CHAPTER 16

Fishes of African Rain Forests
Diverse Adaptations to Environmental Challenges

Lauren J. Chapman

The extraordinary diversity of the terrestrial taxa in African rain forests that has captivated biologists for more than a century is paralleled by unique and highly diverse aquatic faunas. Africa has more than 2,900 known species of indigenous freshwater fishes, over 28% of which are endemic to the rain forest regions of central and west Africa (Roberts 1975; Daget et al. 1984, 1986, 1991; Lowe-McConnell 1988). Forest rivers harbor a rich assortment of species with extraordinary adaptations to the challenges imposed by the forest environment, in addition to a diverse suite of archaic and phylogenetically isolated groups (Roberts 1975; Lowe-McConnell 1988). Yet our knowledge of these faunas goes little beyond catalogues of species lists and a handful of ecological studies from very few sites. Deforestation, species introductions, and wetland degradation all pose serious threats to fishes of the African rain forests, but the nature and severity of their effects remain largely unknown. In this chapter, I review the striking characteristics of African forest fish faunas, with a focus on fish-forest interactions and adaptive responses to environmental challenges. I identify key areas for future study that would permit a more synthetic analysis of fish-forest interactions and end by briefly discussing anthropogenic impacts that may precipitate declines in fish faunal diversity or shifts in community structure.

Fishes of the Forest

DEMOCRATIC REPUBLIC OF CONGO (DR CONGO) VERSUS AMAZON

Much of our knowledge and interest in fish-forest interactions is based on studies of the inundated forest (Igapo) of the Amazon floodplain, where huge areas of forest become inundated with seasonal flooding, and exploitation of the forest by fruit-eating fishes is integral to forest ecosystem function (Goulding 1980). In Africa, true forested floodplains similar to the Amazon are more or less confined to the Congo Basin and a few smaller river basins in Cameroon and Gabon. Other less heavily forested rivers occur in west Africa, Madagascar, and the small patches of forest in western Uganda (figure 16.1).

The two largest forest rivers in the world, the Congo and the Amazon, have more kinds of fishes than any other river basins, and both systems exhibit high endemism (Roberts 1973). They rank the highest in the world for catchment, length, and output (table 16.1), and both arise on very poor, leached podsolitic soils (Wel-
Figure 16.1. Top: Map of the African continent and Madagascar illustrating the major regions of tropical rain forest and the extent of deforestation in these areas. Adapted from National Geographic Atlas of the World (1992), NG Maps/NGS Image Collection. Bottom: Location of selected rivers from the areas of tropical rain forest in Africa: (1) "Liberia", (2) Sassandra; (3) Bandama; (4) Komoe; (5) Volta; (6) Niger; (7) Sanaga; (8) Ogooue; (9) Congo; and (10) "Uganda." Adapted from Skelton 1988.
FISHES OF AFRICAN RAIN FORESTS

However, beyond these characters the two systems are fundamentally different, and our broader knowledge of fish ecology and limnology in the Amazon cannot be translated to the Congo system. The Congo Basin covers an area of approximately 4 million km² and drains the largest expanse of tropical forest in Africa, yet only 34% of the basin is covered by forest, compared with 80% in the Amazon basin (Marlier 1973; Lowe-McConnell 1975; see also table 16.1). Its catchment has been affected by earth movements that have altered the course of the drainage and produced many abrupt changes of elevation (Beadle 1981). The Congo River is thus characterized by many more rapids and waterfalls than the Amazon (figure 16.2), limiting penetration of marine fishes into the basin (Marlier 1973; Lowe-McConnell 1975; Beadle 1981; see also table 16.1). In contrast, the Amazon has a very gentle slope at a low altitude and has consequently received many marine immigrants (Marlier 1973; Beadle 1981). The Congo exhibits only small fluctuations in water level (3 m) compared with the Amazon (15 m or more at Manaus; Lowe-McConnell 1975). This relative lack of fluctuation is due in part to the presence of lakes and swampy depressions in the upper course of the Congo River drainage that absorb the effects of heavy rains. This is not to say that the system is aseasonal; the water-level fluctuations that are bimodal in nature have marked effects on fish ecology in the region. Like the Amazon, the Congo River is characterized by seasonal flooding of extensive areas, particularly in the central basin, where the flooded river inundates huge areas of forest many kilometers from the main river (Lowe-McConnell 1975), creating an enormous area for seasonal exploitation by fishes and other aquatic organisms.

Endingism

Endemism in the Congo region is impressive; exclusive of Lake Tanganyika, 669 species representing 25 families and 168 genera have been recorded in the entire basin, with 82% endemism at the specific level and 42 endemic genera (Poll 1959, 1973; Beadle 1981). In the

| Table 16.1 |
| Characteristics of the Amazon and Congo River Basins |

<table>
<thead>
<tr>
<th>Character</th>
<th>Congo</th>
<th>Amazon</th>
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<tr>
<td>Size</td>
<td>second largest in the world</td>
<td>largest in the world</td>
</tr>
<tr>
<td>Length</td>
<td>4,650 km</td>
<td>5,500 km</td>
</tr>
<tr>
<td>Output</td>
<td>1,400,000 ft/sec</td>
<td>3–4,000,000 ft/sec</td>
</tr>
<tr>
<td>Drainage discharge</td>
<td>3,822,000 km²</td>
<td>5,600,000 km²</td>
</tr>
<tr>
<td>Forest cover</td>
<td>34%</td>
<td>80%</td>
</tr>
<tr>
<td>Water level fluctuations</td>
<td>3 m (central basin)</td>
<td>15+ m (Manaus)</td>
</tr>
<tr>
<td>Topography</td>
<td>highly variable slope (extensive rapids)</td>
<td>gentle slope</td>
</tr>
<tr>
<td>Species richness (fishes)</td>
<td>560+</td>
<td>1,300+</td>
</tr>
<tr>
<td>Marine immigrants</td>
<td>low</td>
<td>high</td>
</tr>
<tr>
<td>Human population density</td>
<td>0–10 people/km²</td>
<td>0–0.4 people/km²</td>
</tr>
<tr>
<td>Deforestation rate (% / yr)</td>
<td>0.2 (Congo)</td>
<td>0.4 (Brazil)</td>
</tr>
</tbody>
</table>

central basin of the Congo River (a region defined in Poll and Gosse 1963 and Poll 1973), which includes much of the drainage, Poll and Gosse (1963) reported 408 fish species from 24 families. New species emerge with new expeditions, and will be likely to do so for some time. Factors contributing to this high endemism may include a wide range of habitats and numerous barriers (rapids and falls) that have contributed to the prolonged isolation of fish communities (Beadle 1981).

