FUNDAMENTALS OF
Tropical Freshwater Wetlands

From Ecology to Conservation Management

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Chapter 12

Fish

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12.1 Introduction

Fish diversity in tropical freshwater wetlands mirrors diversity and heterogeneity of available habitats and their dynamic connectivity. This leads to functional, life history, and taxonomic diversity of local fishes. Wetland fish have to cope with dynamic environmental and ecological conditions and local fish communities contain a mix of species loosely associated with wetlands and wetland-specialized species. When strictly defined, wetlands are characterized by the existence of relatively shallow water or water-saturated soil (often with anaerobic conditions) (see Wasserman and Dalu, 2022, Chapter 1; Job and Sieben, 2022, Chapter 2; Deemy et al., 2022a,b, Chapter 3). However, deeper water habitats are often considered a part of wetlands (e.g., Alho and dos Reis, 2017) and they are especially relevant for fish, as they typically require some shelter from desiccation. In this chapter, both temporary and permanent wetlands are considered, including floodplain systems of large tropical rivers.

High global diversity of tropical wetland fishes is also associated with the fact that this environment is widespread in Africa, the Neotropics (Central and South America) and southeast Asia, and relatively common in northern Australia and New Guinea. Given the poor long-range dispersal abilities of freshwater fishes, tropical wetland fish communities are dominated by different taxonomic groups across continents and biogeographical regions. Several clades of characiform (tetras), siluriform (catfish), and cichlid fishes taxonomically dominate Neotropical regions. In Asia, cypriniforms replace characiforms, while local perciform taxa (such as anabantoids and ambassids) replace cichlids. African wetland ichthyofauna is composed of all main taxonomic groups and cypriniform fishes coexist with characiforms, anabantoids with cichlids, and catfishes are common. Given the much longer

(although more ancient) link between Africa and Neotropics, fish fauna of the two regions is more similar than to Asia. In northern Australia and New Guinea, wetland ichthyofauna is severely taxonomically depauperated. Rainbowfishes (Melanotaenidae: Atheriniformes) occupy niches taken by cypriniforms and characiforms, percichthyids occupy niches inhabited by cichlids and anabantoids elsewhere, and catfishes (Siluriformes) are relatively common. The diverse origin of continental ichthyofaunas enables interesting comparisons of convergent evolution of functional and life-history traits of tropical wetland fishes across regions. To this end, wetland fishes appear especially suitable for a quantitative comparative study on niche space and use within the concept of "periodic table of niches" (Winemiller et al., 2015), which classifies five primary niche dimensions. Those are habitat use, reproductive and life history, trophic ecology, defense mechanisms, and metabolic strategies.

12.2   Flood pulse: dynamic connectivity

The flood pulse concept characterizes how seasonal dynamics in water level connect river channels with associated habitats in the floodplain (oxbow lakes, backwaters, temporary pools, and flooded terrestrial ground), resulting in maintenance of high functional and organismal diversity (see Deemy et al., 2022a,b, Chapter 6). Flood pulse and associated interconnection of habitats is critical for the functioning of most wetlands worldwide, including the functioning of fish communities. It redistributes nutrients and increases primary productivity, creates new habitats and enables spatial redistribution of organisms, including fishes (Junk, 1999). In the tropics, flood pulses are often highly predictable on a seasonal basis and wetland ecosystems, communities and organisms are adapted to those predictable changes. For example, the annual flood pulse of the upper Paraguay River is the major driver of the changes in the fish communities within diverse Pantanal habitats, as it enables species turnover between periods of low and high water (Da Silva et al., 2010).

The flood-pulse concept predicts a greater diversity of trophic resources available for fish species during floodplain inundation. Pool et al. (2017) used stable isotopic data from 17 fish species from Tonle Sap Lake, an extensive seasonal wetland in central Cambodia which is dependent on substantial annual flooding from the Lower Mekong River, to demonstrate that fish indeed expanded their trophic niches during the flood phase, with broader within-species trophic niches and larger interspecific overlaps. In the Rio Grande (southwestern USA), seasonal flooding extended the narrow algivorous trophic niche of an endangered cyprinid (*Hybognathus amarus*) in streams to exploit rich invertebrate resources in adjacent wetland habitats (Magana, 2013). Wetland habitats are often critical for reproductive activities (spawning) and offspring survival (nursery zones) of tropical fishes.

12.3   Wetland habitat types and associated fish fauna

A larger wetland area often translates into a greater diversity of its habitats and hence increases functional and taxonomic richness of its fish community. Tropical wetlands range from extensive areas such as Pantanal (in the Paraguay River Basin), Okavango Delta and Tonle Sap (in the River Mekong Basin) through intermediate size floodplain systems of many tropical rivers to small, isolated habitat patches such as seasonal marshes, and vernal, rain-fed pools of grassland landscapes, exemplified by temporary pools in semiarid southern Mozambique and wetland marshes in southern Brazil. Consequently, the Great Lake of Tonle Sap Wetland supports at least 150 fish species (Campbell et al., 2006) and the estimated fish species richness in Pantanal is over 300 species (Alho and dos Reis, 2017). In contrast, small seasonal wetlands in savanna regions of Africa and southern Neotropics support few (1−9) fish species (Maltchik et al., 2010; Reichard et al., 2017).

