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Fish Ecology in Tropical Streams

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This chapter emphasizes the ecological responses of fishes to spatial and temporal variation in tropical stream habitats. At the global scale, the Neotropics has the highest fish fauna richness, with estimates ranging as high as 8000 species. Larger drainage basins tend to be associated with greater local and regional species richness. Within longitudinal stream gradients, the number of species increases with declining elevation. Tropical stream fishes encompass highly diverse reproductive strategies ranging from egg scattering to mouth brooding and livebearing, with reproductive seasons ranging from a few days to the entire year. Relationships between life-history strategies and population dynamics in different environmental settings are reviewed briefly.

Fishes in tropical streams exhibit diverse feeding behaviors, including specialized niches, such as fin and scale feeding, not normally observed in temperate stream fishes. Many tropical stream fishes have greater diet breadth while exploiting abundant resources during the wet season, and lower diet breadth during the dry season as a consequence of specialized feeding on a subset of resources. Niche complementarity with high overlap in habitat use is usually accompanied by low dietary overlap. Ecological specializations and strong associations between form and function in tropical stream fishes provide clear examples of evolutionary convergence.

Several studies have revealed the major influence of fishes on benthic ecosystem dynamics in tropical streams including effects on primary production and nutrient cycling. Tropical stream fishes are important food resources for humans in many countries, and significant conservation challenges include drainage-basin degradation, pollution, dams, overfishing, and introductions of exotic species.

I. INTRODUCTION

Freshwater fishes may comprise 25% of the vertebrate species on Earth (Stiassny, 1996). Like most major groups, they display greatest taxonomic diversity in tropical latitudes. Much of this diversity is associated with between-habitat (beta) and between-region (gamma) diversity among streams, and although species diversity within a particular habitat or stream (alpha diversity) can be impressive (Winemiller, 1996a), a broad survey of temperate and tropical streams reveals that, on average, tropical streams contain no greater, or only slightly greater,

species richness than comparably sized temperate streams (Matthews, 1998). In this chapter, 'streams' are defined as fluvial systems with channel widths up to approximately 30 m. By applying this simple definition, streams of many different gradients and positions within stream-order networks are included (Fig. 1). Moreover, streams associated with drainage basins of



FIGURE 1 Representative tropical stream habitats: top-left – upland stream, western Benin; top-right – creek draining uplands adjacent to Barotse floodplain, Upper Zambezi River, Zambia; middle-left – clearwater Río Aguaro in Venezuelan llanos; middle-right – blackwater ‘morichal’ in northeastern Venezuela; bottom-left – rainforest stream on Osa Peninsula, Costa Rica; bottom-right – lowland stream in coastal swamp-forest, Tortuguero, Costa Rica (see colour plate section).

different sizes and streams at different elevations will be discussed. Many of the issues and ecological mechanisms that are discussed in the context of stream fishes apply also to rivers (streams with channel widths > 30 m).

In this chapter, we describe the ecological strategies and responses of fishes to spatial and temporal variation in stream habitats at a range of scales. Streams are highly variable in both of these dimensions. Spatially, streams reveal large variation in local microhabitats, longitudinal patterns of zonation along elevation gradients, and inter-regional faunal differences. Temporal variation in many important environmental and ecological factors occurs on daily, seasonal, and inter-annual scales. Thus, it is impossible to make meaningful generalizations about stream fish ecology without a taking a scale-specific approach. This chapter is organised by first examining broad scales of variation in stream fish assemblages and subsequently describing ecological patterns and processes at successively smaller scales.

For many decades, research on tropical stream fishes lagged behind investigation of temperate stream fishes (e.g. Matthews and Heins, 1987), although there has been a significant increase in studies from several tropical regions in recent years, especially from Argentina, Brazil, French Guyana, Venezuela, and parts of West Africa. At present, however knowledge of tropical streams is less extensive than that of temperate areas, and this information shortfall is exacerbated by the fact that tropical regions contain a greater diversity of habitats and a much greater diversity of species. Moreover, our limited knowledge of tropical fish ecology limits our ability to seek broad ecological generalizations (Dudgeon, 2000a). Some of the conceptual models created to predict ecological patterns for temperate stream fishes probably apply well for tropical fishes, but others may not. Here our goal is to summarize current knowledge of stream fish ecology in the tropics, and to identify pertinent gaps in order to stimulate new research.

II. STREAM HABITATS AND FISH FAUNAS IN THE TROPICS

A. Landmasses and Watersheds

Perhaps the most obvious patterns of variation in stream fish assemblages occur at very broad spatial scales contrasting taxonomic composition of faunas from different continents and major river drainage basins. Historical contingencies in the evolution of fish lineages have resulted in biogeographic patterns. These patterns are particularly evident among freshwater-restricted lineages, because land and saltwater barriers impose a high degree of dispersal limitation. Thus, an interesting question is: what is the extent of ecological similarity (convergence) among stream fish assemblages inhabiting habitats with similar characteristics in different regions? We will attempt to address this question as we examine the ecological features of stream fishes, but first we compare and contrast the major geographic, landscape, and taxonomic characteristics within major regions of the Earth.

B. Continental Basins

Freshwater fishes show strong patterns of phylogeography at the continental scale. Detailed discussion of the geological and evolutionary factors associated with present day continental distributions of tropical fishes is beyond the scope of this chapter, but the major ichthyofaunal patterns in each tropical region are reviewed briefly.

1. Neotropics

The South and Central American rivers and streams contain the greatest number of species on Earth, with recent estimates ranging as high as 8000 and 25% of global fish species richness

(Vari and Malabarba, 1998). The main Neotropical orders are the Characiformes (tetras, piranhas, and related forms), Siluriformes (catfishes), Gymnotiformes (electric knifefishes or 'eels'), Perciformes (represented mostly by the Cichlidae), and the Cyprinodontiformes, represented mostly by Poeciliidae (livebearers) and Rivulidae (killifishes). Freshwater families containing relatively few species include the Lepidosirenidae (lungfish), Osteoglossidae (bonytongues), and Synbranchidae (swamp eels). Freshwater fishes of marine origin include the Potamotrygonidae (stingrays), Clupeidae (shads), Engraulidae (anchovies), Atheriniformes (silversides), Gobiidae (gobies), Eleotridae (sleepers), and Achiridae (soles). South America contains great river basins that yield rivers with huge discharges, including the Amazon (ranked first in the world with a discharge of $212\,500\text{ m}^3\text{ s}^{-1}$), Paraná/La Plata (fifth; $18\,800\text{ m}^3\text{ s}^{-1}$), Orinoco (ninth; $17\,000\text{ m}^3\text{ s}^{-1}$), Magdalena (17th; $7\,500\text{ m}^3\text{ s}^{-1}$), and São Francisco (33rd; $2\,800\text{ m}^3\text{ s}^{-1}$). Although small by South American standards, the most ichthyologically significant river basins in Central America are the Usumacinta (southern Mexico) and the San Juan (Nicaragua and Costa Rica). Small independent drainage basins throughout Central America form a dual series of drainages running along east and west versants of the Cordillera Central.

High species richness of freshwater fishes in South America is derived from a combination of historical, geological, and ecological factors. After the breakup of Gondwanaland (ca. 110 million years ago), the continent's complex geological history, including the uplift of the Andes and its effects on drainage systems (including changing the outflow of the Amazon drainage from west, to north, to east), provided many opportunities for vicariant speciation and dispersal (Lundberg *et al.*, 1998). Like other tropical regions, the continent experienced alternating periods of mesic and dry conditions over geologic time (Prance, 1982) yet, because of the continent's relatively low elevation, overall conditions were probably not as dry those that are thought to have prevailed in Africa (see below). Moreover, because of the presence of ancient Guyana and Brazilian Shields, South America probably experienced less marine intrusion, and hence fewer extinctions of freshwater species, than Southeast Asia.

The highest fish species richness in the Neotropics (and in any river on Earth) is within the Amazon Basin. Around 2000 species are known from the region, although the actual number is certainly much higher as many new Neotropical taxa are described each year (Vari and Malabarba, 1998). Most fishes of large-lowland rivers are distributed widely throughout the Amazon Basin, and some species that typically inhabit peripheral streams are also broadly distributed, such as *Hoplias malabaricus* (Erythrinidae), *Rhamdia quelen* (Heptapteridae), *Helogenes marmoratus* (Cetopsidae) and *Acestrorhynchus microlepis* (Acestrorhynchidae). Others apparently have fairly restricted distributions: e.g. *Paracheirodon axelrodi* (Characidae) in the upper Rio Negro drainage; *Hyphessobrycon* spp. (Characidae) and *Corydoras* (Callichthyidae) catfishes in various tributary sub-basins.

