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Fishes of the African Rain Forests

Emerging and Potential Threats to a Little-Known Fauna

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The extraordinary diversity of terrestrial taxa in African rain forests is mirrored by the richness of Africa's aquatic fauna. Africa has more than 2,900 known species of indigenous freshwater fishes, over 28% of which are endemic to rainforest regions of Central and West Africa (Roberts 1975; Lowe-McConnell 1988; Daget et al. 1984, 1986, 1991). The forested rivers harbor a diverse suite of archaic and phylogenetically isolated groups (Roberts 1975, Welcomme 1985, Lowe-McConnell 1988); however, our knowledge of these fish faunas is still very limited and goes little beyond species lists and a handful of ecological studies from very few sites. In fact, much of what we understand of the natural history of riverine fishes derives from the study of large, highly seasonal savanna rivers (Welcomme 1979; Welcomme, chapter 8). The forested rivers differ fundamentally from the better-known savanna floodplain rivers. In the forested rivers, the floodplain can be more restricted in area, and flow regimes are more stable (Welcomme 1985). Forested rivers are often characterized by water that is ion poor, with low pH, low conductivity, a low silt load, and negligible primary productivity. These features lead to a strong dependence on terrestrial input as the main food source and a strong linkage between the phenology of terrestrial taxa and aquatic food availability (Marlier 1973, Lowe-McConnell 1975, Welcomme 1985). These key features of forested rivers are reflected in the ecology of forest fishes, particularly with respect to seasonal patterns of habitat use and foraging ecology.

Deforestation, species introductions, wetland degradation, hydrodevelopment projects, fisheries exploitation, and pollution all pose serious threats to fishes of the African rain forests, but the severity of their effects remains largely unknown. In this chapter, we review some of the key features of African forest fish faunas with a focus on richness and endemism,
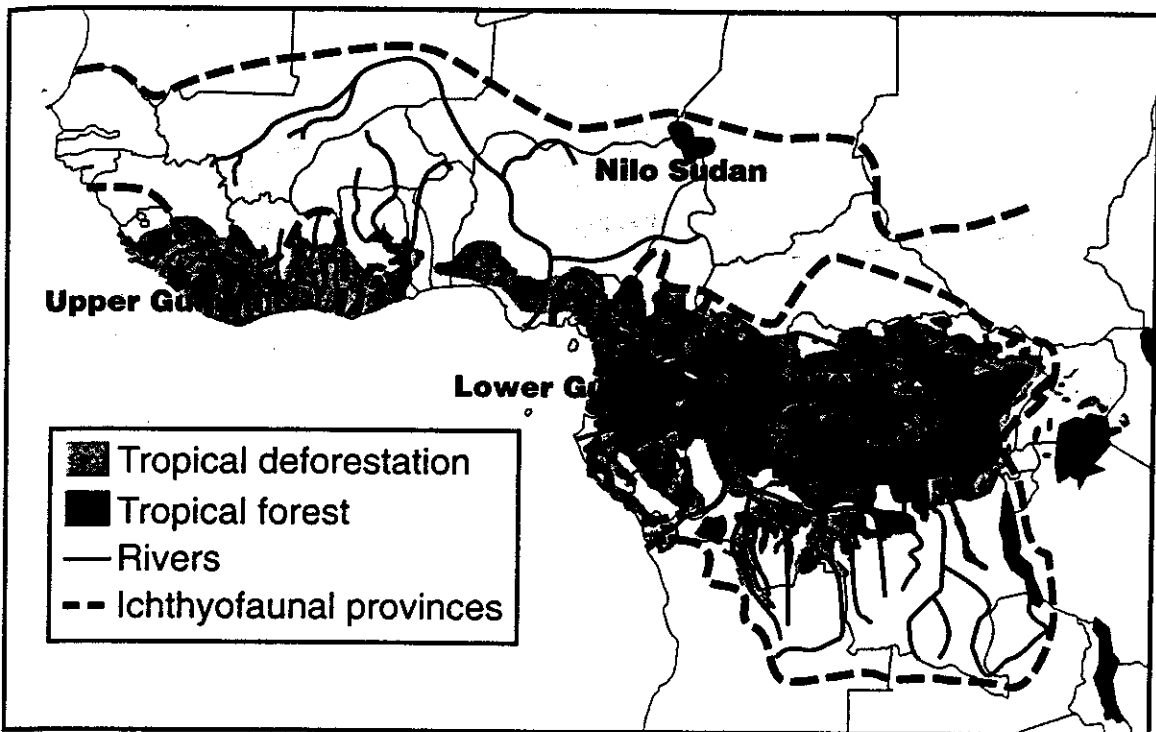
Fig. 9.1. Map of rainforest belt of Central and West Africa, illustrating the major regions of tropical rain forest and the extent of deforestation in these areas (adapted from *National Geographic Atlas of the World* 1992). Also indicated are the major drainages and the Guinean and Congo ichthyofaunal provinces (following Roberts 1975, Reid 1996).

seasonality, and fish-forest interactions. We then discuss potential and emerging anthropogenic threats to the integrity of these little-known faunas.

Characteristics of Forest Fishes

The Amazon versus the Congo

Much of our knowledge of the interactions between fishes and the forest is based on studies of the inundated forest of the Amazon floodplain. In Africa, true forested floodplains similar to those of 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 and Madagascar; and there are small patches of forest in western Uganda (Figure 9.1; Chapman and Chapman, chapter 11; see also Figure 11.1).

Table 9.1. Characteristics of the Amazon and Congo river basins

Character	Congo	Amazon
Length	4,650 km	5,500 km
Discharge	1,400,000 f³/sec	3,000,000– 4,000,000 f³/sec
Drainage	3,822,000 km²	5,600,000 km²
Forest cover	44%	80%
Water level fluctuations	3 m Central Basin	15+ m (Manaus)
Topography	Variable slope (extensive rapids)	Gentle slope
No. of fish species	560+	1,300+
Endemism	82.9%	60%
Marine immigrants	Low	High

Sources: FAO 1981, Marlier 1973, Roberts 1973, World Resources Institute (1994–1995), National Geographic Atlas of the World 1992.

The Congo and the Amazon, the two largest rivers in the world, individually have more fish species than any other river basin, and both exhibit high degrees of endemism (Table 9.1) (Roberts 1973, Revenga et al. 1998). They rank the highest in the world for catchment, length, and output, and both arise on very poor, leached podsolitic soils (Welcomme 1985). However, beyond those characters the two river basins are quite different. The Congo basin covers an area of approximately 4 million km² and drains the largest expanse of tropical forest in Africa, yet only 44% of the basin is covered by forest, compared with 80% in the Amazon basin (Table 9.1) (Marlier 1973, Lowe-McConnell 1975, Revenga et al. 1998). The Congo system is characterized by many more rapids and waterfalls than the Amazon, limiting penetration of marine fishes into the basin (Table 9.1) (Beadle 1981, Marlier 1973, Lowe-McConnell 1975). Relative to the Amazon, where water-level fluctuations are dramatic (more than 15 m at Manaus; Lowe-McConnell 1975), the Congo exhibits only small fluctuations in water level (reaching 2–3 m, from Kisangani to the mouth; Bailey 1986). This more stable regime in the Congo has been attributed to year-round precipitation in the equatorial belt and the balanced input of north and south tributaries. In addition, lakes and swampy depressions in the upper course absorb the effects of the heavy rains (Marlier 1973, Bailey 1986). However, where gradients are low (e.g., Central Congo), large areas still experience seasonal inundation.

