tributaries to spawn in the turbid waters of the Madeira (Goulding, 1980). After spawning, the fishes move back into the lower courses of major tributaries and feed within the flooded forests. During the falling-water phase, the fishes move back into the Madeira channel and migrate upstream and eventually disperse within tributary rivers. In the Río Manoré located further upstream within the Madeira basin in Bolivia, *Prochilodus nigricans* Agassiz, 1829 spawn in the floodplains during the high-water phase, and the young fish

remain in the lower river reaches for a year before migrating with adults to locations in the upper basin during the subsequent falling-water season (Loubens & Panfili, 1995).

In the central Amazon, adult *Semaprochilodus* occupy nutrient-poor blackwater tributaries during the low-water period, and migrate downstream to nutrient-rich floodplains of the Amazon for spawning during the high-water period (Vazzoler *et al.*, 1989; Ribeiro & Petrere, 1990; Vazzoler & Amadio, 1990). After completion of spawning and feeding within the productive floodplains during the high-water phase, great schools of adult and subadult fishes ('piracema') return up nutrient-poor tributary rivers where they feed on detritus and aufwuchs within the flooded forest. The direction of spawning migrations is reversed in some *Prochilodus* populations of the upper Río Paraná–R. La Plata basin of southern South America, where several important spawning and nursery floodplains are located in areas upstream from the main dry season refuges (Godoy, 1967; Bayley, 1973; Bonetto *et al.*, 1981; Agostinho *et al.*, 1993). In general, prochilodontid spawning migrations appear to allow adults and early life stages to feed in productive floodplain habitats during the high-water phase, and allow adults and large sub-adults to disperse to other locations within their river basin during the low-water phase; presumably this reduces the impact of resource competition and predation.

FOODWEB SUBSIDIES FROM MIGRATORY FISHES

In the Orinoco Basin, *Semaprochilodus kneri* (Pellegrin, 1909) descend oligotrophic, blackwater rivers to the floodplains of the whitewater Orinoco where they spawn and remain during the high-water period. The whitewater floodplain ecosystem is highly productive and serves as a nursery area for young *Semaprochilodus*. During the falling-water period, adults and YOY *Semaprochilodus* migrate back into blackwater rivers, where the YOY detritivores are preyed upon by large predatory fishes. Due to low nutrient availability, blackwater rivers support little aquatic macrophyte growth and planktonic primary production is low (Lewis, 1988), yet *Semaprochilodus* species are specially adapted to feed efficiently on detritus and sparse standing stocks of diatoms and other attached algae (Goulding *et al.*, 1988). The factors causing the evolution of this life cycle involving migrations between blackwater and whitewater ecosystems are unknown. Historical biogeography may have played a role (evolutionary history within entirely blackwater drainage basins). Natural selection in the form of predation or competition with whitewater detritivores (including *Prochilodus* species) may be intense within the reduced aquatic habitats of whitewater ecosystems during the dry season.

Systems with little apparent *in situ* primary production nevertheless can support impressive fish biomass. Many nutrient-poor, blackwater rivers in South America support important fisheries, but the basal production supporting this secondary and tertiary production is not apparent. Model simulations have shown that, even at low light intensities, small standing crops of periphyton can support a relatively large consumer biomass (McIntire, 1973). In addition, consumer webs of oligotrophic systems may be augmented by allochthonous sources, such as seeds and terrestrial insects. In contrast to blackwater systems, primary productivity of whitewater floodplain lakes is high (Schmidt, 1973).
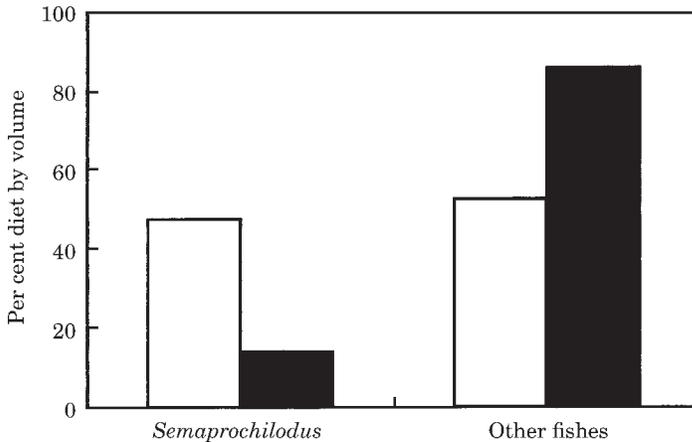
FIG. 4. Volumetric percentages of *Semaprochilodus kneri v.* other fish taxa (collectively) in the diet of Río Cinaruco *Cichla temensis* during falling (□) and low-water (■) periods.