This extraordinarily high level of endemism also occurs in several of the coastal rivers in the region, from Nigeria to DR Congo (Roberts 1975). Endemism is high at the generic level in Madagascar (14 of the 23 genera are endemic; Reinthal and Stiassny 1991) but lower at the specific level (35%, or 23 species). The total richness of the fauna is also low (66 species; Roberts 1975). The rivers draining the small forests of western Uganda are characterized by widespread species and low endemism, although many of the environmental features (high relief, low water-level fluctuations) are shared with the Congo Basin (Greenwood 1966; Chapman, unpublished data).

FOREST VERSUS SAVANNA RIVERS
Most of what we know about the natural history and ecology of African freshwater fishes applies to savanna floodplain rivers; far less is known about forested rivers. This emphasis reflects the importance of savanna floodplain fisheries and the inaccessibility of some forested regions. For example, the forested floodplains of the Congo Basin below Kisangani, which culminate in the
extensive Bangal swamps, tend to retain water to a greater extent than many savanna floodplains. However, fish ecology in this area is largely unknown; the region is almost completely unpopulated by people, and access is extremely difficult (Welcomme 1985).

The forested rivers differ in many respects from savanna rivers. Their floodplains tend to be restricted in area and in some areas internalized over the numerous islands that form between the braided channels in the larger rivers (Welcomme and de Merona 1988). Various factors may contribute to their more stable flow. Flood peaks may be softened by the long retention time of the water in the flooded forests; in some systems the water arrives at different times of the year from different tributaries; and in the equatorial rivers, there are two rainy seasons a year, producing a bimodal flood regime (Welcomme 1979, 1985; Welcomme and de Merona 1988). Forested river waters are frequently impoverished, with low conductivity and negligible silt load, and are often stained brown with humic acids. In combination with heavy shading of the river channel, this tends to produce waters with low levels of primary production (Marlier 1973; Welcomme 1985; Welcomme and de Merona 1988). The main food source is allochthonous plant and animal matter that falls into the water from the surrounding forest. These characteristics of forested rivers have a strong influence on the ecology of forest fish faunas.

Several families and genera of fishes are shared between forest and savanna river systems; however, many species of fishes are not shared, and some tend to have restricted ranges in the equatorial rain forest systems. In west Africa, for example, Daget and Ilitis (1965) distinguished between widespread species found in several savanna rivers, and species much more restricted in range and found in the forested coastal rivers (Welcomme and de Merona 1988).

DOMINANT TAXA AND HABITAT ASSOCIATIONS

The rain forest rivers of Africa are characterized by a diversity of habitats that differ in physico-chemical conditions and species associations. Major habitat types identified in the Congo Basin include the slow-flowing section of the main river, rapids of the main river, marginal waters of the shores, inundated forest, wetlands, and affluent rivers and streams (Poll 1959; Gosse 1963; Matthes 1964; Roberts and Stewart 1976). The main rivers host a greater diversity of microhabitats than smaller streams and wetlands, and are therefore characterized by higher species richness and diversity (figure 16.3). Different habitats pose different environmental challenges for fishes, and the diversity of habitats is reflected in a rich array of adaptations to permit exploitation of even the most extreme conditions.

In the Congo River Basin, detailed information on species richness and habitat associations is available for only a few sites, including Pool Malebo and nearby areas (Poll 1959); Yangambi near Kisangani (Gosse 1963); the Tshuapa River, a large tributary (Matthes 1964); Lake Tumba, a lake of the Congo River below its confluence with the Tshuapa River (Matthes 1964); and the rapids of the Lower Congo River between Kinshasa and Matadi (Roberts and Stewart 1976; see figure 16.2). The dominant families of fishes in these areas of the Congo Basin include the Mormyridae, Bagridae, Clariidae, Mochokidae, Cyprinidae, Characidae, Cichlidae, Citharinidae, and Anabantidae. These families are also represented in many of the other equatorial forest rivers in Africa (table 16.2).

The nocturnal mormyrids are extremely widespread in the rivers of Africa, with the exception of Madagascar (see table 16.2; figure 16.4). They are the dominant family in both richness (75 of the 408 species) and numbers of individuals in the slow-flowing waters of the central
Figure 16.3. The percentage composition of fishes (number of species per family) in major habitats within four regions of the Congo River. The total number of species in each habitat type is indicated at the top of each bar. Data abridged from Poll 1959 (Pool Malebo), Gosse 1963 (Yangambi), and Matthes 1964 (Ikela region and Lake Tumba), compiled by Lowe-McConnell (1973); and from Roberts and Stewart 1976 (lower Congo rapids). The sites are indicated in figure 16.2.

Congo Basin (Poll and Gosse 1963; Beadle 1981). Mormyrids are well known for their exceptionally large cerebellum, related at least in part to their remarkable electrogenic and electrolocation capabilities (Bennett 1971; Hopkins 1981, 1986; Kramer 1990). Many mormyrids are characterized by tubular mouths with small openings that permit probing and extraction of benthic invertebrates (see figure 16.4). They occur in a variety of habitats, including streams and swamps (see figure 16.3), but they are principally fluvial, associating in shoals that are thought to be kept together by the signals from their electric organs (Beadle 1981; Hopkins 1986).

In the central Congo River Basin the catfishes represent 21% of the fish fauna (36 mochokid species, 27 bagrids, and 23 clariids), and many belong to endemic genera (Poll and Gosse 1963, 1973; Lowe-McConnell 1988; see also figure 16.4). The catfishes are mainly nocturnal and have specialized defenses, including a unique arrangement of the pectoral and dor-
Table 16.2
Fish Families Represented in a Selection of African Rain Forest Rivers

<table>
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<tr>
<th>FAMILY</th>
<th>CONGO (16%)</th>
<th>OGOOU (100%)</th>
<th>SANGA (100%)</th>
<th>KOMOUE (62%)</th>
<th>BANDABA (76%)</th>
<th>SASSANDRA (91%)</th>
<th>&quot;LIBERIA&quot;*</th>
<th>&quot;UGANDA&quot;*</th>
<th>AIR BREATHERS*</th>
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Table 16.3 (continued)

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</table>


*Note*: Locations of the rivers are indicated on figure 16.1. Note that many of the regions within “forest” rivers have been heavily deforested.

a “Liberia” and “Uganda” include several small river systems within the forested regions of these countries.

b “Air breathers” refers to families with air-breathing representatives.

c Represented only by introduced species.