Human impacts are more evident in the Congo, where population density averages 15 people/km², as compared with only 4 people/km² in the Amazon basin (Table 9.2). This difference has been reflected in a higher

Table 9.2. Human population density, forest cover, and deforestation in various African watersheds, with data for the Amazon for comparison

Watershed	Basin area (km²)	Population density (no. of people/km²)	Percent forested	Forest loss (%)	Deforestation rate (%/year)
Congo (entire watershed)	3,730,474	15	44	46	7
Congo (Kasai subbasin)	925,172	14	40	66	6
Congo (Sangha subbasin)	180,418	5	64	30	4
Congo (Ubangi subbasin)	613,202	11	26	72	4
Congo (Tanganyikà subbasin)	273,156	33	12	54	13
Ogooue	223,856	4	75	9	5
Nile (entire watershed)	3,254,555	44	2	91	6
Nile (Lake Victoria)	283,168	160	9	89	7
Limpopo	421,168	35	1	99	5
Niger	2,261,763	31	<1	96	6
Amazon	6,144,727	4	73	13	5

Source: World Resources Institute and Worldwatch Institute 1998.

rate of deforestation (7% in the Congo vs. 5% in the Amazon), a greater loss of original forest (46% in the Congo vs. 13% in the Amazon; Table 9.2), and a larger percentage of converted land (Ravenga et al. 1998). Given these dramatic differences between the two systems, we cannot easily translate our broader knowledge of the Amazonian fishes to the Congo fauna. However, the strong interplay between fishes and the forest in inundated regions of the Amazon (Lowe-McConnell 1975; Goulding 1980, 1989) and the implications of deforestation for these interactions (Goulding et al. 1996) highlight the need for more in-depth studies of fish-forest interactions in the Central Congo basin and other heavily forested regions of Africa.

Richness, Endemism, and Patterns of Distribution

By convention, the fish fauna of Africa has been divided into ichthyofaunal provinces based on endemism, palaeogeography, and apparent physical or ecological barriers to dispersal (see Poll 1957, Roberts 1975, Skelton 1988). Several limitations to these traditionally ichthyogeographical accounts have been identified by biogeographers over the past few decades, the most important of which is the need for incorporation of phyletic (cladistic) data and more complete distributional studies (Greenwood 1983, Reid 1996). However, the concept of ichthyofaunal provinces is useful for descriptive and comparative purposes.

Three ichthyofaunal provinces, Upper Guinea, Lower Guinea, and Congo, roughly coincide with the current and past natural distribution of lowland rain forest, excluding recent deforestation, (Figure 9.1) (Roberts 1975, White 1983, Sayer et al. 1992, Reid 1996). Roberts (1975) argues that the contraction and expansion of forested areas during interpluvials and pluvials may have affected the distribution and speciation of fishes. For example, the retreat of rain forest and encroachment of semiarid conditions in the Upper Guinea ichthyofaunal province may account for the disjunct distributions of fishes in the region. He also points out that the Dahomey Gap, which is a nonforested area between the forests of the Upper and Lower Guinea provinces, represents a major biogeographical barrier for many animal taxa. Recent studies recognize the importance of ecology and post-Miocene geology on the distribution of African fishes but emphasize that our current data based on fish systematics and area distributions in African rainforest waters cannot support a rigorous ichthyogeographical analysis (Reid 1996). Nonetheless, it is clear that several fish species inhabiting the running waters of African rain forests occur nowhere else and seem to require the particular ecological conditions perpetuated by large, intact rain forests (Roberts 1975, Reid 1996).

How many fish species occur in the Guinea-Congo ichthyofaunal provinces? This question is key to many important ecological and biodiversity-related concerns. Daget and colleagues' series, *Check-list of the Freshwater Fishes of Africa* (CLOFFA 1–4; Daget et al. 1984, 1986a, 1986b, 1991), has synthesized much of what is known about Africa's freshwater fish biodiversity; however, there is still remarkably little data on many areas, particularly of deeply forested basins. In the rainforest rivers of the Guinea-Congo, the species list continues to grow and is still far from complete (Reid 1996). For example, from the work of Roberts and Kullander (1994) on the Fwa River, Democratic Republic of the Congo, we now know that there are far more species of cichlids than previously thought. In fact, some of this diversity may be represented by riverine species flocks. In their recent review of fish species richness in the Cross River basin, Teugels et al. (1992) reported that previous figures underestimated fish species richness in the basin by 73%. Given these caveats, Reid (1996) offers 1,000 species as an estimate of richness of the Guinea-Congo ichthyofaunal provinces.

Richness varies dramatically among rainforest rivers: from 32 species in the Lobe River to an estimated 669 in the Congo. In an analysis of factors influencing species richness of West African fish communities, most of which were heavily forested, Hugueny (1989) found that species

richness was positively related to area and mean annual discharge. Neither vegetative diversity nor the percent forest cover was a significant predictor of fish species richness. However, on a smaller within-basin scale, the distribution of forest cover seems to be an important predictor of fish community composition. In their study of diversity patterns of fish assemblages in the lower Ntem River basin in Cameroon, Toham and Teugels (1998) found that mean percent canopy closure (bankside cover) was a significant predictor of fish community composition. It is clear from many studies that overhanging vegetation in tropical forests plays an important functional role in determining features of the aquatic system, including water temperature, water chemistry, food availability, and the hydrological regime (Sioli 1964, Fittkau 1967, Marlier 1973, Toham and Teugels 1998). Toham and Teugels (1998) found two distinct groups of fish species; the first one was most often associated with maximal canopy closure, and the second group frequently occurred in waters with an open canopy.

The richness of fish species in many rainforest rivers reflects a high degree of endemism. Based on our current state of knowledge, endemism in the Congo basin is very impressive. Exclusive of Lake Tanganyika, 669 species representing 25 families and 168 genera have been recorded, with 82% endemism at the species level and 25% at the genera level (Poll 1959, 1973; Beadle 1981). This is much higher than the percentage in the Amazon, where endemism is about 60%. New species emerge with new expeditions and will likely do so for some time. This extraordinarily high level of endemism also occurs in several of the coastal rivers from Nigeria to Congo (Roberts 1975). Although species richness is relatively low in Madagascar, endemism is very high: 100% of the truly freshwater fishes (see Reinthal et al., chapter 7) and 14 of the 23 genera (Reinthal and Stiassny 1991). In western Uganda, the rivers draining the small forests are characterized by widespread species and low endemism, though many of the environmental features (high relief, low water-level fluctuations) are shared with the Congo basin (Greenwood 1966; L. Chapman, pers. obs.).

