conditions in seasonal wetlands. Egg characteristics are correlated with the modes of spawning and parental care. For instance, eggs of external bearing loricariid catfishes (*Loricaria* and *Loricariichthys* spp.) have thick zona radiata apparently to protect against abrasion, and the zona granulosa produces secretions that probably contributes to egg adhesion (Suzuki *et al.*, 2000). Among Paraná River loricariids, the cavity nesting loricariids (*Hypostomus* and *Megalancistrus* spp.) have the largest eggs with the thickest zona granulosa.

Migration to spawning habitats favorable for egg and larval development can enhance survival of early life stages. During the wet season in Panama, Brycon petrosus migrate to the headwaters of Panamanian rainforest streams to spawn, and spawning aggregations have been observed on partially submerged leaf litter (Kramer, 1978b). Headwater migrations also have been observed in affluents of the Upper Paraná River. Characiformes such as Salminus maxillosus, Brycon orbignianus, and Prochilodus lineatus, among others, migrate to the headwaters during the wet season to spawn in shallow water (<3 m), and eggs drift downstream while developing. Drifting larvae reach the nursery areas (lagoons) when the river overflows its banks (Agostinho et al., 2003b). In piedmont streams of Venezuela, the small characid Bryconamericus dueterodonoides spawns during the dry season, and larvae drift downstream at night (Flecker *et al.*, 1991). Drifting larvae may be transported to more productive habitats in lower stream reaches, with young fishes migrating back upstream during the ensuing wet season. Other larger Characiformes inhabiting the same streams (e.g. Brycon whitei, Salminus hilarii, and Prochilodus mariae) have evolved a different strategy and migrate to lowland floodplains for spawning during the early wet season. Similar breeding migrations are observed among some of the large cyprinids of Himalayan piedmont streams (e.g. Catla catla, Tor spp.).

Fish spawning migrations in lowland creeks tend to be fairly local, with fishes swimming up or down creeks or laterally across flooded zones in search of productive marshes. These seasonal wetlands contain abundant food (microcrustaceans) and cover (aquatic macrophytes) for early life stages. At the onset of the flood period, the area of these shallow marshes increases rapidly, and per-unit-area densities of larval predators are low. A quarter of the most common species captured from a seasonal marsh associated with a small lowland creek in the Venezuelan llanos only entered the habitat for reproduction and feeding during the wet season (Winemiller, 1989b, 1996a). Most of the fish species encountered in a creek draining marginal wetlands around Lake Victoria in Uganda likewise used the habitat for reproduction and feeding only during the wet season, with downstream migrations during the dry season associated with the onset of anoxic conditions (Welcomme, 1969).

How do reproductive strategies relate to habitat variation and dynamics, and are there consistent patterns of fish reproductive strategies across the tropics? Based on multivariate analysis of 10 life-history and demographic traits of fishes inhabiting a lowland creek in the Venezuelan llanos, Winemiller (1989a) found a continuum that identified three endpoint life-history strategies. This continuum describes essential life history tradeoffs among fishes (Winemiller and Rose, 1992) and other groups of organisms (Winemiller, 1992). Of these three endpoints, the opportunistic strategy is marked by rapid maturation at small size and sustained high reproductive effort. It is associated with small size, low fecundity, frequent reproductive intervals, and extended breeding seasons as exemplified by annual killifishes, guppies (*Poecilia reticulata*), and small characids. The opportunistic strategy among the three identified for increasing fitness under density-independent environmental settings, for example, when population density is reduced by habitat disturbance or predation. Reznick and Endler (1982) have demonstrated that increases in predation intensity on adult guppies in Trinidadian streams results in the evolution of earlier ages and smaller sizes of maturation.

The key attribute of the second endpoint – the equilibrium strategy – is high parental investment for individual offspring, either by egg provisioning, parental care, or usually both. Fishes

Region	Neotropics	Africa	Asia/India/Australi
Opportunistic	Hyphessobrycon	Barbus (small)	Brachydanio
	Nannostomus	Neolebias	Danionella
(early maturation)	Pterolebias	Leptoglanis	Rasbora
(high reproductive effort)	Rachovia	Aplocheilichthys	Pseudomugil
	Brachyrhaphis	Nothobranchius	Dermogenys
	Poecilia	Ethmalosa	0,1
Periodic	Acestrorhynchus	Marcusenius	Cyclocheilichthys
	Brycon	Alestes	Osteochilus
(high fecundity)	Bryconops	Distichodus	Tor
(seasonal spawning)	Myleus	Citharinus	Botia
	Leporinus	Barbus (large)	Bagrichthys
	Curimata	Labeo	Leiocassis
	Prochilodus	Schilbe	Mystus (large)
	Eigenmannia	Bagrus	Bagarius
	Pimelodella	Chrysichthys	Pangasius
	Rhamdia	Clarias	Kryptopterus
	Amblydoras	Synodontis	Osphronemus
Equilibrium	Ancistrus	Polypterus	Heteropneustes
	Loricaria	Protopterus	Channa
(parental care)	Loricariichthys	Gymnarchus	Mogurnda
	Hypostomus	Hepsetus	Oxyeleotris
	Hoplosternum	Pelvicachromis	Scleropages
	Aequidens	Hemichromis	Ctenops
	Biotodoma	Oreochromis	Arius
	Crenicichla	Sarotherodon	
	Geophagus	Tilapia (large)	
	Satanoperca	Serranochromis	
Intermediate – E/P	Pygocentrus	Notopterus	Chaca
	Serrasalmus	Pollimyrus	Mystus (small)
	Gymnotus	Clarias	Sphaerichthys
	Synbranchus	Parauchenoglanis	Trichogaster
Intermediate – E/O	Corydoras	Ctenopoma	Betta
	Belonesox	Pseudocrenilabrus	Hemirhamphodon
	Archocentrus	Tilapia (small)	Luciocephalus
Intermediate – O/P	Astyanax	Micralestes	Puntius
	Moenkhausia	Hemigrammocharax	Melanotaenia
	Roeboides	Chiloglanis	Parambassis

TABLE III	Genera from Each Tropical Region Exemplifying the Trilateral Life-history Strategies of
Winemiller	r (1989a, 1992): Opportunistic (O), Periodic (P), and Equilibrium (E)

exhibiting the equilibrium strategy are mostly of intermediate body size, with low fecundity, large eggs, and well-developed parental care as exemplified by brood-guarding cichlids and catfishes (such as *Hoplosternum littorale* and loricariids). This strategy should maximize parental fitness under conditions where density-dependent mortality is important, especially where food is limiting or the threat from predation is high. The third endpoint – the periodic strategy – is associated with high fecundity, small eggs, a contracted and synchronized spawning period, and little or no parental care, and it was the most common strategy in the assemblage studied by Winemiller (1989a). Most of these periodic strategists were characiformes, gymnotiformes, and siluriformes with intermediate body sizes. In its most extreme manifestation, periodic strategists mature at large sizes, have high fecundities, pulse spawning, and migratory behavior (e.g. *Prochilodus mariae*). This strategy appears to maximize fitness in habitats with strong

seasonal variation in environmental quality and food availability (Winemiller, 1989b; Winemiller and Rose, 1992). Relatively stable habitats, such as low-order streams draining lowland rainforests in central Amazonia, seem to favor opportunistic life-history strategists (e.g. small characiformes and dwarf cichlids such as *Apistogramma* spp.) and equilibrium strategists such as *Hoplias*, *Gymnotus*, and the cichlid genus *Aequidens*.

Small fishes with high reproductive efforts are represented in all tropical regions (Table III), particularly in headwater streams that experience frequent hydrological disturbances, as well as seasonal lowland streams associated with higher species richness. Opportunistic strategists in Africa include the small barbs (Barbus spp.), characiformes (Neolebias and Hemigrammocharax spp.), and killifishes (Aphiosemion, Aplocheilichthys, and Nothobranchus spp.). In the Neotropics, small species of killifishes (Cynolebias, Rachovia, and Pterolebias spp.), poeciliids (*Fluviphylax*, *Neoheterandria*, and *Poecilia* spp.), and characiforms (*Characidium*, Deuterodon, and Hemigrammus spp.) are typical opportunistic strategists (Winemiller, 1989b; Mazzoni and Petito, 1999; Mazzoni et al., 2002). In Asia, the opportunistic strategy is observed among small cyprinids (e.g. Brachydanio, Rasbora, Microrasbora, and some Puntius spp.) and halfbeaks (e.g. Dermogenys spp.). Within the Asian cyprinid genus Puntius, continuously breeding opportunistic strategists and seasonally-spawning periodic strategists can be found in the same stream (de Silva et al., 1985), paralleling the situation seen in Neotropical characids (Winemiller, 1989b). Equilibrium species with well-developed parental care, including mouth brooders, occur in multiple families in the streams of all tropical regions (Table III). Migratory periodic-type fishes with large body sizes, high fecundities and synchronized spawning periods are also found throughout the tropics (Table III). The triangular life history continuum also describes fundamental patterns of variation in reproduction and population dynamics of fish assemblages in temperate floodplain rivers (Winemiller, 1996b; Humphries et al., 1999).