The Amazon Basin is permanently or intermittently connected to the Orinoco via the Casiquiare River (Rio Negro tributary) in southern Venezuela, to the Essequibo River (Guyana) via the headwaters of the Rio Branco (Rio Negro tributary), and to the Paraná River via the Rio Paraguay headwaters in the Pantanal region of southwestern Brazil. Thus, some large species, such as the catfishes *Zungaro jahu* (= *Paulicea lutkeni*) and *Hypophthalmus edentatus*, are distributed across all three major river basins. Even certain small species, such as the knifefish *Eigenmannia virescens* and the tetra *Moenkhausia dichrourea* appear to occur throughout all three river basins. However, given the rapid pace by which new phylogenetic research is changing our view of taxonomy and species distributions, it is possible that re-evaluation of the taxonomic status of wide-ranging species may reveal each of them to be two or more species. Small coastal river basins have depauperate freshwater fish faunas, although invasions by marine species can result in stream assemblages with species richness comparable to streams in large continental basins.

Several major groups of fishes are absent from Neotropical river basins beyond the Amazon. For example, osteoglossiformes are only present in the Amazon and Essequibo basins, and the lungfish (*Lepidosiren paradoxa*) is confined to the Amazon and Paraguay basins. Of relevance to stream ecology is the restriction of some fishes to streams having particular physicochemical characteristics. Three fairly distinctive water types have long been recognized in South America. Whitewaters drain uplands of relatively young geological formations, such as the Andes Mountains, and have comparatively high conductivity, nutrient loads, suspended sediment loads, and tend to have neutral or alkaline pH. Blackwater streams drain lowlands, especially those draining ancient geologic formations, such as the Guyana Shield in northern South America, and have low conductivity, dissolved nutrient concentrations, suspended sediment loads, and more acid pH. Humic acids leached from submerged vegetation produce the dark tea color and pH as low as 3–4. Clearwater streams can be found throughout the continent, but usually drain well-weathered uplands and carry relatively few suspended sediments. Depending on the landscape attributes and hydrology, clearwater streams may have neutral or acid pH, and low or high conductivity and nutrient concentrations. In general, streams with higher turbidity contain more siluriform and gymnotiform fishes since they can navigate and locate food under low light conditions using well-developed olfactory and electric sensory capabilities. Diurnal characiform and cichlid fishes comprise greater fractions of fish assemblages in clearwater and blackwater aquatic systems. Research by Menni *et al.* (1996, 2005, and references therein) in Argentina emphasizes the influence of local physicochemical conditions on stream fish distributions.

The Central American ichthyofauna is dominated by lineages derived from South American ancestors and freshwater species derived from marine lineages. Dispersal from South America into Central America occurred in two phases, with the earlier colonization by so-called secondary-division freshwater groups (Cichlidae, Poeciliidae) during the Late Cretaceous or Paleocene (Myers, 1966; Bussing, 1976). The second phase occurred after the final formation of the Isthmus of Panama during the Pliocene, and included taxa of the Characiformes, Siluriformes, Poeciliidae, and Cichlidae. Dominant marine-derived taxa include Eleotridae, Gobiidae, and mullets (Mugilidae). Several marine taxa (e.g. Centropomidae, Lutjanidae, Pomadasyidae, and Syngnathidae) enter streams and may occur dozens of kilometers inland, where they reside as integral parts of local fish assemblages.

2. Africa

The major rivers of Africa are the Congo (ranked second in the world with a discharge of $40\,480\text{ m}^3\text{ s}^{-1}$), Zambezi (19th; $7\,100\text{ m}^3\text{ s}^{-1}$), Niger (21st; $6\,100\text{ m}^3\text{ s}^{-1}$), and Nile (32nd; $2\,800\text{ m}^3\text{ s}^{-1}$); with the Volta ($1\,260\text{ m}^3\text{ s}^{-1}$) and Senegal ($690\text{ m}^3\text{ s}^{-1}$) also ranked within the top 50 rivers by discharge. Highest species richness (690) occurs in the Congo Basin (Hugueny, 1989), followed by the Niger (211), Volta (137), and Nile (127). The African ichthyofauna is dominated by Osteoglossiformes (weakly electric fishes of the Mormyridae), Characiformes (Alestidae, Hepsetidae, Citharinidae, and Distichodontidae), Cypriniformes (barbs), Siluriformes, Cyprinodontiformes (killifishes), and Perciformes (cichlids and Nile perches). Much of the African continent lies at higher elevation than South America or Southeast Asia, and consequently, fewer marine-derived species are represented in the African freshwater ichthyofauna. Marine-derived groups include anguillid eels and pufferfish (Tetraodontidae). The African ichthyofauna has traditionally been divided into faunal regions: Sudanian, Upper Guinea, Lower Guinea, Congo, East Coast, Zambezi, and South African (Lowe-McConnell, 1987). Distributions of individual species, however, do not necessarily adhere to these regional divisions. Lévêque (1997) provides examples of 10 distributional patterns for fishes of northern Africa.

Most of Africa has strongly seasonal rainfall. The wettest regions are the western and central Congo River Basin, Lower Guinea (Cameroon, Gabon, Central African Republic), and Upper Guinea in the region of the Niger River headwaters (Guinea) and along the coast (Sierra

Leone, Liberia, Cote d'Ivoire). Depending on soil composition and topography, these mesic areas usually contain mosaics of blackwater, clearwater, and whitewater streams. Blackwater streams mostly occur in rainforest areas that are poorly drained with oligotrophic soils. These mesic regions contain the richest and most ecologically-diverse fish faunas on the continent. As in South America and Asia, blackwater streams in Africa tend to support different fish species from whitewater streams; however some species such as *Hepsetus odoe* (Hepsetidae) and *Clarias gariepinus* (Clariidae) are fairly ubiquitous. Characiformes and cichlids tend to be relatively more abundant and diverse in blackwater streams than whitewater streams.

Streams of the Sahel, eastern Africa, and southern Africa lie within regions where seasonal precipitation has given rise to the development of extensive savanna and tropical dry forests. The Upper Niger River floodplains, Nile River, and mainstem Congo River have mostly whitewater characteristics. By contrast, the Upper Zambezi River, which drains sandy soils, has clearwater characteristics but after it accumulates dissolved and suspended solids from tributaries draining clay-rich soils, resembles a whitewater stream in its middle and downstream reaches. Relative to clearwater and blackwater streams, whitewater streams tend to be dominated by cyprinids, catfishes, and mormyrids. Relatively low fish species richness of the Sahel, eastern, and southern African river basins seems to be associated with major historic changes in rainfall as well as contemporary patterns of seasonal precipitation that frequently include extended periods of drought.

3. Asia–Australia

The tropical regions of Asia include southeastern China, the Indian subcontinent, Indo-China, the Malay Peninsula, and the East Indies. The major rivers of tropical Asia are the Brahmaputra (ranked fourth in the world with a discharge of $19\,800\text{ m}^3\text{ s}^{-1}$), Ganges (fifth; $18\,700\text{ m}^3\text{ s}^{-1}$), Mekong (13th; $11\,000\text{ m}^3\text{ s}^{-1}$), and Indus (22nd; $5\,600\text{ m}^3\text{ s}^{-1}$). The Asian fish fauna is dominated by Cypriniformes (barbs and loaches), Siluriformes, anabantoids (gouramis, climbing perches, snakeheads), and mastacembeloids (spiny eels), plus many freshwater species from the estuarine and marine groups including Beloniformes (halfbeaks and needlefish), Atheriniformes, Eleotridae, Gobiidae, and Tetraodontidae. The Cichlidae is represented by just three species (*Etilapia* spp.) in India and Sri Lanka that tolerate brackish water.

The rivers of continental Southeast Asia and the islands of Borneo and Sumatra have the highest fish species richness within Asia. However, despite the complex geologic history and great topographic diversity of Southeast Asia, some elements of the fish fauna reveal surprisingly high inter-basin similarity, with several species broadly distributed from India to western Borneo. Historic sea-level changes resulted in a series of marine intrusions and recessions over low-lying terrain of southeastern Asia that have created many opportunities for allopatric speciation and dispersal. In addition, the great river basins arising in the Himalayan Mountains (Ganges, Mekong, etc.) have provided high habitat diversity along elevation gradients and refuges for species throughout geologic and climatic changes.

Streams in the Australian-New Guinea region drain the land east of Wallace's Line, which divides Borneo and Sumatra in the west from Celebes (Sulawesi) and the Philippines in the east. The Fly is the largest river in this region. Stream fish assemblages contain fewer representatives of freshwater families and more marine-derived and marine taxa such as Mugilidae, Terapontidae, and Toxotidae. Rainbow fishes (Melanotaeniidae) are also an important and diverse group in this region. Thirty-five fish species occur in both New Guinea and the Cape York Peninsula of northeastern Australia, a reflection of land bridges that existed as recently as 6000–8000 years ago (Allen *et al.*, 2002). Northern Australia has over 100 freshwater fish species, with highest richness in the northeast or, and including many marine-derived or marine-dependent species (Allen *et al.*, 2002).