Factors contributing to the high endemism in the Congo basin may include environmental stability over a long period, a wide range of habitats, and numerous barriers (rapids and falls) that have incurred prolonged isolation of fish communities (Beadle 1981, Bailey 1986). In the Congo River, the 350 km of rapids between Stanley Pool and Matadi (Figure 9.2) probably represents the most extensive area of rapids in the tropics (Beadle 1981). The rapids are characterized by high oxygen levels but very low light levels under the rocks, where some rapids-adapted fishes spend much of their time. Roberts and Stewart (1976) recognized
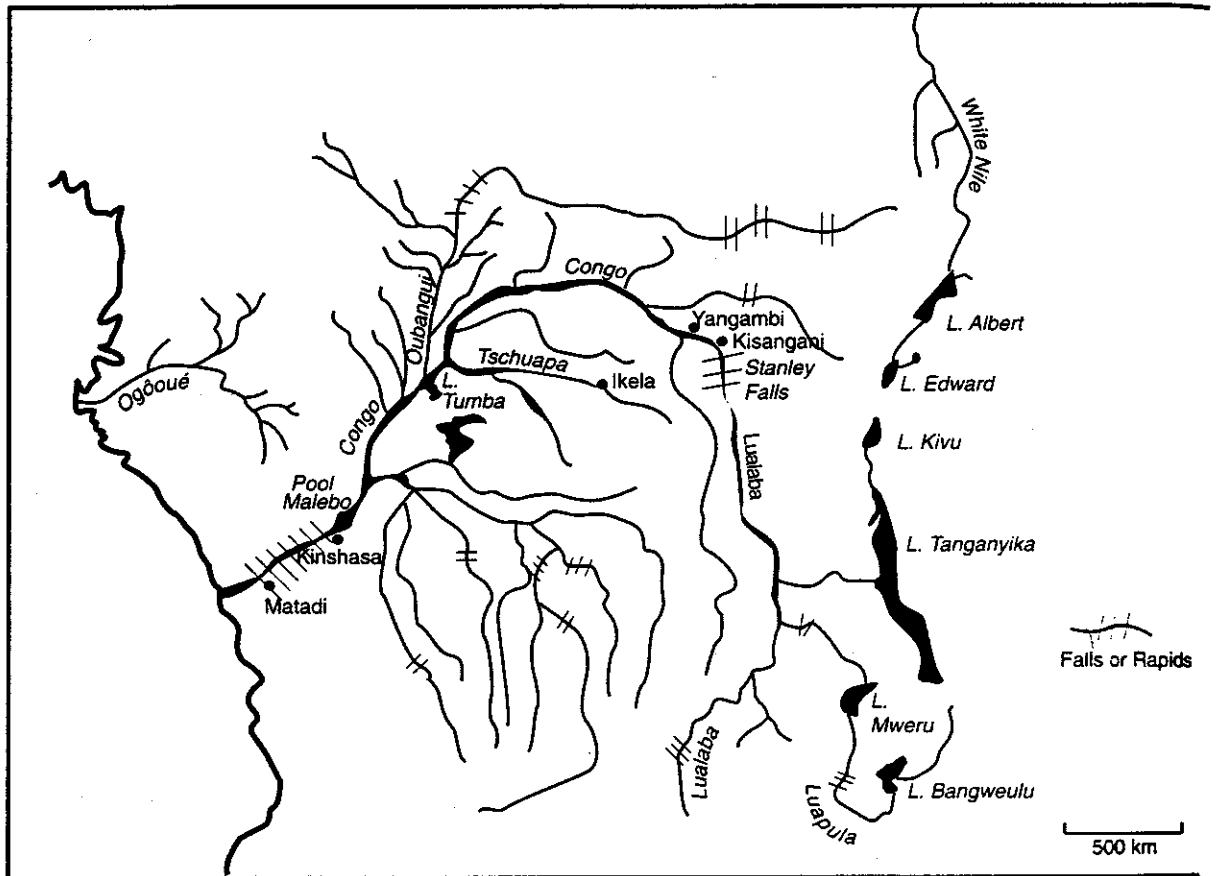
Fig. 9.2. Map of the Congo River basin, indicating the larger tributaries, major survey sites, and adjacent water systems. The tributary rivers east of lakes Tanganyika, Edward, Kivu, and Albert are not shown. (Adapted from Beadle 1981.)

two ecological categories of highly specialized rapids fishes: strongly rheophilic (current loving, 58 species) and hyporheic. The latter group is composed of eight species of fish, which avoid the strong current by burrowing deeply into the interstices of rocks. The most common structural modification of the rapids fishes is reduction of the eyes (Roberts and Stewart 1976). Other characteristic structural modifications include mouths modified as suckers to attach to rocks and dorsoventral flattening of the body (Welcomme 1985, Banister 1996, Welcomme and de Merona 1988). The majority of the rapids fishes in the Congo basin are endemic, and many of them are restricted to the 300-km stretch of 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 rainforest rivers of Africa are characterized by a diversity of habitats, which differ in physicochemical conditions and species associations and may be critical in permitting high numbers of species to coexist. 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 9.3).

Detailed information on species richness and habitat associations is available for only a few sites in the Congo River basin including (see Figure 9.2): Pool Malebo and nearby areas (Poll 1959); Yangambi near Kisangani (Gosse 1963); the Tschuapa River, a large tributary (Matthes 1964); Lake Tumba, a lake of the Congo River below its confluence with the Tschuapa River (Matthes 1964); and the rapids of the Lower Congo River between Kinshasa and Matadi (Roberts and Stewart 1976). In these areas of the Congo basin, the dominant fish families include the Mormyridae, Bagridae, Clariidae, Mochokidae, Cyprinidae, Characidae, Cichlidae, Citharinidae, and Anabantidae (Figure 9.3). These families are also well represented in many of the other equatorial forest rivers in Africa.

Species richness is generally high in the open waters and marginal areas of the main river, where fish communities tend to be dominated by mormyrids, characids, and citharinids. Richness is much lower in the dense swamps within the forested river basins (Figure 9.3). 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 9.2). 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 that can extend for several kilometers. Heavily vegetated swamps, such as papyrus (*Cyperus papyrus*) swamps, where emergent vegetation shades the water from light and wind are often characterized by very low oxygen conditions (Carter 1955; Chapman et al. 1998; Chapman et al., 2000).

Permanent swamps tend to be inhabited by a very specialized fauna adapted for life in deoxygenated waters. The development of air-breathing organs is more common in tropical fresh waters than in other regions (Roberts 1975), and in Africa one finds air-breathing representatives in at least 12 of the families of freshwater fishes (Carter 1957, Roberts 1975,
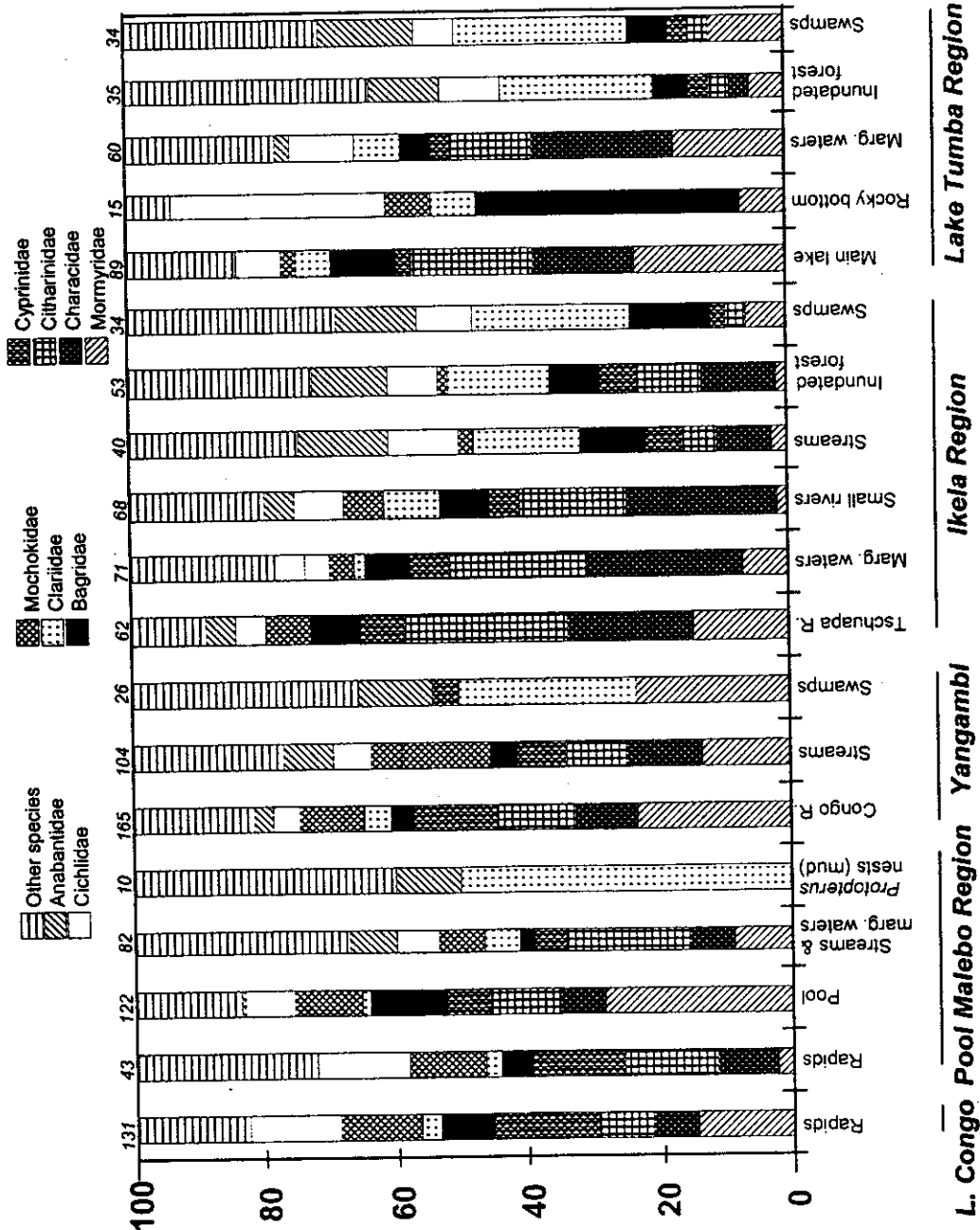
Fig. 9.3. The number of fish species per family (expressed as a percentage of all fish species captured per major habitat) within five regions of the Congo River. The total number of species in each habitat type is indicated at the top of each bar. The sites are indicated on Fig. 9.2 for reference. (Data abridged from Poll 1959; Pool Malebo, Lowe-McConnell 1975; Yangambi, Gosse 1963; Ikela region and Lake Tumba, Matthes 1964; Lower Congo rapids, Roberts and Stewart 1976.)