IV. FEEDING STRATEGIES AND FOOD-WEB STRUCTURE

Fishes in tropical streams display diverse feeding behaviors, including specialized trophic niches not normally observed in temperate stream fishes (e.g. seed, fruit, scale, fin, and mucus feeding). Many tropical freshwater fishes are trophic generalists (Knöppel, 1970), sometimes accompanied by a contraction of the diet during periods of reduced resource availability. An increase in dietary specialization accompanied by a decrease in interspecific dietary overlap has been documented during the dry season for stream fishes in Panama, Costa Rica, and Venezuela (Zaret and Rand, 1971; Winemiller, 1987, 1989c; Winemiller and Pianka, 1990). In Sri Lankan rainforest streams, fishes revealed patterns of niche complementarity in which high overlap in habitat use was accompanied by low dietary overlap (Moyle and Senanayake, 1984; Fig. 6). Dietary specializations in such streams tended to be associated with consumption of allochthonous foods and morphological specializations. Other studies of tropical stream fishes have also documented significant patterns of association between diet and morphology (Watson and Balon, 1984; Winemiller, 1991; Winemiller et al., 1995; Winemiller and Adite, 1997; Hugueny and Pouilly, 1999; Ward-Campbell et al., 2005). The impression that emerges from these studies is that many tropical stream fishes increase dietary breadth to take advantage of abundant resources during the wet season, then resort to more specialized feeding during the dry season when interspecific competition for limited resources favors consumption of foods for which each species has greatest relative foraging efficiency based on morphology. For example, the scale-feeding glass characid, Roeboides dayi, eats large amounts of seasonally-abundant aquatic insects during the wet season, but shifts to a diet of mostly fish scales during the dry season when densities of a diverse array of invertebrate-feeding fishes tend to increase as the habitat diminishes (Peterson and Winemiller, 1997). Like several other scale-feeding

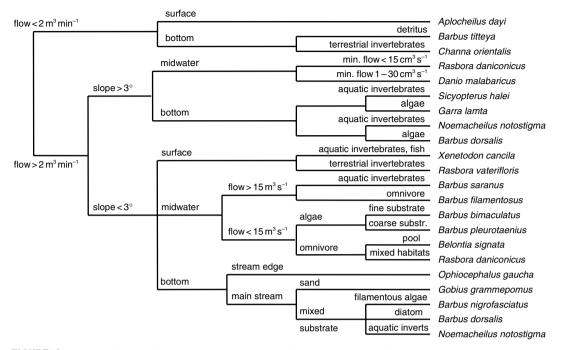


FIGURE 6 Ecological 'key' illustrating the high degree of microhabitat and food resource partitioning reducing ecological overlap among fishes in a Sri Lankan stream (from Moyle and Senanayake (1984)).

Neotropical characids, R. dayi has external teeth on the snout used to dislodge scales from the flanks of fishes, but this morphological specialization is of little service during the wet season when aquatic insects and other invertebrates are plentiful.

Tropical stream fishes occupy almost the entire spectrum of trophic niches that can occur in aquatic communities (Fig. 7). Periphyton grazers are present in stream habitats in almost every region and elevation. Most of them possess inferior mouths, often with fleshy lips, and numerous spatulate teeth for rasping; cyprinids, which lack jaw teeth, often possess horny oral ridges used for rasping. Periphyton is abundant in both high- and low-gradient streams, but can be limited by availability of light and solid substrates. For this reason, specialist grazers may be uncommon in streams with shifting sand substrates, especially where there is dense shading by riparian forest. In lowland streams with muddy beds, the surfaces of aquatic macrophytes or woody debris often support sufficient periphyton to support grazing fishes. In these and other streams, many grazing fishes shift to feeding on detritus and sediments rich in organic matter when periphyton stocks are reduced (as may happen on a seasonal basis). However, detritus is a less nutritious resource for grazers, such as loricariid catfishes (Power, 1984a), and it is probably only consumed when periphyton is scarce.

Phytoplankton is rarely a major component of the diet of tropical stream fishes, perhaps reflecting its relative scarcity in streams compared to lakes and wetlands, but it is a significant component of the diet of the tiny Asian cyprinid *Pectenocypris balaena* (Roberts, 1989). Zooplankton tend to be rare in the water column of upland streams, but many fishes in lowland streams consume large amounts. Most zooplankton feeders, including larvae of nearly all species, consume individual zooplankton, but some African and Neotropical catfishes, such as Hemisynodontis membranaceus and Hypophthalmus edentatus, and the Neotropical cichlid Chaetostoma flavicans have morphological specializations allowing them to consume zooplankton by filter feeding.

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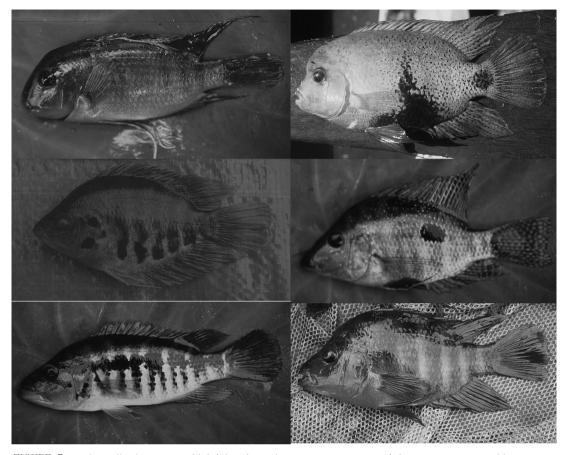


FIGURE 7 Ecologically divergent cichlid fishes from the Tortuguero region of the Costa Rican Caribbean coast: top-left – Neetroplus nematopus (algae grazer); top-right – Vieja maculicauda (detritivore); middle-left – Archocentrus centrarchus (invertebrate picker); middle-right – Astatheros rostratum (invertebrate feeding substrate sifter); bottomleft – Parachromis dovii (piscivore); bottom-right – Amphilophus citrinellus (generalized carnivore). Similar patterns of interspecific dietary and ecomophological diversity are observed among cichlid faunas throughout the Neotropics and tropical Africa (see colour plate section).

Aquatic invertebrates are important food sources for stream fishes throughout the tropics. Taxa consumed depend on stream elevation, topography, and other landscape features that influence aquatic habitat characteristics, but insects of the major aquatic orders are common in the diets of many fishes, and small crustaceans are important dietary items in low-gradient streams. Larger decapod crustaceans and mollusks are also important food, although mollusks and some other taxa can be virtually absent in extreme blackwater conditions of low pH and hardness. Invertebrate meiofauna are selected by specialist feeders, usually tiny benthic fishes such as the burrowing trichomycterid catfishes of the Neotropics, or may be consumed in bulk by sediment feeders (e.g. Neotropical prochilodontids and curimatids).

Terrestrial arthropods are consumed by many tropical fishes, and these allochthonous resources assume greater importance in small forest streams and along the land-water interface of larger streams and wetlands. Their importance in fish diets has been shown in all tropical regions, including Amazonian rainforest (Knöppel, 1970), Sri Lanka (Moyle and Senanayake, 1984) and West Africa (Paugy and Bénech, 1989). Species with surface-oriented morphologies seem to specialize on terrestrial insects (e.g. the characid *Corynopoma riisei* and poeciliid *Alfaro cultratus* in the Neotropics), and the terrestrial invertebrates that live on floating mats of

aquatic vegetation can be of great importance in the diets of fishes associated with such habitats: examples from the Neotropics include *Astronotus ocellatus* (Cichlidae) and the driftwood catfish *Parauchenipterus galeatus* (Auchenipteridae).

Although herbivory upon macrophytes is common in tropical fish assemblages, relatively few tropical fishes consume the non-reproductive tissues of living plants (Agostinho *et al.*, 2003a). Exceptions are Neotropical *Pterodoras* spp. (Doradidae), that sometimes consume large amounts of aquatic macrophytes. *Schizodon* spp. (Anostomidae) specialize on aquatic vegetation, and have morphological adaptations (oral and pharyngeal teeth, gill rakers, alimentary canal) for this diet (Ferretti *et al.*, 1996). Elsewhere, *Tilapia rendalli* in the Upper Zambezi consume large amounts of emergent and floating grasses (Winemiller and Kelso-Winemiller, 2003). More often, are consumed by fishes the non-reproductive parts of macrophytes in the form of detritus: examples include curimatids and prochilodontids in South America, distiched other detritivores have long guts and other morphological and physiological adaptations for extracting energy and nutrients from refractory organic material (Fugi and Hahn, 1991; Delariva and Agostinho, 2001).

Terrestrial plants tissues, especially flowers, fruits and seeds, are very important resources for fishes in tropical streams. Many fruit- and seed-eating fishes have dentition specialized for crushing (e.g. *Brycon*, *Colossoma*, *Myleus*, *Metynnis*, and other bryconine and serrasalmine Characidae), and when seeds are not destroyed, fishes can be significant seed dispersal agents for riparian and floodplain trees in the Neotropics (Goulding, 1980; Souza-Stevaux *et al.*, 1994; Horn, 1997; Mannheimer *et al.*, 2003). Most fishes that feed on fruits and seeds also consume invertebrates, but the proportion depends on season and habitat.

Piscivorous fishes exhibit variable degrees of feeding specialization: some feeding nonselectively while others are highly specialized for the pursuit and capture of particular types of prey in terms of morphology and/or behavior. Piscivores are well represented among the bonytongues (Osteoglossiformes), cichlids, catfishes (especially the Ariidae, Bagridae, Clariidae, Schilbeidae, Siluridae and Pimelodidae), snakeheads (Channidae), centropomids (e.g. barramundi and Nile perches), and characiformes (certain groups within the Atestidae and Characidae). Erythrinids (e.g. Hoplias, Hoplerythrinus) are the most common and widespread piscivores in small Neotropical streams (Araújo-Lima et al., 1995). Other groups contain relatively few piscivorous genera or species (e.g. the Mormyridae, Cyprinidae, and Gymnotiformes). Piscivores tend to be represented by fewer species at lower population abundance than other trophic groups. Most consume their prey whole, but a few piscivores bite pieces of flesh or fins from prey that may be as large or larger than themselves (e.g. the South American Serrasalmus and Cetopsis spp., African Hydrocynus brevis and Ichthyoborus spp., and Asian Channa spp.). Scale-feeding fishes are found in streams of the Neotropical (*Roeboides* spp. and *Exodon para*doxus: Characidae) and Indian-Asian-Australian regions (Chanda nama: Ambassidae). Some members of the Neotropical catfish family Trichomycteridae feed on mucus (Ochmacanthus spp.: Winemiller and Yan, 1989) or blood (e.g. species of Vandellia, Paravandellia, Stegophilus, and Acanthopoma: Machado and Sazima, 1982) from the gill filaments from other fishes. In contrast to this extreme specialization, virtually all piscivores eat aquatic invertebrates during their larval and juvenile stages, and adults of some species continue to include quantities of decapod crustaceans and other large invertebrates in their diets. A few Neotropical piscivores even consume tetrapod vertebrates. Perhaps most remarkable among these is the South American bonytongue Osteoglossum bicirrhosum, which can leap more than a meter above the water surface to capture snakes, birds and bats (Goulding, 1980).

