Conservation of migratory fishes in freshwater ecosystems

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Migratory fishes are natural wonders. For many people, the term migratory fish evokes images of salmon audaciously jumping at waterfalls as they return to their own riverine birthplace to spawn after years of growth in the ocean, but freshwater fishes actually show a broad spectrum of migration strategies. Migratory fishes include small species – three-spined sticklebacks that spawn in coastal streams around the northern Pacific and gobies that move from the ocean into tropical island streams by climbing waterfalls (McDowall, 1988) – as well as some of the largest freshwater fishes in the world, such as the Mekong dog-eating catfish and the Chinese paddlefish (Stone, 2007). Aside from migratory habits, these species have few shared characteristics; they encompass numerous evolutionary lineages, enormous differences in life history, and every possible direction and distance of migration. Biologists treat migratory freshwater fishes as a functional group because their life-history strategy revolves around long-distance movement between ecosystems in a perilous quest to take advantage of both high-quality breeding sites and bountiful feeding areas. As humans have physically blocked fish migrations, degraded breeding and feeding grounds and relentlessly harvested migrants for their flesh and roe, many populations have declined or been extirpated. This chapter will provide an overview of fundamental and applied research that is helping to guide efforts to conserve migratory freshwater fishes.

For practical purposes, we define migratory behaviour as the synchronized movement of a substantial proportion of a population between

distinct habitats, which is repeated through time within or across generations. Modern definitions of fish migrations typically recognise both the adaptive benefits of migrating and individual variation in executing the general strategy (see McDowall, 1988; Lucas & Baras, 2001). Not every individual must move, the timing may vary somewhat from year to year, and the motive for migrating may include seeking refuge from harsh conditions in addition to breeding and feeding. Nonetheless, in most cases, migration is critical to individual fitness and population persistence because it enables specialised use of different habitats for growth and reproduction. Where their migration routes are blocked or key habitats are lost, migratory fishes often suffer rapid and catastrophic losses.

Human appropriation and degradation of the earth's freshwater ecosystems (Vörösmarty *et al.*, 2010; Carpenter *et al.*, 2011) have transformed this reliance on multiple habitats into a detriment for many migratory fishes. Historically, travelling spectacular distances along the same routes swum by their ancestors was sufficiently advantageous to give rise to migrations of over 1400 km among salmon in the Snake River of the USA, whitefish in the Omul River of Russia, sturgeon in Europe's Danube River, and various catfishes in Asia's Mekong River and South America's Amazon River (McKeown, 1984; Lucas & Baras, 2001). Today, these extreme migrants are especially vulnerable to changes in environmental conditions specifically because their long-distance movements expose them to many risks. Barriers and habitat loss have reduced many migratory fish populations, and even entire species. Emblematic cases include the sturgeons and paddlefishes – an ancient lineage of which all extant species appear on the IUCN's Red List of endangered species (Pikitch *et al.*, 2005) – as well as numerous salmon populations along the coasts of North America and Europe that now depend on stringent protections to avoid extirpation (Parrish *et al.*, 1998; Ruckelshaus *et al.*, 2002). The growing literature on declines of migratory fishes across the world suggests that a conservation crisis point is at hand, meriting urgent attention (Chapter 1).

The thesis of this chapter is that conserving migratory fishes is a global challenge that requires balancing numerous biological, social and economic factors. This scenario is not unique to fishes (Wilcove & Wikelski, 2008), but river networks impose special constraints on conservation approaches. Unfortunately, scientific research has long focused on just a handful of migratory fishes. Pioneering books on fish migrations dealt primarily with salmon, eels, shad and sturgeon (e.g. Meck, 1916; Hasler, 1966; Harden Jones, 1968), and taxonomic and

geographic coverage have expanded only in the last few decades (e.g. McKeown, 1984; McDowall, 1988; Lucas & Baras, 2001). Similarly, conservation and management efforts have focused disproportionately on a modest number of high-profile migratory taxa such as salmon and sturgeons (e.g. Ruckelshaus *et al.*, 2002; Landsman *et al.*, 2011), while far more species remain obscure despite their imperillment. Economically valuable migrants can sometimes serve as umbrella species whose conservation will also improve the prospects for other migratory fishes (e.g. Limburg & Waldman, 2009), but many regions are losing migrations quietly without the benefit of such rallying-point species.