Graham 1997). Air-breathing organs show a remarkable diversity in their morphology and origins. These include such innovations as diverticula of the branchial (gill) chambers (e.g., *Clarias, Anabas, Ctenopoma*) and modification of the air bladder (e.g., *Polypterus, Pantodon, Phracto- laemus*). All of the genera of air-breathing fishes are common in the wet- lands of the equatorial forest, the Clariidae and the Anabantidae being the two largest families of air-breathing fishes in the region. African lungfishes (*Protopterus* spp.), the best known of the African air-breathing fishes, are obligatory air-breathers and will die without access to the surface. Other air-breathers (e.g., some clariid catfishes) are facultative and can use their gills when dissolved oxygen levels are high. 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 we have found that it survives by virtue of a low metabolism, a low critical oxygen tension, high hemoglobin, large gills, and extremely efficient use of aquatic surface respiration (ASR) (Chap- man and Liem 1995, Olowo and Chapman 1996, Chapman et al. 1999). Even when a water column is devoid of oxygen, diffusion will maintain a microlayer of well-oxygenated water at the surface (Kramer and Mehegan 1981). Some non-air-breathing fishes, such as *Barbus neumayeri*, skim the surface under extreme hypoxia to exploit the oxygen-rich surface film, a behavior referred to as aquatic surface respiration. This behavior is very common among tropical fishes inhabiting hypoxic habitats (Gee et al. 1978, Kramer and Mehegan 1981, Kramer and McClure 1982, Kramer 1983, Winemiller 1989, Chapman et al. 1995). Species of fish with a sub- terminal mouth (e.g., many catfishes) face the problem of attaching their mouth to the surface film. In our studies, we have found that the upside- down swimming habit of the central African mochokid catfish *Synodontis nigriventris* and the mormyrid *Petrocephalus catostoma* is one solution to this problem (Chapman et al. 1994, Chapman and Chapman 1998).

Seasonality

Seasonality associated with biannual flooding in the Central Congo and other equatorial rainforest rivers and annual flooding in rain forests of higher latitudes (e.g., Upper Lualaba, rivers of Sierra Leone) is reflected in patterns of breeding, growth, and mortality. The main effect of seasonal flooding is an increase in available aquatic habitat through inundation of adjacent low-lying habitat. In the Central Congo basin, gradients are gentle, such that large areas are susceptible to seasonal inundation.

During the high-water period, many fishes move into the inundated forest and forest wetlands to feed and reproduce. Matthes (1964) reported 38% of the 127 fish species of the Ikela region and 26% of the 119 species in the Lake Tumba region of the Congo River as seasonal inhabitants of inundated forest. Clariid catfishes were the most speciose family in the inundated forest, but other groups, including the citharinids, characids, bagrids, and anabantids, were well represented. 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, though it is unclear as to whether individual fish breed once a year or during both flood events (Matthes 1964, Lowe-McConnell 1975). Many fishes migrate upstream as the Congo waters begin to rise and then move laterally into the flooded forest to release young in the forest waters (Matthes 1964, Lowe-McConnell 1975). For example, in Lake Tumba (see Figure 9.2), 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 a conductivity of 24 to 32 us and pH of 4.5 to 5.0 (Dubois 1959, as cited in Beadle 1981). It also has 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).

The reproductive biology of forest fishes varies among species but is clearly geared to seasonal patterns of precipitation and flooding. Some fish are total spawners and have very discrete breeding seasons that correspond with early flooding; others are multiple spawners that tend to spawn from just before 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, Uganda, reproductively mature individuals of the cyprinid *Barbus neumayeri* and the catfish *Clarias liocephalus* are found throughout the year. However, there are definite peaks in reproductive activity that coincide with seasonal peaks of precipitation, when dissolved oxygen levels are relatively high (Chapman and Frankl, 2000).

Fishes that use the flooded forest must have a broad physicochemical tolerance, flexible feeding strategies, and high sensitivity to small changes in water level. In Kibale Forest, inundation of the Dura River basin is modest but still has an important impact on fish ecology in the region. The flooded forest of the Dura River differs markedly in limnological characteristics from the main river. Compared with the main river, in the flooded
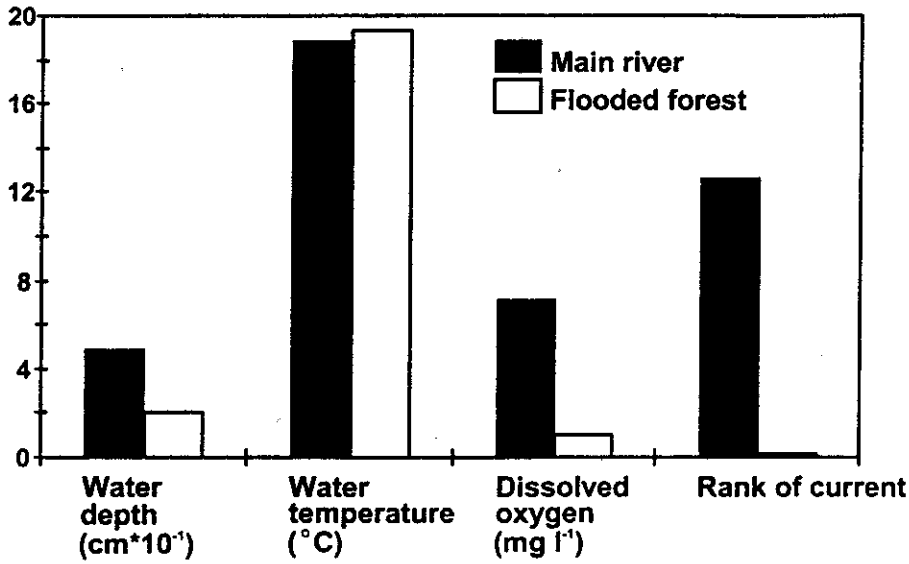
Fig. 9.4. The water depth (cm), water temperature ("C), dissolved oxygen concentration (mg/L), and rank of current for the main waters of the forested Dura River, Uganda, and its associated inundated forest zone.

forest dissolved oxygen content can be very low or moderately hypoxic, current is lower, water temperature higher, and water depth much shallower (Figure 9.4). Fishes that move into the forest must be able to withstand chronic hypoxia and must be sensitive to water-level decline if they are to return to the main channel before being trapped in desiccating forest pools. Certainly, not all fish species move into the forest. In Kibale for example, *Amphilius jacksonii*, a rheophilic catfish with a high metabolic rate and low tolerance to hypoxia, was never found in the flooded forest during a 3-year study of the river (Walsh et al. 2000). However, the cyprinind *Barbus neumayeri* and the air-breathing catfish *Clarias liocephalus* were found in the forest during most months of inundation. The forest is used as a nursery and feeding ground by both species. Although many smaller individuals become trapped when waters fall, many of the fish, including most of the adults, return to the river before isolation of the pools.