Phytoplankton and C_3 macrophytes (plants using the Calvin photosynthetic pathway) are the most nutrious primary production sources in whitewater floodplains, and seem to be more important in supporting fish biomass than their standing biomass would indicate. Although C_4 macrophytes (grasses and sedges using the Hatch–Slack photosynthetic pathway) comprise a major portion of the primary producer biomass in many systems, they seem to be a minor source of energy for aquatic consumers (Hamilton *et al.*, 1992; Forsberg *et al.*, 1993). There is little information on production rates of attached algae (periphyton) in tropical rivers, but their importance as a source of carbon for aquatic organisms has been demonstrated in recent stable isotope studies (Hamilton *et al.*, 1992).

During the period 1992–1998, the ecology of fishes in the Río Cinaurco, a blackwater river in southern Apure State in Venezuela was studied. During the wet season, *Semaprochilodus kneri* and *S. laticeps* Steindachner, 1879, migrate downstream from the Cinaruco to spawn and feed on the rich floodplains of the Orinoco. During the early dry season, great schools of adult and YOY *Semaprochilodus* (the smaller *S. kneri* is most abundant) enter and ascend the Cinaruco. These upstream migrants are preyed upon by resident piscivores, among them the abundant *Cichla temensis* Humboldt, 1833. Juvenile *Semaprochilodus* were estimated to provide *c.* 50% of the prey volume ingested by *Cichla* >40 cm during the falling-water period and about 15% of the volume ingested by *Cichla* during the low-water period (Fig. 4). *Cichla* >40 cm comprise about 60% of the *Cichla* adult population (Jepsen *et al.*, 1997; Winemiller *et al.*, 1997), and they constitute a much greater percentage in terms of population biomass.

Reproduction by *Cichla* follows the falling-water period of heavy feeding on *Semaprochilodus* and should be strongly dependent upon this nutritional source. Body condition and fat stores of *Cichla* increase during this period of falling water levels. As the low-water season progresses, the density of YOY fishes declines and the frequency of *Semaprochilodus* in *Cichla* diets declines markedly. During the middle and late phases of the low-water period, most *Cichla* have empty stomachs, and gonadal maturation occurs in preparation for spawning

just prior to the beginning of the annual floods. The migratory detritivores probably provide *Cichla* and other large piscivores (other common species are the piranha, *Serrasalmus manueli* (Fernández Yépez & Ramírez, 1967), and payara, *Hydrolycus scomberoides* (Cuvier, 1817) of nutrient-poor rivers with a significant nutritional subsidy that permits them to achieve greater fecundities, levels of recruitment, and population densities than those that would be supported by *in situ* food production from the oligotrophic system. Taphorn & Barbarino Duque (1993) estimated Cinaruco-Laguna Larga *C. temensis* at *c.* 71 adults ha^{-1} based on the mark–recapture method. No comparable data are available from other blackwater rivers, but our experiences throughout the Orinoco Basin suggest that the Cinaruco *C. temensis* density well exceeds the average for the basin.