We will begin with an overview of the range of migratory strategies and the diversity of freshwater fishes that migrate. With this broad perspective in mind, we will discuss the conservation predicament created by losses of both key habitats and the connections among them. We will then explore some of the ramifications of declining migrations for metapopulation dynamics, ecosystem processes and human fisheries. Finally, we will discuss some key practical considerations that complicate conservation efforts, including cost-efficiency of restoring connectivity, societal demand for new dams and roads that create barriers, risks of species invasions and contaminant transport, and the tendency to focus on economically valuable species. An exhaustive review of any one of these topics is beyond the scope of this chapter; our goal is to introduce a variety of viewpoints on the challenge of conserving migratory freshwater fishes.

11.1 ECOLOGICAL CLASSES OF MIGRATORY FRESHWATER FISHES

There are four major classes of migration patterns among fishes that depend on freshwater ecosystems for at least part of their life cycle (Myers, 1949; McDowall, 1988). *Potamodromy* describes migrations that occur entirely within freshwaters. Most potamodromous species spend part of the year in either large rivers or lakes, and their migrations take them upstream into tributaries (or occasionally between zones of the same lake). The other three forms of freshwater migratory behavior are classified as *diadromy* (Figure 11.1) because they involve switching between freshwater and saltwater environments, which demands a range of physiological adaptations. Diadromous species that breed in saltwater are *catadromous*; the young travel to freshwater ecosystems to grow and mature before returning to saltwater to complete their life cycle. Among species that breed in freshwaters, some diadromous fishes
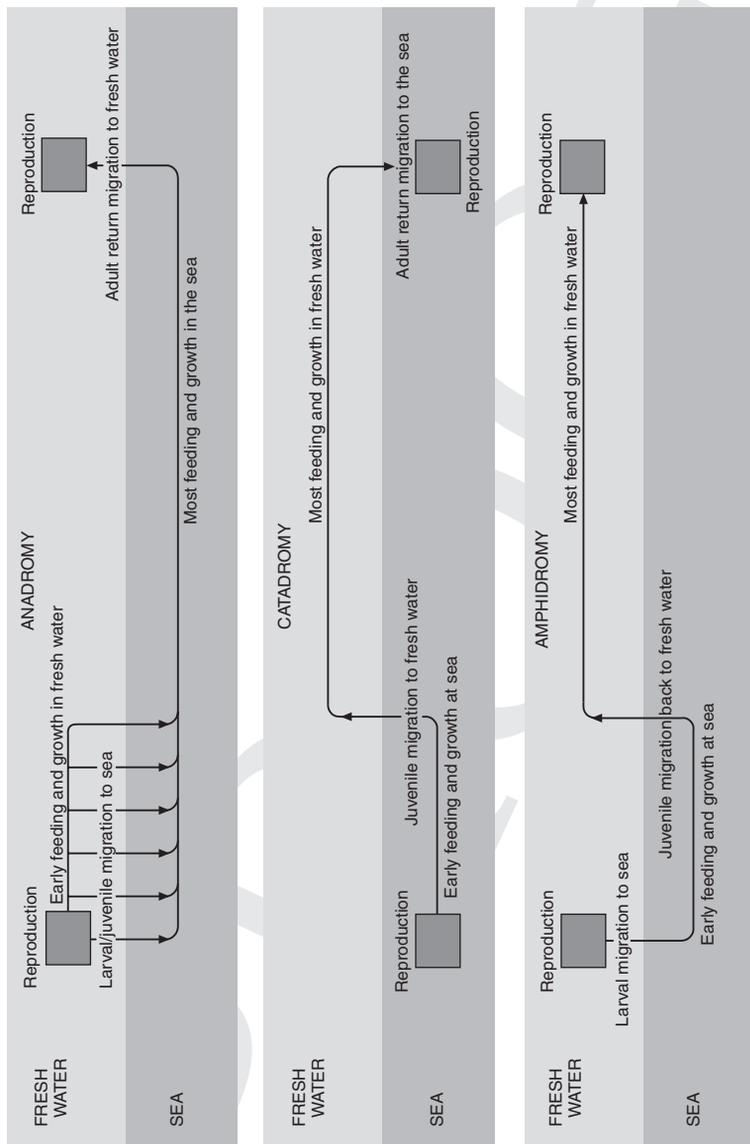
Figure 11.1 Migration patterns between freshwaters and the sea in the three different types of diadromy. The relative timing and importance of freshwater–saltwater transitions are the basis for differentiating among anadromy, catadromy and amphidromy. This diagram is reproduced from McDowall (1997), with kind permission from Springer Science and Business Media.

use marine waters as their primary growth environment (*anadromy*), while others remain in saltwater only briefly prior to returning to freshwater (*amphidromy*).