The feeding-guild structure of several tropical stream fish assemblages has been examined by analysing stomach contents. In a Panamanian stream studied by Angermeier and Karr (1983), the assemblage comprised seven guilds: insectivores consuming aquatic insects (11 species/size

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classes), general insectivores (six species), grazers of algae (five species), omnivores (two species), and one species each of a terrestrial herbivore, a piscivore, and a scale eater. A Sri Lankan stream had a similar guild structure; six species eating aquatic insects, six grazer species, four omnivores, three species feeding on terrestrial insects, two piscivores (that also ate invertebrates), and a detritivore (Moyle and Senanayake, 1984). A small coastal creek in Costa Rica supported seven species feeding on algae and detritus, five piscivores (that also ate invertebrates), and three omnivores; the equivalent species totals for each guild in a larger creek in the same area were six, eleven, and two, respectively, plus eleven species that ate invertebrates and two piscivores (Winemiller, 1987). In an Andean piedmont stream in Venezuela, the fish assemblage was made up of four species feeding on algae and detritus, eight species that ate invertebrates, six omnivores, and a piscivore, whereas a lowland creek in the Venezuelan llanos had equivalent species totals of 9, 21, 12, 6 plus a further 6 species that fed on fish and invertebrates. The dietary data of these four stream assemblages in Costa Rica and Venezuela were analyzed by Winemiller and Pianka (1990) using null-model algorithms. There was statistically-significant guild structure within all assemblages, and niche partitioning within guilds, with the guild structure being more developed during the dry season when, as discussed above, resources are more limited and density-dependent factors influence populations.

Several studies have revealed the important influence of fishes on ecosystem dynamics in tropical streams. Strong effects of a migratory detritivore, Prochilodus mariae, on sediments as well as algal and invertebrate community structure - in a Venezuelan piedmont stream (Río Las Marías) have been experimentally demonstrated by Flecker (1996). Reduced discharge during the dry season results in sedimentation of suspended clay particles. By ingesting and resuspending fine sediments, P. mariae shift the periphyton assemblage from dominance by relatively inedible cyanobacteria to dominance by diatoms. Changes in sediments and algal stocks also influences nutrient dynamics in the ecosystem (Flecker et al., 2002). For reasons not yet understood, P. mariae migrations into the stream are low in the dry season of some years and high in others; consequently, the stream ecosystem shifts between two alternative states depending on the abundance of *P. mariae*. When *P. mariae* are rare, the stream has clear water, a thick layer of fine sediments on the stream bed, and dominance of the periphyton by cyanobacteria which are responsible for high rates of nitrogen fixation. During years when large numbers of *P. mariae* migrate into the stream, it has turbid water, a thin layer of sediments on the stream bed, diatom-dominated periphyton, and lower nitrogen fixation rates. Prochilodus inhabit deep pools and runs, but other benthic herbivorous and detritivorous fishes in Río Las Marías have similar ecosystem 'engineering' effects in shallow riffles (Flecker, 1997). Parodon apolinari (Parodontidae), Ancistrus triradiatus, and Chaetostoma milesi (Loricariidae) prefer to graze algae from stone surfaces, but they will ingest overlying sediments in order to access periphyton; this sediment removal has potential implications for primary production. When Power (1990) experimentally manipulated densities of the Ancistrus spinosus in a Panamanian stream, she found that benthic algal stocks and rates of photosynthesis were greatest under light grazing pressure that removed accumulated fine sediments.

Recent work by McIntyre *et al.* (2007) has shown strong effects of fishes on nutrient cycling in a Neotropical stream (Río Las Marías, Venezuela). Different species varied significantly in the rate at which they excreted nitrogen and phosphorus, with excretion of one or other nutrient – and hence nutrient cycling – being dominated by a relatively small subset of the 69 species in the steam. Simulations showed that elimination of one or more of these species would cause significant reductions in the rate of nutrient cycling, with the greatest changes being associated with loss of fishes targeted by fishermen.

Benthivorous fishes have been shown to undergo seasonal shifts in diet, apparently in response to changes in relative availability of algae and organic-rich sediments. Virtually all benthic algivorous fishes inhabiting a lowland creek in the Venezuelan llanos (Caño Maraca)

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had guts containing mostly algae during the wet season, but diets were dominated by detritus during the dry season (Winemiller, 1990, 1996b). Omnivorous characid fishes in the same system remove periphyton from the roots of floating aquatic macrophytes, and showed less extreme seasonal shifts in the amounts of algae that they ingested. Other consequences of fish consumption of algae have been shown by Power (1983, 1984b) who demonstrated that the distribution of loricariid catfishes – and hence periphyton – in a Panamanian stream was influenced by the threat of predation by wading birds. Because grazing by loricariids reduces algal standing stocks, fish avoidance of shallow-water areas where the predation threat was high led to a 'bath-tub ring' of algae in the shallow marginal areas of deep pools. A small Venezuelan piedmont stream that contained a similar loricariid fauna did not show the same pattern of algal distribution, which has been attributed to the relative rarity of piscivorous birds and/or additional smaller species of grazers in shallow pool margins (Winemiller and Jepsen, 1998).

Pringle and Hamazaki (1997, 1998) experimentally manipulated fish access to benthic periphyton in a Costa Rican lowland stream. In the presence of seven species of algae-gleaning fishes, the periphyton assemblage was dominated by cyanobacteria and chironomid (Diptera) larvae. In the absence of these fishes, diatoms dominated the periphyton, and aquatic insects were more diverse and abundant. The fish effects were modified by the occurrence of periodic scouring flash floods that tended to cause relatively greater reductions of periphyton stocks and insect abundance in fish-exclusion areas. Additional complexity in this system arises from the fact that the effect of fishes, which are diurnal feeders, is modified by decapod crustaceans (prawns) that feed at night. Experiments manipulating access to patches by fishes, prawns, or both revealed an additive effect of diurnal and nocturnal grazers, but a greater effect of diurnal fishes.

Food chains in tropical streams are consistently short, usually only three or four trophic levels (Winemiller, 1990). Food webs are comprised of dozens, if not hundreds of food chains,

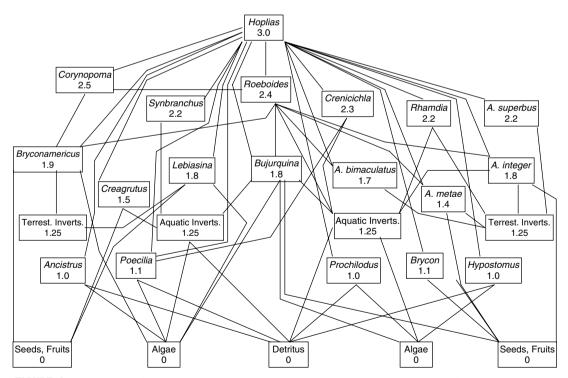


FIGURE 8 Caño Volcán food web (piedmont stream, Venezuela) illustrating the dominant functional groups and trophic links (based on Winemiller, 1990). Algae, detritus, seeds/fruit, aquatic macroinvertebrates, and terrestrial invertebrates have been aggregated. Numbers are estimated trophic level values.

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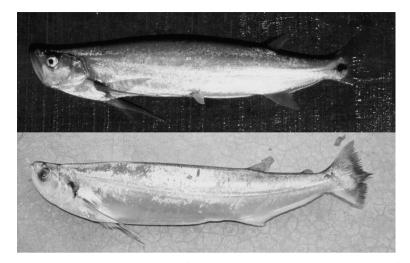


FIGURE 9 Convergent evolution in piscivorous fishes with specialized morphology and feeding behavior: Macrochirichthys macrochirus (Cypriniformes: Cyprinidae) from Southeast Asia and Indonesia (top); Rhaphiodon vulpinus (Characiformes: Cynodontidae) from South America (bottom) (see colour plate section).

originating from aquatic and terrestrial primary producers and detritus to fishes (Fig. 8). In the tropics, stream fishes seem to have claimed, in evolutionary terms, some of the niche space occupied by aquatic invertebrates in temperate regions. Fishes that live as periphyton grazers and detritivores are more common and diverse in the tropics. The abundances of fishes species feeding at lower trophic levels as primary consumers results in direct and relatively efficient conversion of primary production into fish biomass, implying that food chains leading to fish biomass are more efficient in tropical streams than their temperate equivalents. Unfortunately this hypothesis is difficult to test because of a number of potential factors that confound latitudinal comparisons (e.g. phylogenetic history/constraints, latitudinal differences in photoperiod and net annual production, etc.), although it is apparent that tropical freshwater systems frequently support impressively high fish production and harvest (Welcomme, 1985). In surprising contrast to the high fish production in large tropical rivers, however, small streams in Venezuela (Penczak and Lasso, 1991), Borneo (Watson and Balon, 1984), and Brazil (Agostinho and Penczak, 1995; Mazzoni and Lobón-Cerviá, 2000) are less productive then similar-sized streams at temperate latitudes.

As mentioned above, tropical stream fishes reveal consistent patterns of association between feeding behavior and morphology (Moyle and Senanayake, 1984; Watson and Balon, 1984; Wikramanayake, 1990; Winemiller, 1991; Mérigoux and Ponton, 1998). Herbivores and detritivores have long alimentary canals and often possess specialized dentition for scraping or raking materials from substrates. Seed and fruit eaters have intermediate gut lengths and dentition that allows efficient mastication. Zooplanktivorous filter feeders have long, comb-like gill rakers. Piscivores have large, often upturned, mouths, sharp conical or triangular teeth, oro-pharyngeal tooth plates, and short guts. Body shape, fin dimensions and placement, and the relative position of the eyes and mouth combine to indicate swimming behavior and habitat affinities. Because these general patterns are robust, tropical freshwater fishes reveal extensive convergent evolution in ecomorphology (Fig. 9). Convergent morphologies and associated ecological attributes have been demonstrated by statistical comparisons among the assemblages of weakly electric African mormyrids and South American gymnotiformes (Winemiller and Adite, 1997), cichlid fishes from assemblages in Africa, and South America (Winemiller et al., 1995), and entire fish assemblages from lowland habitats in Africa, Central America, South America, and two temperate regions (Winemiller, 1991). One inference arising from

comparative studies is that the highly-diverse Central American cichlids have undergone more recent adaptive radiation than the other fluvial cichlid faunas.