Habitats and physicochemical characteristics of streams vary considerably within the Asian-Australian tropical region depending on topography, geology, and soils. Blackwaters are present

in lowland regions of the Malay Peninsula, Borneo, and New Guinea, while upland streams in the major river basins of India and Southeast Asia tend to have whitewater and clearwater characteristics. In particular, the many rivers that arise in the Himalayas and Tibetan Plateau carry heavy sediment and nutrient loads, and streams draining alluvial floodplains tend to be highly productive with high biomass of macrophytes, invertebrates, and fishes. Northern Australian streams tend to be of the clearwater type, but some blackwater streams can be found in the northeast where rainfall is higher and landscapes more forested.

4. Coastal Drainages and Islands

Streams that drain directly into the sea have fish assemblages that are minor subsets of regional faunas and, with some exceptions, tend to have low endemism. Due to dispersal limitations, these coastal streams can be particularly depauperate. The species that are present are often those with some degree of salinity tolerance, such as the classification of certain groups a secondary freshwater groups proposed by Myers (1966) for Central America and the Caribbean. Salinity tolerance experiments with characid (low tolerance) and poeciliid (higher tolerance) fishes have supported this classification (Winemiller and Morales, 1989). Small coastal drainages in West Africa have fish assemblages that are subsets of the Niger-Chad-Sudan faunal province, although, some drainages contain endemic taxa (Hugueny and Lévêque, 1994). Fish species richness is a function of catchment surface area and discharge African rivers of West, with some areas containing more species and others containing fewer species than predicted by chance (Hugueny, 1989; see also Fig. 2). Patterns of species extinction and colonization associated with climatic variation (extended periods of drought conditions) during the Quaternary Period could account for the latter observation. A strong linear relationship between species richness and catchment area has also been obtained for coastal rivers of the Guyana region of northern South America (Mérigoux *et al.*, 1998). Coastal streams along the Brazilian Atlantic coast can be classified into three groups according to their endemic fish faunas (Buckup, 1999). Fish diversification in these drainages depends on the history of headwater drainage captures and especially vicariance and dispersion caused by sea level changes during the last 300 000 years (Weitzman *et al.*, 1988).

Marine fishes can dominate on islands and peninsular areas that have few species from freshwater-affiliated groups. For example, small streams on the Osa Peninsula of Costa Rica that drain directly into the Pacific Ocean contain only four freshwater species, but support large populations of eleotrids (three species), gobies (two species), mugilids, syngnathids, pomadasyids,

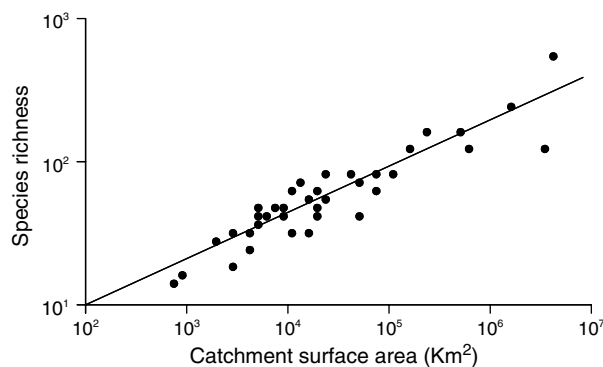


FIGURE 2 Plot showing the relationship between fish species richness and river drainage area in West Africa (from Hugueny, 1989).

lutjanids, gerreids, and tetraodontids (one species each: Winemiller, 1983). Fish assemblages on the Caribbean island of Puerto Rico are comprised entirely of marine and marine-dependent fish species (Covich and McDowell, 1996). *Sicydium plumieri* (Gobiidae) penetrates far inland (to 600 m asl) by climbing over waterfalls using its mouth and suctorial disk (fused pelvic fins). *Sicydium* species from islands (e.g. Hawaii) and coastal regions (e.g. Osa Peninsula) in other regions of the world show similar behavior and distribution.

C. Latitudinal Gradients

A strong correlate of latitudinal gradients in both the Northern and Southern hemispheres is annual variation in photoperiod and solar insolation yielding temperate–subtropical–tropical transitions in environmental conditions. How do patterns of fish species richness in small streams change with latitude in each region? Do any important taxonomic or functional groups of fishes drop out at subtropical or temperate latitudes within major biotic regions?

In the Americas, the northern transition zone occurs in Mexico, with mild temperate conditions in northern Tamaulipas yielding to subtropical conditions in southern Tamaulipas, and a tropical climate prevailing southward from Veracruz. All of Central America, the Caribbean, and South America down to the tropic of Capricorn is tropical, and within these regions, elevation gradients (see below) dominate climatic conditions more than latitude, particularly along the Andean Cordillera.

In northern Central America, there is a replacement of South American families (Characidae, Poeciliidae, Cichlidae) with North American families (Cyprinidae, Catostomidae, and Ictaluridae) (Bussing, 1976), and fish species seem to display less ecomorphological specialization northward across the temperate-tropical transition zone. For example, the species-rich stream-fish assemblages of the Usumacinta Basin of southern Mexico contain cichlids and poeciliids that exhibit a wider range of body sizes and diverse feeding strategies than assemblages from streams in San Luis Potosí and Tamaulipas. These more northern streams typically support one or two native cichlid species (*Herichthys* spp.), all of which are trophic generalists, and a few poeciliids that feed either on periphyton (*Xiphophorus* spp.) or small arthropods (*Gambusia* spp.).

Disregarding the high elevations of the Andes (but see Chapter 8 of this volume), the southern zone of climatic transition in the Western Hemisphere occurs from southern and middle Argentina (temperate) to northern Argentina, Paraguay and the Brazilian states of Paraná and São Paulo (subtropical); areas to the north of this are tropical. There is a decline in the number of families and genera in the ichthyofauna between La Plata-Paraná-Paraguay Basin and the smaller river basins in northern Argentina that is probably associated with historical biogeography more than contemporary climatic factors associated with the latitudinal gradient, although the latter undoubtedly plays a role in the distributions of individual species. Many groups display less ecological specialization at higher latitudes to the south. For example, the geophagine cichlids show large interspecific variation in body size and snout length, and feeding behavior ranging from specialized substrate sifters to epibenthic gleaners in the La Plata-Paraná-Paraguay Basin, whereas the few geophagine species in southern drainages tend to be generalists: i.e. medium-sized, epibenthic omnivores.

In Africa, the northern climatic transition zone occurs mostly in the Saharan region where there are few perennial streams. Subtropical conditions are encountered in the vicinity of the lower Nile in Egypt, where the only streams present are those associated the floodplain drainage. The entire continent south of the Sahara to the Okavango and Zambezi rivers in Botswana and Zambia/Mozambique (respectively) is tropical, the only exceptions being the mountain peaks of east Africa. Despite their situation within the Tropic of Capricorn, Botswana, Zambia and southern Mozambique experience conditions that are more typical of subtropical climates. The region is dominated by flat terrain and floodplains, but the elevation is sufficiently high to

provide temperatures as low as 8°C during June and July. Further southward through South Africa, the climate becomes increasingly temperate.

Many higher taxa that are species-rich in the Congo Basin have few representatives in the drainages of Angola, the Okavango-Zambezi Basin, and the region to the south. For example, the siluriform families Schilbeidae, Bagridae, and Amphiliidae have relatively fewer species in the Zambezi Basin, where cyprinids (especially species of *Barbus* and *Labeo*) and cichlids (particularly *Serranochromis* spp.) assume relatively greater functional importance in stream communities. A few genera are endemic to temperate regions of southern Africa, including *Pseudobarbus* (Cyprinidae) and *Sandelia* (Anabantidae) (Skelton, 1993), but overall species richness decreases as latitude increases. As in the southern Neotropics, there is a decline in morphological and trophic diversity of stream fishes from tropical through to temperate parts of southern Africa. The latitudinal trend in species attributes is less apparent in West Africa, where causal mechanisms may have more to do with biogeography than climatic gradients.

In eastern Asia, the southward transition from temperate to subtropical and to tropical occurs in southern China. In the continental interior, elevation changes in the Himalayas drive climatic transitions more than latitude, and fish assemblages change accordingly (see below). Lowland regions throughout Indochina and the East Indies have tropical climates and high fish species richness. As in southern Africa, the latitudinal transition from tropical to temperate is associated with a decline in the number of higher taxa plus the addition a smaller number of new ones, but this may reflect habitat changes associated with elevation rather than climatic changes associated with latitude. For example, ambassids, ariids, and other marine-derived species are limited to southern, lowland streams, whereas certain hillstream taxa (*Coraglanis* and *Glyptosternon*: Sisoridae) are confined to northern high-elevation regions. Within this group of upland stream fishes, there is also some latitudinal differentiation, in *Glyptothorax* (Sisoridae), for example, there is a group of seven species confined to southern India and another 25 species limited to northern India (Jayaram, 1999).