Because of their great abundance, low position in food chains and migratory nature, prochilodontid fishes are probably extremely important components of South American river food webs. They assimilate primary production from productive, floodplain ecosystems and move it across a wide spectrum of the spatial hierarchy of floodplains. When they enter river channels, they are preyed upon by a variety of piscivores. As they ascend rivers, sometimes for hundreds of kilometres, great schools transport production from one landscape to another. In effect, these algivorous/detritivorous, migratory fishes increase ecological efficiency in food webs and link food webs of landscapes over a wide range of spatial scales. By subsidizing resident piscivores nutritionally in nutrient-poor ecosystems, migratory fishes enhance piscivore fitness and population densities. This could influence the population dynamics of some resident prey populations of the local food web, and could influence indrectly other species and resources *via* cascading trophic interactions (Polis *et al.*, 1996, 1997).

BASIN-WIDE MIGRATIONS BY AMAZON CATFISHES

Although migratory prochilodontids are the largest component of commercial fish catches in South America, pimelodid catfishes support a major commercial fishery in the Amazon estuary in addition to smaller-scale fisheries in the central and western Amazon. Until very recently, the ecology of the large pimelodid catfishes of the Amazon was virtually unknown. Recently, Barthem & Goulding (1997) presented evidence indicating that several species of large pimelodid catfishes, most notably the dourada *Brachyplatystoma flavicans* (Castelnau, 1855) and piramutaba *Brachyplatystoma vaillantii* (Valenciennes, 1840), spawn in the western region of the Amazon Basin in large whitewater tributaries. From these locations in Colombia, Ecuador, Peru, and western Brazil, larvae and small juveniles are transported downstream in the Amazon channel until they arrive in the huge freshwater estuary around Marajo Island in northeastern Brazil. They estimated that a juvenile, riding the strong rain-swollen currents, might travel from the western Amazon to the estuary, a distance of some 3300 km, in as little as 13 days. The estuary supports large populations of juvenile catfishes, and the commercial fishery there is supported by juveniles measuring over 1·0 m fork length (L_F). In the case of *B. flavicans*, adults appear to be completely absent from the estuary, and the average size of *B. flavicans* and *B. vaillantii* in commercial fisheries samples increases as one ascends the Amazon. Colombia's Río Caqueta records the largest average size for *B. flavicans*, and it is the only

location where fairly large numbers of ripe adults have been documented. Barthem & Goulding (1997) argue that immature *B. flavicans*, perhaps beginning at age 3, migrate from the estuary to main river channels of the central and western Amazon. Once sexual maturation is achieved (estimated at age ≥ 4 and 1–2 m L_F), *B. flavicans* are hypothesized to migrate to western tributaries for spawning. The same scenario is proposed for *B. vaillantii*, with the exception that some adults may remain for several months in the estuary where they feed on benthic prey.

If this model of the life cycle of these large catfishes is correct, then it has obvious implications for understanding Amazon River food webs and the management of fish stocks. From a foodweb perspective, these catfishes represent the reverse effect of migratory prochilodontids. Rather than transport production from one landscape to the food web of another, these catfishes transport a top consumer from one landscape to another. If the food web is modelled from a broad geographical perspective, such as the entire Amazon Basin, then the locations of producers and consumers might be irrelevant. Yet, this is unlikely. When a food web is partitioned in space, the potential exists for a variety of dynamics (Holt, 1996; Polis *et al.*, 1996, 1997). For example, immigration of prey (or importation of resources) can subsidize consumer populations to the extent that they are able to suppress the growth of endemic prey populations to a greater extent than would be possible without this subsidy. This mechanism might reduce local species richness and foodweb complexity, or, if a competitive dominant among endemic prey populations is suppressed, it might increase species richness by permitting competitive subordinates to gain a firmer foothold in the community. Similarly, the immigration of a top predator from another landscape could have the same effects on the local community. In addition, the huge spatial separation between adult foraging habitats and the juvenile nursery results in a demographic disconnection between the predator and its resources. Because juveniles and adults are located thousands of km apart, fecundity would be unrelated to foodweb dynamics that regulate juvenile growth, survival and recruitment to the adult population, or at the very least, the response lag time would occur at the scale of a decade or more.