   Large wetlands are typically associated with a large river system composed of a river channel, backwaters, oxbow lakes (which are disconnected from the main river for most of the year), and a multitude of small, temporary streams and pools (Fig. 12.1). In large, complex wetlands, the main river channel serves as a refuge and central migratory pathway for wetland fish (Fig. 12.1A). Tributaries (Fig. 12.1C) and side channels are generally shallower and may be more prone to seasonal changes in environmental and biotic conditions—from water level and temperature, flow conditions and oxygen availability, to the presence of vegetation and predators. Tributaries and side channels may play a similar role to the main river channel but create a finer habitat structure. They also play an important role in fish migrations to flooded temporary habitats of a wetland. Wetlands associated with large rivers may be dominated by forests (e.g., in the Amazon Basin) or shrubs and grasses (e.g., freshwater wetlands in savannas and pampas of southern Brazil), with consequences for the composition of their ichthyofaunas. Backwaters are nonflowing sections of the river channel, connected directly to the main river system. Oxbow lakes (Fig. 12.1B) are former river meanders that lack permanent connections to the flowing section. Oxbow lakes, in particular, harbor seasonally very dynamic fish communities, in response to seasonal fluctuation in water level (Fig. 12.1B, D, and F) and associated conditions and resources (White et al., 2012). Finally, temporary streams (Fig. 12.1E), pools and marshes are exploited by many fish species for feeding and reproduction, utilizing their short-term but high resource availability during the inundated phase. They also act as refuges from predation by larger fishes and provide elevated water temperatures during the daytime, which may increase metabolic activity and growth rates of resident fish. Few species have evolved to be permanent residents of temporary pools.
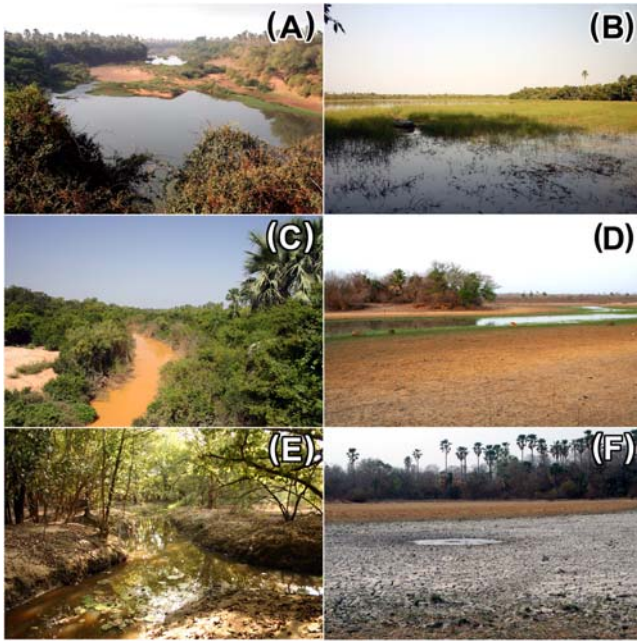
FIGURE 12.1 Wetland habitats associated with the middle reach of the Gambia River. The system consists of fluvial habitats (left panel), with main river channel (A), a series of tributaries (C), and temporary streams (E) and stagnant water habitats (right panel). Oxbow lakes were highly dynamic, with large expanse in area during the wet season (B), shrinking in dry season (D) and occasional desiccation in the driest weeks (F). *Photo courtesy: Martin Reichard.*

To demonstrate the dynamic nature of fish communities associated with wetland systems, I provide examples of fish communities from an extensive wetland system in the middle Gambia River Basin in Senegal, a series of isolated wetland pools in Pantanal, and a small wetland associated with seasonal marshes in southern Brazil.

12.3.1 Example 1: wetland system associated with the middle reach of the River Gambia

The Gambia River is the last of the large West African rivers with a natural flood regime, with no impoundments along its 1120 km long stretch. Its large floodplain is seasonally inundated by river floodwater, creating a network of habitats and allowing fish to move freely across the wetland. A 5-year study was conducted in the Niokolo Koba National Park in the middle reaches of the river. The flow regime of the river is natural, with a peak discharge in September ($\sim 1500 \text{ m}^3 \text{ s}^{-1}$) and minimal flow in May to June ($\sim 4.5 \text{ m}^3 \text{ s}^{-1}$). In the study area, the main river channel never desiccated,

but formed a set of disconnected isolated pools during periods of the lowest flow. A total of 62 fish species from 22 families were recorded over the 5 years (Blažek et al., 2012; White et al., 2012).

In a multiyear analysis, estimates of fish species richness in the main channel (width of approximately 100 m) increased by 50% during the wet season (White et al., 2012). Only one large mormyrid *Mormyrus hasselquisti*, a malapterurid catfish *Malapterurus occidentalis* and a riverine cichlid *Tylochromis intermedius* were recorded exclusively in the main river channel (Blažek et al., 2012), while other species regularly used a wider spectrum of habitats.

Fish species richness in tributaries of the main river, represented by three permanent streams 2−30 m wide, increased in the wet season almost twofold. A claroteid catfish *Chrysichthys mauri*, mochokid catfish *Synodontis schall*, a syngnathid pipefish *Enneacampus ansorgii*, and a gobiid *Porogobius schlegeli* were associated with tributaries and the main river channel (Blažek et al., 2012), indicating their associations with more fluvial conditions. Other species, such as *Ctenopoma petherici* (Anabantidae) (Fig. 12.2D), were present only in temporary floodplain pools in the wet season, and in oxbow lakes and tributaries in the dry season (White et al., 2012).

Oxbow lakes, connected to the main river via temporary channels in the wet season, demonstrated the highest (fourfold) increase in species richness between wet and dry seasons. *Polypterus senegalus* (Polypteridae) (Fig. 12.2H), *Heterotis niloticus* (Osteoglossidae), and *Brienomyrus niger* (Mormyridae) were highly associated with oxbow lakes, though also occurred in other habitat types. During the dry season of some study years, several oxbow lakes desiccated. The last species recorded in such habitats was *Heterobranchus longifilis* (Clariidae) (Fig. 12.2F) that were trapped in desiccating mud and predated by large flocks of marabou storks *Leptoptilos crumeniferus*. Smaller temporary habitats, such as seasonal pools and streams, had diverse ichthyofauna that exploited this seasonal habitat with rising water level. Only an annual killifish *Pronothobranchius gambiensis*, a specialist in desiccating wetland pools, was recorded exclusively in temporary habitats (Blažek et al., 2012; White et al., 2012).

All other species recorded in the wetland used multiple habitats across seasons, despite various affinities to particular habitat types. For example, a small barb *Enteromius niokoloensis* and a small distichodontid *Nannocharax ansorgii* were recorded only in flowing water habitats, be it main river channel, tributary or a temporary stream during the wet season. A large number of species (e.g., *Papyrocranus afer*: Notopteridae, *Schilbe intermedius*: Schilbeidae, *Auchenoglanis occidentalis*: Bagridae (Fig. 12.2C), *Clarias anguillaris*: Claridae, *Brycinus leuciscus* (Fig. 12.2E) and *Rhabdalestes septentrionalis*: Alestidae, *Labeo coubie*, *Enteromius macrops* and *Enteromius baudoni*: Cyprinidae; Fig. 12.2A, *Synodontis nigrita*: Mochokidae, *Hemichromis bimacultus*: Cichlidae and *C. petherici*: Anabantidae; Fig. 12.2D) were common across all wetland habitats (Blažek et al., 2012).
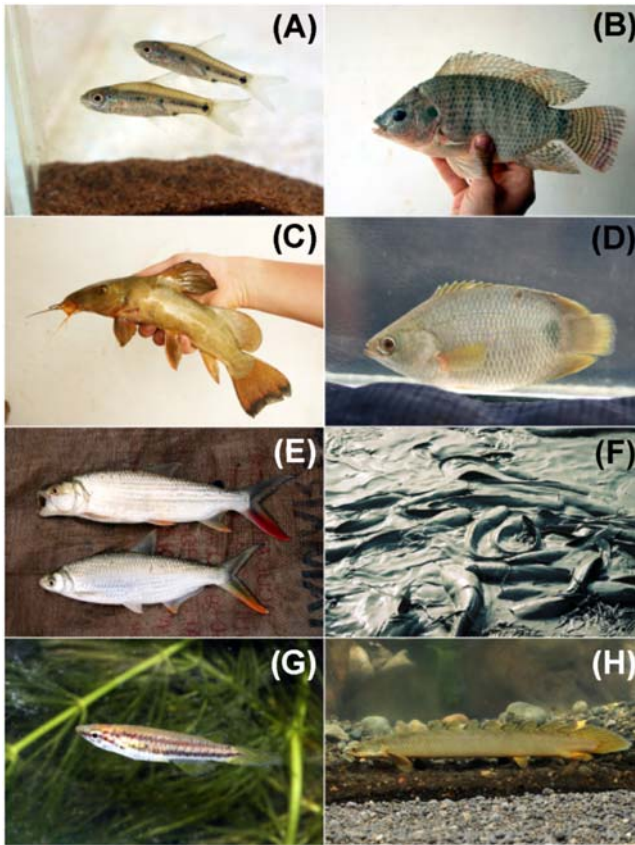
FIGURE 12.2 Characteristic fish species in wetlands of the middle Gambia River.
(A) *Enteromius baudoni* (Cyprinidae) and (B) *Oreochromis niloticus* (Cichidae), (C) *Auchenoglanis occidentalis* (Bagridae), (D) *Ctenopoma petherici* (Anabantidae), and (E: lower) *Brycinus leuciscus* (Alestidae) are examples of species widespread across all wetland habitats. Body shape and colouration of *Alestes baremoze* (Alestidae) (E: upper) is an example of aggressive mimicry of *B. leuciscus*. (F) *Heterobranchus longifillis* are often the last surviving fish in desiccating habitats. (G) *Epiplatys bifasciatus* (Nothobranchiiidae) is an example of an invertivore associated with flooded river margins. (H) *Polypterus senegalus* (Polypteridae) are associated with oxbow lakes, often found in dense vegetation, and adapted to frequent hypoxia. *Photo courtesy: Radim Blažek.*