V. CONSERVATION OF FISH BIODIVERSITY

The high taxonomic and ecological diversity of stream fishes in the tropics provides a unique and extensive record of evolutionary biological diversification for scientific study. Tropical stream fishes provide striking examples of ecological convergence, and the limited dispersal ability of many freshwater fish clades makes them particularly amenable to evolutionary investigations. However, this diverse fauna is not merely of scientific or aesthetic interest. Tropical stream fishes are important food resources for humans and, in large areas of Africa and Asia in particular, freshwater fishes are the primary source of animal protein. They are also the genetic reservoirs of current and future aquaculture stocks. Across much of the tropics, stream fishes are collected for export via the aquarium and ornamental fish trade, and can be of considerable economic importance. Sport fishing in some tropical rivers supports ecotourism that may have potential for expansion. Leaving aside discussion of the complex and unpredictable effects of global climate change on stream fishes (reviewed by Poff et al., 2001), the major threats to stream fishes and the ecological integrity of their habitats, are outlined below. This is followed by a brief account of some possible management responses to alleviate the worst effects of human impacts on stream fishes. A more detailed treatment of conservation issues relevant to tropical streams is given in Chapter 10 of this volume.

A. Drainage-basin Degradation and Land-use Change

The primary threat to the ecological integrity of tropical streams and the long-term survival of their fish faunas is degradation of watersheds by a variety of human activities. The largest impact is from deforestation and conversion of land to agriculture, which modifies light regimes, increases mortality of eggs and larvae due to more ultraviolet radiation reduces, inputs of allochthonous energy and woody debris, and increases sedimentation, nutrient loading, and agrochemical inputs (see review by Pusey and Arthington, 2003). Removal of trees is poorly regulated or practiced illegally in some tropical countries, and the impacts on drainage basins and riparian zones can be devastating. Complete deforestation can lead to streams that are waterless during the dry season, and the wet season run-off from spates that result in soil erosion and transport of sediments, in addition to flash floods of higher amplitude and shorter duration than are experienced under forested conditions. Together, these changes result in the elimination of all but the most resistant and resilient fish species. Complete deforestation of local drainage basins in the Andean piedmont of Venezuela during the last 30 years have reduced fish assemblages in many streams from approximately 25 species to fewer than 10. Resistant species, including Hoplias malabaricus, Poecilia reticulata, and Bujurauina pulcher, are tolerant of habitat disturbances and can reproduce year-round. Migratory species, such as Prochilodus mariae, Brycon whitei, and Salminus hilarii, are eliminated from streams that they formerly occupied during the dry season (Lilyestrom and Taphorn, 1978; Winemiller et al., 1996). In areas of Ecuador with fragmented forests, beta diversity is higher among stream fishes in forested areas relative to sites that have been deforested, indicating greater heterogeneity in species composition (Bojsen and Barriga, 2002). In addition, the percentage of rare species making up assemblages in Ecuadorian streams is positively correlated with canopy cover.

Deforestation of riparian areas in savanna regions can be particularly devastating. Poff *et al.* (2001) report that the number of fish species in a stream draining the Guyana Shield region of southern Venezuela declined from 80 to 5 following riparian deforestation (associated with

highway construction) that resulted in high turbidity, reduced flow, loss of shade, and increased water temperatures. In tropical Asia, where the loss rate of forest cover is estimated from 0.9% to 2.1% per year, deforestation is a major cause of declining fish biodiversity, because the allochthonous materials from riparian zones and seasonally-inundated forest provide important food resources for numerous fishes (Dudgeon, 2000a).

B. Pollution

Many tropical countries lack resources for adequate sewage treatment, and considerable organic matter and other substances are released directly into streams. Throughout tropical Africa, and in parts of tropical Asia, untreated waste from cities, towns and villages are discharged into streams with negative influences on ecosystems and human health. Certain agricultural practices, especially sugar-cane processing, also increase organic loads in streams, and in South America, the use of alcohol fuel for vehicles has greatly increased land conversion. Signs of impacts on streams are widespread: pollution has eliminated fish from 5% of the total length of China's major rivers (Dudgeon (2000a), and pollution impacts are reported to be apparent in most Indian rivers (Natarajan, 1989). Many cities in tropical Latin America still have grossly inadequate sewage treatment, and release industrial wastes into surface waters. Cities in São Paulo State, Brazil, treat only about 8% of their effluents (Agostinho *et al.*, 1995). Excessive loads of dissolved and particulate organic matter result in increased biological oxygen demand and acute and chronic reductions in dissolved oxygen in the water column of streams, with dire consequences for most fish species.

Some forms of agriculture (e.g. rice, cotton), as practiced in developing tropical countries, result in large inputs of pesticides and herbicides into streams. In the Venezuelan llanos, for instance, applications of pesticides in rice fields have resulted in mass mortality of stream fishes. Large floodplain ecosystems may dilute agricultural chemicals (Nico *et al.*, 1994). Excessive loading of dissolved organic matter from sugarcane processing plants causes dry-season fish kills in some streams of the South American llanos that are important seasonal refugia for regional fish populations (Winemiller *et al.*, 1996). Urban and industrial pollution in the Lake Valencia Basin of Venezuela has resulted in depauperate stream fish assemblages and the possible extirpation of at least one endemic species (Provenzano *et al.*, 2003). Mercury contamination from gold-mining operations, which is often combined with degradation of watersheds, has impacted stream fishes throughout the Neotropics (Winemiller and Morales, 1989; Nico and Taphorn, 1994). More subtle effects on fishes have been observed: a pollution gradient in a southern Brazilian river was associated with reductions in oocyte diameter and gonadal indices as well as altered gonadosomatic relationships in *Astyanax fasciatus* relative to conspecifics from unpolluted sites (Schulz and Martins-Junior, 2001).

C. Dams and Impoundments

The impacts of dams on river hydrology and biodiversity are well recognized (Allan and Flecker, 1993; Dudgeon, 2000b). Streams are often impounded to create reservoirs for local water supplies, for aquaculture or sport fishing, or to produce hydroelectric power. Construction of small impoundments for hydroelectric power is increasing in Southern Brazil, because most of the large rivers already have been fully exploited for this purpose. Moreover, it is relatively easy and inexpensive to dam low-order streams, and small impoundments built for various purposes have proliferated throughout the tropics. In arid regions, these impoundments may enhance survival of fishes that would otherwise suffer high mortality when streams dry out periodically. Notwithstanding, the primary concern arising from construction of dams and impoundments is the loss of habitat connectivity and migration corridors, both of which have serious consequences for fish populations (Winemiller *et al.*, 1996; Benstead *et al.*, 1999).

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D. Overfishing

Rural people in many tropical countries rely extensively on fishery resources in small streams. Most higher-order streams contain significant populations of large fishes, even but the smallest lowland streams support stocks of large fishes, such as clariid catfishes (Africa), mastacembelid eels (Asia), and erythrinid characiforms and callichthyid catfishes (South America). Many stream fish populations are greatly overexploited, especially in densely settled areas. The placement of gillnets or barrage-type fish traps across stream channels to intercept migrating fishes usually have significant negative consequences for local stocks. Depletion of particular species that are responsible for high rates of phosphorus or nitrogen excretion can also have implications for nutrient recycling and hence local stream productivity (McIntyre et al., 2007). Catches from heavily-fished streams consist mainly of smaller opportunistic species with high reproductive effort and rapid population turnover. Examples include the small cyprinids and catfishes that are dietary staples of impoverished rural people throughout Southeast Asia, India, and Africa. Improved fishery management could increase productivity if fish populations were allowed to contain greater numbers of larger-bodied adults with higher fecundity. Unfortunately, degradation of aquatic habitats and drainage basins usually accompanies overexploitation, which further reduces stream fish production.

E. Exotic Species

Introductions of exotic (non-indigenous) species are a threat to native fishes and the ecological integrity of streams worldwide. The problem has been better documented in temperate regions, but Lévêque (1997) listed 27 documented exotic fish introductions into African countries. Most other reported cases of inter-continental introductions in the tropics involve African tilapiine cichlids ('tilapias'), originally imported for aquaculture. These fishes thrive in lacustrine habitats in many parts of the Neotropics, but their establishment in streams seems to be limited to low-diversity coastal drainages and degraded habitats where native species were reduced or eliminated prior to tilapia introductions. However, invasions are still proceeding. Many small lakes have been created to support pay-to-fish businesses in Brazil, most of them based on African tilapia. In Maringá municipality (Paraná state), at least 40 of these small businesses use tilapia, and a recent survey of streams in the area found tilapia in all samples, sometimes as the only species present (Fernandes et al., 2003). Tilapia populations also have become established in India and parts of Southeast Asia and northern Australia. Another widespread exotic is the mosquitofish (Gambusia affinis), a North American poeciliid that has been introduced throughout the tropics and subtropics to control mosquito larvae. Like tilapia, mosquitofish populations seem to flourish in degraded streams and low-diversity streams of coastal drainages.

A prevalent problem in the tropics is inter-basin transfers of non-indigenous fishes within regions. Such transfers have increased in southern Brazil over the past two decades. For the most part, species native to the Amazon Basin (e.g. *Cichla* spp., *Astronotus ocellatus* and the sciaenid *Plagioscion squamosissimus*) have become established in the Upper Paraná and Paraguay basins. Many introductions were initially to small impoundments for sport fishing. In addition to being transferred between basins within South America, peacock cichlids (*Cichla* spp.), which are voracious piscivores and popular sportfish, have been introduced to Florida, Hawaii, Puerto Rico, Panama, and Malaysia. As well as deliberate introductions, exotic ornamental fishes frequently are released by accident. The illegal development of fish farms for exotic species along stream banks, and other violations of guidelines designed to prevent escape, have been responsible for the release of an estimated 1.3 billion non-native fishes into streams of a single sub-basin of the Paraná River during floods in January, 1997 (Orsi and Agostinho, 1999). A subsequent increase in lerniosis (a disease caused by the parasitic copepod crustacean *Lernaea cyprinacea*) among native fishes increased sharply (Gabrielli and Orsi, 2000). A striking

example of the extent of exotic fish introductions has been recorded from the Paraiba do Sul River Basin, southeastern Brazil, which is the main center of ornamental fish farming in South America. Magalhães *et al.* (2002) reported 22 non-indigenous ornamental species in a single stream and a reservoir in the region, and there was evidence of reproduction by several species.

