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THE BIOTA OF INTERMITTENT RIVERS AND EPHEMERAL STREAMS: FISHES

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IN A NUTSHELL

- Most fish species in intermittent rivers and ephemeral streams (IRES) survive by using a combination of adaptable colonization and recruitment strategies.
- A few species possess specialized adaptations such as air-breathing that allow them to persist in extreme IRES.
- Fish in IRES are threatened by increased habitat fragmentation (due to factors such as river regulation, water abstraction, and climate change) and the presence of alien species.
- Preservation of IRES with natural flow patterns should be a global management priority to conserve specialized biota such as fish.

4.5.1 INTRODUCTION

There is perhaps no organism more associated with water than a fish, but not all fishes have the same association with water. Although the vast majority of fishes—both marine and freshwater—relies on constant immersion in permanent water, a very small subset has overcome the obvious ecological challenges presented by intermittent rivers and ephemeral streams (IRES) that cease to flow and, in many cases, dry to pools or completely. This chapter is an overview of fishes that reside in waters with temporary, irregular, or ephemeral flow regimes (Chapter 2.2). It considers IRES on four continents and describes aspects of fish presence and diversity within them. A very basic question underlies this chapter: why and how would organisms that breed and feed in water and rely on water for all aspects of their life history live in areas where water presence is seldom guaranteed?

As in many plant and animal groups, there are exceptions to the general fish-in-water rule, and several fish species possess adaptations that enable them to survive out of water for short periods. Climbing perch *Anabas testudineus*, so named for its ability to “crawl” short distances overland, and other members of the family Anabantidae extract oxygen from the air, as do various members of the speciose Gobiidae family and certain catfishes such as the Clariidae. Mudskippers (subfamily Oxudercinae) extract atmospheric oxygen through their skin whereas snakeheads (Channidae) can survive without water by estivating in burrows (Lévêque, 1997; Allen et al., 2002).

As interesting as these fish are, this chapter takes a broader view because most riverine fishes lack specialized breathing organs, much less the ability to estivate. Although understandable in the context of
permanent rivers with constant or near-constant flow, it is salient to note that most fishes that occur in IRES also lack specific physiological adaptations for flow intermittence or drying. Instead, they are riverine fish that respire using their gills and that use their fins and tail for locomotion. They are adapted to live in water, yet they persist in rivers that can be wet one season and dry the next, wet one year and dry the next, or—in extreme circumstances—dry for long and unpredictable periods interrupted by short-lived floods. When the water comes, the fishes appear to come with it or, at the very least, follow soon afterward.

The presence and distribution of fish in IRES is discussed, as well as the relevant abiotic characteristics of the systems on four continents (Africa, Australia, North America, and the Mediterranean area of Europe) to identify global themes and similarities. We then review fish adaptability—particularly with regard to colonization/dispersal ability, recruitment, and specialized adaptations to drying—and the advantages of living in ephemeral waters. We conclude by considering present and future threats to the fishes in IRES and propose a priority list of species and systems that require conservation. Where relevant, we suggest recommendations for management. Despite the potential complexity of such a huge and varied topic, the primary goal of our chapter is to address four simple questions: what kinds of fishes live in IRES, why do they live there, how do they live there, and what threatens their existence?

4.5.2 THE FISH FAUNA OF IRES
AFRICAN IRES AND THEIR FISHES

The majority of the African continent is generally dry (annual rainfall <500 mm), and as a consequence, xeric and seasonal savannah aquatic ecosystems dominate the continent and surround the moist forests of Central and West African lowlands and coasts (Thieme et al., 2005). These ecosystems are characterized by IRES that flow briefly but are otherwise often dry (Fig. 4.5.2).

Five families of African freshwater fishes (out of a total of approximately 30) are regularly associated with IRES (Lévêque, 1997): the lungfishes (Protopteridae), the annual killifishes (Nothobranchiidae), the air-breathing catfishes (Clariidae, Fig. 4.5.3a), the Cichlidae (Fig. 4.5.3b), and the Cyprinidae (Fig. 4.5.3c). Fishes in these families are all widespread (Lévêque, 1997; Thieme et al., 2005; Snoeks et al., 2011).
FIG. 4.5.2
South African examples of IRES: (a) the Buffels River in the Karoo environs and (b) a dry savannah tributary of the Limpopo River system.

Photos: Courtesy P. Skelton.

FIG. 4.5.3
Examples of African fish species from IRES include: (a) the air-breathing African sharp-tooth catfish *Clarias gariepinus*, (b) the Mozambique tilapia *Oreochromis mossambicus*, and (c) the chubbyhead minnow *Enteromius anoplus*.

Photos: Courtesy P. Skelton.
AUSTRALIAN IRES AND THEIR FISHES

Australia is the driest inhabited continent and has a climate that renders most of its rivers intermittent to some degree. This comparative lack of water means the continent contains a small total number of freshwater fish species (approximately 300: Allen et al., 2002). Given Australia’s aridity and the unpredictability of flows, it is not surprising that an even smaller subset of species (fewer than 30) occurs in the continent’s center where annual rainfall averages far less than 500 mm (Wager and Unmack, 2000). Indeed, catchments in Australia’s arid interior represent the realistic limit of habitable waterways for fish, with many rivers entirely ephemeral and reliant solely on unpredictable flooding and rainfall. A good example is the Todd River, which flows—very rarely—through the central Australian town of Alice Springs but most of the time is a dry sandy channel. The characterization of Australia as a desert surrounded by an ocean with a few small rivers on the periphery is very appropriate; a large section of the western interior contains no large rivers at all and the two largest rivers to the east of this area—the Diamantina and the Cooper—have among the most unpredictable flow regimes on Earth (Puckridge et al., 1998).

As in Africa, the fish fauna of Australia’s most extreme IRES is limited to a small number of families. Catfishes (Plotosidae, Fig. 4.5.4a), perches (Terapontidae and Percichthyidae, Fig. 4.5.4b), and the bony herring Nematolosa erebi are the larger species, although few exceed 40 cm in total length.
The smaller species include glassfishes (Ambassidae), gobies (Gobiidae), gudgeons (Eleotridae, Fig. 4.5.4d), and rainbowfishes (Melanotaenidae, Fig. 4.5.4c).