Fish-Forest Trophic Interactions

One of the most notable features of fishes in forest waters is their dependence on food of allochthonous origin. The forest rivers are often characterized by black water with low pH, low conductivity, and a modest silt

load. In combination with the heavy shading induced by the forest canopy, the contribution of phytoplankton to primary production tends to be extremely low (Welcomme and de Merona 1988). Nutrients of allochthonous forest products (e.g., leaves, vegetation debris, terrestrial insects) are therefore often important sources of input into the system, and they can form the basis of the food webs (Lowe-McConnell 1975, Welcomme 1985, Bailey 1986, Welcomme and de Merona 1988). Some allochthonous foods show a high degree of seasonal availability, 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. There, many fishes move into the inundated forest to feed on forest products. For example, Goulding (1980) reported 40 fruit and seed species (38 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*) (Goulding 1980). Unfortunately, we understand far less about fish-forest trophic interactions in African equatorial forest rivers, but localized studies suggest a strong interdependence between aquatic and terrestrial ecologies (Reid 1996). Interestingly, 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 (Goulding 1980). However, it is clear that several species rely on forest foods. Reid (1996) reports that several fishes in rainforest rivers of Cameroon feed on plant and animal debris from the rainforest canopy and riverbanks. In fact, windblown terrestrial insects constitute as much as 90% of the diet of the killifish *Epiplatys sexfasciatus* (Reid 1996). Terrestrial insects were also common in 30% of the fish species studied by Matthes (1964) in the region of Lake Tumba and 17% of the fishes in the rivers of the Ikela region. In the river fishes of the Yangambi region of the Congo basin, Gosse (1963) reported terrestrial insects as present in the diet of 13 of 16 species he examined and common in the diet of eight of those species.

Forest Elephant–Fish Interactions

Aquatic and terrestrial ecologies are closely interdependent in a number of other contexts, one of which is the creation or maintenance of aquatic habitat by terrestrial organisms. For example, Brossert (1982) found that the distribution of small annual cyprinodont fishes (killifishes) in Gabon

was associated with the distribution of forest elephant footprints. These annual fishes lay their eggs in small temporary pools in which the eggs remain dormant during the drier periods. In Kibale Forest of Uganda, we have found that the forest elephants play an important role in the maintenance of valley swamp pools. Forest elephants periodically visit the papyrus swamps that choke the forest river valleys. Their wallowing activities create open pool habitat that is quickly invaded by swamp fishes, increasing local fish productivity (L. Chapman and C. Chapman, pers. obs.). As the pools fill with dense swamp vegetation, catch per unit effort declines.

Threats to Forest-Fish Interactions

Deforestation, species introductions, wetland degradation, hydrodevelopment projects, overfishing, and pollution all threaten the integrity of rainforest fish faunas. Unfortunately, the lack of baseline ecological studies precludes us from predicting impacts of anthropogenic change. Nevertheless, from what we understand about accelerating rates of land conversion in the region and studies in other tropical regions, we can anticipate the nature and severity of such perturbations. Dramatic losses in aquatic biodiversity have been documented in many tropical regions. Studies in the Gombak River basin of Southeast Asia showed that 41% of the native fish species were lost between 1969 and 1990. Mohd (1994) attributed this loss to a combination of logging, highway construction, and land conversion to agriculture. Similarly, by 1992 only 29 of the 54 indigenous fish species of Singapore were still extant in the wild (Dudgeon 1992). Factors implicated included loss of migratory routes, overfishing, and pollution. In the Santarem area of the Amazon, more than 90% of the floodplain forest has been destroyed. Adult tambaqui (a characid) and other fruit- and seed-eating fishes, which were once important to the local fisheries, are now rare. Goulding et al. (1996) point out that this is probably due more to habitat destruction than overexploitation.

Deforestation

Although Africa has more semiarid and desert areas than any other continent, rain forest probably covered about 3,620,000 km^2 of continental Africa before anthropogenic land conversion. The majority of the rain forest was found in Central Africa (74%) and West Africa (19%), with small patches in East Africa (7%). Deforestation has reduced rain forest in Central Africa to 55% of its original area but has been much more severe

in West Africa (72% loss) and East Africa (72% loss) (Martin 1991; Chapman and Chapman, chapter 11).

With respect to forested watersheds, the Congo has lost 46% of its original forest and currently experiences a deforestation rate of 7% (Revenga et al. 1998). However, deforestation varies among subbasins from 30% to 72% (see Table 9.2). Variation in deforestation rates reflects in part differences in population densities among the subbasins (see Table 9.2). Some forested watersheds are still relatively intact. For example, the Ogooue watershed of Gabon is 75% forested and has lost only 9% of its original forest cover. Again, this stability is due in part to the low population density in the region (4 people/km^2). In general, though, deforestation in the African rain forest has been more dramatic than in the Amazon basin, where loss of original cover is estimated at 13%, with a current deforestation rate of 5% per year. The link between high population density and forest conversion is particularly evident when comparing the forested rivers of Central Africa with some of the savanna watersheds. For example, the Nile watershed has a population density of 44 people/km^2 and a 91% loss of original forest; the Limpopo has a population density of 35 people/km^2 and a 99% loss of original forest; and the Niger has a population density of 31 people/km^2 and a 96% loss of original forest (Ravenga et al. 1998). In Madagascar, the eastern rainforest region, which includes several small rivers that drain the forested slopes, is largely deforested (84% loss). 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).

Deforestation threatens forest fish faunas in several ways: indirectly through its effects on water quality and flow regimes and directly through loss of allochthonous input. Deforestation of the watershed leads to changes in the seasonal flood regime. In forested watersheds, vegetation and topsoil aid in retaining water. When the forest is removed, flood peaks tend to become higher and shorter, because runoff is not delayed by the forest's holding capacities. Dramatic changes in the flood regime can negatively affect fish populations that require a smoother seasonal transition (Welcomme 1985). In addition, the scouring effects of unnatural sporadic peaks in discharge could potentially deplete algal and insect biomass and force fish downstream (Pringle and Benstead 2001) as is seen in high-gradient tropical streams that experience flash floods (Chapman et al. 1991).

Removal of vegetation decreases the rate of evapotranspiration and the interception of precipitation and therefore increases runoff and sediment

yield. In many tropical forested and savanna rivers, annual sediment yield is low (Chapman and Chapman 2002). Sedimentation increases dramatically in the forested rivers after deforestation (Douglas et al. 1992, 1993; Chapman and Chapman 2002; Chapman and Chapman, chapter 11). 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 in the upper regions of the watershed (Marlier 1973, Eckholm 1976). Reduced-impact logging can minimize the runoff effects of logging. In peninsular Malaysia, two small catchments were selectively logged, one using conventional logging and the other using reduced-impact logging (Yusop and Suki 1994). In the first year after logging, values for suspended solids in the conventionally logged catchment were 12 times those of the control, and high levels persisted until the fifth year. There was, however, only a doubling of suspended solids in the catchment that experienced reduced-impact logging, and the system recovered to predisturbance levels within 2 years.