d Represented by both native and introduced species.
Figure 16.4. Selected fish genera found in African rain forest rivers: (A) Protopterus (Protopteridae); (B) Polypterus (Polypteridae); (C) Pantodon (Pantodontidae); (D) Gnathonemus (Mormyridae); (E) Campylomormyrus (Mormyridae); (F) Alectes (Characidae); (G) Hydrocynus (Characidae); (H) Belonophago (Citharinidae); (I) Citharinus (Citharinidae); (J) Barbus (Cyprinidae); (K) Labeo (Cyprinidae); (L) Clarus (Clariidae); (M) Synodontis (Mochokidae); (N) Bagrus (Bagridae); (O) Lates (Centropomidae); (P) Oreochromis (Cichlidae); (Q) Gobiocichla (Cichlidae); (R) Ctenopoma (Anabantidae). Drawings adapted from Greenwood 1966; Lowe-McConnell 1975; and Welcomme 1985.
sal fin spines (Alexander 1966; Roberts 1973). All have barbels and small eyes. The mochokids are primarily bottom dwellers, feeding from soft deposits with their ventral mouth. However, a few species habitually swim upside down, taking food or oxygen from the surface film (Roberts 1975; Chapman et al. 1994). The clarid catfishes are often found over muddy bottoms and are omnivorous feeders. Many have a respiratory organ in the branchial chamber, which permits them to use atmospheric air to meet their oxygen demands in oxygen–scarce waters (Liem 1987; Chapman 1995). Some members of the genus Clarias are capable of terrestrial locomotion during wetter periods (Bruton 1979; Liem 1987). The family Bagridae includes very large predatory catfishes and several small species that live in fast flowing waters of the Congo River (Poll 1957, 1959; Lowe-McConnell 1988).

The Cyprinidae is one of the most abundant and widespread freshwater fish families in Africa and is well represented in many of the rain forest rivers, with the exception of Madagascar. It is the dominant taxon in many of the small forest rivers of western Uganda (Chapman, unpubl. data) and represents 13% of the fish fauna in the central Congo River Basin (Poll and Gosse 1963; Lowe-McConnell 1988). The genus Barbus (figure 16.4) includes several species in the Congo Basin (Poll 1973), many of which are small species that feed primarily on benthic invertebrates and vegetation debris (Matthes 1964). Other cyprinids of the genus Lakeo are mud and detritus feeders and are largely open water forms (Matthes 1964). In the Congo Basin, the cyprinids are most common in the rivers and streams and rare in wetlands (see figure 16.3). This differs from patterns observed in the small forest streams and rivers of Uganda, where some Barbus species are extremely tolerant of hypoxia and are abundant in wetland habitats (Chapman and Liem 1993).

The characiforms (characids, cichariniids, heptetids) are widespread in the rain forest rivers of Africa, with the exception of Madagascar, and compose 18% of the fish fauna of the central Congo Basin (Poll and Gosse 1963; Lowe-McConnell 1988; see table 16.2 and figure 16.4). Most members of the family Characidae are silvery, iridescent, laterally compressed, open water fishes that are active in the daytime (Roberts 1973). In the Congo River, the group includes large piscivorous forms (e.g., Hynobryrus) in the open waters and smaller omnivorous species, plankton feeders, and surface insect feeders (Gosse 1963; Matthes 1964). The Cichariniidae include an interesting group of deep-bodied, mud-sucking fishes that occupy the benthic zone of the open river (e.g., Citharinus, figure 16.4). Also included in this family is a remarkable group of long slender fishes, found mainly in the Congo Basin, which are specialized to feed on the fins of other fishes (e.g., Phago and Belonophago, Matthes 1961), and several species of macrophyte feeders (Distichodus spp.) that tend to occupy marginal waters (Matthes 1964). The family Heteropteriidae includes only one species, the primitive characiform Heptetus ovo, a large predatory fish.

Cichlids are found in most forest rivers in Africa (see table 16.2), representing 8% of the central Congo Basin fauna in terms of species richness (Poll and Gosse 1963; Lowe-McConnell 1988). However, with the exception of the Lower Congo rapids, where the endemism and abundance of cichlids are remarkably high, they seldom constitute a major portion of the individual fishes at a site, and species tend to be few at any one site (Roberts and Stewart 1976). A similar pattern occurs in the forested rivers of Uganda (Chapman, unpublished data). Endemism of cichlids at the specific and generic levels is high in DR Congo, but the spectacular radiations that have produced large species flocks are limited to the Great Lakes of east Africa (Greenwood 1981, 1994; Kaufman et al. 1996). The cichlids
include the tilapiines, which are important food fish (both when caught in the wild and when produced in aquaculture), as well as many other small species (see figure 16.4). In the Congo River Basin they are found in a variety of habitats, including the inundated forest zone, but seldom inhabit the hypoxic waters of swamps (see figure 16.3).

The Anabantidae is also a widespread family in equatorial forest rivers and is one of the few fish taxa to be well represented in swamps (see table 16.2 and figure 16.3). A labyrinthine respiratory organ in the suprabranchial cavity permits use of atmospheric air and enables survival in the deoxygenated water of dense swamps. Many anabantids feed on benthic invertebrates or surface insects of allochthonous origin (Matthes 1964; Greenwood 1966).

Many other families are represented in the rain forest rivers of Africa (see table 16.2 and figure 16.4). Some of the most widespread families tend to be species poor. This includes many air-breathing fishes that can be found in the dense interior of deoxygenated swamps, like the lungfishes (*Protopterus dolloi* and *P. annectens*) and polypterids (seven species; Poll 1973). The ability to disperse through swampy divides and their resilience to extreme physicochemical conditions facilitated by air breathing may contribute to the widespread distribution and low endemcity of many air breathers.

Although specific associations of fishes characterize different habitats of the Congo Basin and other forested rivers in Africa (see figure 16.3), community composition changes over the year as fishes move to different habitats with the seasons (Lowe-McConnell 1975). In addition, community composition will vary among years owing to annual variation in the onset, magnitude, and duration of flooding. The dynamic nature of the community composition is not unique to forest rivers; in fact, it is probably more dramatic in savanna rivers, with their more extensive floodplains. Such seasonal shifts in habitat use and interannual variation in the relative abundance of species may be important in permitting high numbers of species to coexist (Lowe-McConnell 1975; Chapman and Chapman 1993).