A second major dimension of life-history variation among freshwater migratory fishes regards the potential number of breeding bouts in a fish's lifetime, known as *parity*. A large majority of migratory species are capable of breeding repeatedly (*iteroparity*), including almost all potamodromous fishes. In contrast, some migratory species invest all of their resources in one large reproductive bout that is inevitably followed by death (*semelparity*). Semelparous migrants include all lampreys and anguillid eels as well as some salmonids, clupeids (shad and herring) and sticklebacks. Despite the fame of Pacific salmon for mass mortality after spawning, the majority of salmonid species are at least partially iteroparous (Quinn, 2005).

Convergent evolution of each of the four migration strategies and two parity states in many lineages attests to the advantages conferred by stereotyped migrations (McDowall, 1988, 1997). For most potamodromous and diadromous fishes, the underlying motivation for large-scale migrations is to take advantage of prime breeding and feeding areas that are geographically distinct, much the same as for migratory birds and mammals (Baker, 1978). Some fish migrations are also used to seek refuge from inhospitable environmental conditions (Lucas & Baras, 2001), although these movements often align with feeding or breeding cycles as well. In all anadromous fishes and most potamodromous species, feeding and growth occur in a relatively large ecosystem with high productivity (ocean, lake or large river), and breeding is concentrated in smaller, less-productive streams and rivers. In contrast, catadromous species achieve most of their growth in a small ecosystem (stream, lake) before returning to the ocean to spawn. Amphidromous species both breed and grow in freshwater environments, but retain a marine larval phase that enables dispersal and colonisation (McDowall, 1988).

Strong latitudinal patterns in the frequency of each diadromous strategy underscore the match of the growth phase to the more productive environment; catadromous and amphidromous fishes predominate in the tropics where rivers and lakes are more productive than most marine habitats, while anadromous species take advantage of the high productivity of oceans compared to rivers and lakes at higher latitudes (Gross *et al.*, 1988). At the same time, the

less-productive environment is thought to feature less risk of predation for young fishes, making it appealing as a nursery area despite lower potential growth rates (McDowall, 1988; Lucas & Baras, 2001). The importance of ecosystem productivity and predation presumably also govern the direction of potamodromous fish migrations, although the most advantageous direction to migrate likely depends on both dietary and reproductive requirements. For example, most of the large minnows and alestid fishes in African lakes use the lacustrine environment for growth but move into tributaries to spawn (Leveque, 1997). Intriguingly, large tropical rivers often contain some species that move upstream to breed in headwaters and others that move downstream to breed in floodplains and deltas – these fish may literally migrate past each other (Lucas & Baras, 2001).

The ecology of potamodromous fishes has received far less attention than that of diadromous species, despite the fact that the majority of the world's migratory freshwater fishes are potamodromous. The total number of diadromous species worldwide is estimated to be around 250 (McDowall, 1997), which is comparable to the sum of potamodromous species documented in case studies of just the Mekong River (165 species; Baran & Myschowoda, 2009), Canada (34 species; Lucas & Baras, 2001) and South American rivers (at least 67 species; Carolsfeld *et al.*, 2004). Roughly one-third of Canadian freshwater fish species are potamodromous (Lucas & Baras, 2001) and most major tropical rivers include at least a few dozen species (e.g. Welcomme, 1985; Carolsfeld *et al.*, 2004). Moreover, potamodromous species dominate fish biomass in many tropical (e.g. Carolsfeld *et al.*, 2004; McIntyre *et al.*, 2008; Ziv *et al.*, 2012) and temperate (Klingler *et al.*, 2003; Cooke *et al.*, 2005) rivers during their migrations, suggesting that they play essential roles in ecosystems.