Increased sedimentation and higher turbidity can lead to the decline of plankton through a reduction in light penetration and the disappearance of many benthic rheophilic 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, Welcomme 1983). These include insect groups such as the Ephemeroptera, Plecoptera, and Trichoptera. Severe modification can result in shifts to invertebrate communities dominated by small burrowing forms such as larval chironomids. The silt can also provide anchorage for vegetation that can block low-order streams (Welcomme 1983). On the floodplain, excessive siltation can choke the standing waters, which then disappear at a rate faster than they are created.

In their review of the effects of logging on tropical riverine systems, Pringle and Benstead (2001) found no studies that dealt specifically with effects of increased sedimentation on tropical fishes. However, in temperate systems, studies (focusing primarily on salmonids) have found negative effects that include smothering of eggs and entrapment of fry by consolidated sediments, mortality of juvenile and adult fish due to clogging of opercular cavities and gill filaments, and sublethal effects such as reduced feeding and growth, respiratory impairment, reduced tolerance to disease and toxicants, and physiological stress (Lloyd 1987, Waters 1995). Other serious impacts are the loss of habitat for fry that require interstitial space in riffles, the filling of pools, and the blanketing of structural cover (Waters 1995). Goulding et al. (1996) comment that floodplain deforestation

in the Amazon had resulted in a dwindling amount of wood that is naturally carried downstream.

High-intensity logging or clear-cut felling can also result in a dramatic decline in the supplies of deadfall and course woody debris, which play an important role in the stability of the stream and create higher structural diversity for fishes and other aquatic organisms.

Clearing of the forests also leads to increased sunlight and higher water temperatures. Marlier (1973) reported changes in chemical composition associated with increased solar insolation for small watercourses in the eastern Congo. Waters from deforested areas had higher pH and a higher concentration of salts than protected waters. In addition, removal of riparian vegetation can lead to fundamental shifts in the resource base of the stream from a food web founded on allochthonous materials to a food web where primary production may be very important. Of course, the primary production may be impeded to some degree by much higher turbidity in deforested watersheds.

We understand little about the potential effects of forest clearance on the productivity of aquatic taxa in African rain forests. The productivity of some taxa could increase, as was seen in epilithic algal communities in streams at the Hubbard Brook Experimental Forest, New Hampshire (Ulrich et al. 1993) and streams of Tasmania (Davies and Nelson 1994), in many benthic invertebrate communities invaded by tolerant taxa (e.g., Stone and Wallace 1998), and in the salmonid standing crops in deforested areas of the northwestern United States (Welcomme 1985). However, given that many rainforest rivers in Africa have relatively low primary productivity and rely largely on allochthonous input, destruction of the forest may result in a decline in the productivity of certain taxa. 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. Such an effect has been observed in the Amazon basin, where the economically important characid *Colossoma macropomum* (the tambaqui) has declined near the major city of Manaus. The decline of the frugivorous tambaqui has been attributed to overfishing and the disappearance of the inundated forest feeding grounds (Marshall 1995). Welcomme (1983) notes that in heavily forested systems such as the Amazon, Congo, and Mekong, trees appear to act as a nutrient sink, and their disappearance from the fundamentally poor systems may have long-term impacts on nutrient balance.

We have found no published data on the effects of sedimentation on the richness of African rainforest fish communities; however, recent studies

have demonstrated the impacts of sediment inundation of lacustrine habitats in Lake Tanganyika. The Lake Tanganyika watershed is undergoing deforestation at an alarming rate (see Table 9.2), producing rapid erosion and the discharge of large volumes of sediment into the clear littoral and sublittoral environments of Lake Tanganyika (Cohen et al. 1993). In their study of disturbed and undisturbed littoral-sublittoral communities, Cohen and his colleagues (1993) found low species richness among fishes and ostracods associated with adjacent watershed deforestation. They suggested that the high sediment yields in disturbed sites may have mediated this decline in fish and ostracod richness by reducing light penetration, thereby decreasing the maximum depth of primary productivity; by binding or releasing nutrients or toxics; by filling cracks and crevices with sediment and reducing habitat heterogeneity; and by decreasing the surface area available for algal growth and invertebrate colonization. In a later study of the same region, Alin et al. (1999) showed that the species richness and density of fishes, mollusks, and ostracods were negatively correlated with sedimentation.

It is likely that the extensive deforestation taking place in Africa will have adverse impacts on aquatic ecosystems and the distribution and abundance of fish species. Within the countries of Africa that host closed-canopy forest, an average of 3.2% of the country has protected status (see Chapman and Chapman, chapter 11). Some important aquatic habitats containing endemic fishes are found within these protected areas, such as the Cross River National Park of Nigeria; however, many key aquatic habitats receive no protection. Reid (1996) notes two prime examples: Lake Barombi Mbo, a small crater lake in Cameroon that hosts an endemic flock of cichlids, and Lake Bermin, Cameroon, which hosts eight endemic species of *Tilapia*-derived cichlids. Unfortunately, it is rare that the location of protected areas has been designed to protect aquatic systems in Africa, and in many countries, there is even a tradition to permit extraction of aquatic resources within park boundaries (see chapter 11 and Mugisha, chapter 20).

Species Introductions

Madagascar hosts an extraordinary fish biota, with levels of endemism upwards of 90% across the region. The majority of the endemics are restricted to freshwater habitats, and 61% of these are found exclusively in the running waters of the eastern and northeastern humid rain forests (Stiassny 1996). Sadly, forested freshwater regions in Madagascar have undergone some of the most severe habitat degradation in Africa (IUCN

1985, Reinthal and Stiassny 1991; Reinthal et al., chapter 7). In their recent survey of Malagasy fish communities in the heavily degraded forests of the central and eastern highlands, Reinthal and Stiassny (1991) reported attrition of the endemics. However, deforestation is only one of two major factors that was correlated with attrition of the freshwater fish fauna. The introduction of nonindigenous species introductions was the other. Reinthal and Stiassny (1991) found the fish communities were dominated by nonindigenous species, and most sites were composed entirely of introduced species. Since the first introduction of the goramy (*Osphronemus goramy*) in 1957, the list has grown to 27 nonindigenous species (Stiassny 1996). Stiassny and Raminosoa (1994) point out that, precluding change in current trends, few Malagasy endemic fishes will survive (see also Reinthal et al., chapter 7).

Within continental Africa, the transfer or introduction of nonnative fish 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 introductions have been undertaken to expand sport fisheries or for biological control (Ogutu-Ohwayo and Hecky 1991). Lake Victoria represents the most dramatic example of biodiversity loss associated with species introductions in Africa. We have seen a mass extinction of indigenous fishes in Lake Victoria that has coincided with the introduction of Nile perch *(Lates niloticus)* and other anthropogenic perturbations to the system. It is estimated that over 50% of the more than 600 endemic species of haplochromine cichlids disappeared between 1980 and 1986, and many are presumed to be extinct (Ogutu-Ohwayo 1990a, 1990b, 1994; Kaufman 1992; Witte et al. 1992a, 1992b; Kaufman et al. 1996, 1997). Similar changes in the fish fauna have occurred with the introduction of Nile perch into other lakes in the region (e.g., Lakes Kyoga, Nabugabo) (Ogutu-Ohwayo 1990a, 1990b, 1993, 1994; Chapman et al. 1996a, 1996b; Schofield and Chapman 1999).