**Responses to Environmental Challenges**

**SEASONALITY**

Water level is often the most seasonally varying environmental parameter in tropical rivers, the effects of which can match the importance of temperature in many temperate waters. Although water levels are less dynamic in most African forest rivers than in the Amazon region, the ecology and behavior of the fishes are still geared to changes in available habitat mediated by seasonal rains. The pronounced seasonality associated with biannual flooding in the equatorial rain forest rivers and annual flooding in rain forests of higher latitudes (such as Sierra Leone) is reflected in patterns of breeding, growth, and mortality.

The main effect of seasonal flooding is an increase in available habitat. The degree of expansion varies with the topography of the system, and the most pronounced effects can be observed in shallow forested wetlands and flat river basins bordered by low relief forest that becomes inundated. In high-gradient channels, like the rapids of the lower Congo, the effects of the floods are reflected in changes in current velocity, with less extensive habitat expansion. In intermittent forest streams, habitats may shift rapidly from fast-flowing waters during flooding to small isolated stagnant pools during the drier periods.

Seasonal flooding can also induce marked changes in the physico-chemical environment, but the nature of the shift varies among habitats. For example, dissolved oxygen is extremely low during the dry season in many wetlands and stagnant pools of intermittent forest streams. Studies in Kibale National Park of Uganda have demonstrated the strong interaction...
between seasonal flooding and habitat in contributing to variation in dissolved oxygen levels. Kibale Forest is drained by two major ever-flowing rivers, the Dura and Mpanga Rivers; both are tributaries of Lake George (figure 16.5). These rivers are choked by papyrus (*Cyperus papyrus*) swamps for several kilometers and are fed by numerous small forest streams. Average monthly oxygen levels are extremely low in the swamps but vary markedly with season. In the Rwembaita Swamp of central Kibale, oxygen averaged only 1.5 mg/L over a two-year period but showed a strong increase to more than 3.5 mg/L during peak flood conditions (figure 16.6). A small intermittent tributary showed higher values of dissolved oxygen than the swamp (mean = 3.3 mg/L), with less dramatic seasonal variation than the swamp. In the ever-flowing Njuguta River, a tributary of the larger Mpanga River, dissolved oxygen was consistently high throughout the year (mean = 6.3 mg/L), with little seasonal variation (see figure 16.6). The dramatic changes in the oxygen environment of wetlands and other seasonally hypoxic (oxygen-scarce) waters may permit seasonal access to fishes otherwise unable to exploit these areas, or provide conditions suitable for seasonal spawning.

During the high-water period, many fishes move into the inundated forest and forest wet-

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**Figure 16.5.** Map of the major river systems that drain Kibale Forest (Dura River and Mpanga River) and the sampling sites for dissolved oxygen concentration and the gill size of the cyprinid *Barbus neumayeri*. Site 1: Rwembaita Swamp, a dense papyrus swamp; site 2: Inlet Stream East, a small intermittent feeder stream of the Rwembaita Swamp; site 3: Njuguta River, an ever-flowing tributary of the Mpanga River; site 4: a forest site on an ever-flowing section of the Mpanga River. Dotted lines mark the boundaries of Kibale National Park.
Figure 16.6. Mean dissolved oxygen levels (mg/L) for three sites from Kibale National Park: a papyrus swamp (Rwembaita Swamp; figure 16.5, site 1), a small intermittent stream (Inlet Stream East; figure 16.5, site 2), and an ever-flowing river (Njuguta River; figure 16.5, site 3). Each value represents the mean of duplicate samples at a series of sites in each system over a two-year period. Seasonal variation in oxygen levels in the Rwembaita Swamp are shown relative to the seasonal pattern of rainfall (mm). No data are available for the sampling periods indicated by X.
lands to feed and reproduce. Growth during the flood period is rapid because fishes are widely dispersed in new habitats where food is plentiful. In the Congo River, where there are two floods a year, fishes tend to have two breeding seasons, although it is unclear as to whether individual fish breed once per year or during both flood events (Matthes 1964; Lowe-McConnell 1975). Many fishes migrate upstream as the Congo River waters begin to rise and then move laterally into the flooded forest to release the young in the forest waters (Matthes 1964; Lowe-McConnell 1975). For example, in Lake Tumba, a large lake in the Congo River Basin (see figure 16.2), fishes penetrate tens of kilometers into the inundated forest to spawn and feed during high water. This seasonal strategy may contribute to the richness of the Lake Tumba fish fauna. The water of the lake is chemically impoverished, with very low primary productivity, but the floods allow fishes to find food and nursery areas far from the lake in the inundated forest (Lowe-McConnell 1975). In the Yangambi area (see figure 16.2), Gosse (1963) reported juveniles of many fish species using the inundation zones where insect larvae, rich bottom deposits, and zooplankters provide young with abundant food supplies. As water levels fall, the juveniles move out of the inundation zone to the floating meadows or marginal macrophytes, which provide cover from predators like *Hydrocynus* (Gosse 1963; Lowe-McConnell 1975).

Some fish are total spawners and have very discrete breeding seasons, while others are multiple spawners that tend to spawn from just prior to the onset of the floods until peak floods. Other species in equatorial forest rivers breed throughout the year but show strong peaks in spawning activity. For example, in the valley swamps and forest rivers of Kibale Forest, reproductively mature individuals of *Barbus neumayeri* and *Clarias lincephalus* are found throughout the year. However, there are definite peaks in reproductive activity coinciding with seasonal peaks of precipitation, when oxygen levels are relatively high (Chapman and Frankl, unpublished data). This seasonal pattern may permit the young to access seasonally available habitat and may minimize exposure of eggs to the extreme hypoxia that characterizes the dry season in the valley swamps.

The flood regimes are more predictable than other kinds of variability and have permitted adaptive responses to evolve. New habitat increases environmental heterogeneity, alters community composition, and may contribute to higher levels of species diversity than would be supported by a more stable regime (Roberts 1973).

**FISH-FOREST TROPHIC INTERACTIONS**

One of the key features of forest waters is the dependence of fishes on food of allochthonous origin. The forest rivers are often black-water rivers with low pH, low conductivity, and a low silt load. In combination with the heavy shading induced by the forest canopy, the contribution of phytoplankton to primary production within forest rivers tends to be extremely low (Welcomme and de Merona 1988). Nutrients of allochthonous forest products (vegetation debris, insects, and so on) are therefore often the most important source of input into the system and form the basis of the food webs (Lowe-McConnell 1975; Welcomme 1985; Welcomme and de Merona 1988). Fishes must adapt themselves to the seasonal availability of allochthonous foods, and the main feeding time is the high-water season, when forest areas are more accessible (Lowe-McConnell 1975).