VI. MANAGEMENT TO ALLEVIATE HUMAN IMPACTS AND RESTORE DEGRADED STREAMS

Appropriate drainage-basin management is essential to avoid stream sedimentation, altered hydrology, and increased loads of nutrients and organic matter. Protection of vegetation cover, maintenance of the integrity of riparian zones, and reductions in point- and non-point-source pollution are essential components of conservation and management strategies for stream fishes. Appropriate regulations exist in many tropical countries, but, for a variety of reasons, are not enforced or are enforced weakly. In some regions land-use practices are unregulated, or follow traditions that have existed for centuries. Sociological and economic tools and incentives will be an essential part of any solution to the persistent environmental problems associated with poverty in developing tropical countries.

Dam construction should, ideally, be limited to streams where fishes do not migrate or where such migrations are not an essential part of the life cycle or breeding. In regions where fish migrations occur (as in most of the tropics), dams should be limited to one or few tributaries within drainage basins thereby preserving some connectivity within system. In cases where this approach is impractical due to economic or social imperatives, research will be needed on the construction of appropriate fish passageways combined with monitoring of their effectiveness.

Relative to temperate streams, very little research has been conducted on tropical stream fishes in support of management. More research is needed on many aspects of the biology numerous poorly-known species, such as fish-habitat relationships and factors influencing population dynamics and production (for further information, see below). Existing fisheries regulations are weakly enforced in many tropical regions, and community-based approaches to regulate fishing effort that involve local people need to be developed and implemented. Promotion of existing examples of self-regulation (e.g. the Tonlé Sap fishery in Cambodia), including descriptions of possible pitfalls and shortcomings, could offer models for the management of tropical stream resources. Inter-basin and inter-regional transfers of fishes must be halted by legislation and all other means. While some exotic introductions are well intended, most still occur in a context of ecological naivety. The potential benefits of exotics pose unacceptable risks for native biota, and eradication of established exotics is virtually impossible in most instances. As an alternative, increased efforts to explore the suitability of native fishes for aquaculture and sport fishing are needed.

VII. RESEARCH NEEDS

Despite the many threats to tropical stream fishes, and the societal and economic constraints upon measures to address them, the steps needed to improve both the scientific foundations for management of tropical stream fishes and the effectiveness of management can be described succinctly (Stiassny, 1996). One of the most pressing needs is additional surveys of habitats and biotic diversity in regions of the tropics, such as the Congo Basin, where the ichthyofauna is still poorly known. Existing survey data need to be taxonomically verified and updated, and regional databases should be compiled and maintained for analysis of new impacts, long-term trends, and management

needs. Regional databases could be combined to facilitate analysis of broader-scale biogeographic patterns, regional variation in species richness, and invasions by exotic species.

Knowledge of critical fish-habitat relationships in tropical streams lags far behind that available for temperate streams. This information is essential for assessment of human impacts and management of fish stocks. Incredibly, the habitat affiliations of most tropical stream fishes remain undocumented, and habitat use at critical stages of their life cycles (e.g. breeding) is often not well understood. This information will be essential to broader understanding of the influence of environmental variation at different scales on fish-habitat relationships. Population and assemblage dynamics, both seasonally and inter-annually, as well as the reproductive biology and life-history strategies of the great majority of tropical stream fishes remain undocumented. In addition to such fundamental research, studies are needed to assess the negative impacts of human activities (e.g. channel obstructions, deforestation, nutrient enrichment) on fish populations and the stream ecosystems that support them. Such studies could pave the way for development of new approaches or technologies to mitigate impacts (e.g. fish passageways, riparian management, wetland restoration).

Much greater understanding of species interactions (especially food webs) and their influence on population dynamics in species-rich communities is required for effective fisheries management, and this information gap is particularly large for tropical freshwater systems. Continued and improved assessment of past and current management practices on fish populations will be needed if we are to achieve sustainable harvest of fish stocks.

REFERENCES

- Adebisi, A.A. (1988). Changes in the structural and functional components of the fish community of the upper Ogun River, Nigeria. *Arch. Hydrobiol.* **113**, 457–463.
- Abes, S.S., and Agostinho, A.A. (2001). Spatial patterns in fish distributions and structure of the ichthyocenosis in the Água Nanci stream, upper Paraná River Basin, Brazil. *Hydrobiologia* 445, 217–227.
- Agostinho, A.A., and Penczak, T. (1995). Populations and production of fish in two small tributaries of the Paraná River, Paraná, Brazil. *Hydrobiologia* **312**, 153–166.
- Agostinho, A.A., Barbieri, G., and Verani, J.R. (1991). Idade e crescimento do cascudo preto *Rhinelepis áspera* (Siluriformes, Loricariidae) no rio Paranapanema, bacia do rio Paraná. UNIMAR, Maringá 13, 249–258.
- Agostinho, A.A., Vazzoler, A.E.A. de M., and Thomaz, S.M. (1995). The high Paraná River Basin: limnological and ichthyological aspects. In "Limnology in Brazil". (J.G. Tundisi, C.E.M. Bicudo, and T. Matsumura-Tundisi, Eds.), pp. 59–103. ABC/SBL, Rio de Janeiro, Brazil.
- Agostinho, A.A., Gomes, L.C., and Julio, H.F., Jr (2003a). Relações entre macrófitas e fauna de peixes: implicações no controle de macrófitas. In "Ecologia e Manejo de Macrófitas Aquáticas" (S.M. Thomas and L.M. Bini, Eds.), pp. 261–279. Editora da Universidade Estadual de Maringá, Maringá, Brazil.
- Agostinho, A.A., Gomes, L.C., Suzuki, H.I., and Júlio, H.F., Jr (2003b). Migratory fishes of the upper Paraná River Basin, Brazil. In "Migratory Fishes of South America: Biology, Fisheries and Conservation Status" (J. Carolsfeld, B. Harvey, C. Ross, and A. Baer, Eds.), pp. 19–99. World Fisheries Trust, Victoria, Canada.
- Allan, J.D., and Flecker, A.S. (1993). Biodiversity conservation in running waters. BioScience 43, 32-43.
- Allen, G.R., Midgley, S.H., and Allen, M. (2002). "Field Guide to the Freshwater Fishes of Australia". Western Australian Museum, Perth.
- Alves, C.B.M., and Vono, V. (1997). A ictiofauna do córrego Gameleira, afluente do rio Grande, Uberaba (MG). Acta Limnologica Brasiliensia 9, 23–31.
- Amaral, M.F., Aranha, J.M.R., and Menezes, M.S. (1998). Reproduction of the freshwater catfish *Pimelodella pap-penheimi* in Southern Brazil. *Stud. Neotrop. Fauna Environ.* 33, 106–110.
- Amaral, M.F., Aranha, J.M.R., and Menezes, M.S. (1999). Age and growth of *Pimelodella pappenheimi* (Siluriformes, Pimelodidae) from an Atlantic Forest stream in Southern Brazil. *Braz. Arch. Biol. Tec.* 42, 449–453.
- Angermeier, P.L., and Karr, J.R. (1983). Fish communities along environmental gradients in a system of tropical streams. *Environ. Biol. Fish.* 9, 117–135.
- Aranha, J.M.R., Takeuti, D.F., and Yoshimura, T.M. (1998). Habitat use and food partitioning of the fishes in a coastal stream of Atlantic forest, Brazil. Rev. Biol. Trop. 46, 955–963.

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Araújo-Lima, C.A.R.M., Agostinho, A.A., and Fabré, N.N. (1995). Trophic aspect of fish communities in Brazilian rivers and reservoirs. In "Limnology in Brazil" (J.G. Tundisi, C.E.M. Bicudo, and T. Matsumura-Tundisi, Eds.), pp. 105–136. ABC/SBL, Rio de Janeiro, Brazil.

Arratia, G.F. (1983). Preferencias de habitat de peces siluriformes de águas continentales de Chile (Fam. Diplomystidae y Trichomycteridae). Stud. Neotrop. Fauna Environ. 18, 217–237.

Balon, E.K. (1975). Reproductive guilds of fishes: a proposal and definition. J. Fish. Res. Bd. Can. 32, 821-864.

Balon, E.K., and Stewart, D.J. (1983). Fish assemblages in a river with unusual gradient (Luongo, Africa Zaïre system), reflections on river zonation, and description of another new species. *Environ. Biol. Fish.* 9, 225–252.