The southern tropical–temperate transition occurs over northern Australia, with tropical climates largely restricted to the northernmost coastal regions, especially eastern portions of the continent. Ichthyofaunal change along the southern latitudinal gradient appears to be weak, with greater faunal variation associated with the longitudinal axis that is more strongly associated with precipitation and geology (Allen *et al.*, 2002).

D. Elevation Gradients

Topography and climate at different elevations influence stream geomorphology, and discharge dynamics. High elevation streams in the tropics have fast currents, and are characterized by plunge pools, riffles, and rapids dominated by boulders and cobbles, with few or no aquatic macrophytes (see also Chapter 8 of this volume). Strong currents select for species that have adaptations for maintaining position in rapid current and foraging on substrates (Fig. 3). Benthic fishes associated with swift currents often have dorsoventrally compressed bodies, reduced swim bladders, and large, broad pectoral and pelvic fins; these provide a surface for pressure from the water current to press against the substrate. Examples include genera from a number of families including *Amphilius* (Amphilidae), *Euchiloglanis* (Sisoridae), *Balitora*, *Homaloptera* (Balitoridae), *Psilorhynchoides* (Psilorynchidae) and *Parodon* (Parodontidae). In some cases, the body and fins form a suction cup that enhances adhesion to the substrate, as in *Sicydium* (Gobiidae), *Gobiesox* (Gobiosocidae), *Gastromyzon* (and other Balitoridae), and certain *Euchiloglanis* (Sisoridae). *Pseudecheneis sulcatus* (Sisoridae), which lives in high elevation streams from Nepal to northern Burma, has an oval patch of 13–14 transverse muscular folds on the ventral surface of its thoracic region that are used for adherence to surfaces. The same mechanism is observed in the dorsal suction pad (modified dorsal spines) of marine remoras

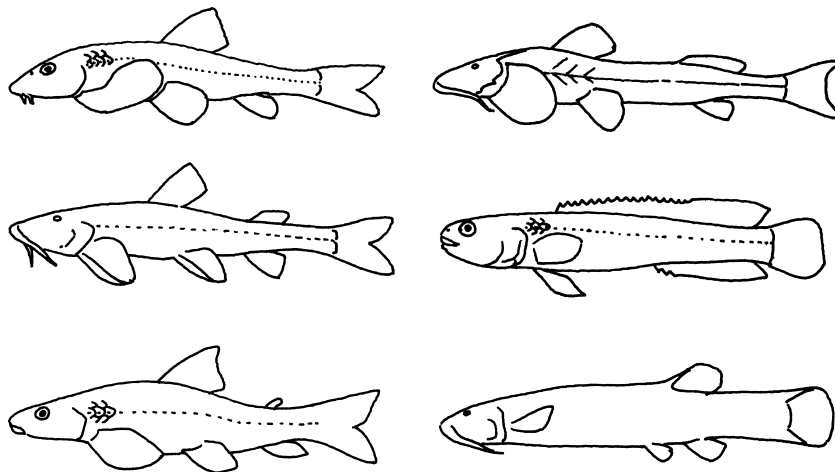


FIGURE 3 Illustration of fishes that inhabit high-gradient streams highlighting the relationship between body shape and position normally occupied in water column: top-left – Asian balitorid loach; top-right – Asian sisorid catfish; middle-left – African amphiliid catfish; middle-right – African cichlid; bottom-left – South American parodontid characin; bottom-right – South American trichomycterid catfish.

(Echeneidae). Other fishes use their fleshy mouths and oral suction to adhere to solid surfaces, notably the Loricariidae, Astroblepidae, as well as some Mochokidae (*Chiloglanis*) and the sisorid *Oreoglanis siamensis*. Another ecomorphological syndrome observed in fishes inhabiting high-elevation streams is body elongation and fossorial behavior. This syndrome is observed in South America (trichomycterid catfishes), Africa (clariid catfishes) and Asia (cobitid loaches).

Allochthonous resources, including drifting terrestrial invertebrates and detritus, are important in high-elevation streams. Periphyton and associated invertebrates provide the other major food resource for mountain and hillstream fishes. Spates and periodic scouring floods displace aquatic organisms, increase mortality (especially on juveniles), move sediments and restructure habitats, decrease the availability of benthic food resources and influence on the intensity of biotic interactions involving fishes (Dudgeon, 1993). As a result, fish populations are subject to large fluctuations and ecological interactions may be only weakly density dependent. However, because virtually no research has been conducted on the ecology of fishes in tropical high-elevation streams, this proposition is largely inferred from work conducted on temperate stream fishes (e.g. Grossman *et al.*, 1998).

At middle elevations (piedmont and other upland regions), streams have well-defined pool-riffle geomorphology, high substrate diversity (bedrock, cobble, gravel, sand, and terrestrial litter), and seasonal discharge variation, including periodic spates and flash floods during the wet season. Fish species tend to segregate according to pool-glide-riffle mesohabitats. For example, *Ancistrus triradiatus* (Loricariidae), *Lebiasina erythrinoides* (Lebiasinidae) and *Synbranchus marmoratus* (Synbranchidae) were essentially restricted to shallow riffle and glide habitats in Caño Volcán, a Venezuelan piedmont stream (K. O. Winemiller, unpublished observations). Even within pools, species used different areas of the habitat: *Aequidens pulcher*, *Crenicichla gayi* (Cichlidae) *Hypostomus argus* (Loricariidae), *Rhamdia* sp., *Hoplias malabaricus*, and *Prochilodus mariae* (Prochilodontidae) occurred on or close to the bottom in mid-pool; the characids *Astyanax* spp., *Bryconamericus beta*, *Brycon whitei*, *Roeboides dayi* were in mid-water at mid-pool; *Corynopoma riisei* occurred close to the surface in mid-pool; and *Poecilia reticulata* (Poeciliidae), *Bryconamericus deuteronoides*, and *Creagrutus melasma* (Characidae) were found in shallow water near pool margins. Juveniles of many larger species also were confined largely to shallow riffle, glide, and pool edge habitats with high structural complexity.

Similar patterns of habitat segregation, which may be associated with morphological specialization, have been reported from upland and lowland streams in other parts of the Neotropics (Angermeier and Karr, 1983; Arratia, 1983; Winemiller, 1983; Sabino and Castro, 1990; Flecker, 1997; Aranha *et al.*, 1998; Sabino and Zuanon, 1998; Mazzoni and Lobón-Cerviá, 2000; Lemes and Garutti, 2002) and other tropical regions (Inger and Chin, 1962; Moyle and Senanayake, 1984; Schut *et al.*, 1984; Bhat, 2005).

At low elevations, streams have slow currents, pools, runs, sloughs, organic-rich sediments, abundant and diverse aquatic macrophytes, allochthonous and autochthonous resources, and seasonal patterns of discharge. In lowland streams of large continental basins, water level varies predictably in response to seasonal precipitation. During the wet season, high discharge often maintains stream channels at bank-full levels for several months. Depending on local topography, lateral flooding of riparian zones may be extensive. Many fishes migrate upstream from larger, deeper channels to spawn in these shallow flooded areas that serve as productive nursery habitats (Welcomme, 1969; Winemiller, 1996a). Thus, reproductive activity is synchronized with the flood season with one spawning peak per year. In some parts of Asia that experience two monsoonal floods each year, stream fishes generally spawn twice (Dudgeon, 2000a).

Rapid remineralization of nutrients associated with organic matter accumulated in sediments during the dry season can lead to releases of inorganic nutrients into the water column during the wet season. In savanna regions with few trees to intercept solar radiation, this increased nutrient availability promotes production rates by aquatic macrophytes and periphyton, resulting in high rates of production of aquatic invertebrates and juvenile fishes. Some lowland streams that drain the floodplains of large rivers provide important deepwater habitats during the dry season, as well as conduits for fish lateral migrations in response to seasonal changes in water level (see also Chapter 7 of this volume). Fishes inhabiting broad lowland marshes that are often associated with floodplains partition their use of habitat based on water depth and vegetation structure (Winemiller, 1987, 1990). Small fishes vulnerable to predation occupy the shallowest marginal areas and dense stands of aquatic vegetation, including root masses of Water hyacinth (*Eichhornia crassipes*; Pontederiaceae) and other floating plants. Larger fishes, including piscivores and those feeding lower in the food web but protected from predation by virtue of size or possession of spines or armor, occupy deeper open-water areas. In the Neotropics, Nocturnal knifefishes (Gymnotiformes) and catfishes from various families hide in vegetation or woody debris during daytime, but swim in open waters at night.