12.3.2 Example 2: seasonal wetland pools of Northern Pantanal in Brazil

Seasonal pools are characteristic habitats for wetland fishes. Tondato et al. (2013) compared fish communities from ten temporary pools and linked species presence to habitat characteristics. The composition of fish communities (based on a sample of 8735 individuals from 29 species) varied among ponds

but was not associated with the level of isolation from other aquatic habitats. Instead, fish communities were structured by water depth, macrophyte vegetation richness and cover. Beta diversity was high, with only 14 species detected in more than three pools. Characids such as *Markiana nigripinnis* and *Moenkhausia sanctaefilomenae* and a cichlid *Crenicichla vittata* were associated with deep water. In contrast, *Hoplias malabaricus* (Erythrinidae), *Aequidens plagiozonatus* (Cichlidae) and *Synbranchus marmoratus* (Synbranchidae) lived in shallow and nonvegetated areas. A catfish *Trachyleopterus striatulus* (Auchenopteridae), a gymnotiform *Eigenmannia trilineata* (Sternopygidae) and a small characiform *Psellogrammus kennedyi* (Characidae) inhabited pools and areas with greater richness and extent of macrophyte cover. Finally, many smaller fish species were generally widespread across the pools and habitats, especially *Hypessobrycon elachys* and *Serrapinnus calliurus* (Characidae), which composed 54% and 31% of all collected fish individuals, respectively (Tondato et al., 2013). Representative species are illustrated in Fig. 12.3.

12.3.3   Example 3: pools associated with shallow marshes in southern Brazil

The region with the highest abundance of small wetlands is located between the permanent lakes Lagoa do Peixe and Laguna dos Patos in a coastal plain of Rio Grande do Sul state in Brazil. A total of 25 fish species were recorded in 9 small wetland pools formed on flooded grassland vegetation (Maltchik et al., 2010; Lanés et al., 2016). Three of the species were annual killifishes (*Austrolebias minuano* (Fig. 12.4D), *Austrolebias wolterstorffi*, and *Cynopoecilus fulgens* (Fig. 12.4C): Rivulidae), surviving habitat desiccation as diapausing embryos in dry mud. Of the other species, adult *H. malabaricus* (Erythrinidae), *Callichthys callichthys* (Callichthyidae) (Fig. 12.4F), and *Synbranchus marmoratus* (Synbranchidae) (Fig. 12.4E) are reported to temporarily survive desiccation in mud, a clear adaptation to life in wetlands. Many species used the pools opportunistically and could not have survived habitat desiccation. One half of fish diversity in wetland pools was composed of characiform fishes, with dominant species being small-bodied *Astyanax eigenmanniorum* (Fig. 12.4H), *Hyphessobrycon igneus*, and *Cheirodon interruptus*. Another very common species was a live-bearing poecilid *Phalloceros caudimaculatus* (Lanés et al., 2016). In general, population density of annual species declined throughout the season, from high abundance in the wettest period (when annual killifishes hatched) to very low abundance near pool desiccation. In contrast, population densities of nonannual species varied greatly, as fish entered and left small wetland pools during periods of connection within the grassland matrix (Lanés et al., 2016). Such broad coexistence between specialized annual fish species and nonannual fish species is in contrast with the occurrence patterns of six annual killifish
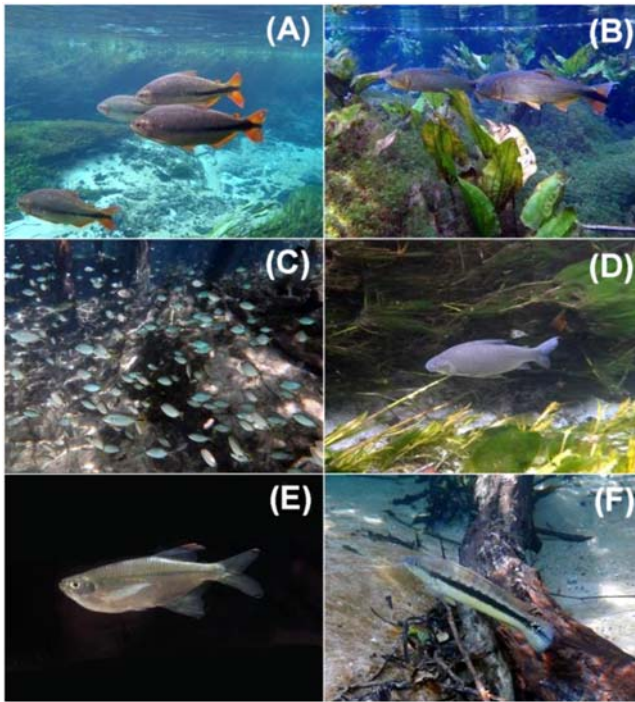
FIGURE 12.3 **Characteristic fish species of Pantanal.** Underwater photographs of (A) a frugivorous *Brycon hilarii* (Characidae), (B) its aggressive mimic *Salminus brasiliensis* (Characidae), (C) large shoal of omnivorous *Astyanax lacustris* (Characidae), (D) detritivorous *Prochilodus lineatus* (Prochilodontidae), (E) *Pseudocorynopoma doriae* (Gasteropelecidae) specialised on feeding terrestrial insects from water surface (Alestidae), and (F) *Crenicichla lepidota* (Cichlidae), a resident invertivore with equilibrium life history and parental care. *Photo courtesy: Martin Reichard.*

species from ephemeral wetland pools in Venezuelan Llanos. There, arrival of nonannual fishes to pools formerly disconnected from the permanent water bodies during elevated water level resulted in the complete disappearance of annual fish species (Nico and Thomerson, 1989).