- Benstead, J.P., March, J.G., Pringle, C.M., and Scatena, F.N. (1999). Effects of a low-head dam and water abstraction on migratory tropical stream biota. *Ecol. Appl.* 9, 656–668.
- Bhat, A. (2005). Ecomorphological correlates in tropical stream fishes of southern India. *Environ. Biol. Fishes*, 73, 211–225.
- Bistoni, M.A., and Hued, A.C. (2002). Patterns of fish species richness in rivers of the central region of Argentina. Braz. J. Biol. 62, 753-764.
- Bojsen, B.H., and Barriga, R. (2002). Effects of deforestation on fish community structure in Ecuadorian Amazon streams. *Freshw. Biol.* 47, 2246–2260.
- Buck, S., and Sazima, I. (1995). An assemblage of mailed catfishes (Loricariidae) in southeastern Brazil: distribution, activity, and feeding. *Ichthyol. Explor. Freshw.* 6, 325–332.
- Buckup, P.A. (1999). Sistemática e Biogeografia de Peixes de Riachos. In "Ecologia de Peixes de Riachos" (E.P. Caramaschi, R. Mazzoni, and P.R. Peres-Neto, Eds.), Série Oecologia Brasiliensis, Vol. 6, pp. 91–138. PPGE-UFRJ, Rio de Janeiro.
- Bührnheim, C.M., and Fernandes, C.C. (2001). Low seasonal variation of fish assemblages in Amazonian rain forest streams. *Ichthyol. Explor. Freshw.* 12, 65–78.
- Bührnheim, C.M., and Fernandes, C.C. (2003). Structure of fish assemblages in Amazonian rain-forest streams: effects of habitat and locality. Copeia, 2002, 255–262.
- Burcham, J. (1988). Fish communities and environmental characteristics of two lowland streams in Costa Rica. Revista Biologia Tropical 36, 273–285.
- Bussing, W.A. (1976). Geographical distribution of the San Juan Ichthyofauna of Central America with remarks on its origin and ecology. In "Investigations of the Ichthyofauna of Nicaraguan Great Lakes" (T.B. Thorson, Ed.), pp. 157–175. University Nebraska Press, Lincoln.
- Campos, H.C. (1982). Zonacion de los peces em los rios del sur de Chile. Actas del VIII Congreso Latinoamericano de Zoologia. (P.J. Salinas, Ed.), pp. 1417–1431. Mérida, Venezuela.
- Cardona, M., Roman-Valencia, J.L.L., and Hurtado, T.H. (1998). Composicion y diversidad de los peces de la quebrada San Pablo en el alto Cauca, Colombia. *Bol. Ecotrop. Ecossistemas Trop.* **32**, 11–24.
- Casatti, L., Langeani, F., and Castro, R.M.C. (2001). Peixes de riacho do Parque Estadual Morro do Diabo, bacia do alto rio Paraná, SP. Biota Neotropica, Vol. 1, No. 1, http://www.biotaneotropica.org.br/v1n12/pt/abstract?inventory + BN 1122001.
- Castro, R.M., and Casatti, L. (1987). The fish fauna from a small forest stream of the upper Paraná River Basin, Southeastern Brazil. Ichthyol. Explor. Freshw. 7, 337-352.
- Chapman, L.J., and Kramer, D.L. (1991). The consequences of flooding for the dispersal and fate of poeciliid fish in an intermittent tropical stream. Oecologia 87, 299–306.
- Chapman, L.J., Kramer, D.L., and Chapman, C.A. (1991). Population dynamics of the fish *Poecilia gilli* (Poeciliidae) in pools of an intermittent tropical stream. J. Anim. Ecol. 60, 441–453.
- Chernoff, B., and Willink, P.W., Eds. (1999). A Biological Assessment of the Aquatic Ecosystems of the Upper Rio Orthon Basin, Pando, Bolivia. Bulletin of Biological Assessment 15, Conservation International, Washington, DC.
- Costa, W.J.E.M. (1984). Peixes fluviais do sistema lagunar de Maricá, Rio de Janeiro, Brazil. *Atlântica* (Rio Grande, Brazil) 7, 65–72.
- Costa, W.J.E.M. (1987). Feeding habits of a fish community in a tropical coastal stream, Rio Mato Grosso, Brazil. Stud. Neotrop. Fauna Environ. 22, 145–153.
- Covich, A.P., and McDowell, W.H. (1996). The stream community. In "The Food Web of a Tropical Rain Forest" (D.P. Reagan and R.B. Waide, Eds.), pp. 434–459. University of Chicago Press, Chicago.
- Delariva, R.L., and Agostinho, A.A. (2001). Relationship between morphology and diets of six Neotropical loricariids. J. Fish Biol. 58, 832–847.
- de Mérona, B. (1981). Zonation ichthyologique du bassin du Bandama (Côte d'Ivoire). Rev. Hydrobiol. Trop. 16, 103-113.
- de Pinna, M.C.C., and Winemiller, K.O. (2000). A new species of Ammoglanis (Siluriformes, Trichomycteridae) from Venezuela. Ichthyol. Explor. Freshw. 11, 255–264.
- de Silva, S.S., Schut, J., and Kortmulder, K. (1985). Reproductive biology of six *Barbus* species indigenous to Sri Lanka. *Environ. Biol. Fish.* **3**, 201–218.
- Dudgeon, D. (1993). The effects of spate-induced disturbance, predation and environmental complexity on macroinvertebrates in a tropical stream. *Freshw. Biol.* 30, 189–197.

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- Dudgeon, D. (2000a). The Ecology of tropical Asian rivers and streams in relation to biodiversity conservation. *Annu. Rev. Ecol. Syst.* **31**, 239–263.
- Dudgeon, D. (2000b). Large-scale hydrological changes in tropical Asia: prospects for riverine biodiversity. *BioScience* **50**, 793–806.
- Edds, D.R. (1993). Fish assemblage structure and environmental correlates in Nepal's Gandaki River. Copeia, 1993, 48–60.
- Fernandes, R., Gomes, L.C., and Agostinho, A.A. (2003). Pesque e pague: negócio ou fonte de dispersão de espécies exóticas? Acta Sci. (Brazil) 25, 115-120.
- Ferretti, C.M.L., Andrian, I.F., and Torrente, G. (1996). Dieta de duas espécies de Schizodon (Characiformes, Anostomidae), na planície de inundação do Alto Rio Paraná e sua relação com aspectos morfológicos. Bol. Inst. Pesca (Brazil) 23, 171–186.
- Flecker, A.S. (1996). Ecological engineering by a dominant detritivore in a diverse tropical stream. *Ecology* 77, 1845–1854.
- Flecker, A.S. (1997). Habitat modification by tropical fishes: environmental heterogeneity and the variability of interaction strength. J. N. Am. Benthol. Soc. 16, 286–295.
- Flecker, A.S., Taphorn, D.C., Lovell, J.A., and Feifarek, B.P. (1991). Drift of characin larvae, *Bryconamericus deuterodonoides*, during the dry season from Andean piedmont streams. *Environ. Biol. Fish.* **31**, 197–202.
- Flecker, A.S., Taylor, B.W., Berhardt, E.S., Hood, J.M., Cornwell, W.K., Cassatt, S.R., Vanni, M.J., and Altman, N.S. (2002). Interactions between herbivorous fishes and limiting nutrients in a tropical stream ecosystem. *Ecology* 83, 1831–1844.
- Fraser, D.F., Gilliam, J.F., MacGowan, M.P., Arcaro, C.M., and Guillozet, P.H. (1999). Habitat quality in a hostile river corridor. *Ecology* 80, 597-607.
- Fugi, R., and Hahn, N.S. (1991). Espectro alimentar e relações morfológicas com o aparelho digestivo de três espécies de peixes comedores de fundo do Rio Paraná, Brasil. *Rev. Bras. Biol.* 51, 873–879.
- Gabrielli, M.A., and Orsi, M.L. (2000). Dispersão de *Lernaea cyprinacea* (Linnaeus) (Crustacea, Copepoda) na região norte do estado do Paraná, Brasil. *Rev. Bras. Zool.* 17, 395–399.
- Gaigher, I.G. (1973). The habitat preferences of fishes from the Limpopo River System, Transvaal and Mozambique. *Koedoe* 16, 103–116.
- Garutti, V. (1989). Contribuição ao conhecimento reprodutivo de Astyanax bimaculatus (Ostariophysi, Characidae), em cursos de água da bacia do Paraná. *Rev. Bras. Biol.* 49, 489–495.
- Goulding, M. (1980). "The Fishes and the Forest". University of California Press, Berkeley.
- Grossman, G.D., Ratajczak, R.E., Jr, Crawford, M., and Freeman, M.C. (1998). Assemblage organization in stream fishes: effects of environmental variation and interspecific interactions. *Ecol. Monogr.* 68, 395–420.
- Horn, M.H. (1997). Evidence for dispersal of fig seeds by the fruit-eating characid fish *Brycon guatemalensis* Regan in a Costa Rican tropical rain forest. *Oecologia* 109, 259–264.
- Hugueny, B. (1989). West African rivers as biogeographic islands: species richness of fish communities. Oecologia 79, 236–243.
- Hugueny, B. (1990). Richesse des peuplements de poissons dans le Niandan (Haut Niger, Afrique) en fonction de la taille de la riviére et de la diversité du milieu. *Rev. Hydrobiol. Trop.* 23, 351–364.
- Hugueny, B., and Lévêque, C. (1994). Freshwater fish zoogeography in west Africa: faunal similarities between river basins. *Environ. Biol. Fish.* **39**, 365–380.
- Hugueny, B., and Pouilly, M. (1999). Morphological correlates of diet in an assemblage of West African freshwater fishes. J. Fish Biol. 54, 1310–1325.
- Humphries, P., King, A.J., and Koehn, J.D. (1999). Fish, flows and flood plains: links between freshwater fishes and their environment in the Murray-Darling River system, Australia. *Environ. Biol. Fish.* 56, 129–151.
- Ibarra, M., and Stewart, D.J. (1989). Longitudinal zonation of sandy beach fishes in the Napo River Basin, Eastern Ecuador. *Copeia*, **1989**, 364–381.

Inger, R.F., and Chin, P.K. (1962). The freshwater fishes of North Borneo. Fieldiana, Zool. 45, 1–268.

- Jayaram, K.C. (1999). "The Freshwater Fishes of the Indian Region". Narendra Publishing, Delhi.
- Jiménez, J.L., Román-Valencia, C., and Cardona, M. (1998). Distribución y constancia de las comunidades de peces em la Quebrada San Pablo, Cuenca del Rio La Paila, Alto Cauca, Colombia. *Actual. Biol.* 20, 21–27.
- Knöppel, H.-A. (1970). Food of central Amazonian fishes: contribution to the nutrient-ecology of Amazonian rain-forest streams. Amazoniana 2, 257–352.

Kramer, D.L. (1978a). Reproductive seasonality in the fishes of a tropical stream. Ecology 59, 976–985.

- Kramer, D.L. (1978b). Terrestrial group spawning of *Brycon petrosus* (Pisces: Characidae) in Panama. *Copeia*, 1978, 536–537.
- Kramer, D.L., Lindsey, C.C., Moodie, G.E.E., and Stevens, E.D. (1978). The fishes and aquatic environment of the central Amazon Basin, with particular reference to respiratory patterns. *Can. J. Zool.* 56, 717–729.
- Lemes, E.M., and Garutti, V. (2002a). Ecologia da ictiofauna de um córrego de cabeceira da bacia do alto rio Paraná, Brasil. *Iheringia* **92**, 69–78.