Much of what we understand about the use of flooded forest by fishes comes from studies of the inundated forest of the Amazon. Here many fishes move into the inundated forest zone to feed on forest products. For example, Goulding (1980) reported forty fruit and seed species (thirty-eight genera) that were exploited by fishes in the Rio Machado of the Amazon Basin.
Adaptations to fruit eating include the strongly developed dentition for seed crushing seen in some Amazonian species (e.g., *Colossoma* and *Myleus*), which act as seed predators. Other species ingest the seeds whole and serve as dispersal agents (Goulding 1980). Unfortunately, we understand far less about the inundated forest regions of African equatorial forest rivers. Specialized fruit eaters like those of the Amazon do not seem to be as apparent; the African fish faunas seem to lack taxa with strongly developed dentition that characterizes some of the Amazonian species (Goulding 1980). However, it is clear that several species rely on forest foods during the inundation period. Matthes (1964) reported 38% of the 127 fish species of the Ikela region and 26% of the 119 fishes in the Lake Tumba region of the Congo River as seasonal inhabitants of the inundated forest zone. Foods of terrestrial origin in the stomach contents of these fishes included vegetative material (leaves, twigs, flowers, fruits, seeds), terrestrial invertebrates (such as ants, termites, coleopterans, dipterans, and spiders), and detritus (Matthes 1964). Some fishes inhabiting the margin of the inundated forest also benefit from allochthonous forest foods that fall into the water or emerge floating from the interior.

**RAPIDS**

The 350 km of rapids in the Congo River between Stanley Pool (near Kinshasa) and Matadi (see figure 16.2) probably represents the most extensive area of rapids in the tropics (Beadle 1981). The rapids are characterized by an abundance of oxygen but very low light levels under the rocks, where some rapids fishes spend much of their time. Some remarkable endemic adaptations characterize the fish fauna of this region. The most common structural modification of the rapids fishes is reduction of the eyes. Of the sixty-six highly specialized rapids fishes that Roberts and Stewart (1976) found in their study of the rapids of the lower Congo River, twenty-six species had small or minute eyes, five species had eyes reduced in size and partially or completely covered by skin and other tissues, and one species had no eyes. Other characteristic structural modifications include mouths modified as suckers to attach to rocks, dorso-ventral flattening of the body, horizontal positioning of paired fins (which are often enlarged), and loss of accessory air-breathing organs in some clarid catfishes (Welcomme 1985; Welcomme and de Merona 1988; figure 16.7). Members of the family Amphiliidae are well adapted to life in strong currents. They are elongated, streamlined fishes that possess sucker-like mouths or enlarged fins with which they can cling to the substrate (Welcomme 1985; Welcomme and de Merona 1988; see also figure 16.7). Elongated forms occur in other rapid-adapted fishes, including the polypterid *Calamoichthys calabaricus*, the mormyrid *Mormyrops longiceps* (see figure 16.7), and the cichlid *Gobiocichla wondari* (Welcomme and de Merona 1988).

Most of the rapids fishes in the Congo Basin are endemic, and many of them are restricted to the extensive rapids between Pool Malebo and Matadi (Roberts and Stewart 1976). The families most represented in this radiation are the Mormyridae, Bagridae, Mochokidae, and Cichlidae. The radiation of endemic rapids species of cichlids is particularly surprising given that cichlids seldom comprise more than a few species in other riverine faunas.

Our estimates of the diversity and endemism of fish faunas of the rapids habitats is conservative, because these fishes are not well known, particularly those from the Ubangui, the Kasai, and the Lualaba regions of the Congo Basin (Roberts and Stewart 1976). Sampling is difficult, and surveys have been few. Additional sampling will no doubt yield new species in this region and novel adaptations to this extreme environment.
Figure 16.7. Adaptations to swift current in some African fishes that inhabit the rapids of the rain forest rivers: (A) Gymnallabes typus (elongated body); (B) Mormyrops longiceps (elongated body); (C) Amphilius platychir and (D) its sucker-like mouth; (E) Chiloglanis micropogon and (F) its elaborate sucker-like mouth. Drawings adapted from Welcomme and de Merona 1988, courtesy of IRD (Institut de Recherche pour le Développement).

DEOXGENATION

Oxygen scarcity (hypoxia) is widespread in tropical freshwaters, particularly in heavily vegetated swamps, marshes, inundated forest areas, and the dry-season pools of intermittent watercourses (Carter and Beadle 1930; Carter 1955; Kramer et al. 1978; Chapman and Kramer 1991; Chapman and Liem 1995; Chapman et al. 1998). In these habitats, the availability of oxygen is strongly influenced by the flood cycles, and these two factors create strong seasonal changes in habitat availability. Hypoxic habitats are well represented in the rain forests of Africa. Extensive wetlands, including enormous areas of swamp forest, lie in the central Congo Basin, north of the confluence of the Congo and Oubangui Rivers (see figure 16.2), and several shallow lakes (including Lake Tumba) are associated with these swamps. Swamp forests are also prevalent in some lowland areas of west Africa, which grade into extensive mangrove in coastal areas. In the forests of east Africa, one finds river valleys choked with wetlands, which can extend for several kilometers. The permanent swamps in east Africa and parts of central Africa are dominated by papyrus (Cyperus papyrus) (Carter 1955). Along sections of the Congo River, Vossia cuspidata (hippo grass) replaces papyrus, and the permanent forested swamps of the central Congo Basin are dominated by Cyrtosperma senegalense and the palm Raphia (Howard-Williams and Gaudet 1985). Papyrus is relatively rare in west Africa, where it is replaced by Cyrtosperma senegalense and Vossia.

Heavily vegetated swamps where emergent
vegetation shades the water from light and wind are often characterized by very low oxygen conditions. For example, the dense canopy of *Cyperus papyrus* (which averages 4–5 m in height) intercepts more than 90% of incoming radiation (Thompson et al. 1979; Jones and Mithuri 1985). In combination with high rates of organic decomposition, these conditions contribute to extreme hypoxia in the dense interior of some papyrus swamps, which can average less than 1.0 mg/L for much of the year (Carter 1955; Chapman and Liem 1995; Chapman et al. 1999; see also figure 16.6). Temporary peripheral swamps that form part of the inundation zone can be characterized by higher oxygen levels if the vegetation permits exposure to light and mixing. These less hypoxic wetlands are extremely important nursery and breeding areas for fishes on a seasonal basis.