**NORTH AMERICAN IRES AND THEIR FISHES**

In North America, the greatest concentration of IRES with large basin areas and fish populations occurs in western deserts or central grassland biomes, where variable climate and hydrology (both seasonal and stochastic) results in stream drying for much of the year. Opportunistic fish species are common in such habitats (Poff and Allan, 1995; McManamay et al., 2014), and examples include central stoneroller *Campostoma anomalum*, creek chub *Semotilus atromaculatus*, Sonora sucker *Catostomus insignis*, and logperch *Percina* spp. (Fig. 4.5.5a–d, respectively). In contrast, true desert fishes such as pupfish in the genus *Cyprinodon* are restricted to drying habitats or isolated pools (Minckley and Deacon, 1991). IRES can also be important for economically important species such as coho salmon *Oncorhynchus kisutch* which move from permanent rivers into these habitats for spawning and juvenile rearing (Wigington et al., 2006).

**FIG. 4.5.5**

North American fish species found in IRES include: (a) central stoneroller *Campostoma anomalum*, (b) creek chub *Semotilus atromaculatus*, (c) Sonora sucker *Catostomus insignis*, and (d) logperch *Percina caprodes*.

*Photos: Courtesy K. Gido.*
IRES OF MEDITERRANEAN EUROPE AND THEIR FISHES

IRES dominate surface runoff in semiarid areas of Mediterranean Europe (Cushing et al., 1995; Estrela et al., 1996). These Mediterranean rivers are characterized by sequential, seasonally predictable flooding (late autumn-winter) and drying (summer-early autumn) phases that vary markedly in intensity from year to year (Gasith and Resh, 1999). This hydrological variability means that fish in Mediterranean rivers persist in some of the most hydrologically unstable and diversely stressed river systems worldwide (Bonada and Resh, 2013).

Mediterranean rivers contribute significantly to the diversity of European freshwater fish because most endemic fish in Europe occur in areas with Mediterranean climates (Griffiths, 2006; Reyjol et al., 2007; Freyhof and Brooks, 2011). Levels of endemism are especially high in southern peninsulas, presumably because these regions have acted as refugia during glacial periods (review in Blondel et al., 2010). Moreover, these basins show considerable faunal similarities with North African and Middle Eastern basins (Reyjol et al., 2007). Although most endemic fishes come from the Cyprinidae (Fig. 4.5.6),

**FIG. 4.5.6**

Fish in IRES in Mediterranean Europe include endemic cyprinids such as (a) *Luciobarbus microcephalus* and (b) the hybrid complex *Squalius alburnoides*.

*Photos: Courtesy F. Ribeiro (a) and S. Carona (b).*
endemic species also occur in other families such as the Cobitidae, Cyprinodontidae, Gobiidae, and Petromyzontidae (but see review in Tierno de Figueroa et al., 2013). Overall, peri-Mediterranean areas are currently considered biodiversity hot spots for freshwater fish in Europe (Reyjol et al., 2007).

### 4.5.3 Why Do Fish Live in IRES?

The fundamental reasons that fish live in IRES are access to resources and the ability to maintain their populations across large areas. Given that a subset of riverine species colonizes IRES, it follows that these species have evolved to capitalize on the specific or general resources provided by each basin or catchment.

Despite their variable hydrology (Chapters 2.2 and 2.3), IRES contribute substantially to the overall functioning of river ecosystems, and the sometimes erratic wetting and drying cycles create massive increases in resources in recently inundated areas (Arthington et al., 2005; Kingsford et al., 2006; Balcombe et al., 2007). Review papers on the significance of headwater streams, many of which are intermittent, emphasize their importance to aquatic animals by providing an interface for trophic subsidies (Chapter 4.7) and a viable habitat for migratory species (Freeman et al., 2007; Meyer et al., 2007; Chapter 4.8). These systems often have high levels of resource availability through terrestrial subsidies (Courtwright and May, 2013) or through reduced competition for existing resources.

Although many IRES are highly stochastic environments, the dynamics of their fish communities can often be predicted by where the IRES occurs in the landscape and the climatic and topographic factors that determine the amount, location, and timing of surface flow (e.g., Magalhães et al., 2002b; Filipe et al., 2010; Oliveira et al., 2012). Within basins, species richness, abundance, and biomass generally increase downstream, with summer shortage of water often limiting fish occurrence in headwaters (Pires et al., 1999; Corbacho and Sanchez 2001; Magalhães et al., 2002b; Filipe et al., 2010). Nevertheless, the mechanisms driving increasing diversity have been found to vary. For example, Ostrand and Wilde (2002) reported species turnover from highly tolerant, cyprinodontid-dominated communities upstream to less-tolerant cyprinid-dominated communities downstream, whereas Whitney et al. (2015) found community structure was nested and the few species that occurred in upstream habitats were a subset of downstream communities. Regardless, patterns of higher fish diversity downstream are generally driven by greater stability and proximity to refugia habitats in larger rivers (Schlosser, 1987; Roberts and Hitt, 2010) and illustrate the importance of maintaining hydrological connectivity among habitats in these dynamic systems.

Examples from the four continents considered in this review illustrate that many species of fish in IRES are able to take advantage of either seasonal population booms of prey species or the exclusivity of isolated (and drying) wetlands. For example, the Afro-Asian air-breathing catfish family Clariidae includes widespread large-bodied African species such as *Clarias gariepinus* and *Clarias anguillaris*, both of which are predominantly associated with extreme environments (Bruton, 1979a,b). Indeed, as waterholes recede and dry in African systems, large numbers of Clariidae catfish are frequently the only and last aquatic survivors (Fig. 4.5.7).