Lowland streams in coastal regions are strongly influenced by proximity to the sea, and the hydrology and physicochemistry of those near sea level may be affected by tidal fluxes. Coastal stream faunas usually contain marine elements, some of which (e.g. eleotrids, mullets and certain gobies) have life cycles that require a period of residence in estuarine or marine habitats (Winemiller, 1983; Winemiller and Morales, 1989; Winemiller and Leslie, 1992). Streams on coastal alluvial plains can show faunal transitions over distances of only a few kilometers (Winemiller and Leslie, 1992): in French Guiana, for example, fish assemblages at locations 3–10 km from the coast contained only two marine-derived species, *Megalops atlanticus* (Megalopidae) and *Eleotris amblyopsis* (Eleotridae) (Mérigoux *et al.*, 1998). These transitions are driven by biotic factors (giving rise to functional species replacements) in addition to differential responses to physicochemical factors. In eastern Costa Rica, for example, the large omnivorous/detritivorous cichlid, *Vieja maculicauda*, is common in coastal lagoons and streams, but is replaced in upland streams by *Tomocichla tuba*, another cichlid of similar size and feeding habits. In the coastal lowlands, these species never co-occur although they may be present in habitats less than a kilometer apart. Similar patterns of spatial segregation are observed among other functional 'equivalents' in the coastal zone (e.g. the poeciliids *Brachyrhaphis parismina* on the coast and *B. holdridgei* inland).

Several studies have examined variation in fish assemblages over broad elevation gradients in the tropics. Bistoni and Hued (2002) found that fish species richness in Argentinean streams was correlated with altitude, distance from source, and stream order. Other studies of lotic fish assemblages in Chile (Campos, 1982), Ecuador (Ibarra and Stewart, 1989), Colombia (Jiménez *et al.*, 1998), and southern Brazil (Abes and Agostinho, 2001) identified significant patterns of species distribution and assemblage structure in relation to physicochemical conditions and elevation gradients. One of the best illustrations of the strong effect of a large-scale elevation gradient on fish assemblages comes from a study of the Gandaki River, Nepal (Edds, 1993). Assemblage structure at 81 sites distributed between 50 and 3100 m asl was strongly correlated with stream bed gradient and other physical and environmental features associated with elevation.

E. Stream Size and Habitat Gradients

Stream size generally co-varies with order within drainage networks. First- and second-order streams in drainage system headwaters are narrow, but pools vary and depth depends on topographic gradients and substrates. As stream order increases, stream mesohabitats become larger and more diverse with well-defined pool-riffle structure, especially in areas with high topographic relief (Schlosser, 1987). As small tributaries coalesce into higher order streams, mesohabitats become larger but often less differentiated, particularly in low-gradient landscapes with deep alluvial substrates. Stream depth and width do not necessarily co-vary, and broad lowland streams can be quite shallow when compared to high gradient streams of the same drainage system.

The number of species generally increases in a downstream direction. Several factors contribute to this trend: larger mesohabitats; shorter distance to downstream source populations; reduced barriers to migration from downstream locations; and more stable habitats (fewer local extinction events). In addition to accumulation of additional species, species turnover also occurs along streams especially over long gradients involving major elevation changes (Edds, 1993). Among lowland streams, patterns of species turnover may be stronger within coastal streams due to the influence of marine-dependent species, such as eleotrids and some gobies, as well as invasions by marine lutjanids and carangids (Winemiller and Leslie, 1992). A similar trend can be observed in small streams that drain directly to large rivers, with more species and genera present relative to similar-sized streams affluent to lower-order streams (Penczak *et al.*, 1994; Agostinho and Penczak, 1995; Pavanelli and Caramaschi, 1997, 2003).

In the Bandama Basin of West Africa, fish assemblages show a pattern of longitudinal zonation into three sections: headwaters subject to seasonal desiccation with relatively few species of small fishes (characids, rivulids, and *Barbus* spp.); a long middle reach with high species diversity; and a short lower reach where brackish water sometimes penetrates several kilometers inland and marine and marine-dependent fishes are present (de Mérona, 1981). The middle reach contains high habitat diversity with a succession of deep pools and shallow swift riffles. Genera characteristic of riffles include *Nannocharax* (Citharinidae), *Amphilius* (Amphiliidae), and *Aethiomastacembelus* (Mastacembelidae). Species common in slower pool areas of the middle reach include the alestiids *Alestes baremoze*, *Brycinus macrolepidotus*, *B. nurse* and *Hydrocynus forskalii*, and the catfish *Schilbe mandibularis* (Schilbeidae).

In upland streams of Sri Lanka, fish species richness increases downstream from waterfalls in the headwaters (Moyle and Senanayake, 1984). Stream discharge increases, slope decreases, and new fish species are added at locations successively lower in the longitudinal gradient, so that richness increases from one or two species at upstream sites to as many as 14 species further downstream. Upstream sites support benthic fishes adapted to life in swift currents, such as the benthopelagic cyprinids *Garra lamta* and *Noemacheilus notostigma* (Balitoridae)

and small pelagic species with rapid life cycles (e.g. *Rasbora daniconius*: Cyprinidae). Carnivorous *Ophiocephalus gaucha* (Channidae) and herbivorous *Awaous* (= *Gobius*) *grammepomus* (Gobiidae) were confined to the most downstream sites.

The Luongo River in northern Zambia has an unusual pattern of longitudinal zonation, with swift high-gradient sections in both the upper and lower reaches separated by a long middle section with low gradients and sluggish flow (Balon and Stewart, 1983). The three sections of the river are separated from the middle reach by waterfalls that appear to serve as effective barriers to dispersal and, as a result, the two high-gradient reaches contain mostly fishes associated with turbulent waters but with almost no species in common. The Luongo also has a fairly high number of endemic fish species. Rather different habitat associations occur in the Limpopo River Basin of Mozambique and the Transvaal region of South Africa.

Gaigher (1973) identified five groups: widespread species with non-specific habitat affinities (e.g. *Barbus paludinosus*, *Clarias gariepinus*), species that are widespread but absent from coldwater, high-elevation streams (e.g. *Micralestes acutidens*: Characidae; *Labeo cylindricus*: Cyprinidae), pool-dwelling species from low-elevation warm-water streams (e.g. the mormyrid *Petrocephalus catostoma* and the mochokid catfish *Synodontis zambezensis*), species confined to middle- and high-elevation streams with perennial flow (e.g. *Barbus lineomaculatus* and the cichlid *Chetia flaviventris*), and species with restricted distributions and/or habitat requirements, such as lungfish and specialized catfish (e.g. *Protopterus annectens* and *Amphilius platyichir*), that are most at risk of local extirpation by human impacts.

Research from the temperate zone indicates that small headwater streams have more stochastic environments (in terms of discharge, depth, and water quality) and tend to have more randomly-assembled local communities made up of species with good colonizing ability (Schlosser, 1987; Grossman *et al.*, 1998). In tropical systems, headwater streams, especially those at low elevations, often show lower assemblage variability than larger downstream reaches as seen, for instance in small headwater streams of central Amazonian rainforests (Schwassman, 1978). The composition of these assemblages is fairly constant and fluctuations in population densities are low (Bührnheim and Fernandes, 2001, 2003). Likewise, monthly variations in the fish assemblage of Caño Volcán, a small headwater stream in the Andean piedmont, was much lower than that seen in Caño Maraca, a lowland creek in the Venezuelan llanos (Winemiller, 1987). In contrast to these Neotropical systems, fish assemblages in headwaters of the upper Ogun River in Nigeria exhibited large seasonal changes (Adebisi, 1988). These streams are reduced to series of isolated pools during the dry season, when samples were dominated by omnivorous species, such as *Brycinus* spp. and *Tilapia zillii* (Cichlidae), and insectivores (e.g. smaller mormyrid species and the bagrid catfish *Chrysichthys auratus*). During the early stages of the wet season, large piscivorous fishes, including some mormyrids (*Mormyrops deliciosus*), tigerfish (*Hydrocynus forskalii*) and bagrids (*Bagrus docmak*), begin to appear in gillnet catches.

The patch-dynamics model of species richness in streams predicts that highest species richness occurs in habitats with intermediate spatio-temporal scales of disturbance. This prediction was tested by Mérigoux *et al.* (1999) who examined the relationship between variation in habitat characteristics and species richness of juvenile fishes at 20 sites in tributaries of the Sinnamary River, French Guiana. Habitat variability accounted for only 36% of variation in species richness in multiple-regression models, but this may reflect the influence of rare species on total community variation, and analyses restricted to common species might show stronger support for the patch dynamics model. Furthermore, the Sinnamary River is bisected by a major impoundment that is likely to influence population changes of highly-mobile species. Seasonal and inter-annual environmental variation probably influences species with different life history strategies in dissimilar but predictable ways (as discussed below) so that, even if

there are winners and losers in a given habitat patch during any particular period, the fish assemblage would appear relatively stable when viewed over longer temporal scales.