12.4 Reproductive strategies and spawning migrations

Reproductive strategies of wetland fishes, and their association with flood pulse dynamics, can be exemplified by fishes from the Pantanal (Alho and dos Reis, 2017). Four main types of reproductive strategy were classified. Long-distance migratory species annually migrate upstream to spawn, their eggs and larvae being passively carried down by the water current. Juveniles feed on resources from highly productive lowland wetlands. In Pantanal, catfishes such as *Pseudoplatystoma reticulatum* and *Pseudoplatystoma*
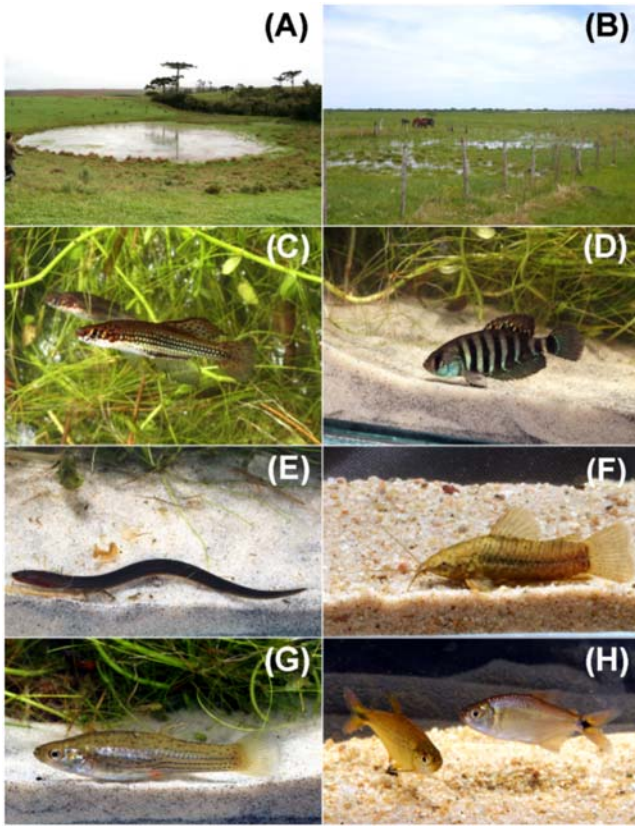
FIGURE 12.4 **Shallow marshland pools in southern Brazil and associated fish species.** Highland (A) and lowland (B) wetland habitats are associated with pastures. Annual killifishes *Cynopoecilus fulgens* (C) and *Austrolebias minuano* (D) (Rivulidae) survive habitat desiccation as dormant embryos. *Synbranchus marmoratus* (Synbranchidae) (E) and *Callichthys callichthys* (Callichthyidae) (F) are species with adaptations to hypoxia. *Jenynsia multidentata* (Poecilidae) and *Astyanax eigenmanniourum* (Characidae) are frequent visitors of small seasonal wetlands. *Photo courtesy: Martin Reichard (A, B) and Radim Blažek (C−H).*

corruscans (both Pimelodidae) or characiforms *Salminus brasiliensis* (Fig. 12.3B), *Brycon hillari* (Characidae), *Megaleporinus macrocephalus* (Anostomidae), and *Prochilodus lineatus* (Prochilondontidae) (Fig. 12.3D) are typical examples of long-distance upstream migrants (Alho and dos Reis, 2017).

The second strategy includes fish species that perform small migratory movements between flooded wetland habitats such as oxbow lakes and the river channel to spawn in the rivers during seasonal floods. Examples from Pantanal include a characiform *Mylossoma duriventre* (Serrasalmidae) and gymnotiform knife fishes *Gymnotus* spp. (Gymnotidae). The third strategy

includes fish that migrate from the river to flooded wetlands to spawn, such as piranhas (i.e., *Serrasalmus* spp., and *Pygocentrus* spp.: Serrasalmidae) and another predatory fish *H. malabaricus* (Erythrinidae). The fourth reproductive strategy includes fishes that do not perform any spawning migrations, such as many cichlids (Alho and dos Reis, 2017).

The Mahakam River in East Kalimantan, Indonesia, supports a complex wetland composed of river channels, lakes, pools, and swamps (Christensen, 1992). Fish reproductive strategies like those in the Pantanal can be defined in the local fish community. An example of a long-distance migratory behavior associated with reproduction is reported for a cyprinid *Thynnichthys vaillanti*, which migrates 300−400 km upstream to spawning grounds. Another common cyprinid fish in the region, *Leptobarus hoevenii*, lays its eggs on flooded wetland vegetation at the peak of the wet season. Their juveniles grow in shallow, plankton-rich areas of the lakes. *Barbonymus schwanenfeldii* inhabit the main river during the dry season and migrate to the small tributaries to spawn on gravel and sand substrates as water levels rise during the wet season. Staying in breeding areas for extended periods, they produce successive egg batches continuously throughout most of the wet season and their offspring drift downstream to grow in shallower and warmer stagnant waters. Finally, an anabantoid fish (*Helostoma temminckii*: Helostomatidae) migrated only short distances into flooded forest where spawning occurred and juveniles left that habitat with decreasing water level (Christensen, 1992).

12.5 Latitudinal aspects

Position on latitudinal gradient greatly affects regional seasonality in precipitation, flooding, and wetland connectivity. While subtropical regions experience a single rainy season and major seasonal dynamics, equatorial wetlands may be less seasonal or exhibit two phases of rainy and dry seasons every year. This has consequences for life history, migration and timing of reproduction for many wetland fish species. For example, annual killifishes of the genus *Nothobranchius* inhabit seasonal wetland pools in African savanna. In equatorial regions with two rainy seasons, *Nothobranchius* fishes may complete two generations per year, separated by desiccation of their habitats and population persistence in the form of diapausing eggs buried in dry sediment. In more subtropical wetlands, a single generation is produced per year, because habitats only appear during a single rainy season (Reichard, 2015). Similarly, in south India, Sri Lanka and Sumatra, two monsoonal floods per year translate into two reproductive seasons of local fishes (Dudgeon, 2000).