The term “boom and bust” is frequently used to describe the ecology of both aquatic and terrestrial systems in Australia’s dry inland (Kingsford et al., 2006; Wardle et al., 2013) and is also applicable to the other areas considered in this overview. The primary driver is rainfall leading to population “booms” followed by drought resulting in “busts.” Studies in central Australia report the occurrence of
several fish species in rivers that flow only briefly and subsequently become dry for prolonged periods (Glover and Sim, 1978; Bailey and Long, 2001; Kerezsy et al., 2013). Similarly, Lake Eyre, the large terminal lake in South Australia into which the Cooper and Diamantina rivers drain intermittently, is a temporary haven for massive numbers of desert species such as the sardine-like Lake Eyre hardyhead *Craterocephalus eyresii* and the bony herring. However, these populations die in their millions, often soon after the flows recede and the lake begins evaporating (Ruello, 1976). Temporary “booms” of algae, zooplankton, and invertebrates (Chapters 4.2 and 4.3) in these mostly dry areas explain the sudden influx of massive numbers of fish.

Although it is tempting to consider that IRES may be inferior aquatic systems due to their fluctuating hydrology, this anthropocentric notion is probably misguided. Instead, it appears that IRES provide ecological advantages to resident fish species, as indicated by a study of juvenile Arkansas darter *Etheostoma cragini* in Colorado. Labbe and Fausch (2000) found that individuals that had migrated into ephemeral reaches of Big Sandy Creek were in better condition than individuals that remained in perennial reaches. Another characteristic of IRES that influences the structure of fish communities in some areas is the tight linkage with terrestrial subsidies. For example, Courtwright and May (2013) showed that the diets of brook trout *Salvelinus fontinalis* in intermittent headwater streams primarily consisted of terrestrially derived insects. Even after the supply of terrestrial insects was experimentally removed from these streams, fish did not switch to consuming aquatic insects.

Population and species maintenance is also likely facilitated by a dispersed metapopulation (Chapter 4.9) spread throughout a network of IRES. In Mediterranean IRES, for example, after flows decline in late spring, fish such as barbels either disperse along river segments in search of suitable dry-season refuges (*Luciobarbus bocagei*—Alexandre et al., 2016) or stay in deep pools most likely to persist through summer (*Barbus haasi*—Aparicio and Sostoa, 1999). Following flow resumption, chub *Squalius torgalensis* leave dry-season refuges and move into previously dry areas, in the process promoting the mixing of populations that were previously separated (Pires et al., 2014). This behavior is likely to facilitate demographic rescue in the most isolated habitats as well as contributing to local population recovery and overall persistence.
4.5.4 HOW DO FISH SURVIVE IN IRES?

Fish communities in IRES fall into two main categories: a large group of riverine species that maintain populations by migratory behavior, and a small group with specialized adaptations enabling them to persist in water-limited habitats. Fish adaptations to IRES are diverse and span a range of life history attributes as well as tolerance to extreme or unusual water quality parameters and climatic conditions. In extreme cases (Box 4.5.1), fishes have specific ways of surviving in areas where complete desiccation occurs. Nevertheless, most fishes in IRES are riverine species that have been able to adapt to and benefit from the conditions imposed by ephemerality.

Fish dispersal in seasonal rivers is a widespread phenomenon with a clear adaptive element that allows dispersal and occupation of available habitats when aquatic connections exist (Cambray, 1990; Gratwicke and Marshall, 2005). In African IRES, fish migrations include both upstream and downstream longitudinal movements and lateral migrations from the main channel into flooded margins (Table 4.5.1). The lateral migrations allow for rapid feeding and breeding by smaller species in order for the majority of the fish populations to return to the main channel with the receding floodwaters. Many fish are trapped in residual pans and floodplain pools, and generally eaten to extinction by birds, mammals, and humans (van der Waal, 1998; Barson and Nhiwatiwa, 2010; Tweddle et al., 2015). A similar fate awaits the residual populations in the pools of drying rivers (Minshull, 2008). Species found surviving in sandy bed pools of the Motloutse tributary of the Limpopo in South Africa include the air-breathing sharp-tooth catfish C. gariepinus, various cyprinids, and the cichlid Oreochromis mossambicus (van der Waal, 1997). The same group of species has been found to recolonize floodplain pans on the Save River in the Zimbabwean lowveld (Barson and Nhiwatiwa, 2010), and a similar community survived in residual pools of the Kunyeri River, the feeder river to Lake Ngami, which dried in 1982 (Paul Skelton, personal observations).

In Australian IRES, fishes similarly migrate throughout ephemeral systems when flows occur, with the majority also colonizing floodplains and other off-channel areas (Balcombe et al., 2007). In the east Simpson Desert in arid Australia, Kerezsy et al. (2013) identified two main groups of colonists (Table 4.5.1) that migrated through floodwaters to temporary habitats in the highly ephemeral Mulligan River. Extreme colonizing species migrated at least 300 km upstream from the closest permanent water and mostly comprised small-bodied species such as desert rainbowfish, glassfish, the plotosid catfish silver tadan, the terapontid spangled perch Leiotherapon unicolor, and bony herring. In contrast, conservative colonizing species, including the percichthyid yellowbelly and the terapontids Barcoo grunter Scortum barcoo and Welch’s grunter Bidyanus welchi, generally stayed within 150 km of the closest permanent water and remained in deeper sections of inundated channel. Conservative colonists were generally larger-bodied species with longer life spans.

In North American prairie streams, high flows and floods similarly facilitate connectivity of habitats and allow fishes from downstream perennial reaches to colonize upstream intermittent habitats (Franssen et al., 2006; Table 4.5.1). However, floods in these systems can be infrequent (2–5 years; Franssen et al., 2006). Whitney et al. (2015) reported complete extirpation of fishes in a small desert stream following wildfire and noted that recolonization was delayed because of the presence of an intermittent reach between the perennial habitat in this tributary stream and the potential refugia population in the main streams of the river network. A recent survey of this system shows the fish communities have yet to return to this area a full two years after the wildfire (K. Gido, unpublished data). Thus, connectivity of fish habitat in IRES is linked to hydrology and recovery from disturbance can take weeks, months, or
even years. Genetic evidence can provide a longer term evaluation of the importance of connectivity in IRES (Chapter 4.9). For example, genetic analysis of Rio Grande sucker *Pantosteus plebeius* in desert stream networks shows that low-elevation reaches separated by dry reaches are greater barriers to gene flow than higher-elevation perennial reaches (Turner et al., 2015).