Much of the environmental variation in low-gradient tropical streams is relatively predictable in accordance with seasonal precipitation. Rising water levels create new aquatic habitats, increase ecosystem productivity and total production, and stimulate fish reproduction (Lowe-McConnell, 1964, 1987; Winemiller, 1996a). During the dry season, aquatic habitats contract, production decreases, and water quality often declines (with low dissolved oxygen and high hydrogen sulfide), so that fish mortality increases. Fish samples from isolated dry-season pools tend to contain many species with special respiratory adaptations (Lowe-McConnell, 1964; Winemiller, 1996a), including fishes capable of efficiently skimming the oxygen-rich surface layer (Kramer *et al.*, 1978, Winemiller 1989a). This annual wet-dry cycle is probably associated with essentially density-independent population dynamics during the early part of the wet season, followed by increasing importance of density-dependent regulation of populations (e.g. by food limitation and predation) as water levels drop during the dry season. It is not uncommon for lowland streams in the tropics, particularly those in savanna regions, to be reduced to a series of isolated pools during the dry season. Chapman and Kramer (1991) concluded that populations of *Poecilia gilli* in isolated pools in small, high-gradient streams in Costa Rica are regulated more by density-independent factors linked to extreme hydrologic changes (spates or drying), compared to fishes in low-gradient streams that experience more gradual and predictable hydrological changes (Chapman *et al.*, 1991).

Fish species richness was correlated with water depth in a survey of habitats in the Niandan River in eastern Guinea (Hugueny, 1990) and in three streams in western Guinea (Pouilly, 1993), and this trend seems to be typical of most tropical drainages. Table I summarizes information on stream width, dominant fish species, and taxonomic richness at the species and genus level for stream surveys from tropical regions worldwide. Species richness ranges from 4 to 83, with lowland streams tending to support more species than upland and mid-elevation streams. Species richness is positively correlated with stream width ($r = 0.46$, $df = 43$, $p = 0.0015$) as is generic richness, although the latter relationship is weaker ($r = 0.31$, $df = 43$, $p = 0.047$). The average number of species in lowland streams of around 15 m width was similar in the Neotropics (23) and Asia (25) but slightly lower in Africa (20.5), and may be due to the absence of data for streams from the Congo – the most species-rich basin in Africa for fishes. The ratio of number of species to number of genera was lower for Neotropical streams (1 : 20) than those in Asia (1 : 37) and Africa (1 : 50) and, although more surveys were included for the Neotropics, this result is unlikely to be an artifact. The number of coexisting congeneric species in African and Asian streams (e.g. cyprinids such as *Barbus* in Africa versus *Puntius* and *Rasbora* in Asia) does indeed appear to be generally higher than in the Neotropics, although the effects of locality and habitat are also influential.

Angermeier and Karr (1983) studied fish assemblage-habitat relationships in a series of low-gradient streams entering Lake Gatún, Panama. The number of species of algivores and omnivores increased with stream width; insectivore richness increased also but declined in the widest streams. Average total biomass of algivores and fishes feeding on terrestrial plants (seeds, fruits) both increased linearly with stream width, whereas insectivore biomass showed the opposite trend (Fig. 4). Such data illustrate the general pattern that algal food is more available in relatively open and unshaded downstream reaches within densely forested landscapes. The abundance of small fishes (<40 mm standard length), by contrast, decreased with stream width but tended to be higher in pools than riffles and runs (Angermeier and Karr, 1983). Many small fishes in tropical streams use shallow areas, including pool margins, as refugia from piscivorous fishes; for example, 21 of 29 species inhabiting an Amazonian stream were located along the margins (Sabino and Zuanon, 1998). In Trinidadian streams, the killifish *Rivulus hartii* is abundant in small tributaries where piscivores are absent, but also uses shallow marginal

TABLE I Taxonomic Richness in Tropical Stream Fish Assemblages at Different Elevations and Regions: Location, Mean Stream Width (m), Number of Species, Number of Genera, Dominant Species, and Literature Source

Site	Width	Species	Genera	Dominant species	Source
High elevation (>1000 m above regional lowlands)					
Gandaki, Nepal	–	4	3	<i>Schizothorax richardsoni</i>	Edds, 1993
Mergulhão, Brazil	5	26	8	–	Aranha <i>et al.</i> , 1998
San Pablo, Colombia	7	19	18	<i>Brycon henri</i>	Cardona <i>et al.</i> , 1998
Mid elevation (100–1000 m above regional lowlands)					
Córrego Capivara, Brazil	20	26	20	<i>Phalloceros caudimaculatus</i>	Uieda and Barretto, 1999
R. Pardo, Brazil	3	19	15	<i>Astyanax fasciatus</i>	Castro and Casatti, 1987
Córrego Cedro, Brazil	–	21	20	<i>Poecilia reticulata</i>	Lemes and Garutti, 2002
C. Gameleira, Brazil	–	8	7	<i>Astyanax bimaculatus</i>	Alves and Vono, 1997
C. Tabajara, Brazil	2.5	18	15	–	Uieda, 1984
Morro do Diabolo, Brazil	9	22	19	–	Casatti <i>et al.</i> , 2001
C. Acaba Saco, Brazil	4.5	28	19	<i>Loricaria</i> sp.	Miranda and Mazzoni, 2003
C. Água Boa, Brazil	2.5	35	32	<i>Ancistrus aguaboensis</i>	Miranda and Mazzoni, 2003
C. Cavalo, Brazil	3	36	23	<i>Ancistrus minutus</i>	Miranda and Mazzoni, 2003
Chajéradó, Colombia	<10	19	14	–	Sánchez-Botero <i>et al.</i> , 2002
Chajéradó, Colombia	<30	18	16	–	Sánchez-Botero <i>et al.</i> , 2002
Caño Volcán, Venezuela	6	20	16	<i>Bryconamericus beta</i>	Winemiller, 1990
R. Todasana, Venezuela	5.5	9	9	<i>Sicydium plumieri</i>	Penczak and Lasso, 1991
Tosso, Benin	7	16	11	<i>Brycinus longipinnis</i>	K. O. Winemiller, unpublished observations
Parakou, Benin	15	11	10	<i>Barbus boboi</i>	K. O. Winemiller, unpublished observations
Sina Sinarou, Benin	12	11	7	<i>Barbus callipterus</i>	K. O. Winemiller, unpublished observations
Kouande, Benin	3	13	5	<i>Barbus macrops</i>	K. O. Winemiller, unpublished observations
Perma, Benin	15	12	7	<i>Sarotherodon galilaeus</i>	K. O. Winemiller, unpublished observations
Tchan Duga, Benin	2	14	9	<i>Epiplatys</i> sp.	K. O. Winemiller, unpublished observations
Low elevation (<100 m above regional lowlands)					
Sábalo, Costa Rica	5	21	19	<i>Poecilia gilli</i>	Burcham, 1988
Quebrada, Costa Rica	2.5	21	20	<i>Eleotris amblyopsis</i>	Winemiller and Leslie, 1992

(continued)

TABLE 1 (continued)

Site	Width	Species	Genera	Dominant species	Source
Agua Fría, Costa Rica	26	56	42	<i>Astyanax fasciatus</i>	Winemiller and Leslie, 1990
Camaronal, Costa Rica	5.5	16	16	<i>Astyanax fasciatus</i>	Winemiller, 1983
Pedro Miguel, Panama	–	12	12	<i>Gephyrocharax atricaudata</i>	Zaret and Rand, 1971
Tarumã, Brazil	2.5	6	6	<i>Aequidens tetramerus</i>	Knöppel, 1970
Barro Branco, Brazil	1	17	15	<i>Aequidens tetramerus</i>	Knöppel, 1970
Stream-41, Brazil	<3	11	10	<i>Hemigrammus</i> sp.	Bührnheim and Fernandes, 2003
Gavião, Brazil	<3	19	18	<i>Hyphessobrycon heterorhabdus</i>	Bührnheim and Fernandes, 2003
Porto Alegre, Brazil	<3	12	12	<i>Hemigrammus</i> sp.	Bührnheim and Fernandes, 2003
R. Indaiá, Brazil	–	8	8	<i>Deuterodon iguape</i>	Sabino and Castro, 1990
R. Ubatiba, Brazil	13	22	20	<i>Astyanax cf. hastatus</i>	Costa, 1984
R. Mato Grosso, Brazil	3	17	16	–	Costa, 1987
Z. Campus, Brazil	2.8	27	21	<i>Astyanax bimaculatus</i>	Lobón-Cervía <i>et al.</i> , 1994
Z. Barbará, Brazil	2.6	24	22	<i>Astyanax bimaculatus</i>	Lobón-Cervía <i>et al.</i> , 1994
R. Fazenda, Brazil	20	21	21	<i>Deuterodon cf. pedri</i>	Uieda and Uieda, 2001
I. Guaraná, Brazil	–	29	27	–	Sabino and Zuanon, 1998
R. Ubatiba, Brazil	2.5	22	19	<i>Deuterodon cf. hastatus</i>	Mazzoni and Lobón-Cervía, 2000
Nareuda, Bolivia	10	38	–	<i>Corydoras loretoensis</i>	Chernoff and Willink, 1999
Maraca, Venezuela	22.5	83	72	<i>Cheirodon pulcher</i>	Winemiller, 1990
Siapa trib, Venezuela	5	34	27	<i>Bryconops giancopinii</i>	K. O. Winemiller, unpublished observations
Siapa trib, Venezuela	4	36	28	<i>Moenkhausia copei</i>	K. O. Winemiller, unpublished observations
Siapa trib, Venezuela	5	26	23	<i>Characidium</i> sp.	K. O. Winemiller, unpublished observations
Siapa trib, Venezuela	8	20	20	<i>Apistogramma uaupesi</i>	K. O. Winemiller, unpublished observations
Kambo, Guinea	–	23	21	<i>Chiloglanis occidentalis</i>	Pouilly, 1993
Balisso, Guinea	–	29	26	<i>Epiplatys</i> sp.	Pouilly, 1993
Kilissi, Guinea	–	16	16	<i>Brienomyrus brachyistius</i>	Pouilly, 1993
Bugungu, Kenya	–	14	9	<i>Barbus kerstenii</i>	Welcomme, 1969
Kataba, Zambia	5	12	7	<i>Aplocheilichthys</i> sp.	Winemiller, 1993
Kapuas-6, Borneo	5	21	16	–	Roberts, 1989
Kapuas-37, Borneo	5	33	22	–	Roberts, 1989
Bulu, Borneo	2	16	12	<i>Noemacheilus spiniferus</i>	Watson and Balon, 1984
Payau, Borneo	2	23	18	<i>Osteochilus kahajenensis</i>	Watson and Balon, 1984
Kaha, Borneo	4	32	22	<i>Glaniopsis hanitschi</i>	Watson and Balon, 1984