The conservation of migratory freshwater fishes is a global challenge. Diadromous fishes use (or once used) virtually every coastal river basin on Earth (McDowall, 1988), and potamodromous species can be found in most inland river networks and lakes as well as many coastal drainages. Unfortunately, there exists neither a comprehensive map of diversity patterns among the world's migratory freshwater fishes nor a systematic assessment of their endangerment. These undertakings would be of great value for research and conservation, but the diversity patterns summarised above provide context for understanding why migratory fishes are so often imperiled.

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11.2 TRIPLE JEOPARDY: DEPENDENCE ON MULTIPLE HABITATS AND THEIR INTERCONNECTIONS

Animals have evolved complex life histories to allow utilisation of multiple environments that collectively maximise lifetime reproductive success by taking advantage of the opportunities (and avoiding the costs) afforded by each place (Wilbur, 1980). In some cases, the spatial dimension of this transition is trivial; for instance, most insects and amphibians undergo a radical metamorphosis from larval to adult morphotypes, but the spatial distance between their respective habitats is often small. Nonetheless, such transitions expose these species to a form of double jeopardy; threats in either of their two critical habitats can lead to extirpation, even if the other habitat remains pristine (e.g. Todd *et al.*, 2011). Migratory animals face this same double jeopardy, but also a third major challenge (i.e. triple jeopardy) due to the necessity of suitable conditions in the migration corridors connecting their often-distant feeding and breeding habitats (Wilcove & Wikelski, 2008). Compared to aerial migrations of birds or insects, migratory mammals and fishes experience an especially stringent form of triple jeopardy in that their pathway itself is often physically blocked. Thus, conserving fish migrations requires ensuring appropriate conditions in the habitats used as breeding grounds and feeding areas, but also protecting migratory corridors that are not obstructed by dams, road crossings or other barriers (Figure 11.2).

The importance of recognising this triple jeopardy scenario is underscored by cases where migratory freshwater fishes have declined due to changes in just one of the three essential habitats. For instance, restored spawning grounds in California's Shasta River attract anadromous coho salmon, but low flow and high temperatures lead to mortality of young fish before they are ready to migrate to the ocean (Jeffres & Moyle, 2012). That losses of spawning or nursery grounds will compromise population viability is obvious, but degradation of feeding habitats can be just as problematic. Long-term variation in salmon populations in the northern Pacific Ocean indicate that climatic control of marine productivity drives fluctuations in anadromous fish stocks (Finney *et al.*, 2002; Irvine & Fukuwaka, 2011), thereby illustrating both the importance of feeding areas and the necessity of accounting for human impacts on the marine realm when seeking to conserve diadromous species. Striped bass declines in Chesapeake Bay through the 1970s illustrate a different type of anthropogenic influence on feeding areas; this downturn was driven
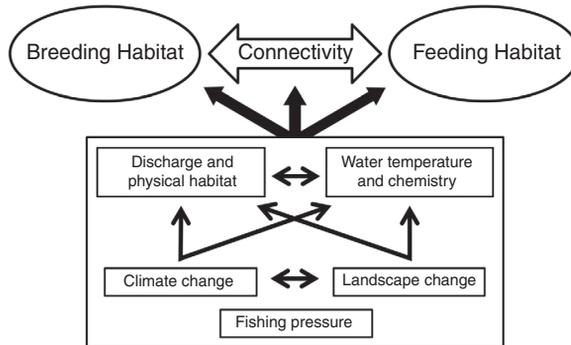
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Figure 11.2 Conceptual model of the triple jeopardy faced by migratory fishes. Population declines can be driven by loss or degradation of breeding habitat, feeding habitat, or the migration corridor that connects breeding and feeding habitats. Major classes of anthropogenic change, and the resulting stressor pathways, leading to habitat loss or degradation are indicated in the lower box.

by overfishing in the marine waters where they spend years growing to adult size (Richards & Rago, 1999).