In Mediterranean rivers, large numbers of chub *S. torgalensis* move away from dry season pools following flow resumption. Movements continue throughout the period of hydrological connection, with some individuals migrating long distances upstream. This movement pattern is likely to facilitate the mixing of individuals that were spatially separated, as well as rapid colonization of dewatered areas at variable distances from the dry season refugia and the flux of individuals and genes throughout river segments (Pires et al., 2014).
### 4.5.4 HOW DO FISH SURVIVE IN IRES?

**Table 4.5.1 Examples of fish adaptations in IRES in Australia, North America, Mediterranean Europe, and Africa**

<table>
<thead>
<tr>
<th>Adaptation</th>
<th>Examples</th>
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<tr>
<td><strong>Specific adaptations to drying habitats</strong></td>
<td></td>
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<tr>
<td>Australia</td>
<td>Gobies (<em>Chlamydogobius</em> spp.) occur throughout Australia’s arid areas and extract oxygen from the atmosphere using a pharyngeal organ (<em>Thompson and Withers, 2002</em>)</td>
</tr>
<tr>
<td>North America</td>
<td>Physiology of pupfish (<em>Cyprinodon</em> spp.) allows them to withstand extreme temperatures and salinities (<em>Minckley and Deacon, 1991</em>). Species such as bowfin <em>Amia calva</em> can gulp air during periods of hypoxia (<em>Johansen et al., 1970</em>)</td>
</tr>
<tr>
<td>Europe</td>
<td>Fishes in Mediterranean rivers lack specific adaptations to survive in drying habitats but are tolerant of environmental variability (<em>Ferreira et al., 2007</em>)</td>
</tr>
<tr>
<td>Africa</td>
<td>Lungfish breathe air using a lung and estivate in cocoons during the dry period (<em>Greenwood, 1986</em>). Air-breathing catfish (<em>Clariidae</em>) have an epibranchial arborescent organ to extract oxygen from the atmosphere and survive longer than other species in drying habitats (<em>Bruton, 1979a</em>)</td>
</tr>
<tr>
<td><strong>Recruitment strategies</strong></td>
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<tr>
<td>Australia</td>
<td>In central Australia, seven species have been demonstrated to spawn continuously to take advantage of irregular flows: bony herring <em>Nematolosa erebi</em>, banded grunter <em>Amiataba percoides</em>, carp gudgeon <em>Hypleoleotris</em> spp., yellowbelly <em>Macquaria</em> sp., rainbowfish <em>Melanotaenia splendida tatei</em>, glassfish <em>Ambassis</em> sp., and spangled perch (<em>Kerezsy et al., 2011</em>). Ephemeral areas such as floodplains provide nursery habitat for juvenile fish across the continent</td>
</tr>
<tr>
<td>North America</td>
<td>Pelagic spawning fishes in the genera <em>Macrhybopsis</em>, <em>Notropis</em>, <em>Platygobio</em>, and <em>Hybognathus</em> broadcast eggs during floods to decrease likelihood of desiccation and potentially reduce predation of eggs and larvae (<em>Perkin et al., 2014</em>)</td>
</tr>
<tr>
<td>Europe</td>
<td>Fishes in Mediterranean rivers generally show early maturity and high fecundity, and some are multiple spawners (<em>Ferreira et al., 2007</em>). Species spawning early in the season are less prone to recruitment failures associated with drought but may be negatively affected by floods (<em>Magalhães et al., 2007</em>)</td>
</tr>
<tr>
<td>Africa</td>
<td><em>Nothobranchius</em> killifish grow and mature rapidly, spawn continuously and lay tough, drought-resistant eggs in the substrate. Embryonic development is phased and suspended for variable periods (diapause) in tune with drought and rainfall periodicity (<em>Nagy, 2014</em>). Sharp-tooth catfish spawn on flooded grassy shores of lakes and rivers with the onset of rains and local floods (<em>Bruton, 1979b</em>). Floodplains of savannah rivers are important breeding and nursery areas for many species during flooding (<em>Lowe-McConnell, 1985</em>)</td>
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The role of flows and flooding as drivers of biological processes such as fish recruitment was encapsulated in the original Flood Pulse Concept by Junk et al. (1989), and holds true for many IRES, particularly those where flows occur regularly (e.g., at a particular time of year) despite having variable volumes (Table 4.5.1). The annual flood cycle of tropical savannah rivers in Africa is described by Lowe-McConnell (1985, 1987), Welcomme (1979, 1986) and Lévêque (1997). In these rivers, sustained rainfall over several weeks or months results in a well-defined single or multiple flood peak that overflows into shallow floodplains; fishes respond by migrating upstream to breed (van der Waal, 1997; Gratwicke and Marshall, 2005). Similarly predictable responses occur in Mediterranean rivers (e.g., assemblages in some intermittent reaches are composed chiefly of young-of-year fish soon after flow resumes; Skoulikidis et al., 2011) and in North American IRES.

At local scales, habitat size is an important driver of fish community structure in IRES. In many IRES, juvenile fishes occupy shallow habitats and likely benefit from warmer water temperatures and increased resources (Labbe and Fausch, 2000; Martin et al., 2013). As waters recede, simplification of the food web occurs, with smaller habitat areas associated with simpler food webs and shorter food chains (McHugh et al., 2015; Chapter 4.7). These patterns are similar in IRES worldwide: predictable flooding occurs, fish breed, and small and/or shallow areas function as nurseries.

The Flood Pulse Concept has been modified for application to less-predictable systems such as boom-and-bust IRES in Australia. Rather than being driven by an annual, predictable flood, many Australian rivers have far more variable hydrological conditions. Working in central Australia, Puckridge et al. (1998) shifted the conceptual emphasis from floods to flow regimes and demonstrated that flows of any magnitude and/or duration could elicit an ecological response in unpredictable rivers. Concentrating...
on fish recruitment in more temperate systems in the southeast, Humphries et al. (1999) developed the low-flow recruitment hypothesis, concluding that for many Australian fishes—and specifically smaller species—over-bank flooding was not a requirement for successful recruitment. Subsequent studies continue to redefine the role of flow in recruitment success for fish that are adapted to living in variable Australian rivers (King et al., 2003; Cockayne et al., 2015). The general conclusion remains that Australian fishes, persisting as they do in unpredictable rivers, appear to have variable and sometimes elastic reproductive strategies in order to capitalize on the fickle conditions. For example, most fish species living in arid regions have been demonstrated to breed continually—a useful trait when an annual flow is not guaranteed (Kerezsy et al., 2011; Table 4.5.1).