Large wetlands are associated with seasonal flood pulses and they appear to possess higher alpha diversity (more locally coexisting species) and beta diversity (species turnover across local habitats) but a lower gamma (between regions) diversity estimate. Migratory behavior and subsequent

dispersal of juveniles support larger ranges and many fish species of seasonally variable wetlands have wider distributions. For example, in Africa, species-rich small barbs (i.e., *Enteromius* spp., Cyprinidae) do not rely on flood pulses and have often evolved into local endemics. In contrast, other cyprinid fishes, *Labeo* spp., exploit larger rivers associated with flood pulses, resulting in wider distributions of certain species but lower taxonomic diversity (Paugy et al., 2003).

In addition to lower seasonality and hence higher benefit from narrower specialization to particular ecological niches, long-term climate and habitat stability maybe responsible for generally greater species richness of tropical wetlands. Local communities in the less-seasonal tropics may be saturated while fish communities at higher (but still tropical) latitudes may have been depauperated in the past due to climate-driven extinctions (droughts), with too little time since recolonization to saturate their communities (Hugueny and Paugy, 1995). To what extent ecological or historic contingencies are responsible for taxonomic diversity gradients is hotly debated, with data on wetland-associated fishes providing important contributions to this debate (Oberdorff et al., 2019).

12.6   Life history strategies

Life-history strategies of wetland fishes are best described by a triangular life-history continuum (Winemiller and Rose, 1992). In this classification system, species are divided according to reproductive strategies and consequent demographic structure. Fishes from each of the three main strategies use resources in their specific manner.

Periodic strategy is perhaps the most characteristic for species that utilize seasonally dynamic connectivity of wetland habitats. The periodic strategy is characterized by short and synchronized reproductive periods, typically coinciding with the peak of the rainy season, increase in main channel discharge and high connectivity across the floodplain. Species with the periodic strategy have high fecundity (number of eggs) and relatively smaller eggs, with little energetic investment into individual offspring. Those species often live in large shoals and migrate to spawning places. Their mating system is promiscuous, with multiple spawners of both sexes releasing their gametes synchronously. It contains many species with a lifespan expectancy of one year, resulting from major mortality that occurs soon after reproductive season. Alternatively, longer-lived species with a periodic strategy survive across several breeding cycles. This strategy is associated with density-independent (environmental) mortality of egg and juveniles and periodic availability of resources and developmental conditions. Species employing this periodic reproductive strategy are capital breeders. Capital breeders store energy acquired over long term and allocate it into their short reproductive bouts.

Many larger cypriniform (e.g., *Thynnichthys vaillanti* and *Labeo senegalus*) and siluriform (e.g., *Pangasius pangasius*) fishes in Asia and Africa, and characiform (e.g., *P. lineatus*) (Fig. 12.3D) and siluriform (*P. corruscans*, Pimelodidae) fishes in the Neotropics are typical representatives of species with a periodic strategy.

Equilibrium strategy is characterized by less pronounced reproductive seasonality, with breeding distributed almost continuously over the seasonal cycle, irrespective of environmental fluctuations. There is much higher investment into individual offspring, either in terms of resources (nutritional value of the egg yolk) or in parental care. Fishes with equilibrium strategy have larger eggs and overall lower fecundity, divided into more frequent batches. Parents employ various modes of active contribution to offspring survival. This often leads to formation of stable pairs that share parental care duties. Alternatively, harem systems are established with dominant males guarding a territory with resources needed for reproduction (i.e., a substrate or habitat patch) and females protect their clutches. Equilibrium strategy results in less fluctuating population dynamics as recruitment is often driven by density-dependent processes and because recruitment and mortality are continuous. Equilibrium strategy is not associated with upstream or lateral spawning migrations.

Cichlid fishes are perhaps the most known examples employing equilibrium life history strategy, from guarding eggs and offspring in a nest to elaborate cases of parental care such as mouthbrooding. Many catfishes (e.g., loricarids in the Neotropics), basal teleosts (e.g., *Gymnarchus* and *Polypterus* in Africa; Fig. 12.2H) or labyrinth fishes in Asia (*Channa*, *Betta*, *Trichopterus*: Anabantidae) also employ equilibrium strategy with extensive parental care.

Opportunistic strategy is described by high investment into rapid sexual maturation and production of offspring, often at the expense of potential late-life fecundity and survival. Seasonality of reproductive effort is typically low but may be associated with availability of habitat or resources that are needed for successful reproduction. This strategy appears common in fishes that suffer strong mortality from predation or frequent habitat disturbance that is less predictable than a seasonal flood pulse. Fish species with an opportunistic strategy have low fecundity, because they reproduce at small size and are income breeders. Income breeders convert energy acquired during their reproductive period into immediate reproductive effort.

Small species associated with marginal wetland habitats are typical opportunistic breeders. Cyprinodontiforms, such as killifishes (Nothobranchiidae in Africa, Rivulidae in the Neotropics, and Aplocheiliidae in Asia) (Fig. 12.2G) or livebearers (Poecilidae in the Neotropics) (Fig. 12.4G) are representative examples of this strategy. Some of the smallest fishes in the world belong to this life history category, including Asian *Danionella* and *Paedocypris* from peat swamp forest wetlands. Small

cypriniforms (such as *Rasbora* in Asia and *Enteromius* in Africa) or characiforms (such as *Hyphessobrycon* in the Neotropics) (Fig. 12.4H) are other typical examples of fishes with an opportunistic life history.

It is important to emphasize that this triangular life-history continuum has three endpoints but there is a lot of variation in the life history space that falls into intermediate regions. Given the triangular shape, some species would be characterized as a transition between two of the three strategies, with a mix of traits and features representative of those two endpoints. For example, a species that blends features of periodic and opportunistic strategy would have a temporally constrained reproductive season that spans a period of several weeks or months but is not year-round (e.g., *B. schwanenfeldii*). Consequently, stored energy (capital breeding) may be utilized at the start of reproductive season, with a contribution of new resources (income breeding) as the reproductive season progresses. Overall, wetland fishes represent the full spectrum of life-history strategies, with a periodic strategy typical for seasonal migrants to large wetland habitats and an opportunistic strategy most typical for long-term residents in small wetlands.

12.7   Trophic ecology

Wetland fishes are characterized by high plasticity in the composition of their diet. As tropical wetlands are dynamics systems, many fishes opportunistically expand their trophic niche during periods of food availability (Pool et al., 2017). In a Pantanal pool fish community, herbivory and planktivory disappeared during the dry season, while detritivory, invertivory, piscivory, lepidophagy (scale consumption), and generalist omnivorous strategies persisted throughout the year cycle (Novakowski et al., 2008).