CONCLUSIONS

Fishes are major components of tropical river food webs, and function as conduits of energy and matter flow through ecosystems. When compared with temperate river fishes, tropical fishes demonstrate more diversity of species and ecological niches, herbivory, detritivory, omnivory, trophic specialization at all levels, and examples of large-scale seasonal movements in response to water-level fluctuations. Trophic interactions in tropical rivers are linked in space and time within nested hierarchies. Foodweb structure and function are greatly influenced by water-level fluctuations and fish movement at different spatio-temporal scales. This study presented several examples based on recent research in South America and Africa.

Now some of the salient features of how fish movement influences foodweb structure/function in tropical floodplain rivers are summarized using heuristic models focused on local and regional spatial scales. At the spatial scale of
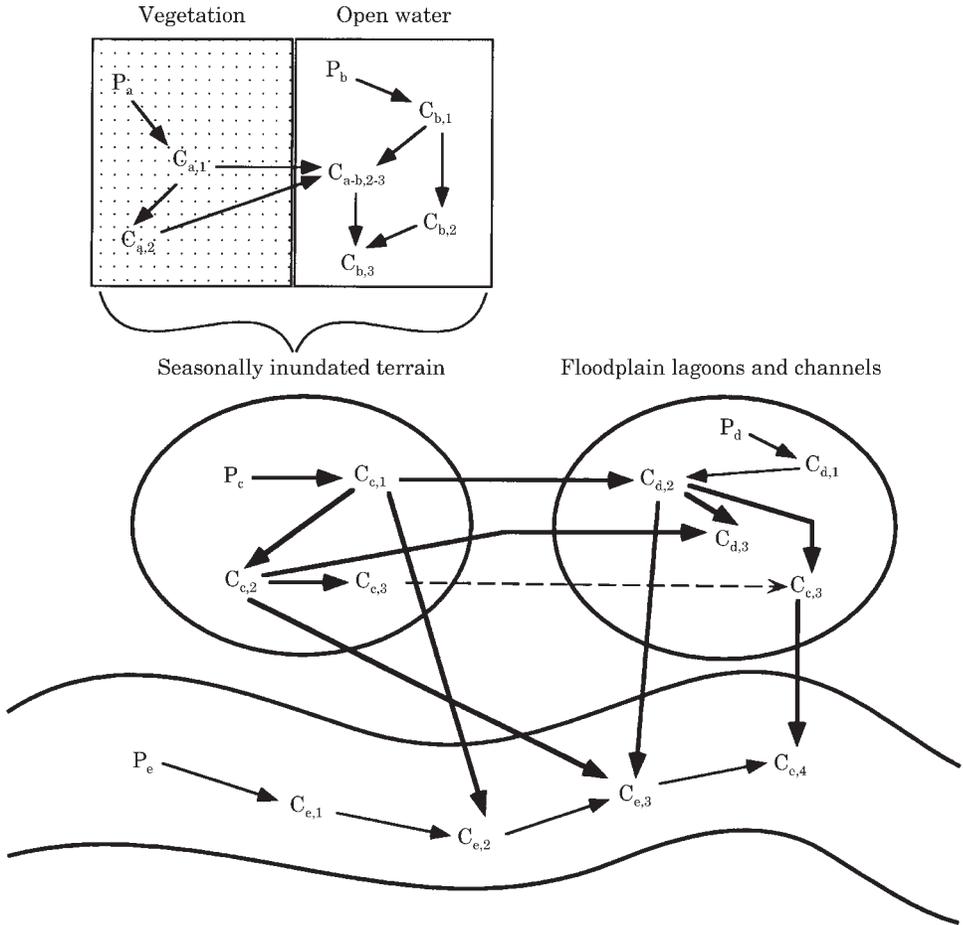
FIG. 5. Schematic diagram illustrating how fishes move production across floodplain habitats at local scales: movement from densely vegetated mesohabitats to open-water mesohabitats (top); and movement from seasonal to permanent aquatic floodplain habitats and movement from floodplains to the river channel (bottom) (P, primary production; C_1, primary consumers; C_2, secondary consumers; C_3, tertiary consumers; solid arrows represent foodweb links; bold arrows represent major pathways; dotted arrow represents migration by consumers; see discussion for examples).