Although movement and recruitment allow the majority of fishes in IRES to successfully utilize such areas to complete their life cycles, certain species have evolved specialized adaptations or increased tolerances to survive when areas dry to such a degree that oxygen and water itself become limiting factors (Table 4.5.1). In extreme environments such as desert rivers in Africa, fish diversity declines toward peripheral habitats prone to severe and prolonged desiccation. The diverse assemblage of African cichlids includes several eurytopic genera such as Oreochromis, Sarotherodon, and Tilapia that frequent seasonally fluctuating habitats of savannah ecosystems (Trewavas, 1983). Oreochromis species, in particular, are physiologically adapted to extremely harsh conditions, including hypersaline lakes and warm springs (Trewavas, 1983; Hecht and Zway, 1984; Nyingi and Agnèse, 2011).

The Anabantidae, commonly referred to as “labyrinth” fishes due to their superbranchial air-breathing organ, is another African family that survives in temporary water bodies. However, the air-breathing and terrestrial habits of African anabantid species such as the many-spined climbing perch Ctenopoma multispine are less associated with the desiccation of the environment and more with tolerating deoxygenation of swampy environments and undertaking overland breeding migrations during wet periods (Benl and Foersch, 1978; Bruton and Kok, 1980; Sayer and Davenport, 1991).

Air-breathing is a vital adaptation for survival in extreme drying habitats. The last species present in drying pools of African rivers and floodplains is the sharp-tooth catfish (e.g., Bell-Cross and Minshull, 1988; Barson and Nhiwatiwa, 2010), and provided the substrate is not completely desiccated, this species’ capabilities, including the ability to leave a drying water body and move overland, facilitate its survival (Bruton, 1979a,b; van der Waal, 1998). In contrast, complete desiccation of the environment can be survived by two groups of African fish: the lungfishes and the annual killifishes (Box 4.5.1). Although the species encountered in the harsh peripheral pools are characteristically ecological “pioneers” and “residuals” such as Clarias catfish (van der Waal, 1998), only “extremophile” species with special adaptations to surviving desiccation (Greenwood, 1986; Watters, 2009) exist in remote disconnected rain-filled pans.

Extreme IRES in Australia similarly provide habitat for fish species with specific adaptations that allow them to survive. Small gobies of the genus Chlamydogobius are distributed throughout Australia’s arid interior, primarily in shallow artesian springs and residual waterholes that persist following flooding. In these hot, extremely shallow (frequently <3 cm deep, A. Kerezsy, personal observation) and oxygen-poor habitats, the gobies extract atmospheric oxygen using a pharyngeal organ (Thompson and Withers, 2002). Another specialized Australian fish, the salamanderfish Lepidogalaxias salamandroides, is found only in acidic peat flats in Western Australia and survives without water for several months by estivating in burrows (Allen et al., 2002). Although most of Australia’s IRES fish are pioneers rather than extremophiles, their survival capabilities in some of the world’s most unpredictable rivers are indicative of their adaptations, exemplified by “Australia’s toughest freshwater fish” (Box 4.5.2).

Unlike Australia and Africa, there are no North American fishes capable of estivation. Instead, fishes occupying IRES in this region are often capable of breathing air (gar), withstanding extreme physiological
conditions (some minnows and pupfish), rapid population growth (mosquito fish), or a combination of these traits. Perhaps the ultimate survivor of naturally extreme environments is the desert pupfish *Cyprinodon macularius*, which can withstand temperatures up to 45°C and salinity to 70 ppt (Lowe and Heath 1969).

### 4.5.5 Threats to Fishes in Intermittent Rivers

Extended drying periods and below-average rainfall are normal climatic perturbations in arid areas. Although the consequences are often catastrophic for a particular cohort of fishes in a catchment, recovery occurs when a series of wetter-than-average months or years replenish formerly dry reaches and rejuvenate catchments. Examples discussed previously, such as the mass die-off of fish in outback Australia or the failure of fish to recolonize IRES in North America following wildfire, are not permanent changes but merely examples of the immense variability within such systems. Given time and flows, fish are likely to recolonize both areas when conditions are suitable. However, natural perturbations such as these can be amplified by anthropogenic changes such as river regulation (and resulting fragmentation of habitats), the imposition of alien species, and the looming problems associated with climate change (Table 4.5.2).
### Table 4.5.2 Examples of threats to fish in IRES in Australia, North America, Mediterranean Europe, and Africa