There is a tight link between trophic ecology and morphological features. Feeding habits can be estimated from stomach contents, stable isotopic signature, but also inferred indirectly from dentition, mouth and jaw morphology, and gut length (Keppeler et al., 2020). These morphological features are convergent across main tropical wetland regions and strongly correlate with realized trophic niche. Generalized predatory body shape (slender body, posterior position of dorsal fin) or herbivorous and detritivorous species with very long guts have evolved across disparate regions with tropical wetlands. In addition to typical trophic niches, tropical fishes in general, and species inhabiting larger wetlands in particular, employ some trophic specialization (e.g., frugivory) that are not commonly observed in other fishes. Tropical wetland fishes also occupy trophic niches that are usually taken by aquatic invertebrates in temperate regions. For example, there are more detritivorous fishes in the tropics compared to temperate regions (Winemiller et al., 2007) and some miniaturized cypriniform species (*Paedocypris*, *Danionella*) feed on meiofauna such as rotifers (Kottelat et al., 2006). In the following paragraphs, I outline some typical trophic guilds of tropical wetland fish species.

Invertivory: Feeding on aquatic invertebrates is a common trophic habit among tropical wetland fishes. Insects and crustaceans are the most common prey given their generally high abundance, compared to other aquatic invertebrates. In approximately 25% of fish species in a Pantanal pool, insects were main prey consumed during both the dry and wet season (Novakowski et al., 2008). In addition to aquatic invertebrates, many species feed on terrestrial invertebrates that fall or land on the water surface. Some species specialize on such a diet using upturned (superior) mouths, including the cypriniform *Aplocheilus lineatus* (Aplocheilidae) from Asia, the osteoglossiform *Pantodon buchholzi* (Pantodontidae) from Africa and the characiform *Pseudocorynopoma doriae* (Gasteropelecidae; Fig. 12.3E) from the Neotropics. Archerfishes (*Toxotes* spp., Toxotidae: Perciformes) are capable of shooting down their aerial and terrestrial insect prey by spitting jets of water. Many other fish species consume invertebrates when they become abundant.

Herbivory and detritivory: Herbivorous fish can exploit various plant resources of the wetland. Aquatic vegetation, when available, is the most widely consumed plant resource. Terrestrial plants are accessible seasonally in flooded habitats and are only consumed by specialized species that resort to other food in the dry season. In Africa, *Coptodon rendalli* (Cichlidae) is an example of a species that feeds heavily on floating and emergent vegetation. In the Neotropics, *Pterodoras granulosus* (Doradidae) seasonally consumes large quantity of macrophytes, though it is classified as a feeding generalist (Winemiller et al., 2007). A lot of vegetation is consumed during its decay, as detritus. Several species of Curimatidae in the Neotropics (Fig. 12.3D) and Distichodontidae in Africa feed heavily on plant detritus and contribute significantly to organic matter transfers and nutrient cycling within wetlands. Finally, phytoplankton is consumed by some specialized fish species (e.g., the small cypriniform *Pectenocypris balaena* [Cyprinidae] from the Kapuas, Borneo), though this resource is not stable or available across longer time periods in typical tropical wetlands. The fact that phytoplankton feeding requires morphological specialization (such as specialized gill rakers), which limits exploitation of other resources, constrains its wider utilization among tropical wetland fishes.

Frugivory: Many wetland fishes feed on seeds and fruits that become more available during floods. The most known and studied species from this trophic guild is *Colossoma macropomum*, but at least 275 fish species are reported to feed on fruits and seeds (Horn et al., 2011). Frugivory is very common in the Neotropics (at least 150 species), dominated by herbivorous serrasalmids (*Myleus*, *Colossoma*, *Metynnis*, *Piarctus*; Characiformes), large omnivorous catfishes (Doradidae, Pimelodidae) and generalist small- and medium-sized characids and cichlids (Horn et al., 2011), including *Brycon hilarii* (Fig. 12.3A). Fruit-eating fishes can play important roles as seed dispersers, with considerable consequences for plant-recruitment dynamics in

some wetlands. In the Peruvian Amazon, two large fruit-eating fish species (*C. macropomum* and *Piaractus brachypomus*, Serrasalmidae) consumed 35% of the fruit species available to fishes (Anderson et al., 2009). Hence, frugivory is not an exclusive feature of larger characiforms. A study from a savanna stream in Central Brazil reports that fruits and seeds were an important component of the diet of eight species, being most abundant in four species of *Astyanax* tetras (Characidae) whose diets contained 45%−73% of this item (de Melo et al., 2004).

In Africa, less information is available on fruits and seeds in the diet of wetland fishes. However, they are consumed at least by some larger catfish species (e.g., *Clarias* spp. and *Schilbe* spp.) and morphological features such as the muscular gizzard of *H. niloticus* (Osteoglossidae, Osteoglossiformes) or the special oral dentition of some characiforms (e.g., *Brycinus* and *Alestes* spp.: Alestidae and *Distichodus* spp.: Distinchodontidae) from the Congo Basin suggests that these fishes are likely foraging on fruits and seeds (Horn et al., 2011). In tropical Asia, at least 55 species of freshwater fishes from nine families are known to consume fruits regularly or occasionally, including many cyprinids (e.g., *Tor* spp., *Barbonymus* spp., *Leptobarbus* spp.) and *Pangasius* catfishes (Horn et al., 2011).

Piscivory: Predation on other fish is also a relatively widespread trophic specialization among wetland fishes, often combined with invertivory. Many species opportunistically feed on small juvenile fish. In fact, fish were the dominant prey of 31% of the species in dry and wet periods in a Pantanal pool, with the characiforms *Acestrorhynchus pantaneiro* (Acestrorhynchidae), *Plagioscion ternetzi* (Sciaenidae), *Raphiodon vulpinus* (Cynodontidae), *S. brasiliensis* (Characidae), *Serrasalmus marginatus*, and *Pygocentrus nattereri* (both Serrasalmidae) being exclusive piscivores (Novakowski et al., 2008). Specialized larger piscivorous species may employ a sit-and-wait strategy (e.g., *Hepsetus* spp. in Africa, *Hoplias* spp. in the Neotropics or *Channa* sp. in Asia) or pursue their prey (e.g., *Hydrocynus* spp. in Africa and *Pygocentrus* spp. in the Neotropics). *S. brasiliensis* is an example of aggressive mimicry, whereby a predatory species blends within shoals of its prey, *B. hilarii* (Fig. 12.3A and B) (Bessa et al., 2011).

Specialists: Several species of *Roeboides* (Characidae) and *Catoprion* (Serrasalmidae) feed on fish scales (lepidophagy). Few species are specialist lepidophages. For example, *Roeboides prognathus* feeds almost entirely on scales (and possesses highly specialized tooth and jaws to dislodge scales) while *Roeboides bonariensis* combines invertivory with occasional lepidophagy (Sazima, 1983). At least one wetland lepidophagous species, a small characid *Probolodus heterostomus* employs aggressive mimicry, similar to piscivorous *S. brasiliensis*. Other extreme diet specializations of wetland fish include selective feeding on hard incrustations of cyanobacteria by adult *Annamia normani* (Balitoridae) from Vietnam (Herder and Freyhof, 2006), molluscivory by a catfish *Nedystoma dayii* (Ariidae) from New Guinea

(Hyslop, 1999) and specialized feeding on microcrustaceans by *Moenkhausia dichroura* (Characidae) (Novakowski et al., 2008).