Basic data on international transfers are available for some heavily forested regions. For example, Welcomme (1981) reports seven international transfers of inland fish species into Congo: *Astatoreochromis alluaudi* (for control of snail vectors of bilharzia), *Clarias lazera* (for experimental fish culture and predation on stunted tilapia), *Heterotis niloticus* (escape from aquaculture installations), *Lepomis gilbbosus* (for forage for *Micropterus salmoides*), *Micropterus salmoides* (for control of stunted tilapia), *Sarotherodon macrochir* (for aquaculture), and *Tilapia rendalli* (as a food fish). In Kibale National Park of Uganda, two introduced fishes (*Poecilia reticulata* and *Oreochromis niloticus*) have been recorded in one of the

major rivers draining the forest. In our survey of 20 crater lakes in western Uganda, we found between one and three species of introduced tilapia in all lakes, introduced guppies in seven lakes, and introduced Nile perch in one lake. Further spread is inevitable given the prevalence of introduced tilapia and other nonnatives in Uganda and accelerating interest and donor support for aquaculture activities in the region.

Fish introductions will continue to be made, and it is therefore critical that we begin to understand the community dynamics associated with such transfers. There are two issues particularly relevant to the introduction of exotic fishes into aquatic systems. First, we must know what limits the spread of nonindigenous species 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 rainforest waters.

Wetland Degradation

The continued degradation of wetlands in East and Central Africa also poses problems for fish populations. In many areas of Africa, wetlands are harvested sustainably for a variety of purposes including gathering materials for roofing, furniture, and fish traps. However, since the 1950s, there has been an expanding and accelerating trend for 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 the Democratic Republic of Congo, to 70% in Liberia (World Resources Institute 1994).

Continued degradation will threaten the water-holding capacity and will affect microclimates and other functional values of wetlands (Howard-Williams and Thompson 1985). In addition, we now believe that continued large-scale 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 seasonal feeding and breeding grounds for many species. Matthes (1964) reported 26 fish species as inhabitants of the swamps in the Ikela region of the Congo basin, and Gosse (1963) reported a similar number from the swamps of the Yangambi region. Many of these species are highly adapted to the extreme conditions of the

dense swamp interior; loss of wetland means loss of habitat for these fishes, 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 than in the main part of the wetland 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 the marginal swamp pools of the Central Congo provide cover for many of the small fishes endemic to the region. In these swampy regions, they can hide 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.

By limiting movement and demanding specialization for extreme hypoxia, wetlands may also contribute to faunal diversification (Chapman and Liem 1995, Olowo and Chapman 1996, Chapman et al. 1999). For air-breathing fishes, large swampy divides are not likely to be a barrier to dispersal. However, for hypoxia-intolerant non-air-breathers, dense swamps may limit movement and serve as an isolating mechanism leading to faunal diversification. For non-air-breathers that can survive in the dense interior of papyrus, use of dense swamps is likely to be limited by the efficiency of oxygen uptake. This may result in geographical variation between swamp populations and populations from open-water sections of the drainage. For example, we have found significant differences between the gill morphology, physiology, respiratory behavior, and life history parameters of 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). We have also found genetic differences among these populations that suggest that these swamps pose an ecological and genetic barrier for this species (Chapman et al. 1999). Currently in Uganda, swamp channelization has been adopted as a means of creating agricultural land and improving transport through swamps. This channelization, however, may remove barriers among populations whose genetic integrity was maintained by swampy divides or may facilitate the expansion of introduced species whose dispersal was limited by dense swamps.

Hydrodevelopment Projects

Although large areas of the continent are still comparatively free of major regulatory structures, most large rivers of Africa have at least one main-

stream dam, and some (e.g., Nile) have more. Welcomme (chapter 8) lists all dams over 100 km² and notes that there are also a large number of medium-sized dams (reservoir sizes 10–100 km²). The overriding factor in stream and river regulation is alteration of the flood regime, either for flood control, hydroelectric power production, or irrigation and water storage. In Central Africa, the Lufira, Lualaba, and Congo rivers have been regulated for hydroelectric power, but the immense potential of the Congo River (estimated at 1 million MW) has been largely untapped. At present, a capacity of about 2,000 MW has been realized, and about 2% of the population has access to electricity; most of the currently available power is used by mining companies (Bailey 1986). There has been a tremendous proliferation of smaller hydroprojects, particularly in South Africa and West Africa (see Day, chapter 3, and Gordon, chapter 4).

Although there are few studies on the impacts of dams in forested rivers of Africa, Welcomme (chapter 8) reviews several accounts of the impacts of dams on savanna rivers. One major impact below dams is the creation of barriers to migration. Welcomme suggests that the initial 50% reduction in catch in the Niger River below the Kainji Dam—whereby the characids, mormyrids, and clariids declined in favor of the predatory Nile perch (*Lates niloticus*)—was due to the concentration of migratory species below the dam, which provided an easy target for predators. A second major impact below dams is the regulation of flow, which prevents or decreases inundation of downstream floodplains (e.g., Pongolopoort Reservoir, Pongolo River; Manantali Dam, Senegal River; Kainji Dam, Niger River; see Welcomme, chapter 8). The construction of the Bakolori Dam on the River Sokoto reduced the magnitude of the wet-season floods that supported an extensive floodplain agricultural system and a fishery on which an estimated 50,000 people depended (Adams 1985). There was a substantial decline in both wet- and dry-season fishing; fishing virtually ceased in some villages or became confined to the wet-season riverbed.

Many impacts have also been well documented above dams in Africa, the most significant of which has been the development of major fisheries in large impoundments (see Welcomme, chapter 8). The fisheries have often included species from the original riverine community, but there have frequently been major changes in community structure. Again, much of what we know about impoundment communities derives from studies of savanna river impoundments. However, the principles are likely to apply to forested rivers. The decreased flow, changes in plankton abundance, development of thermal stratification and a deoxygented hypolimnion can result in changes in community structure to exclude rheophilic species,

increase the abundance of planktivorous fish, and eliminate fish species in the hypolimnion or increase the numbers of hypoxia-tolerant species.

As one example, in May 1964, the dam at Akosombo across the Volta River in Ghana was closed and the formation of the Volta Lake began. There were, unfortunately, no quantitative data showing the relative abundance of species available before impoundment, but a few studies of the Black Volta, which was topographically and ecologically similar to Akosombo Gorge, were compared with the early years after the first period of filling. The most characteristic features of the changes in fish fauna during the first few years after filling were an increase in plankton feeders; a great decrease in mormyrids in the lake as compared with the river; a drop in the characid *Alestes*, a predatory fish; and an increase in tilapia (Petr 1967, 1968; Reynolds 1973). The tremendous decline in the mormyrids was attributed in part to an anoxic hypolimnion that developed below about 20 m in depth (Petr 1968). Mormyrids are well known for their exceptionally large cerebellum, which incurs a very high oxygen demand, and many of these species seem very sensitive to low oxygen conditions, which may preclude their use of deoxygenated bottom waters. The main changes in the structure of the fish community following the damming of the River Niger at Kainji were a decline in the numbers of benthic insectivores, primarily the mormyrids, and an increase in the numbers of omnivores, predators, and planktivores (Lewis 1974).

In forested rivers, the flooding of shoreline vegetation is likely to have important consequences for the inshore community. In the Volta Lake, trees submerged by flooding provided a suitable substrate for periphyton in the epilimnion of both inshore and offshore areas; the periphyton in turn provided food and shelter for aquatic invertebrates such as *Povilla adusta*, which became extremely abundant and important as a food source for many fish species (Petr 1970).