<table>
<thead>
<tr>
<th>Threat</th>
<th>Examples</th>
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<tbody>
<tr>
<td><strong>Fragmentation</strong></td>
<td></td>
</tr>
<tr>
<td>Australia</td>
<td>Rivers throughout Australia’s Murray-Darling Basin have been regulated since colonization, resulting in declines of many native species</td>
</tr>
<tr>
<td>North America</td>
<td>Fragmentation in IRES caused by poorly designed road crossings as well as heavily engineered dams. Many fish species have been extirpated upstream of impoundments</td>
</tr>
<tr>
<td>Europe</td>
<td>Habitat loss and fragmentation associated with damming contribute significantly to the decline of native fishes</td>
</tr>
<tr>
<td>Africa</td>
<td>Instream dams and weirs in dry areas are a major development in Africa and probably cause the decline of fish populations in these areas by interrupting fish migrations</td>
</tr>
<tr>
<td><strong>Alien species</strong></td>
<td></td>
</tr>
<tr>
<td>Australia</td>
<td>Carp, redfin perch, and goldfish threaten the Murray-Darling Basin; <em>Tilapia</em> spp. threaten native assemblages in the tropics; and gambusia are problematic across the continent</td>
</tr>
<tr>
<td>North America</td>
<td>IRES in the western United States are most prone to invasive fish species, including many sport fishes native to eastern United States such as bass (<em>Micropterus</em> spp.), sunfish (<em>Lepomis</em> spp.), and catfish (<em>Ictalurus</em> spp. and <em>Amieurus</em> spp.). Small cyprinids and gambusia are also common invaders of IRES. <em>Tilapia</em> (<em>Oreochromis</em> spp.) escaping from aquaculture facilities have exploited IRES in southern latitudes</td>
</tr>
<tr>
<td>Europe</td>
<td>Mediterranean rivers are a hot spot for fish invasions, including highly successful invaders such as common carp, pumpkinseed <em>Lepomis gibbosus</em>, and gambusia</td>
</tr>
<tr>
<td>Africa</td>
<td>In southern Africa, widespread translocation of sharp-tooth catfish via interbasin transfers and humans threaten many fish species in IRES. Carp and Mozambique tilapia (<em>Oreochromis mossambicus</em>) are invasive in dry areas of South Africa and Namibia</td>
</tr>
<tr>
<td><strong>Groundwater extraction</strong></td>
<td></td>
</tr>
<tr>
<td>Australia</td>
<td>Long-term extraction of groundwater from Australia’s Great Artesian Basin has likely impacted springs and IRES waterholes reliant on this groundwater in the arid zone</td>
</tr>
<tr>
<td>North America</td>
<td>Massive declines in surface water in IRES can be attributed to groundwater extraction, particularly in the Great Plains region of the United States</td>
</tr>
<tr>
<td>Europe</td>
<td>Water extraction threatens native fish in most Mediterranean rivers</td>
</tr>
<tr>
<td>Africa</td>
<td>The cave catfish in Namibia (<em>Clarias cavernicola</em>), restricted to a single cave lake, is threatened by a declining water table due to groundwater extraction</td>
</tr>
<tr>
<td><strong>Climate change</strong></td>
<td></td>
</tr>
<tr>
<td>Australia</td>
<td>More intense droughts are likely to reduce the number of IRES that receive periodic flows, resulting in reduced habitat for fish species</td>
</tr>
<tr>
<td>North America</td>
<td>Same as for Australia</td>
</tr>
<tr>
<td>Europe</td>
<td>Mediterranean rivers already experience substantial reductions in water availability, which will worsen with longer and more severe droughts expected under altered future climates</td>
</tr>
<tr>
<td>Africa</td>
<td>Climate change could threaten source tributaries in montane regions where fish species such as the Maloti minnow <em>Pseudobarbus quathlambae</em> is relict and fragmented into small isolated populations. Increased drought frequency in mesic areas in southern Africa such as the Karoo could threaten IRES</td>
</tr>
</tbody>
</table>
DROUGHT AND CLIMATE CHANGE

Within the context of the four continents considered in this overview, summer drying and drought is particularly significant for fish in Mediterranean rivers and North American IRES because, unlike some species from Africa and Australia, the persistence of fish in Mediterranean and North America IRES is strictly dependent upon perennial surface waters which act as refuges and sources of colonists after flow resumes (Robson et al., 2013; Chapter 4.8). Although large pools with well-developed canopies generally hold the richest assemblages and the highest overall abundances of native species (Magalhães et al., 2002a; Pires et al., 2010), the presence of networks of heterogeneous refuges may be critical in promoting adequate conditions for the persistence of species and life stages with different habitat requirements.

Fish assemblages in IRES on all four continents show considerable stability in the face of present-day droughts, probably due to the way historical hydrological filters have winnowed the pools of native species to those best adapted to cope with the prevailing patterns of variability (see also Hershkovitz and Gasith, 2013). Although species abundances can decline significantly in dry years (Bernardo et al., 2003; Skoulikidis et al., 2011), small and transient changes in species richness, composition, and rank abundance are normal (Magalhães et al., 2007). Indeed, except in some upstream reaches, local assemblages appear to be resilient to droughts (Chapter 4.8) and are capable of recovering to their former structure.

More frequent and severe droughts associated with climate change are likely to exacerbate intermittence and loss of hydrological connectivity, especially in small- and middle-sized streams (Giorgi and Lionello, 2008). This is likely to have severe impacts on native fishes, with species facing a trade-off between adaptation to new conditions or dispersal to new habitats (Filipe et al., 2013). Prolonged and intensified drought in Mediterranean regions of North America may result in dramatic changes or gradual shifts in freshwater populations and communities (Resh et al., 2013), and climate warming will increase periods of intermittence in arctic rivers, further fragmenting populations of Arctic grayling *Thymallus arcticus* (Betts and Kane, 2015). At broader scales, it seems likely that there will be considerable shifts in species richness and composition, with declines or local extinctions of the most sensitive species and their replacement by more resistant species (Magalhães et al., 2007; Filipe et al., 2013; Table 4.5.2).

WATER EXTRACTION, RIVER REGULATION, AND FRAGMENTATION OF HABITAT

Arguably the greatest threat to IRES biota is the fragmentation of their habitats. Fish ecology in IRES is driven by source-sink dynamics, and therefore long-term survival is underpinned by colonization opportunities. Barriers that inhibit these movements are particularly detrimental to the natural functioning of species and ecosystems. Perkin et al. (2014) proposed an ecological “ratchet mechanism” to describe how dams inhibit the ability of fish populations to recolonize areas following drying, often leading to basin-wide extirpations (Fig. 4.5.10). Increasing human populations are causing increases in disturbance frequencies and more severe drying, which is predicted to increase extirpations in these highly fragmented systems.