One sees myriad adaptations (physiological, morphological, and behavioral) by fishes to the respiratory challenges imposed by oxygen-scarce waters. Permanent swamps tend to be inhabited by a specialized fauna adapted for life in deoxygenated waters. The development of air-breathing organs is more common in tropical freshwater swamps than anywhere else (Roberts 1975), and in Africa one finds air-breathing representatives in at least nine of the families of freshwater fishes (see table 16.2). All of the genera of air-breathing fishes are common in the swampy regions of equatorial forest (Roberts 1975; Beadle 1981). The largest air-breathing families of the equatorial forest are the Clariidae and the Anabantidae. Unlike gills, which seem to be evolutionarily homologous among species, air-breathing organs show remarkable diversity in their structural morphology and their origins (figure 16.8). These include such innovations as diverticula of the branchial chambers (as in *Clarias, Anabas, and Ctenopoma*) and modification of the air bladder (as in *Polypterus, Pseudonutum,* and *Phractolaimus*). Air-breathing fishes combine the use of dissolved and atmospheric oxygen; however, there is great variation in the degree of dependence on atmospheric air and in the degree of the development of gills and air-breathing organs (Carter 1957; Johansen 1970). Some species, like the lungfishes (*Protopterus spp.;* see figure 16.4), a widespread taxa in equatorial forest swamps, are obligatory air breathers and will die without access to the surface. Other species, including the air-breathing *Clarias,* have well-developed gills and can meet their oxygen requirements using water breathing at higher oxygen levels.

Air breathing permits the lungfish to withstand extended periods of desiccation that can characterize dry-season conditions in some wetlands. Methods for surviving prolonged dry periods vary among lungfish species and include secreting subterranean cocoons (*Protopterus annectens*; see figure 16.8), lying in water-filled subsurface burrows (*Protopterus dolloi*; see figure 16.8), or burrowing into moist regions of the substrate (*Protopterus aethiopicus*; this species is also known to aestivate like *Protopterus annectens* [Greenwood 1987]).

Although air-breathing fishes tend to be widespread in swamps of equatorial Africa, some non-air breathers also survive in dense wetlands. For example, the small cyprinid, *Barbus neumayeri,* is found in the interior of papyrus swamps of Kibale Forest in Uganda, where it survives by virtue of a low critical oxygen tension, high hemoglobin, large gills, and extremely efficient use of aquatic surface respiration (Chapman and Liem 1995; Olowo and Chapman 1996). Even when a water column is devoid of oxygen, diffusion will maintain a microlayer of well-oxygenated water at the surface. Some water-breathing fishes, like *Barbus neumayeri,* skim the surface under extreme hypoxia to exploit the oxygen-rich surface film, a behavior referred to as aquatic surface respiration, or ASR (Kramer and Meeghan 1981; see figure 16.8). ASR is common among non-
air-breathing fishes from hypoxic habitats (Gee et al. 1978; Kramer and McClure 1982; Kramer 1983; Winemiller 1989; Chapman et al. 1995); however, species of fishes with subterminal mouths (like many catfishes) face the problem of attaching their mouth to the surface film. The upside-down swimming habit of the central African mochokid catfish, *Synodontis nigriventris*, is one solution to this problem (see figure 16.8). This catfish exhibits reverse countershading and can be found swimming inverted (Daget 1948), a habit often associated with exploitation of the water surface for feeding or respiration (Chapman et al. 1994).

Roberts (1973) noted an interesting link between oxygen-deficient habitats and parental
care in fishes of the Amazon and Congo Basins. He observed that in these large tropical rivers, parental care occurs primarily in fishes in which the adults breed in swamps and other oxygen-deficient habitats. For example, in the African lungfish (Protopterus spp.), a nest is constructed and guarded by the male (Johnels and Svensson 1954; Bouillon 1961; Greenwood 1987). In the central Congo Basin P. dolloi excavates a burrow that receives air through a chimney-like structure, without which the eggs would be deprived of oxygen (see figure 16.8). The small anabantid fish Ctenopoma damasi and the characoid Hepsetus adae construct floating nests of foam in which the eggs are supported (Berns and Peters 1969; Roberts 1973).

Although the dense interior of heavily vegetated wetlands in African forests is depauperate with respect to fish species richness, these habitats may still contribute to the maintenance of fish faunai structure and diversity for a number of reasons. First, wetlands provide important habitats for some fishes that are rare in other habitats (such as Phractolamus, Ctenopoma, and some clarid catfishes). Second, swamps may contribute to faunal diversification. For air-breathing fishes, papyrus swamps and other large swampy divides are not likely to be a barrier to dispersal. However, for hypoxia-intolerant water breathers, dense swamps may limit movement and serve as an isolating mechanism. For water breathers that can survive in the dense interior of papyrus, the use of, and dispersal through, papyrus are likely to be limited by oxygen availability and the efficiency of oxygen uptake in the species. This may result in geographical variation between swamp populations and populations from open-water sections of the drainage. For example, there are significant differences in the gill morphology, critical oxygen tension, respiratory behavior, and life-history parameters between B. neumayeri from a papyrus swamp in the Kibale Forest of Uganda and B. neumayeri from other sites in the drainage with higher oxygen levels (Chapman and Liem 1995; Olowo and Chapman 1996). The relationship between the gill size of Barbus neumayeri and dissolved oxygen concentration at four sites in Kibale indicates that this variation can occur over very small geographical scales in response to local oxygen conditions (figure 16.9). Recent data have revealed very low dispersal rates between the swamp and river or stream populations, but one that would be theoretically sufficient to homogenize gene frequencies (Chapman et al. 1999). However, randomly amplified polymorphic DNA (RAPD) markers indicated significant genetic differentiation among sites, suggesting habitat-specific selection pressures on dispersers (Chapman et al. 1999).

Unfortunately, we understand very little about the ecology of fishes in the wetlands of African rain forests, particularly in the huge expanses of wetland in the central Congo Basin. Oxygen seems to play a major role in structuring wetland communities, but it is not the only factor of importance. The interaction between oxygen and other physicochemical parameters in affecting fish movement patterns and distribution has received little attention. Often wetlands and other hypoxic habitats, like areas of the inundated forests, serve as nursery areas. It is important that we begin to examine the strategies developed to cope with such environmental challenges during the early stages of life and how the conditions of these habitats affect growth and development. In addition, oxygen levels vary with seasonal flooding, permitting swamp access to many species that are unable to cope with dry-season conditions. To evaluate the importance of rain forest wetlands for fish ecology, evolution, and fisheries production, we need to examine, in much more detail and over a much broader geographical scale, the seasonal patterns of wetland use and physico-
Figure 16.9. Scatter plot showing the relationship between mean percent gill size for four populations of Barbus neumayeri from Kibale National Park, Uganda, and mean dissolved oxygen concentration (mg/L). Mean percent gill size represents the relative position within the estimated range of total gill filament length for freshwater fishes, following Palzenberger and Pohla 1992. Values of dissolved oxygen represent the means of two years of monthly samples for the Rwembaite Swamp (1), the Inlet Stream East (2), and the Njuguta River (3), and the mean of three months of samples for the Mpanga River (4). Numbers refer to the locations indicated on Figure 16.5.

chemical thresholds for movement in and out of wetland sites.