Both breeding and feeding habitats in rivers have been compromised by widespread alterations of substrate, flow, temperature and chemistry (Vörösmarty *et al.*, 2010; Carpenter *et al.*, 2011) that lead to mismatches with migratory life-history strategies that have evolved to suit the natural properties of rivers. In particular, critical life-history events such as spawning and larval rearing are generally timed to match patterns of discharge and temperature (Poff *et al.*, 1997; Lytle & Poff, 2004). For example, the American paddlefish relies on temperature, flow and turbidity cues indicative of spring high-flows to ensure that river conditions are conducive to larval growth (Jennings & Zigler, 2009). Alteration of these spawning cues has had demonstrable negative effects on paddlefish recruitment (Pracheil *et al.*, 2009). Moreover, when migrating upstream, many species depend on appropriate channel complexity and hydrology to create low-energy corridors for efficient swimming, but human activities can eliminate these favourable conditions (McElroy *et al.*, 2012).

Intensive alteration of the landscape associated with agriculture, urbanisation and forestry leads to degradation of breeding and feeding habitats through physical changes (e.g. substrate and hydrology) as well as shifts in temperature and chemistry that are not directly visible yet can have profound effects (Allan & Castillo, 2007). Migratory fishes

often travel long distances to reach productive feeding areas, but the detrital, algal, invertebrate and prey fish resources that they seek may have been diminished by changing substrate, flow and chemistry. In breeding habitats, substrate composition is critical for the spawning and early life history of many migratory fishes. For example, lamprey larvae bury themselves in soft, fine sediments on stream bottoms, and changes in sediment stability or composition can lead to larval mortality and eventually population declines (Renaud, 1997; Smith *et al.*, 2012). Pacific salmon require a different kind of substrate; their large eggs must be buried in gravel to protect them from predators and ensure adequate water flow for oxygenation (Quinn, 2005). Land-use changes can dramatically elevate watershed inputs of sediment that lead to burial of coarse substrates in silt (Allan & Castillo, 2007), while dams starve downstream areas of sediment as they trap particles within impoundments (Vörösmarty *et al.*, 2003). Either of these changes can disrupt the availability of food resources for young fishes, which must feed intensively to survive and grow. Human activities may also boost the exposure of fry to predators through species introductions and habitat alteration. For instance, predation by non-native trout on young humpback chubs – a native migratory species at risk of extinction – within the Grand Canyon of the Colorado River is facilitated by clear-water conditions below dams (Marsh & Douglas, 1997).

Although maintaining the integrity of both breeding and feeding grounds is essential, so too is ensuring unobstructed migration corridors connecting these habitats. The general consequences of dams and fragmentation are discussed in detail elsewhere in this book (Chapters 4 and 10); hence, we will only outline a few key issues relevant to migratory fishes here. Dams, weirs and road culverts that act as barriers to fish migrations are pervasive in the world's rivers (Reidy Liermann *et al.*, 2012). Millions of dams block fish movement through river networks (Lehner *et al.*, 2011), yet culverts and other structures associated with road crossings are many times more numerous. For instance, there are 38 times as many road crossings as dams in tributaries of the North American Great Lakes (Januchowski-Hartley *et al.*, 2013), and a substantial proportion of these road crossings partially or entirely block fish movement (Januchowski-Hartley *et al.*, 2014). Yet, even as dams and culverts are gaining attention for their detrimental effects on stream-resident and migratory fish species in developed countries, new dams, weirs and road crossings continue to proliferate in poorer countries to meet development and economic needs

(Kareiva, 2012; Laurance & Balmford, 2013). Unfortunately, even progressive discussions of the consequences of infrastructure expansion sometimes fail to consider an aquatic perspective (e.g. Laurance & Balmford, 2013).

The impact of dams and culverts on the downstream migration of fry and adults can be just as damaging as blocking upstream movement. Small dams and culverts probably pose few challenges for moving downstream during high flows, although they may become problematic when discharge is low (Benstead *et al.*, 1999). However, passing over the spillway or through the turbines of a large dam can impart severe injury or death due to high-velocity contact or acute turbulence (Coutant & Whitney, 2000). Safe passage downstream is further complicated by variation among species and life stages in their position and orientation in the water column (Coutant & Whitney, 2000; Williams *et al.*, 2012). Screening systems (Williams, 2008) and surface bypass routes (Johnson & Dauble, 2006) have been developed to divert juvenile salmonids away from the turbines of dams in the Columbia River system (USA), but these methods may not be broadly applicable to other diadromous or potamodromous fishes (Cada, 1990; Coutant & Whitney, 2000). Sensor-packed 'robo-fish' are now providing insights into the experience of larger fishes passing over dams or through hydroelectric turbines; each route often leads to immense instantaneous accelerations (> 95 times gravity) due to direct physical contact with the spillway (100% incidence) or turbine blade (62% incidence; Duncan, 2013). These examples and many others (Chapter 4) illustrate the importance of designing safe passage methods for fishes of all sizes that face dams and road culverts while migrating up- and downstream.