5. Fish Ecology in Tropical Streams 143

- Lemes, E.M., and Garutti, V. (2002b). Ictiofauna de poção e rápido em um córrego de cabeceira da bacia do alto rio Paraná. Com. Mus. Ciênc. Tecnol. PUCRS, Sér. Zool., Porto Alegre, 15, 175–199.
- Lévêque, C. (1997). "Biodiversity Dynamics and Conservation : The Freshwater Fish of Tropical Africa". Cambridge University Press, Cambridge.
- Lilyestrom, C.G., and Taphorn, D.C. (1978). Aspectos sobre la biología y conservación de la palambra (Brycon whitei) Myers y Weitzman, 1960. Rev. UNELLEZ Ciénc. Tecnol., Guanare, Venezuela 1, 53–59.
- Lobón-Cerviá, J., Utrilla, C.G., and Querol, E. (1994). An evaluation of the 3-removal method with electrofishing techniques to estimate fish numbers in streams of the Brazilian Pampa. Arch. Hydrobiol. 130, 371–381.
- Lowe-McConnell, R.H. (1964). The fishes of the Rupununi Savanna District of British Guiana, South America. Pt I. Ecological groupings of fish species and effects of the seasonal cycle on the fish. J. Linn. Soc. (Zool.) 45, 103–144.
- Lowe-McConnell, R.H. (1979). Ecological aspects of seasonality in fishes in tropical waters. In "Fish Phenology" (P.J. Miller, Ed.), pp. 219–241. Symposium of the Zoological Society, No. 44, London Academic Press.
- Lowe-McConnell, R.H. (1987). "Ecological Studies in Tropical Fish Communities". Cambridge University Press, Cambridge.
- Luiz, E.A., Agostinho, A.A., Gomes, L.C., and Hahn, N.S. (1998). Ecologia trófica de peixes em dois riachos da bacia do rio Paraná. Rev. Bras. Biol. 58, 273–285.
- Lundberg, J.G., Marshall, L.G., Guerrero, J., Horton, B., Malabarba, M.C.S.L., and Wesselingh, F. (1998). The stage for Neotropical fish diversification: a history of tropical South American rivers. In "Phylogeny and Classification of Neotropical Fishes" (L.R. Malabarba, R.E. Reis, R.P. Vari, Z.M.S. Lucena, and C.A.S. Lucena, Eds.), pp. 13–68. EDIPUCRS, Porto Alegre, Brasil.
- Machado, F.A., and Sazima, I. (1982). Comportamento alimentar do peixe hematófago Branchioica bertonii (Siluriformes, Trichomycteridae). Ciênc. Cult. 35, 344–348.
- Magalhães, A.L.B., Amaral, I.B., Ratton, T.F., and Brito, M.F.G. (2002). Ornamental exotic fishes in the Gloria reservoir and Boa Vista stream, Paraíba do Sul River Basin, state of Minas Gerais, southeastern Brazil. Comun. Mus. Cienc. Tecnol. PUCRS, Ser. Zool., Porto Alegre 15, 265–278.
- Mannheimer, S., Bevilacqua, G., Caramaschi, E.P., and Scarano, F.R. (2003) Evidence for seed dispersal by the catfish Auchenipterichthys longimanus in an Amazonian lake. J. Trop. Ecol. 19, 215–218.
- Martin-Smith, K.M. (1998). Relationships between fishes and habitat in rainforest streams in Sabah, Malaysia. J. Fish Biol. 52, 458–482.
- Matthews, W.J. (1998). "Patterns in Freshwater Fish Ecology". Chapman and Hall, New York.
- Matthews, W.J., and Heins, D.C. (1987). "Community and Evolutionary Ecology of North American Stream Fishes". University Oklahoma Press, Norman.
- Mazzoni, R., and Lobon-Cerviá, J. (2000). Longitudinal structure, density and rates of a Neotropical stream fish assemblage: River Ubatiba in the Serra do Mar, Southeast Brazil. *Ecography* 23, 588–602.
- Mazzoni, R., and Petito, J. (1999). Reproductive biology of a tetragonopterinae (Osteichthyes, Characidae) of the Ubatiba fluvial system, Maricá, RJ. Braz. Arch. Biol. Technol. 42, 455-461.
- Mazzoni, R., Caramaschi, E.P., and Fenerich-Verani, N. (2002). Reproductive biology of a Characidiinae (Osteichtyes, Characidae) from the Ubatiba River, Maricá, RJ. Braz. J. Biol. 62, 487–494.
- McIntyre, P., Jones, L.E., Flecker, A., and Vanni, M.J. (2007). Fish extinctions alter nutrient recycling in freshwaters. PNAS 104, 4461–4466.
- Menezes, M.S., and Caramaschi, E.P. (1994). Características reprodutivas de Hypostomus grupo H. punctatus no rio Ubatiba, Marica, RJ (Osteichthyes, Siluriformes). Rev. Bras. Biol. 54, 503–513.
- Menni, R.C., Gómez, S.E., and López Armengol, F. (1996). Subtle relationships: freshwater fishes and water chemistry in southern South America. *Hydrobiologia* 328, 173–197.
- Menni, R.C., Miquelarena, A.M., and Volpedo, A.V. (2005). Fishes and environment in northwestern Argentina: from lowland to Puna. *Hydrobiologia* 544, 33–49.
- Mérigoux, S., and Ponton, D. (1998). Body shape, diet and ontogenetic diet shifts in young fish of the Sinnamary River, French Guiana, South America. J. Fish Biol. 52, 556-569.
- Mérigoux, S., Ponton, D., and de Merona, B. (1998). Fish richness and species-habitat relationships in two coastal streams of French Guiana, South America. *Environ. Biol. Fish.* 51, 25–39.
- Mérigoux, S., Hugueny, B., Ponton, D., Statzner, B., and Vauchel, P. (1999). Predicting diversity of juvenile Neotropical fish communities: patch dynamics versus habitat state in floodplain creeks. Oecologia 118, 503–516.
- Miranda, J.C., and Mazzoni, R. (2003). Composição da ictiofauna de três riachos do alto rio Tocantins, GO. Biota Neotropica v3 (n1) http://www.biotaneotropica.org.br/v3n1/pt/abstract?article + BN 00603012003.
- Moyle, P.B., and Senanayake, F.R. (1984). Resource partitioning among the fishes of rainforest streams in Sri Lanka. J. Zool. Lond. 202, 195–223.
- Myers, G.S. (1966). Derivation of the freshwater fish fauna of Central America. Copeia, 1966, 766-773.
- Natarajan, A.V. (1989). Environmental impacts of Ganja basin development on Renepool and fisheries of the Ganga river system. Can. Spec. Publ. Aquat. Sci. 106, 545–560.
- Nico, L.G., and Taphorn, D.C. (1994). Mercury in fish from gold-mining regions in the upper Cuyuni River system, Venezuela. *Fresenius Environ. Bull.* 3, 287–292.

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- Nico, L.G., Schaeffer, D.J., Taphorn, D.C., and Barbarino-Duque, A. (1994). Agricultural chemical screening and detection of chlorpyrifors in fishes from the Apure drainage, Venezuela. *Fresenius Environ. Bull.* 3, 685–690.
- Orsi, M.L., and Agostinho, A.A. (1999). Introdução de espécies de peixes por escapes acidentais de tanques de cultivo em rios da bacia do Rio Paraná, Brasil. *Rev. Bras. Zool.* 16, 557–560.
- Paugy, D., and Bénech, V. (1989). Poissons d'eau douce des bassins côtiers du Togo (Afrique de l'Ouest). Rev. Hydrobiol. Trop. 22, 295–316.
- Pavanelli, C.S., and Caramaschi, E.P. (1997). Composition of the ichthyofauna of two small tributaries of the Paraná River, Porto Rico, Paraná State, Brazil. *Ichthyol. Explor. Freshw.* 8, 23–31.
- Pavanelli, C.S., and Caramaschi, E.P. (2003). Temporal and spatial distribution of the ichthyofauna in two streams of the Upper Rio Paraná Basin. *Braz. Arch. Biol. Technol.* 46, 271–280.
- Penczak, T., and Lasso, C. (1991). Problems of estimating populations parameters and production of fish in a tropical rain forest stream in northern Venezuela. *Hydrobiologia* **215**, 121–133.
- Penczak, T., Agostinho, A.A., and Okada, E.K. (1994). Fish diversity and community structure in two small tributaries of the Paraná River, Paraná state, Brazil. *Hydrobiologia* 294, 243–251.
- Peterson, C.C., and Winemiller, K.O. (1997). Ontogenetic diet shifts and scale-eating in *Roeboides dayi*, a Neotropical characid. *Environ. Biol. Fish.* 49, 111–118.
- Poff, L., Angermeier, P., Cooper, S., Lake, P., Fausch, K., Winemiller, K., Mertes, L., Rahel, F., Oswood, M., and Reynolds, J. (2001). Climate change and stream fish diversity In "Future Scenarios of Global Biodiversity" (O.E. Sala, T. Chapin, and E. Huber-Sannwald, Eds.), p. 315–349. Springer–Verlag, New York.
- Pouilly, M. (1993). Habitat, écomorphologie et structure des peuplements de poisons dans trios petits cours d'eau tropicaux de Guinée. *Rev. Hydrobiol. Trop.* 26, 313-325.
- Power, M.E. (1983). Grazing responses of tropical freshwater fishes to different scales of variation in their food. Environ. Biol. Fish. 9, 103-115.
- Power, M.E. (1984a). The importance of sediment in the grazing ecology and size class interactions of an armored catfish, *Ancistrus spinosus. Environ. Biol. Fish.* **10**, 173–181.
- Power, M.E. (1984b). Depth distribution of armored catfish: predator-induced resource avoidance? *Ecology* 65, 523-528.
- Power, M.E. (1990). Resource enhancement by indirect effects of grazers: armored catfish, algae, and sediment. *Ecology* 71, 897–904.
- Prance, G.T. (1982). "Biological Diversification in the Tropics". Columbia University Press, New York.