Threats to Forest-Fish Interactions

Three of the most serious potential threats to the maintenance of fish faunal structure and diversity in African rain forests are deforestation, wetland degradation, and species introductions. However, the independent or interactive effects of these factors are largely unknown for many African waters. Fish biology in African rain forests suffers from a lack of baseline ecological studies, which would provide more solid grounds for predicting impacts of anthropogenic change. Nevertheless, from what we understand about accelerating rates of land conversion in the region, the continued introductions of non-native species, and studies in other tropical regions, we can anticipate the nature and severity of such perturbations.

Deforestation in rain forest areas is particularly severe in west Africa, averaging 90% of the original forest cover from Sierra Leone to Nigeria. However, the central DR Congo region is also threatened from all directions, with loss of rain forest estimated at 57% (World Resources Institute 1994; see figure 16.1). Other areas of central Africa are experiencing similar loss. In Madagascar, the eastern rain forest region is largely deforested (84%
loss), a region including several small rivers that drain the forested slopes. In Uganda, remaining forests are primarily isolated fragments; deforestation has been severe, with an estimated 86% loss of tropical moist forest (World Resources Institute 1994; see Wilkie and Laporte, this volume).

Deforestation threatens forest fish faunas on several dimensions, indirectly through the effects of forest removal on water quality and flow regimes, and directly through loss of allochthonous input generated by the forest. Deforestation of the watershed leads to changes in the seasonal flood regime. In forested watersheds, vegetation and topsoil aid in retaining water. With removal of the forest and topsoil, flood peaks tend to become higher and shorter, because runoff is not delayed by the holding capacities of the forest. Dramatic changes in the flood regime can negatively impact fish populations that require a smoother seasonal transition (Welcomme 1985).

Increased turbidity is associated with increased sedimentation and siltation, and much of the increased silt load of tropical rivers in recent history has been associated with the deforestation of land in the upper regions of the watershed (Marlier 1973; Eckholm 1976). In the Ulu Segama rain forest of Malaysia, Douglas et al. (1992) found that logging resulted in a dramatic eighteenfold increase in sediment yield immediately after the bulk of the catchment had been logged. One year after logging, the system had not recovered, although sediment yields were much reduced, to 3.6 times those of the undisturbed forest. Increased sedimentation and higher turbidity can lead to the decline of plankton through a reduction in light penetration, and to a decline in fish production, as well as the disappearance of many benthic animals that are sensitive to mud on their integument and gills or lose their interstitial habitats to clogging by silt (Chutter 1968; Burns 1972; Marlier 1973). Clearing of the forests also leads to increased sunlight and higher water temperatures. Marlier (1973) reported changes in chemical composition associated with increased solar insulation for small watercourses in the eastern Congo Basin. Waters from deforested areas had higher pH and a higher concentration of salts than protected waters.

We understand little about the potential effects of forest clearance on the productivity of fish populations in African rain forests. It is possible that productivity could increase, as was seen in the salmonid standing crops in deforested areas of the northwestern United States and in many benthic invertebrate communities that were invaded by tolerant taxa (Wencomme 1985). However, given that many rain forest rivers in Africa have relatively low primary productivity and rely largely on allochthonous input, destruction of the forest may result in a decline in aquatic productivity. In areas of the central Congo Basin where flooding allows fishes to find food, refuge, and breeding areas in the inundated forest, the consequences of deforestation may be particularly severe.

Although data are few on the impact of flooded forest conversion in African rain forests, the recent history of the Mekong system of Asia provides a basis on which to speculate. In Cambodia, the Mekong River floods into the Grand Lac, a seasonally fluctuating lake, and surrounding floodplain (formerly forest). Many fishes move into the Grand Lac as it fills and then move out into the inundated zone, returning to the lake and migrating downriver as waters fall in the dry season (Lowe-McConnell 1975). Chevey and Le Poulain (1940) found that growth of some cyprinids was faster in the flooded forest than in the open lake and the river, which they attributed to abundant fish food in the forest.

Subsequent to their study, the forest surrounding the Grand Lac area of the Mekong
was cleared for agriculture and firewood. This
clearance was accompanied by a decline of
about 50% in the fishery in twenty-five years
(Welcomme 1985). The decline was attributed
to erosion and silting in the Mekong Basin
and the dramatic decline of allochthonous food
arising from the deforestation. Silting led to
increased turbidity of waters, which in the case
of the Grand Lac coincided with a drop in pri-
mary production reflected in decreased fish
production. Welcomme (1985) reports that the
process was reversed during the late 1970s
when political troubles led to a collapse of the
human population in the region, which per-
mitted the forest around the Grand Lac to
regenerate. Forest regeneration coincided with
an increase in fish populations, which may have
been related to the renewal of forest resources
and reduced fishing pressure.

In Madagascar, forested freshwater regions
have undergone some of the most severe habitat
degradation in Africa (IUCN 1985; Reithal
and Stiassny 1991). In their survey of Madagascar
fish communities in the heavily degraded forests of the central and eastern highlands,
Reinthal and Stiassny (1991) reported severe attrition of the endemics. Despite intensive
sampling in freshwater habitats, they recorded
only six endemic species of the twenty-eight
freshwater endemics known from Madagascar.
However, deforestation is only one of two major
factors that correlated with severe attrition of the freshwater fish fauna. Exotic species intro-
ductions was the other. Reinthal and Stiassny
(1991) found that the fish communities were
dominated by exotic species, and most sites were
composed entirely of introduced species, the
most common of which were the tilapiine Ore-
ochromis mossambicus and two poeciliid fishes,
Xiphophorus helleri and Gambusia holbrooki.