mesohabitats within the inundated floodplain, much of the primary production that enters directly into aquatic food webs (i.e. periphyton) is concentrated in aquatic macrophyte beds. A subweb of consumers occupies these macrophyte beds, but many fishes from the open-water mesohabitat forage on aquatic invertebrates along the edge of vegetation. Ambush predators concentrate their feeding activities at the interface between macrophyte beds and open water. The net movement of primary and secondary production is from aquatic vegetation to open water, and fishes are the principal agents of transport (Fig. 5), although patches of floating macrophytes can break away and transport organisms physically to other locations (Sazima & Zamprogno, 1985). As ephemeral floodplain habitats dry up, herbivorous and carnivorous fishes move to floodplain creeks and lagoons (Fig. 5). Some of these fishes remain in these permanent aquatic habitats of the floodplain as components of local food webs.
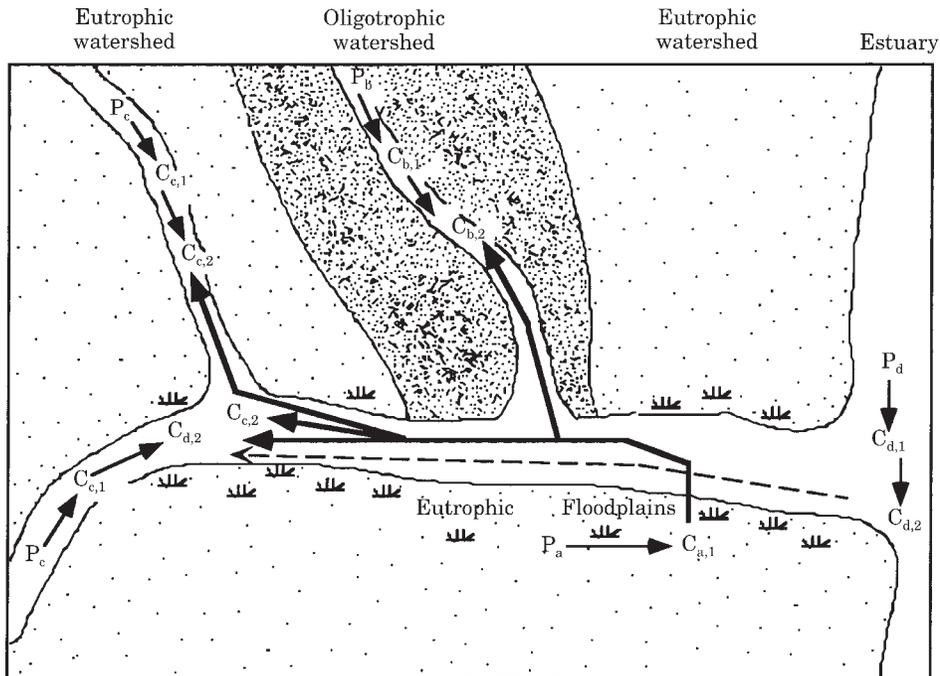
FIG. 6. Schematic diagram illustrating how long-distance longitudinal migrations by fishes link food webs at regional scales: algivorous fishes ($C_{a,1}$) move from whitewater floodplains (a, sparse stippling) to river channels (c) and blackwater rivers (b) draining oligotrophic floodplains (dense stippling); predatory catfishes ($C_{d,2}$) migrate from estuaries (d) to river channels (P, primary production; C_1, primary consumers; C_2, secondary consumers; solid arrows represent foodweb links; thick solid arrows represent foodweb links involving migrations; dotted arrow represents migration by consumers).

Other fishes move to the primary river channel at rates and in numbers that vary depending on resistance to poor water quality, degree of mobility, and habitat preferences. The fishes that enter the channel during the falling-water period are very important food resources for channel-dwelling piscivores (Fig. 5). The dynamics of the movement of production from floodplains toward the river channel is very heterogeneous in time and space. The movement of fishes into the river channel occurs as a pulse during 1–3 months during the falling-water period. Greater understanding of the spatial and temporal heterogeneity of fish movement is crucial for managing fish stocks of floodplain rivers. For example, certain areas may be critical nursery areas or migration routes for fishes that arrive eventually in lagoons or rivers that have important fisheries. Rural people throughout the Venezuelan llanos have described such areas to us, however, virtually no research has been done to substantiate these important claims. In some cases, these habitats are being degraded before their importance to regional fish production is understood.