Fishing Pressure

There are few areas in Africa where fishing is not practiced, but it is often very difficult to keep records of multigear fisheries that operate from many landings dispersed along a system that may traverse several countries. However, Welcomme (chapter 8) notes that, in general, growing human population densities have led to increased pressure on inland fish resources. This pressure affects fish assemblages through selective fishing on larger individuals and large species. Again, fisheries research has concentrated on the fisheries of major floodplains and lakes and has neglected the major forested basins. However, there are some estimates of catch avail-

able for forested rivers. Freshwater catch in the Congo River has been estimated at 82,000 tonnes (Welcomme 1985). This makes up a large proportion of the total estimate for the Democratic Republic of the Congo, which approximates 114,000 tonnes (Jackson and Ssentongo 1988). The best-known fisheries in the Congo are those associated with lakes and wetlands, but the river itself is fished throughout, mostly to accommodate local demands for fresh catch (Bailey 1986). Artisanal and traditional fisheries account for 90% of the national catch of the Democratic Republic of the Congo (DRC) (Mino-Kahozi and Mbantshi 1997). National fish output has not kept pace with population growth in the DRC, so large quantities of fish are imported. Jackson and Ssentongo (1988) provided estimates of the potential and estimated total catch for several African countries. They reported many areas of Africa where the total annual catch is near the potential catch, including heavily forested areas such as Gabon (90% of potential catch) and the Central African Republic (75%). However, in some largely forested regions, such as the DRC, the total annual catch is estimated at only 41% of the potential total catch. A detailed study of the status and future development of the fisheries in the Korup Rainforest in Cameroon showed that the great majority of working members of the populations were engaged in fishing activities for at least a part of the year (Reid 1989). In Korup and elsewhere in Africa, almost all fishes are used, whatever the size, so the economic species concept does not strictly apply. Reid (1989) found no signs of a general overfishing anywhere in the region and deduced that the fisheries resource in the Korup region is sustainable at present intensity. However, a fish-poisoning problem is emerging. Natural plant products, primarily the poison vine *Strychnos aculeata,* are commonly used in Korup as toxic agents in fish capture. However, Reid (1989) reported that people were also using Gammalin 20, an organochlorine insecticide that produces deleterious environmental effects. The fishermen talk of poor fishing in formerly rich mangrove channels due to an obliteration of the entire aquatic biota by Gammalin.

Welcomme (1985) presented data on the basin area and catch for major African rivers. Although it has been argued that tropical black waters are less capable of supporting sustained fishing pressure than savanna rivers, some of the major forested rivers have a catch that is higher than would be predicted on the basis of their basin area (Figure 9.5). However, much more work needs to be done to elucidate patterns of productivity and to derive more accurate measures of total and potential catch in the forested rivers of Africa.
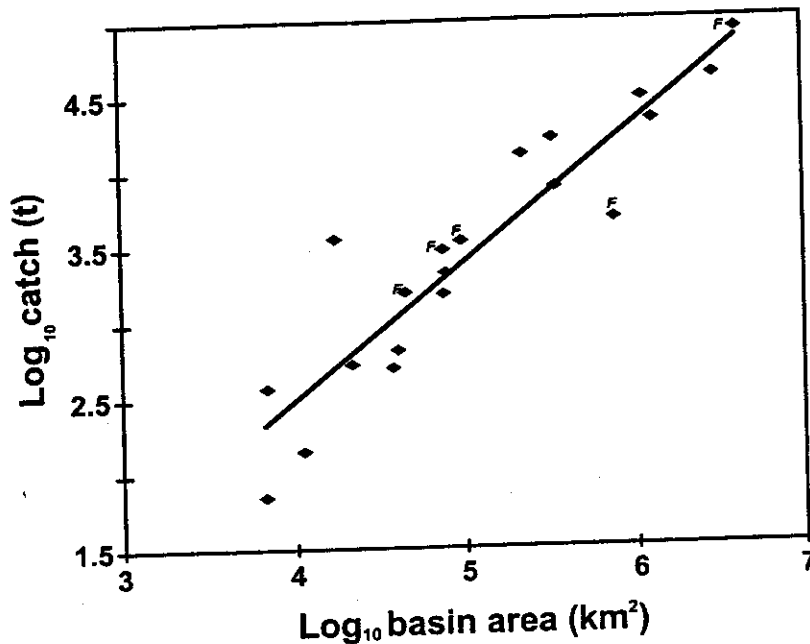
Fig. 9.5. Bilogarithmic relationship between basin fish catch (t) and basin area (km²) for African rivers. Sites marked F represent forested rivers. (Data abridged from Welcomme 1985.)

Pollution

At present, the impacts of pollution on the rainforest rivers of Africa are limited relative to other continents (see Welcomme, chapter 8). However, human population pressure bordering the forested waters of Africa is increasing, as are pollution and degradation in several areas. In the Congo basin, unregulated artisanal and industrial mining for diamonds and gold has been responsible for the physical pollution of certain rivers. For example, the Bakwanga Mining Company, which dredges for industrial diamonds, deposits 6 million to 7 million tonnes of silt, sand, and clay into the Mbuji-Mayi river system and the tributaries of the Lubilanji and Sasai rivers annually (Mino-Kahozi and Mbantshi 1997).

Pollution from poor urban management in the equatorial rain forests is also a growing problem. Many sanitation facilities in the Democratic Republic of the Congo (DRC) are out of order because of lack of maintenance, and sewage is discharged directly into watercourses (Mino-Kahozi and Mbantshi 1997). Similar problems are reported from Cameroon, where many rivers run through large industrial plantations where large quantities of chemical fertilizers, insecticides, fungicides, herbicides, and

so on are washed untreated into the rivers (Folack 1997). Industrial plants and factories are also a source of pollutants in the DRC because most plants do not recycle their waste and lack treatment facilities, and most of them discharge effluents directly into watercourses (Mino-Kahozi and Mbantshi 1997).

There is increasing use of pesticides near watercourses associated with increased human settlement and agriculture along the waterways of the Congo basin. After the crops are harvested, pesticides are often washed away by runoff and erosion into the watercourses. As noted above, pesticides and herbicides also enter the waterways through use in local fisheries that release the chemical upstream, creating downstream contamination for several kilometers (Mino-Kahozi and Mgantshi 1997).

Conclusions

In general, the equatorial rainforest rivers of Africa are characterized by rich fish faunas with high endemism. These fishes interact with the forest on several dimensions. Of particular importance are (1) the heavy reliance on foods derived from the forest to compensate for the low level of primary productivity and (2) the use during seasonal flooding of inundated areas that serve as breeding and nursery grounds. Seasonal flooding affects the availability of oxygen and food, increases environmental heterogeneity, and alters community composition.

Rainforest fish communities are threatened by several human activities, including deforestation, wetland degradation, species introductions, hydrodevelopment projects, fishing pressure, and pollution. Unfortunately, protected-area management in Africa is rarely based on watershed protection or the richness of aquatic communities. Deforestation threatens fish faunas indirectly through effects on water quality and flow regimes and directly through loss of allochthonous input. The application of reduced-impact logging and maintenance of riparian buffer strips offer options to decrease impacts of deforestation, but they require a high level of management. The continued degradation of wetlands in Africa may also precipitate a decline in the diversity and richness of fish communities through loss of habitat, destruction of refugia, and faunal mixing. Even when forest and wetlands are maintained, the continued introduction of nonindigenous species threatens the integrity of fish faunas, as evidenced in the recent history of the rivers of Madagascar. Hydrodevelopment projects can limit migratory pathways, alter water chemistry and flow, reduce downstream floodplain habitat, alter primary productivity, and affect the

composition of invertebrate communities, causing a shift in the composition and abundance of fish assemblages. Increased fishing pressure associated with human population growth and settlement along watercourses is not being curbed by current management and has led to recommendations for more local management initiatives (see Welcomme, chapter 8). Pollution is also an ever-increasing problem, though still localized in the equatorial rainforest regions.

We understand very little about the potential independent and interactive effects of anthropogenic impacts on fish-forest interactions. Of critical importance in the future are distributional surveys to identify priority areas for conservation and to evaluate the spread of nonindigenous species. There are many areas of the equatorial rain forest that have never been adequately sampled, and our knowledge of the true richness of areas is very weak. Of equal importance are the expansion and acceleration of basic ecological studies and empirical studies linking terrestrial degradation with aquatic ecosystem change.

Acknowledgments

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