Historically, management of Australia’s rivers was primarily concerned with mitigating their intermittence in the century immediately following settlement of the continent by Anglo-Europeans, and provides a useful case study of the negative effects of human-induced fragmentation, particularly on fish populations. The development of river regulation and irrigation infrastructure is best exemplified by the highly modified Murray-Darling Basin, where the rivers have been “controlled” by large headwater reservoirs as well as a series of smaller weirs and locks further downstream (Lintermans, 2007). These structures
achieved their intended purpose to allow towns and agricultural districts to develop, but it transpired—that they had unfavorable outcomes for native biota. Native fishes in these IRES evolved with adaptations to boom-and-bust cycles permitting temporary migration and access to floodplains and anabranches. However, river regulation created a series of permanent reaches separated by barriers (weirs) that effectively stifled such behavior. As a result, native fishes declined, their migratory behavior was compromised, and the rivers deteriorated in health (Reynolds, 1983; Harris and Gehrke, 1997).

Many of the largest species, such as the Murray cod *Maccullochella peeli*, its close relative the trout cod *Maccullochella macquariensis*, the Macquarie perch *Macquaria australasica*, the silver perch *Bidyanus bidyanus*, and the freshwater catfish *Tandanus tandanus*, are now listed as threatened species, and river rehabilitation and remediation are now recognized as crucial to the recovery of the Murray-Darling Basin. Removal of weirs, the installation of fishways and fish ladders, and the provision of environmental watering by state and federal management agencies are some of the measures that seek to redress the river regulation of yesteryear and aim to restore the ecological balance in these systems.

**ALIEN SPECIES**

Alien fish species are present in all four of the continental areas considered in this overview. The most widespread alien fishes are small-bodied live-bearers such as gambusia *Gambusia holbrooki*,

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**FIG. 4.5.10**

Conceptual diagram of the ecological ratchet mechanism caused by interactions between habitat fragmentation and drought. Ratchets can operate as mechanisms for population expansion or decline (shown here) and involve forward movement without reciprocated reverse movement through four states in a fragmented riverscape: (A) before drought, (B) onset of drought, (C) height of drought, and (D) following drought. Fish abundance is equal to the number of symbols. If a drought subsides (dashed line of insert in B), then a “pseudo-ratchet cycle” ensues.

Reproduced with permission from Perkin et al. (2014).
large-bodied cyprinids such as carp *Cyprinus carpio*, and the slightly smaller cichlids (predominantly *O. mossambicus*; Table 5.4.2). Like their terrestrial counterparts, nonnative fishes that succeed in foreign environments possess broad dietary and habitat requirements. Unsurprisingly, those that inhabit IRES share traits common to native species inhabiting the same environments: the ability to colonize during flows, the ability to recruit successfully, and the ability to survive during periods of suboptimal water quality. In Australia’s Murray-Darling Basin, for example, carp breeding “hot spots” have been demonstrated to occur in shallow off-river habitats. An unlucky consequence of environmental flows intended to ameliorate the effects of river regulation is that their provision seems to benefit this alien species (Rayner et al., 2009; Conallin et al., 2012).

Worldwide, alien fishes generally originated from importation of foreign species to bolster local food, provide sport, or as ornamental fishes (Table 4.5.2). An exception is the widespread presence of gambusia which was originally transferred around the world in the early 20th century to combat malaria. However, the unfortunate results are no different and this species has been implicated in the decline of many native fishes (Howe et al., 1997; Fairfax et al., 2007). The translocation of native species to IRES outside their natural range is an equally problematic phenomenon, with salient examples including bass (*Micropterus* spp.) in the United States and sharp-tooth catfish throughout southern Africa (Table 4.5.2).

### 4.5.6 CONSERVATION PRIORITIES FOR FISH IN IRES

Conservation of fish in IRES relies upon habitat conservation to maintain periodic flow connectivity and enable ephemeral areas to experience regular and/or irregular wetting episodes. As such, and as a first priority, areas that currently experience natural or near-natural flow regimes should be preserved to maintain their intact ecological functions (Table 4.5.3). Progress toward this goal is piecemeal at best in the four areas considered in this overview (Table 4.5.3). This is concerning, particularly as flow

<table>
<thead>
<tr>
<th>Table 4.5.3  Examples of conservation priorities in IRES in Australia, North America, Mediterranean Europe, and Africa</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Priorities</strong></td>
</tr>
<tr>
<td><strong>Preservation of IRES with natural flows</strong></td>
</tr>
<tr>
<td>Australia</td>
</tr>
<tr>
<td>North America</td>
</tr>
<tr>
<td>Europe</td>
</tr>
<tr>
<td>Africa</td>
</tr>
</tbody>
</table>


## Table 4.5.3 Examples of conservation priorities in IRES in Australia, North America, Mediterranean Europe, and Africa—cont’d

<table>
<thead>
<tr>
<th>Priorities</th>
<th>Examples</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Repair/remediation of regulated rivers to reinstate natural flows and improve habitat</strong></td>
<td></td>
</tr>
<tr>
<td>Australia</td>
<td>Remediation activities including environmental flows and modification of structures to allow fish passage should continue in regulated rivers including IRES in the Murray-Darling Basin, southeastern Australia</td>
</tr>
<tr>
<td>North America</td>
<td>Several fishways on IRES have been built and there is a program to retrofit road crossings to allow fish passage. Some dam removal projects have recently occurred</td>
</tr>
<tr>
<td>Europe</td>
<td>Fish passage and environmental flows that mimic natural flow variation are increasingly recognized as critical to maintain biodiversity and river health</td>
</tr>
<tr>
<td>Africa</td>
<td>Installation of fishways in IRES is advocated but not widely practiced in Africa</td>
</tr>
<tr>
<td><strong>Priority native species</strong></td>
<td></td>
</tr>
<tr>
<td>Australia</td>
<td>Recovery actions should focus on the requirements of listed endangered species (e.g., silver perch and freshwater catfish in the southeast, Balston’s pygmy perch <em>Nannatherina balstoni</em> in the southwest)</td>
</tr>
<tr>
<td>North America</td>
<td>Many species are candidates, including large-river pelagic spawning fish (<em>Hybognathus</em> spp., <em>Macrhybopsis</em> spp.), pupfishes (<em>Cyprinodon</em> spp.), and live-bearers (<em>Poecilia</em> spp.) occupying intermittent spring habitats</td>
</tr>
<tr>
<td>Europe</td>
<td>Although endemic and threatened species with restricted distributions are strong candidates, conservation of biodiversity is increasingly recognized to depend on assemblage rather than species-specific conservation plans</td>
</tr>
<tr>
<td>Africa</td>
<td>Annual killifish are often localized and face threats from habitat destruction and agriculture, including overgrazing of riverine floodplains and marginal swamps. Lungfish are systematically exploited by subsistence fishers; increased human population pressures could threaten their existence</td>
</tr>
<tr>
<td><strong>Priority alien species</strong></td>
<td></td>
</tr>
<tr>
<td>Australia</td>
<td>Control actions should focus on carp and redfin perch in the south, tilapia in the north, and gambusia across the continent</td>
</tr>
<tr>
<td>North America</td>
<td>Control of alien species should focus on isolated habitats where control is practical and on all forms of nonnatives. Predatory fish (e.g., largemouth bass and tilapia) probably have the most detrimental effects</td>
</tr>
<tr>
<td>Europe</td>
<td>Control of invasive species such as common carp and topmouth gudgeon <em>Pseudorasbora parva</em> in source habitats deserve special attention, but effective legislation and public awareness are also critical to reduce introductions</td>
</tr>
<tr>
<td>Africa</td>
<td>Genetic contamination of indigenous <em>Oreochromis</em> species is a major threat to isolated and temporary populations. Deliberate introduction of aliens into refuge sites is a potential threat in many IRES; air-breathing catfish (<em>Clarias</em>) are especially problematic in this respect</td>
</tr>
</tbody>
</table>
regulation continues to compromise IRES in areas such as Africa (Table 4.5.2) and climate change is likely to exacerbate anthropogenic water needs worldwide (Chapters 1 and 5.1).