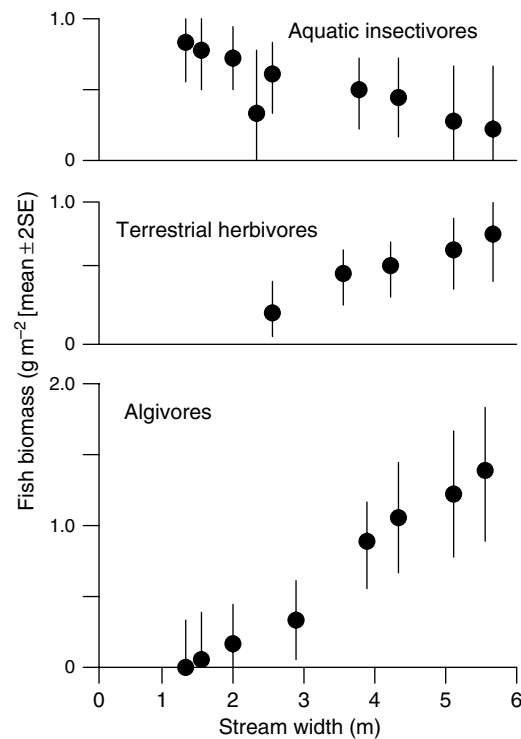


FIGURE 4 Relationship between stream width and fish biomass (density per unit area) for three feeding guilds in lowland streams of Panaman (from Angermeier and Karr, 1983).

habitats of rivers (where predaceous fishes occur) for dispersal, foraging, and reproduction (Fraser *et al.*, 1999).

At a smaller spatial scale, a few studies have demonstrated how tropical stream fishes partition different areas (microhabitats) in pool habitats. Zaret and Rand (1971) showed how fishes use different vertical and lateral regions of a stream pool in Panama (Fig. 5). Comparable patterns of spatial segregation occur in small streams of the Andean piedmont in Venezuela (K. O. Winemiller, unpublished observations), and similar findings have been reported for fishes inhabiting pools of rainforest streams in Borneo (Inger and Chin, 1962), Sri Lanka (Moyle and Senanayake, 1984; Schut *et al.*, 1984), the Amazon (Sabino and Zuanon, 1998), and southeastern Brazil (Sabino and Castro, 1990; Mazzoni and Lobón-Cerviá, 2000). All such studies note that interspecific variation in body shape and fin placement indicates the manner in which fishes use microhabitats. In a study of three upland streams in coastal Guinea, West Africa, during the dry season, Pouilly (1993) found consistent differences in assemblages in low-velocity pool habitats and high-velocity riffles and runs, with a strong association between morphology and habitat. Fishes in shallow high-velocity habitats further partitioned space based on substrate type, but those in pools had weaker associations between morphology and interspecific segregation of space. Martin-Smith (1998) recorded lower species richness but higher fish abundance in riffles of a Borneo stream where the assemblage was dominated by seven benthic balitorid species; 18 species of cyprinids occurred in pools, whereas 13 species were ubiquitous occurring in both habitats. In a Brazilian rainforest stream, algivorous loricariid catfishes with high dietary overlap showed evidence of spatial segregation by microhabitat and were active during different periods (Buck and Sazima, 1995).

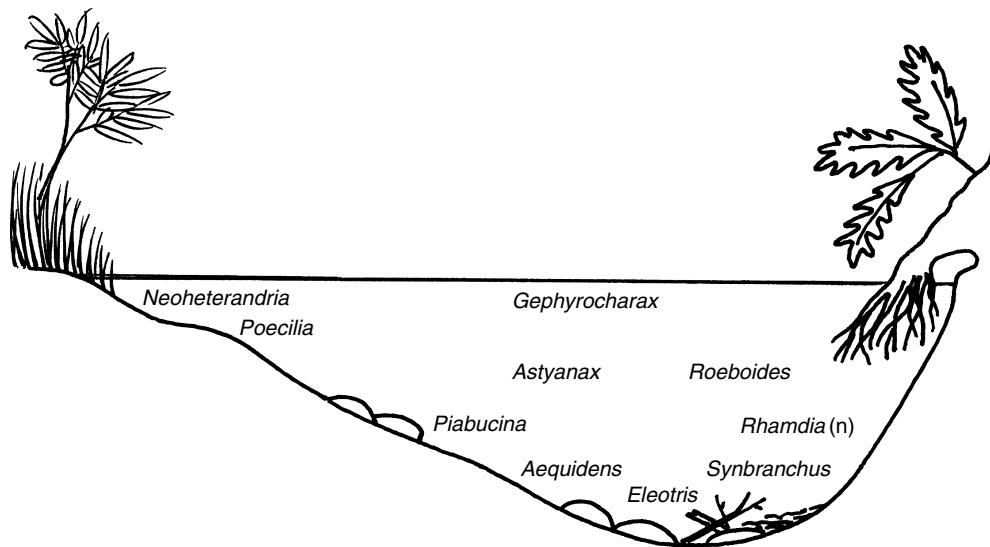


FIGURE 5 Relative vertical and horizontal positions occupied by fishes within a cross-section view of a dry-season pool in lowland stream in Panama where (n) designates nocturnal fishes; based on Zaret and Rand (1971).

III. REPRODUCTIVE STRATEGIES AND POPULATION DYNAMICS

Given the taxonomic diversity of tropical stream fishes and their distribution among various habitats and regions, it is not surprising that they also display diverse strategies and modes of reproduction. Virtually any attribute associated with reproduction reveals high interspecific variation. The challenge is to understand how these different modes of reproduction allow fishes to be adapted to patterns of environmental variation in streams. To organize thinking along these lines, two frameworks for interpreting modes of reproduction as adaptive strategies will be examined. The first is the reproductive guild concept of Balon (1975) in which physiological, morphological, and behavioral features of adult and early life stages of fishes are understood in terms of the physicochemical and ecological challenges imposed by aquatic habitats. The second is Winemiller's (1989a, 1992) trilateral life-history continuum that proposes optimal demographic and reproductive strategies for different patterns of environmental variation.

There is marked interspecific variation in age and size of sexual maturity and, indeed, the smallest of all vertebrates are fishes from tropical marine and freshwater habitats. The trichomycterid *Ammoglanis pulex* (de Pinna and Winemiller, 2000) is a miniature, worm-like catfish that does not exceed 15 mm length and lives among the interstices of coarse sand substrates in clearwater rivers of the Guyana Shield region of South America. The cyprinid *Danionella translucida* from Burma is slightly smaller (<12 mm standard length; Roberts, 1986), and probably feeds on meiofauna. Tropical fresh waters also contain some of the largest bony fishes on Earth, including the Mekong catfish (*Pangasianodon gigas*: Pangasiidae) and the Amazonian Pirarucu (*Arapaima gigas*: Arapaimidae), but these massive species do not normally inhabit streams less than 30 m wide. Other notably large tropical stream fishes are certain Asian carps (Cyprinidae: *Catlocarpio siamensis*, for example), South American electric 'eels' (actually Gymnotiformes: Electrophoridae), detritivorous prochilodontids (South America), herbivorous and piscivorous characids (South America), schilbeid and clariid catfishes (Africa and Asia), pimelodid catfishes (South America), ariid catfishes (Asia-Australia), barramundi (Asia-Australia), and lungfishes (South America, Africa, and Australia). Fish growth can be quite rapid in many lowland tropical ecosystems, so some of these large tropical species (exceeding 5 kg) probably

mature in their second year. Studies of age and growth in tropical stream fishes are still scarce (Agostinho *et al.*, 1991; Amaral *et al.*, 1999), mostly due to the difficulty of age determination by standard methods.