12.8 Community perspectives on trophic ecology

Several tropical wetland fish communities have been thoroughly investigated in relation to trophic ecology of individual species and their coexistence, including seasonal shifts in diet, interspecific diet overlaps and the extent of specialization. Overall consensus highlights that body size is not directly linked to trophic level in wetland fishes while some functional traits like body form and dentition enable adequate prediction of trophic level for particular fishes (Keppeler et al., 2020). For example, two related small *Aphyocharax* species (2−5 cm long) coexisting in Pantanal substantially vary in their diet, with *Aphyocharax dentatus* being consistently piscivorous over the entire season while *Aphyocharax anisitsi* was consistently invertivorous (Corrêa et al., 2009).

Regular sampling over a 1-year period in the Pantanal identified two strict herbivores (*P. granulosus* and *Piaractus mesopotamicus*) and several strict piscivores (e.g., *S. brasiliensis*, *P. nattereri*, *Serrasalmus* spp., *Rhaphiodon vulpinus*) (Corrêa et al., 2011). However, the diet of most fishes varied seasonally among periods of large-scale flooding. *Gymnogeophagus balzanus*, for example, fed on other fishes during the wet phase and switched to aquatic invertebrates during the dry season (Corrêa et al., 2011). Invertivorous *A. anisitsi* switched between aquatic insects (mainly dipteran larvae) in the wet season and terrestrial insects (mainly Hymenoptera) during the dry season (Corrêa et al., 2009). Most variability, however, is associated with the expansion of trophic niches during the wet season. Seasonal variation in trophic specialization and resource partitioning was reported to be higher during the wet season when food was more diverse (Corrêa et al., 2011; Polačik et al., 2014; Pool et al., 2017) while others reported greater resource partitioning during dry periods when food was scarce, with individual species feeding on a diet they specialize on (e.g., Prejs & Prejs, 1987).

In another study from Pantanal, omnivory was most common (29 out of 101 fish species), 16 species were fish predators, 12 herbivorous, 18 detritivorous, 8 fed on zooplankton, 7 were invertivorous, 2 were lepidophagous, 4 species fed on a diet composed from small fish and invertebrates and 4 combined zooplankton and aquatic insects (de Resende, 2000). For the Neotropics in general, Araujo-Lima et al. (1995) reported that all trophic guilds, except planktophagous, are well represented in wetlands, with the detritivorous species having the largest biomass in 8 of the 10 studied floodplains. Planktivorous species are not lacking from tropical wetlands and Novakowski et al. (2008) listed a small characid *M. dichroura* as a specialist consumer of microcrustaceans. Herbivory (combined with frugivory) is much more common in the wet season. *Astyanax abramis* (Characidae),

Loricaria sp. (Loricariidae) and *Trachydoras paraguayensis* (Doradidae) fed predominantly on fruits and seeds, but also consumed small portions of leaves, and filamentous and unicellular algae (Novakowski et al., 2008).

In Africa, data from two Okavango Delta oxbow lakes (madibas) revealed that *C. rendalli* (Cichlidae) was a strict herbivore, *Hepsetus odoe* (Hepsetidae: Characiformes) and *Hemichromis fasciatus* (Cichlidae) were strictly piscivorous and *Schilbe mystus* was an invertivore. *Marcusenius macrolepidotus* was an invertivore, feeding on insects and zooplankton. Other species, including small cyprinids (*Enteromius* spp.) and a small alestid *Brycinus lateralis* fed on a range of diet items with a preference for aquatic and terrestrial insects. Finally, *Serranochromis* spp. (Cichlidae) also fed opportunistically, but often had smaller fish in their stomach (Gilmore, 1979).

In wetlands of the upper Zambezi basin, 10 coexisting catfish species were grouped into four main trophic categories. The largest species (*Clarias gariepinus* and *C. ngamensis*: Clariidae) were piscivorous, smaller clariids and *S. intermedius* (Schilbeidae) combined piscivory with invertivory, while six *Synodontis* species (Mochokidae) scavenged on fish remains and further fed on aquatic insects, seeds and detritus. Finally, *Chiloglanis neumanni* (Mochokidae), *Amphilius uranoscopus* and *Zaireichthys rotundiceps* (both Amphiliidae) were small omnivores that inhabited smaller streams rather than wetlands (Winemiller and Kelso-Winemiller, 1996).

In Angabanga River Wetlands in New Guinea, two introduced species dominated local fish communities (Hyslop, 1999). Asian *Trichogaster pectoralis* (Osphromenidae) was a detritovore feeding on detritus, diatoms and higher plant material. Invasive African *Oreochromis niloticus* (Cichlidae) was classified as a microherbivore, feeding predominantly on unicellular green algae. Native species often fed on benthic invertebrates (e.g., *Neosilurus brevidorsalis*: Plotosidae and *Ophioeleotris aporos:* Eleotridae), while others were herbivorous (*Cestraeus goldiei*: Mugilidae) or piscivorous (*Lates calcarifer*: Latidae) (see Pegg et al., 2022, Chapter 16). Two species were diet specialists—a molluscivore catfish *N. dayii* (Ariidae) and a microcrustacean specialist pipefish *Hippichtys spicifer* (Syngnathidae) (Hyslop, 1999).

12.9 Specific adaptations of wetland fishes

12.9.1 Low oxygen conditions (hypoxia)

Many wetland habitats are, at least temporarily, oxygen-depleted. Declines in dissolved oxygen levels leading to hypoxia are a natural component of many swamps and backwater habitats within tropical wetlands. Hypoxia arises due to poor water circulation, stratification and decay of flooded organic matter. In deeper wetland habitats, thermal stratification may exacerbate hypoxic conditions in the lower part of the water column. In small shallow wetland water bodies, diel-cycling hypoxia develops when microbial and

vegetation respiration at night depletes oxygen levels and normoxic condi-
tions are restored once aquatic vegetation and phytoplankton start photo-
synthesizing during the light phase (Díaz and Breitburg, 2011).

Wetland fish possess various anatomical, physiological and behavioral
adaptations to cope with hypoxia. Increased ventilation rate is employed during
mild hypoxia in species such as zebrafish, *Danio rerio* (Danionidae). A more
efficient response is aquatic surface respiration when fish skim the water sur-
face and breath in the oxygen-enriched layer of water. Surface respiration is
used only after increased gill ventilation rate is inefficient to sustain oxygen
levels because it increases the risk of predation as fish leave their refugia.
Some species associated with hypoxic wetland habitats can facultatively
breathe air. For example, many loricariid and callichthyid catfish species in the
Neotropics breathe air during periods of hypoxia (Perry, 2011). Other species
are obligate air breathers, including African lungfishes (*Protopterus* spp.),
Neotropical *Arapaima gigas* (Arapaimidae) and many Asian anabantoids (e.g.,
Trichogaster spp., *Anabas testudinus*). Air-breathing has evolved in fishes inde-
pendently at least 38 times (Graham, 2011) and represents a trait more common
than generally assumed. In some cases, air-breathing even enables wetland fish
to survive long-term exposure to drying mud, with African (*Protopterus* sp.)
and Neotropical (*Lepidosiren paradoxa*) lungfishes seasonally aestivating in
dry mud. Long-term survival of adult fish in mud is also reported in cal-
lichthyid catfishes of the Neotropics (*Callichthys* spp., *Hoplosternum* spp.;
Fig. 12.4F), anabantiods (*Ctenopoma* spp.; Fig. 12.2D) and clariids (*Clarias*
spp. *Heterobranchus* spp.) in Africa, and *Channa* spp. in Asia.