At the regional-landscape scale, long-distance migrations by fishes have three potential effects on food webs. First, migratory algivorous/detritivorous fishes move secondary production from one landscape to another (Fig. 6), which could influence the dynamics of primary production and resource competition among secondary consumers in the ecosystem receiving the migrants. Because all of

these migratory fishes use productive, whitewater floodplains as their nursery grounds, it is doubtful that emigration of algivore/detritivores represents a significant depletion of nutrients. Second, and probably more importantly, the resident piscivores of the ecosystem receiving the immigrants may gain a significant nutritional subsidy that could increase their population densities to levels at which trophodynamics between these predators and resident prey populations are affected. In this case, a variety of direct and indirect foodweb interactions could affect standing stocks of *in situ* resources and populations. A quantitative understanding of the role of migratory fishes in food webs of ecosystems that receive them is obviously essential for the management of piscivore stocks, but it may be important for understanding the dynamics of certain other components of the food web as well. Third, migration by large piscivores can elevate the mortality of certain fish populations in ecosystems that receive the migrants, and this could change, directly or indirectly, predator–prey dynamics among other components of the food web. In addition, long-distance migrations correlated with particular life stages (such as those shown by Amazonian *Brachyplatystoma* species) reduce the potential for density-dependent feedback mechanisms between conditions in the juvenile nursery area and conditions in the adult river channel habitat that influence fecundity and the recruitment of larvae into the nursery area. The management implications of long-distance migrations by predatory catfishes are obvious (Barthem & Goulding, 1997); different phases of the life cycle located in different geographical regions must be tied together in a quantitative model of population dynamics. Migration routes must be identified (a difficult task), and anthropogenic perturbations that impede migrations must be eliminated (Barthem *et al.*, 1991). Dams already obstruct the migration routes of a great number of migratory prochilodontid populations throughout South America (Goulding, 1988; Bayley & Petrere, 1989; Quirós, 1989; Agostinho *et al.*, 1993; Winemiller *et al.*, 1996; Barbarino Duque *et al.*, 1998).

We have not addressed the potential influence of longitudinal migrations associated with reproduction and recruitment involving movement between tropical freshwater and marine habitats. Many of the issues and mechanisms that we have reviewed for tropical rivers would apply equally to movement across the freshwater–marine ecotone. Many examples can be cited of long-distance migration by marine fishes from the sea into tropical rivers where they may reside for several months or years. Anguillid eels migrate hundreds of km up the Zambezi and other African rivers (Skelton, 1993). Following the closure of the Kariba Dam on the Middle Zambezi, a resident population of *Anguilla bengalensis* Peters, 1852 persisted for several years (Balon, 1974). In Central America, tarpon *Megalops atlantica* Valenciennes, 1864, sawfish *Pristis perotteti* Müller & Henle, 1838, and bullsharks *Carcharinus leucas* Müller & Henle, 1841 migrate up to Río San Juan and enter Lake Nicaragua, where historically they supported fisheries (Thorson, 1971, 1982). In Central America, the mountain mullet *Agonostomus monticola* (Bancroft, 1836) is a long-distance migrant that is a dominant species in mountain and piedmont streams (Cruz, 1987). A variety of fishes from marine families (e.g. Achiridae, Centropomidae, Eleotridae, Gobiidae, Lutjanidae, Sciaenidae, Syngnathidae) move in and out of tropical coastal rivers where they reside and function as natural components of

freshwater food webs (Winemiller, 1983; Winemiller & Leslie, 1992; Adite & Winemiller, 1997). The often complex life cycles and movements by these marine and peripheral freshwater fishes have a major effect on foodweb structure and dynamics in coastal rivers of the tropics.

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