In areas where flow and/or connectivity has been altered, recovery efforts for IRES and their fish species (especially those that are listed as endangered) should focus on ameliorating the effects of fragmentation, alien species, and other threats so that populations can recover and persist over time (Table 4.5.3). Recovery strategies may seek to conserve native species; eradicate alien species; and/or restore IRES, their catchments, and their flow regimes at multiple spatial scales. A more formal investigation of global conservation priorities with a focus on fish in IRES is warranted given the pervasive themes of native fish decline, alien fish invasion, and the continued fragmentation of IRES that are so obvious in this overview.

4.5.7 CONCLUSIONS

This chapter has sought to profile fish species and communities in IRES on four continents and should be considered an overview rather than a comprehensive summary. Several key themes emerge about the characteristics of IRES fishes, the roles they play in these rivers, the threats they face, and some potential strategies for their conservation.

Fish presence and persistence in IRES is underpinned by two key factors: the adaptations of the fish species that enable them to survive in such systems, and the integrity of the catchments themselves. The breadth of adaptations, and especially the convergence of similar traits across different families and on different continents, demonstrates evolution by natural selection in progress. They also remind us that fish, already highly diverse, are capable of adapting to living in virtually any area where water is either permanently or occasionally present.

IRES are, by their very nature, fickle and unpredictable environments. In years when floods do not occur or when rainfall is below average, fish populations will decline and may become locally extirpated. If these conditions persist, recovery might not occur for several years. However, as long as IRES or at least some sections of them remain in reasonable ecological health and are physically capable of reconnecting with parent rivers or more permanent reaches, one aspect of their ecology that is predictable is that when water returns, fish will reappear. Different flow regimes (Chapter 2.2) may elicit different biological responses between seasons but over long time frames, fish persistence in such systems is driven by the regular or irregular patterns of wetting and drying. No matter how different each flood or flow seems, there will be ecological similarities.

One similarity is how IRES fishes contribute significantly to food webs and secondary production. For example, the contribution that fish in IRES can make to arid-zone food webs is superbly demonstrated throughout the Australian inland where a consistent pattern of ecological succession plays out after high flows. Erratic floodwaters provide migration pathways that are quickly utilized by colonizing fish species. Migratory fish-eating birds, notably large-bodied species such as pelicans and cormorants (Fig. 4.5.11), arrive in huge numbers shortly afterward. Then, as the waterholes dry, terrestrial predators and scavengers including rodents, reptiles, and both native and introduced large mammals consume the stranded survivors (R. Kingsford and A. Kerezsy, personal observations; Chapter 4.6).

Intensive human settlement and the subsequent alterations to river catchments have had the most severe impacts on IRES (Chapter 5.1), because even the most hardy and adapted fish species
cannot survive the effects of rivers that cease to flow entirely, dam walls that are too high to scale, or the diseases, predation, and displacement that can occur when alien species are liberated in a reach or catchment. Ameliorating such disruptions is likely to remain a key challenge for river managers worldwide, especially as our global population and commensurate demand for water grow. Although IRES are often overlooked by regulatory agencies as essential habitats for fishes, this chapter illustrates the wide diversity of these habitats and their importance in maintaining healthy river ecosystems.

Our recommendations provide a comparatively simple approach to conserving IRES and their fish communities, even though the implementation of strategies and actions is likely to be extremely complicated. In the first instance, IRES that retain their natural flow regime and that are unaffected by river regulation and water extraction should be identified and allowed to remain in their natural state. Such areas have obvious conservation and research potential, and also provide reference areas for remediation of other rivers, reaches, and areas (whether intermittent or permanent).

In areas where human-induced perturbation has occurred, and especially in areas that are known to provide habitat for rare, endangered or unusual species, research and management aimed at restoring or remediating IRES should be undertaken if possible. This multifaceted and onerous task involves research on specific species, their ecological requirements, and specific threats and stressors. Often, on-ground works are needed, integrating disciplines ranging from biology to engineering. Examples include the installation of fish ladders on weirs to facilitate movement, the resnagging of river channels, the reinstatement of the natural flow regime by managing flows, and the removal or control of alien species using techniques such as physical removal and chemical control. Although complex and expensive, this work is necessary to preserve the ecological integrity of aquatic ecosystems where water itself is not always present. In this regard, the fact that humans have a natural tendency to link fish with water is a definite advantage: if we can explain that IRES are facing an uncertain future, the most graphic evidence for many people will be the decline or absence of native fishes.
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REFERENCES


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