Anatomically, adaptations to hypoxia maybe associated with the presence
of lungs (*Polypterus* and *Erpetoichthys* from Africa) or a respiratory gas
bladder (e.g., African *Heterotis*, *Papyrocranus*, *Notopterus*, and
Gymnarchus, Neotropical *Arapaima*, *Erythrinus* or *Lebiasina*, and Asian
Chitala and *Pangasius*). In many fishes, the ancestral connection between
alimentary canal and swim bladder was lost. To enable air respiration, those
fishes evolved various, often very specialised, anatomical and physiological
adaptions to cope with hypoxia. Neotropical *Electrophorus electricus*
became an obligate air breather, possessing extensive respiratory epithelium
which covers its mouth, branchial arches and the inner part of its operculum,
while *Synbranchus marmoratus* (Synbranchidae) (Fig. 12.4E) evolved similar
respiratory epithelium but retained the capability to extract oxygen from
water. In Africa, three clariid catfish genera (*Clarias*, *Heterobranchus* and
Dinotopterus) evolved large paired suprabranchial chambers that extend
from skull to pectoral girdle, with a similar adaptation present in Asian
Heteropneustes fossilis (Heteropneustidae). Neotropical loricariid catfishes
swallow air and extract oxygen in their stomach, while some Neotropical cal-
lichthyids and Asian cobitids (*Misgurnus*, *Lepidocephalichthys*) extract oxy-
gen in the posterior part of their gut (Graham, 2011). In Africa and Asia,
anabantoid fishes (e.g., *Ctenopoma* and *Trichopterus*) possess a labyrinth

organ formed by vascularized expansion of the epibranchial bone of the first-gill arch. Comparing three Neotropical wetland species that coexist in Pantanal, Jucá-Chagas (2004) observed that *Hoplosterum littorale* (extracting oxygen in intestine) was 2−3 times more efficient in oxygen extraction than *L. paradoxa* (obligatory air breather with lungs) and *Hoplerythrinus unitaeniatus* (with vascularized swim bladder), and *H. unitaeniatus* had to take twice as many breaths to retrieve sufficient oxygen compared to the other two species (Jucá-Chagas, 2004).

12.9.2 Habitat desiccation

Many wetland habitats combine aquatic and desiccated phases over their annual cycle. The most typical response of wetland fishes is to leave the desiccating habitat with receding water. Fish can sense gradients in oxygen levels and water flow and typically follow receding waters to leave desiccating habitats. Many fish are trapped in desiccating pools and predated by piscivorous birds when their density and catchability are high, providing a considerable nutrient transfer link between aquatic and terrestrial components of wetland habitats.

Various species survive short-term desiccation in wet mud, including callichthyid catfish in the Neotropics and clariid catfishes in Africa. These species have well-developed organs for air-breathing to survive receding water levels that are often associated with hypoxia. African lungfishes (*Protopterus* spp.) survive dry periods by burrowing into the mud and aestivating in a subterranean cocoon or even inside a cocoon made of dried mucus on bare land (Chew et al., 2015). Neotropical lungfish (*L. paradoxa*) are not tolerant to body desiccation and dig deep burrows that retain water throughout the dry phase of the habitat (de Almeida-Val et al., 2015).

Annual killifishes survive desiccated phases of their habitats as dormant embryos encased in egg envelopes with thick chorion to protect them from water loss. Annual killifishes have repeatedly evolved annual life cycles in the Neotropics (Fig. 12.4C and D) and in Africa, perhaps 3−4 times on each continent (Furness et al., 2015), though it is also possible that a shared preadaptation enabled them to switch to a developmental mode that includes diapauses (Reichard, 2015). In these fishes, an entire generation can survive for up to 11 months per year as dormant embryos (Vrtílek et al., 2018). During the wet phase, annual killifish develop rapidly. They utilize the aquatic period of their pools until it dries up, with daily reproduction starting in as few as two weeks after hatching (opportunistic life history strategy). They may sustain populations in pools that are inundated for as few as three weeks, though inundations of one to three months are more typical even in the driest region of their range (Vrtílek et al., 2018). Their embryos develop in aquatic habitat for a few days before the first diapause (Diapause I) is initiated by anoxic conditions in pool sediments. Greater oxygen availability

during habitat desiccation initiates re-establishment of the active development and its halt at Diapause II. Another bout of development occurs when the substrate is disturbed and wetted during the initial rains of a new rainy season. Embryos reach Diapause III which apparently serves to slow down metabolism until conditions for hatching are optimal (wetland inundation) (Reichard and Polačik, 2019). It is notable that all clades of annual killifishes (in Africa and Neotropics) undergo the same system of three diapauses. This adaptation enables annual killifishes to colonize wetlands which lack regular connection to permanent water bodies. Other species colonize such habitats by overland migration (e.g., African *Claris gariepinus* and Asian *A. testudinus*). Recently, colonization of isolated wetlands through endozoochory (as eggs transported in the alimentary canal of wetland birds) was confirmed in various fish species (Silva et al., 2019; Lovas-Kiss et al., 2020).

12.10   Summary and conclusions

Tropical wetlands provide a rich network of habitats for freshwater fish. While most wetland fish diversity is connected to large alluvial systems, some fish species are adapted to periodic desiccation of their habitats. Tropical wetlands are subject to strong seasonal fluctuations and therefore even trophic specialists expand their diet temporarily. Functional traits associated with trophic niches are convergent across continents (see Cuthbert et al., 2022, Chapter 17; Gálvez et al., 2022, Chapter 18). Wetland fish fauna have evolved characteristic adaptations associated with particular life histories, including the ability to breath air during hypoxia, survive desiccation, and having characteristic body shapes to energetically maximize resource acquisition. The threats to wetland fishes through habitat degradation, impoundments, water pollution, water extractions, and arrival of non-native species are detailed in Chapters 13 (Moraes et al., 2022), 14 (Tarakini et al., 2022), 16 (Pegg et al., 2022), 19 (Irvine et al., 2022), 20 (Greenfield, 2022), and 22 (Marambanyika et al., 2022).

Acknowledgments

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