Tropical stream fishes display a wide range of values for fecundity and egg size – traits that tend to vary inversely in fishes. Some species spawn only a few eggs or give birth to one or a few well-developed offspring per clutch. Many annual killifishes spawn a few eggs at intervals of a day to a few days throughout their adult lifespan, whereas, the unusual poeciliid *Tomeurus gracilis* releases a single fertilized egg per spawning event, and South American freshwater stingrays give birth to a few fully-developed offspring each time they reproduce. In contrast, some tropical stream fishes have batch fecundities well over 100 000 (e.g. *Brycon*, *Labeo*). The relative investment in reproduction depends on fish size, fecundity, egg size, and spawning interval. Egg diameters in African teleosts vary from 0.6 mm (*Micralestes acutidens*) to 3.2 mm (*Chrysichthys maurus*) (Lévêque, 1997); egg diameter ranged from 0.45 mm (*Steindachnerina argentea*: Curimatidae) to 4.0 mm (*Ancistrus triradiatus*) in fishes among teleosts from a stream in the Venezuelan llanos (Winemiller, 1989b). Spawning may occur daily in certain killifishes but only once per year in many species of high-fecundity batch spawners. In many cases, the interval between spawning events seems to be correlated with the periodicity of major environmental variation in streams: in the case of partial spawners, short intervals between reproductive bouts are associated either with rather constant habitats or with habitats that undergo stochastic variation over short time scales in the order of weeks. Most fishes in small central Amazonian rainforest streams, relatively constant habitats, are partial spawners (Schwassman, 1978). Livebearing poeciliid fishes of rainforest streams in Costa Rica breed continuously, but also display seasonal patterns of reproductive effort (Winemiller, 1993).

The ultimate environmental driver for variations in habitat quality and quantity, and hence breeding events, is probably stream hydrology (Schwassman, 1978; Lowe-McConnell, 1979). Total spawners respond to large-scale environmental variation that is largely predictable, usually on an annual scale in relation to the flood regime. Most stream fishes spawn just before, but more often just after, the onset of flooding to take advantage of expanded, productive aquatic habitats. In floodplain areas, many species migrate up tributary creeks to spawn in seasonally flooded marshes (Welcomme, 1969; Winemiller, 1989b, 1996a). In upland streams, spates and scouring floods during wet seasons favor spawning in small tributary streams or small embayments created when rain-swollen tributaries join the mainstem. Some fish species in upland streams have extended spawning periods, including Characiformes, such as *Corynopoma riisei* (Winemiller, 1989b), *Astyanax bimaculatus* (Garutti, 1989), and *Characidium* sp. (Mazzoni *et al.*, 2002); the loricariid *Hypostomus punctatus* (Menezes and Caramaschi, 1994); and the pimelodid *Pimelodella pappenheimi* (Amaral *et al.*, 1998). Some fishes, such as *Roebooides dayi* and the cichlid *pulcher* *Aequidens* even have dry-season spawning peaks (Winemiller, 1989b). In Panamanian lowland streams, several characiform species reproduce throughout the dry season, but others breed during the wet season (Kramer, 1978a).

One of the most fascinating aspects of tropical stream fish reproduction is the variation observed in parental care. Parental care can be organized according Balon's (1975) reproductive guilds framework (Table II). Open substrate spawners scatter eggs and milt in the water column or over substrates in a seemingly non-selective manner. Most of these species have relatively high fecundity and small eggs, with high larval mortality. Brood hiders may spawn in the water column above or in contact with specific substrates, often gravel or aquatic vegetation, that provide cover for developing eggs and larvae. Brood hiders may have low or high fecundity and breed at frequent intervals (e.g. killifishes that burrow into loose, humic-rich substrates to spawn) or seasonally (e.g. many medium-sized Neotropical and African characids). Substrate guarders usually deposit fertilized eggs onto vegetation, root wads, or in holes. These species usually do not construct a nest, but defend the area around their eggs for one to a few

TABLE II Genera from Each Tropical Region Providing Examples of the Reproductive Guilds Described by Balon (1975)

Region	Neotropics	Africa	Asia/Indo-Pacific/Australia
Open substrate spawners	<i>Brycon</i>	<i>Alestes</i>	
	<i>Creagrutus</i>	<i>Opsaridium</i>	<i>Brachydanio</i>
	<i>Prochilodus</i>	<i>Labeo</i>	<i>Chela</i>
	<i>Pimelodella</i>	<i>Schilbe</i>	<i>Pangasius</i>
	<i>Rhamdia</i>	<i>Ctenopoma</i>	
Brood hiders	<i>Hyphessobrycon</i>	<i>Arnoldichthys</i>	<i>Osteochilus</i>
	<i>Moenkhausia</i>	<i>Neolebias</i>	<i>Puntius</i>
	<i>Copella</i>	<i>Barbus</i>	<i>Rasbora</i>
	<i>Pterolebias</i>	<i>Synodontis</i>	<i>Melanotaenia</i>
	<i>Rachovia</i>	<i>Nothobranchius</i>	<i>Parambassis</i>
Substrate guarders	<i>Pygocentrus</i>	<i>Heterotis</i>	<i>Notopterus</i>
	<i>Serrasalmus</i>	<i>Polypterus</i>	<i>Mogurnda</i>
	<i>Gymnotus</i>	<i>Notopterus</i>	<i>Oxyeleotris</i>
	<i>Sternopygus</i>	<i>Citharinus</i>	
Nest guarders	<i>Aequidens</i>	<i>Protopterus</i>	<i>Betta</i>
	<i>Crenicichla</i>	<i>Gymnarchus</i>	<i>Osphronemus</i>
	<i>Ancistrus</i>	<i>Hepsetus</i>	<i>Trichogaster</i>
	<i>Hoplosternum</i>	<i>Clarias</i>	<i>Channa</i>
	<i>Synbranchus</i>	<i>Hemichromis</i>	<i>Heteropneustes</i>
External bearers	<i>Osteoglossum</i>	<i>Arius</i>	<i>Scleropages</i>
	<i>Loricariichthys</i>	<i>Oreochromis</i>	<i>Betta</i>
	<i>Loricaria</i>	<i>Sarotherodon</i>	<i>Channa</i>
	<i>Geophagus</i>	<i>Haplochromis</i>	<i>Sphaerichthys</i>
	<i>Oostethus</i>	<i>Serranochromis</i>	<i>Luciocephalus</i>
Internal bearers	<i>Potamotrygon</i>	<i>Dasyatis</i>	<i>Himantura</i>
	<i>Belonesox</i>		<i>Dermogenys</i>
	<i>Brachyrhaphis</i>		<i>Hemirhamphodon</i>
	<i>Poecilia</i>		<i>Nomorhamphus</i>
	<i>Xiphophorus</i>		

days before leaving the area. Nest guarding takes many forms among tropical stream fishes, including creation of depressions on the substrate, cavities within dense stands of aquatic macrophytes, and bubble nests (a froth formed at the surface by 'blowing' mucus-coated bubbles). Nest guarders may remain with their broods for several weeks after hatching. They typically have relatively low batch fecundity and large eggs, but the bubbly-nest-building Asian belontiids, some of which lay tiny eggs and have high fecundity, are an exception to this rule. The external bearers include the mouth brooders and fishes that carry adhesive eggs and larvae on their body surface, usually the ventrum as in *Loricaria* (Loricariidae) and *Oostethus* (Syngnathidae). Mouth brooding has evolved multiple times in many highly divergent taxa (Table II). Internal bearing (ovoviparity and viviparity) has likewise evolved in a range of taxa; however, it appears to be uncommon among African stream fishes.

Balon (1975) has explained the relationships between environmental conditions, parental care, and the anatomical and physiological adaptations of eggs, larvae and reproductive adults. He viewed reproductive guilds as adaptive strategies for maximizing larval survival in spatially and temporally heterogeneous habitats. Behaviors such as nest construction and brood guarding (i.e. frequent 'mouthing' of eggs and larvae, fanning, etc.) can decrease silt accumulation and increase water circulation and delivery of dissolved oxygen to developing early life stages. Placing eggs in bubble nests at the water surface increases oxygen availability under anoxic