Within Africa, the transfer or introduction
of non-native species has been widespread and
continues (FAO/CIFA 1985). The primary
purpose of such transfers has been to maintain
or increase fish yield, although some introduc-
tions have been undertaken to expand sport
fisheries or to exert biological control (Ogutu-
Ohwayo and Hecky 1991). The most dramatic
and catastrophic introduction involves the
transfer of the Nile perch (Lates niloticus) into
Lake Victoria. Lake Victoria is the largest tropi-
cal lake in the world and shares its waters with
Uganda, Kenya, and Tanzania. It is not a rain
forest environment, but it illustrates the basic
cycles of events that can follow the introduc-
tion of non-native predators into aquatic sys-
tems. More than 50% of the endemic fishes
disappeared from Lake Victoria between 1980
and 1986, and many are presumed extinct
(Kaufman 1992; Witte et al. 1992a, 1992b;
Kaufman et al. 1997). The introduced Nile
perch is proposed to have been a major contrib-
utor to the mass extinction; the decline in
endemic haplochromines is almost reciprocal
with the increase in Nile perch (Ogutu-
Ohwayo 1990a, 1990b; Kaufman 1992; Witte et
al. 1992a, 1992b). As recently as 1978, the hap-
lochromine fauna was intact; haplochromines
contributed about 80% of the biomass and Nile
perch less than 2%, with the remainder con-
sisting of the introduced Oreochromis niloticus
and native non-cichlids (Kaufman 1992). By
1983 in Kenya and by 1986 in Tanzania, the
Nile perch constituted more than 80% of the
catch (Kaufman 1992). The situation in Lake
Victoria has been followed most closely by the
international community, because of its eco-
nomic importance and extremely high endemism. But similar changes have occurred
with the introduction of the Nile perch into
other lakes in the region (such as Lakes Kyoga
and Nabugabo; see Ogutu-Ohwayo 1993;
Chapman et al. 1996b) and with the introduc-
tion of other fish predators in other tropical
freshwaters (such as the introduction of Cichla
ocellaris into Gatun Lake, Panama; see Zaret

The distribution of introduced fishes in the
waters of African rain forests is not well known, and should be addressed. Sites of early surveys in the central Congo Basin (Pool Malebo, Lake Tumba, and the Tschuapa River) should be revisited to evaluate spread and impact of non-native species. In Kibale National Park of Uganda, two introduced fishes (*Pseudocirrhinus reticulatus* and *Oreochromis niloticus*) have been recorded in one of the major rivers draining the forest. At this point they are rare, with no apparent impact; however, spread is inevitable given the prevalence of introduced tilapia and other non-natives in Uganda and accelerating interest and donor support for aquaculture activities in the region. Fish introductions will continue to be made either for biological management or by accidental transfer, and it is therefore critical that we begin to understand the community dynamics associated with such transfers. Two issues are particularly relevant to the introduction of exotic fishes into aquatic systems. First, we must know what limits leaks of exotics from the intended site of introduction into other water bodies. Second, we must know the characteristics of refugia that can be exploited by indigenous species when confronted with an introduced predator or competitor (Chapman et al. 1996a, 1996b). The situation in Madagascar should be an alarm signal to the potential impacts of introductions into other African rain forest waters.

The continued degradation of wetlands in east and central Africa also poses problems for fish populations. In many areas of Africa, wetlands are harvested in a sustainable manner for a variety of purposes. However, an expanding and accelerating trend is large-scale drainage and conversion to agricultural land (Denny and Turyatunga 1992). Wetlands are also threatened by irrigation schemes, improved transport along waterways, industrial pollution, and mining extracts. Estimates of wetland loss range from 40% in Cameroon to 50% in DR Congo to 70% in Liberia (World Resources Institute 1994).

Continued degradation of wetlands will obviously threaten the functional values of wetlands in their water-holding capacity and effects on microclimates (Howard-Williams and Thompson 1985). But in addition, wetland conversion may contribute to a decline of fish diversity through loss of habitat, destruction of refugia, and faunal mixing. Permanent and seasonal swamps are important year-round habitats for some indigenous fishes and are seasonal feeding and breeding grounds for many species. Loss of wetlands means loss of habitat for these species, many of which are important to local fisheries. Of particular importance are the marginal wetlands or ecotones, where the emergent wetland meets the open waters of lakes and rivers. Here oxygen levels are higher because of interaction with the open waters of the river or lake, and fish do not encounter the respiratory challenges imposed by the dense swamp interior. The vast swampy regions that border the shores of Pool Malebo and marginal swamp pools in the central Congo Basin provide cover for many of the small fishes endemic to the region from larger predatory species that may not be able to feed effectively in the structural complexity of the swamp vegetation (Poll 1959). Loss of wetland may contribute to loss of refugia for prey species from swamp-intolerant predators. Finally, by limiting movement and demanding specialization for extreme hypoxia, wetlands may contribute to faunal diversification (Chapman and Liem 1995; Olowo and Chapman 1996; Chapman et al. 1999). Valley swamps in some forest rivers, like those of Uganda, create formidable barriers to the dispersal of some fishes. However, swamp channelization has been adopted as a means of creating agricultural land and improving transport through swamps. In the steeper valleys, the straight, cleared channels reduce hydraulic resistance and decrease the water-holding capacity of the wetland, which encourages fast removal and more dramatic seasonal flooding.
(Denny and Turyatunga 1992). In addition, there is the question whether channelization will remove barriers among populations whose genetic integrity was maintained by swampy divides or facilitate the expansion of introduced species whose dispersal was limited by dense swamps.

Unfortunately, baseline biological data on the interactions of fish, forests, and wetlands are inadequate to make potent predictions with respect to the consequences of continued wetland loss. However, it is clear that wetland loss will precipitate change in fish communities and potentially lead to a decline in fish diversity and biomass.

In tropical rain forests, monitoring, regeneration, and restoration programs have focused primarily on terrestrial communities. However, in reviewing threats to fish-forest interactions in African rain forests, it is clear that aquatic systems are resources that, along with the forests, are subject to significant use and conversion. In addition, aquatic systems absorb the impacts of land-use change and thereby accumulate and consolidate information on terrestrial change over broad spatial scales in flowing river systems, and broad temporal scales in static lake environments (Hellowell 1986; Crisman 1988). Lakes and reservoirs have a history because of their tendency to accumulate materials. In contrast, the renewal of water in flowing systems reflects terrestrial input at any given time. The value of aquatic faunas and water quality as indicators of terrestrial change has long been recognized (Hellowell 1986; Crisman 1988); however, the vast majority of the work on aquatic bioindicators has focused on temperate systems. Future work in rain forest waters should include studies linking the degradation and restoration of tropical forest communities with aquatic ecosystem dynamics to empirically examine relationships between the degradation and restoration of a tropical forest and the structure and composition of aquatic communities. Predictive models of terrestrial change (land-cover and forest-community composition) based on characters of fish and benthic invertebrate communities would be extremely useful in anticipating and ameliorating the impacts of terrestrial change on aquatic communities.

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