Dams, weirs and road culverts can also exert indirect effects on migratory fishes by changing ecosystem structure and functioning. Large dams alter thermal regimes, hydraulics and fluxes of sediment and nutrients for tens of kilometres downstream (Ward & Stanford, 1983; Poff *et al.*, 2007). In turn, these abiotic alterations drive changes in substrate and physico-chemical characteristics (Ligon *et al.*, 1995), as well as lateral connectivity between the channel and floodplains (Bayley, 1995). Attendant ecological changes may include decreased recruitment of riparian vegetation (Scott *et al.*, 1996), altered fish community structure (Bain *et al.*, 1988; Perkin & Gido, 2012) and decreased community resilience to disturbances (Sedell *et al.*, 1990). Moreover, large dams disrupt the very environmental signals (e.g. discharge, temperature) that many fishes use as migratory cues (Lehner *et al.*, 2011). Overall,

migratory fishes that must rely on fragmented river systems experience wildly different conditions than those typical of the free-flowing rivers in which their migratory life histories evolved.

In addition to dependence on multiple habitats and their connections, migratory species often cross political boundaries. As a result of such trans-jurisdictional movements, it is challenging to incorporate the entire geography and life history of migratory species into management decisions (e.g. Pracheil *et al.*, 2012). Where fish move between areas overseen by multiple governing bodies that differ in their priorities and constituencies, they will often be subject to contrasting regulations (e.g. catch limits) and practices (e.g. habitat restoration). The difficulty of establishing, maintaining and funding coherent management strategies is likely to increase dramatically with the number of jurisdictions involved. Thus, institutions that operate at the actual scale of migrations could improve conservation outcomes by aligning the actions of disparate players. For example, the Great Lakes Fishery Commission, which coordinates federal and state governments across the North American Great Lakes, has helped unify the management of migratory lake sturgeon (Welsh, 2004).

The summary above has merely scratched the surface with regard to the ways and places in which loss of breeding habitat, productive feeding grounds and riverine connections have negatively affected freshwater migratory fishes. The salient point is that degradation of any one of these three key habitats can be sufficient in itself to eliminate a migratory population. Accounting for this triple jeopardy scenario can help to ensure that interventions target the habitats that most limit long-term prospects for migratory fish populations.

11.3 ECOLOGICAL AND SOCIETAL IMPLICATIONS OF DECLINING FRESHWATER FISH MIGRATIONS

The ramifications of population declines of migratory fishes extend well beyond their local ecosystem. The reproductive success of individual migrants contributes not only to their own population, but also to persistence of their species as a whole. As the diversity and population sizes of migratory fishes are diminished, ripple effects are often felt across entire ecosystems based on shifts in the rates of fundamental processes like primary production and organic decomposition. Beyond the river channel, human populations often depend on migratory fishes for sustenance, commerce and recreation. Reducing

or eliminating fish migrations runs can rob communities of a key food supply as well as an integral dimension of their cultural identity. We now address each of these implications of declining migrations in turn.

11.3.1 Long-term conservation in a metapopulation context

Practical constraints often require that conservation efforts focus on just a subset of a species' range, but metapopulation theory suggests that these localised efforts can have long-term benefits for the species as a whole (Hanski, 1999). A metapopulation is a network of patchily distributed populations that are connected via dispersal or migration of individuals – a scenario that could apply to most migratory fish species. The exchange of genes and individuals stabilises the dynamics and enhances the persistence of both individual populations (Brown & Kodric-Brown, 1977) and the metapopulation as a whole (Hanski, 1999), partly by reducing the deleterious effects of inbreeding, mutation load and genetic drift. Conversely, if any one population in the network dwindles or is extirpated, loss of its genetic diversity can reduce the effective size of the entire metapopulation, thereby increasing genetic drift and risk of extinction (Frankham, 1995). These and other aspects of fish metapopulation dynamics are more fully discussed in Chapter 10.