Pringle, C.M., and Hamazaki, T. (1997). Effects of fishes on algal response to storms in a tropical stream. *Ecology* 78, 2432–2442.

- Pringle, C.M., and Hamazaki, T. (1998). The role of omnivory in a Neotropical stream: separating diurnal and nocturnal effects. *Ecology* **79**, 269–280.
- Provenzano, F.R., Schaefer, S.A., Baskin, J.N., and Royer-Leon, R. (2003). New, possibly extinct lithogenine loricariid (Siluriformes, Loricariidae) from Northern Venezuela. *Copeia*, 2003, 562–575.
- Pusey, B.J., and Arthington, A.H. (2003). Importance of the riparian zone to the conservation and management of freshwater fish: a review. *Mar. Freshw. Res.* 54, 1–16.
- Reznick, D., and Endler, J.A. (1982). The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). Evolution 36, 160–177.
- Roberts, T.R. (1986). Danionella translucida, a new genus and species of cyprinid fish from Burma, one of the smallest living vertebrates. Environ. Biol. Fish. 16, 231–241.
- Roberts, T.R. (1989). The freshwater fishes of western Borneo (Kalimantan Barat, Indonesia). *Mem. California Acad. Sci.* 14, 1–210.
- Sabino, J., and Castro, R.M.C. (1990). Alimentação, período de atividade e distribuição espacial dos peixes de um riacho da floresta atlântica (Sudeste do Brazil). *Rev. Bras. Biol.* 50, 23-36.
- Sabino, J., and Zuanon, J. (1998). A stream fish assemblage in Central Amazônia: distribution, activity patterns and feeding behavior. *Ichthyol. Explor. Freshw.* 8, 201–210.
- Sánchez-Botero, J.I., Garcez, D.S., and Palacio, B.J. (2002). Distribuón de la ictiofauna y actividad pesquera en la microcuenca del Rio Chajeradó Atrato Medio, Antioquia Colombia. Actualidades Biológicas, Medellín, Colômbia 24, 157–161.
- Schlosser, I. (1987). A conceptual framework for fish communities in small warmwater streams. In "Community and Evolutionary Ecology of North American Stream Fishes" (W.J. Matthews and D.C. Heins, Eds.), pp. 17–24. University Oklahoma Press, Norman.
- Schulz, U.H., and Martins-Junior, H. (2001). Astyanax fasciatus as bioindicator of water pollution of Rio dos Sinos, RS, Brazil. Braz. J. Biol. 6, 615–622.
- Schut, J., de Silva, S.S., and Kortmulder, K. (1984). Habitat associations and competition of eight Barbus (=Puntius) species (Pisces, Cyprinidae) indigenous to Sri Lanka. Netherlands J. Zool. 34, 159–181.
- Schwassman, H.O. (1978). Times of annual spawning and reproductive strategies in Amazonian fishes. In "Rhythmic Activity of Fishes" (J.E. Thorpe, Ed.), pp. 187–200. Academic Press, London.

5. Fish Ecology in Tropical Streams 145

- Skelton, P.H. (1993). "An Illustrated Guide to the Freshwater Fishes of Southern Africa". Southern Book Publishers, Halfway House, South Africa.
- Souza-Stevaux, M.C., Negrelle, R.R.B., and Citadini-Zanette, V. (1994). Seed dispersal by the fish *Pterodoras granulosus* in the Paraná River Basin, Brazil. J. Trop. Ecol. 10, 621–626.
- Stiassny, M.L.J. (1996). An overview of freshwater biodiversity: with some lessons from African fishes. *Fisheries* 21, 7–13.
- Suzuki, H.I., Agostinho, A.A., and Winemiller, K.O. (2000). Relationship between oocyte morphology and reproductive strategy in loricariid catfishes of the Paraná River, Brazil. J. Fish Biol. 56, 791–807.
- Uieda, V.S. (1984). Ocorrência e distribuição de peixes em um riacho de água doce. Rev. Bras. Biol. 44, 203-213.
- Uieda, V.S., and Barretto, M.G. (1999). Composição da ictiofauna de quatro trechos de diferentes ordens do rio Capivara, Bacia do Tietê, Botucatu, SP. *Rev. Bras. Zoociênc.* 1, 55-67.
- Uieda, V.S., and Uieda, W. (2001). Species composition and spatial distribution of a stream fish assemblage in the east coast of Brazil; comparison of two field study methodologies. *Braz. J. Biol.* 61, 377–388.
- Vari, R.P., and Malabarba, L.R. (1998). Neotropical ichthyology: an overview., eds. In "Phylogeny and Classification of Neotropical Fishes" (L.R. Malabarba, R.E. Reis, R.P. Vari, Z.M.S. Lucena, and C.A.S. Lucena, Eds.), pp 1–11. EDIPUCRS, Porto Alegre.
- Ward-Campbell, B.M.S., Beamish, F.W.H., and Kongchaiya, C. (2005). Morphological characteristic in relation to diet in five coexisting Thai fish species. J. Fish Biol. 67, 1266–1279.
- Watson, D.J., and Balon, E.K. (1984). Structure and production of fish communities in tropical rain forest streams of northern Borneo. Can. J. Zool. 62, 927–940.
- Weitzman, S.H., Menezes, N.A., and Weitzman, M.J. (1988). Phylogenetic biogeography of the Glandulocaudini (Teleostei: Characiformes, Characidae) with comments on the distributions of other freshwater fishes in Eastern and Southeastern Brazil. In "Proceedings of a Workshop on Neotropical Distribution Patterns" (P.E. Vanzolini and W.R. Heyer, Eds.), pp. 379–427. Academia Brasileira de Ciências, Rio de Janeiro.
- Welcomme, R.L. (1969). The biology and ecology of the fishes of a small tropical stream. Zool. J. Linn. Soc. 158, 485-529.
- Welcomme, R.L. (1985). River fisheries. FAO Fish. Tech. Pap. 262, 1-330.
- Wikramanayake, D. (1990). Ecomorphology and biogeography of a tropical stream fish assemblage: evolution of assemblage structure. *Ecology* 71, 1756–1764.
- Winemiller, K.O. (1983). An introduction to the freshwater fish communities of Corcovado National Park, Costa Rica. Brenesia 21, 47–66.
- Winemiller, K.O. (1987). "Tests of Ecomorphological and Community Level Convergence among Neotropical Fish Assemblages". Unpublished Ph.D. dissertation, University of Texas, Austin.
- Winemiller, K.O. (1989a). Development of dermal lip protuberances for aquatic surface respiration in South American characid fishes. Copeia, 1989, 382–390.
- Winemiller, K.O. (1989b). Patterns of variation in life history among South American fishes in seasonal environments. Oecologia 81, 225–241.
- Winemiller, K.O. (1989c). Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan llanos. *Environ. Biol. Fish.* 26, 177–199.
- Winemiller, K.O. (1990). Spatial and temporal variation in tropical fish trophic networks. Ecol. Monogr. 60, 331-367.
- Winemiller, K.O. (1991). Ecomorphological diversification of freshwater fish assemblages from five biotic regions. Ecol. Monogr. 61, 343-365.
- Winemiller, K.O. (1992). Life history strategies and the effectiveness of sexual selection. Oikos 62, 318-327.
- Winemiller, K.O. (1993). Reproductive seasonality in livebearing fishes inhabiting rainforest streams. Oecologia 95, 266–276.
- Winemiller, K.O. (1996a). Dynamic diversity: fish communities of tropical rivers. In "Long-term Studies of Vertebrate Communities" (M.L. Cody and J.A. Smallwood, Eds.), pp. 99–134. Academic Press, San Diego.
- Winemiller, K.O. (1996b). Factors driving spatial and temporal variation in aquatic floodplain food webs. In "Food Webs: Integration of Patterns and Dynamics" (G.A. Polis and K.O. Winemiller, Eds.), pp. 298–312. Chapman and Hall, New York.
- Winemiller, K.O., and Adite, A. (1997). Convergent evolution of weakly-electric fishes from floodplain habitats in Africa and South America. *Environ. Biol. Fish.* 49, 175–186.
- Winemiller, K.O., and Jepsen, D.B. (1998). Effects of seasonality and fish movement on tropical river food webs. J. Fish Biol. 53 (Suppl. A), 267–296.
- Winemiller, K.O., and Kelso-Winemiller, L.C. (2003). Food habits of tilapiine cichlids of the Upper Zambezi River and floodplain during the descending phase of the hydrologic cycle. J. Fish Biol. 63, 120–128.
- Winemiller, K.O., and Leslie, M.A. (1992). Fish communities across a complex freshwater-marine ecotone. *Environ. Biol. Fish.* 34, 29–50.
- Winemiller, K.O., and Morales, N.E. (1989). Comunidades de peces del Parque Nacional Corcovado luego del cese de las actividades mineras. Brenesia 31, 75–91.

146 *Winemiller* et al.

- Winemiller, K.O., and Pianka, E.R. (1990). Organization in natural assemblages of desert lizards and tropical fishes. *Ecol. Monogr.* 60, 27-55.
- Winemiller, K.O., and Rose, K.A. (1992). Patterns of life-history diversification in North American fishes: implications for population regulation. *Can. J. Fisb. Aquat. Sci.* **49**, 2196–2218.
- Winemiller, K.O., and Yan, H.Y. (1989). Obligate mucus feeding in a South American trichomycterid catfish. Copeia 1989, pp. 511–514.
- Winemiller, K.O., Kelso-Winemiller, L.C., and Brenkert, A.L. (1995). Ecological and morphological diversification in fluvial cichlid fishes. *Environ. Biol. Fish.* 44, 235–261.
- Winemiller, K.O., Marrero, C., and Taphorn, D.C. (1996). Perturbaciones causadas por el hombre a las poblaciones de peces de los llanos y del piedemonte Andino de Venezuela. *Biollania Guanare, Venezuela* 12, 13–48.
- Zaret, T.M., and Rand, A.S. (1971). Competition in tropical stream fishes: support for the competitive exclusion principle. *Ecology* 52, 336-342.