Metapopulation dynamics are likely to characterise many migratory fishes because migrations divide the life cycle into phases of spatial segregation and potential mixing among populations. Among diadromous species, catadromous fishes often have the opportunity to mix while spawning in marine waters, whereas riverine breeding areas used by anadromous and amphidromous species are isolated (although straying occurs; e.g. Hamann & Kennedy, 2012). A similar dichotomy exists among potamodromous fishes; some species migrate to many distinct feeding areas in headwaters but mix freely while spawning downstream in floodplains (e.g. prochilodontids in South American rivers; Collins *et al.*, 2013), while others share feeding grounds in lakes or large river channels but scatter into separate tributaries to breed (e.g. migrants in the North American Great Lakes; Landsman *et al.*, 2011). We might speculate that genetic exchange among populations that converge upon shared breeding areas would enhance metapopulation persistence, but also diminish the likelihood of intraspecific differentiation like that observed in some salmonids (Quinn, 2005) and clupeids (Leggett & Carscadden, 1978). In any case, comparisons of metapopulation

structure, genetic exchange and breeding site fidelity across diadromous and potamodromous species would clarify the degree to which conservation strategies need to be tailored to particular migration patterns.

In keeping with metapopulation theory, sockeye salmon fisheries in Alaska show regional stability despite interannual variability in the size of each constituent population (Schindler *et al.*, 2010). The key insight is that while the populations of breeding stock using each river fluctuate considerably, the independence of these dynamics in space and time effectively stabilises the aggregate catch. This model system exemplifies the benefits of conserving a portfolio of populations where mixing and rescue processes can occur via natural connections. Conversely, metapopulation models and research on resident stream fishes underscore the ease of losing ecological connectivity in river systems due to inherent limitations on dispersal pathways in dendritic systems (Gotelli & Taylor, 1999; Fagan, 2002). By extension, the benefits of restoring feeding and breeding areas – or alleviating barriers to movement between them – are expected to be substantial for metapopulations of migratory fishes.

11.3.2 Ecosystem consequences of declining migrations

Looking beyond fishes themselves, ecosystem dynamics often depend upon influxes of energy and nutrients delivered by fish migrations. Indeed, anadromous fishes have been proposed as keystone species for terrestrial vertebrates (Willson & Halupka, 1995). A growing body of research is elucidating the many pathways by which fish migrations can drive ecosystem processes via material subsidies, disturbance, food web interactions and effects on ecosystem processes (Flecker *et al.*, 2010). This work demonstrates that loss of migratory fishes can greatly alter the character of aquatic ecosystems, thereby adding another motive for conservation efforts.

Studies on the ecosystem roles of migratory fish originated with and continue to focus particularly on anadromous salmon, which achieve the majority of their growth in the marine environment but generally die after spawning in freshwater streams and lakes. During spawning they have two major effects on stream ecosystems: disturbance of the substrate during nest-building (Moore *et al.*, 2004) and addition of nutrients from excretion and decomposing carcasses and eggs (Naiman *et al.*, 2002). Fish-derived nutrients are incorporated by algae (Wipfli *et al.*, 1998), invertebrates (Hicks *et al.*, 2005) and resident fishes (Rinella *et al.*, 2012), and are even transferred to terrestrial vegetation (Bilby *et al.*,

2003). This subsidy can have a positive feedback on salmon fisheries as juveniles benefit from the nutrients provided by spawning adults (Bilby *et al.*, 2003; Rinella *et al.*, 2012). These effects are context-dependent; nutrient inputs are most important when substrate size is large and therefore less prone to disturbance, when run size is large relative to ecosystem size, and when background nutrient levels are low (Janetski *et al.*, 2009; Flecker *et al.*, 2010).

There is growing evidence that excretion by live adults is also an important pathway for subsidies that complements inputs from decaying salmon carcasses (Tiegs *et al.*, 2011). This finding raises the possibility that iteroparous species also provide substantial nutrient subsidies despite high spawner survival rates. For instance, suckers are iteroparous, potamodromous species that are abundant across much of North America (Cooke *et al.*, 2005), and their large migrations can constitute a major component of stream nutrient dynamics (Hall, 1972; Flecker *et al.*, 2010; Childress *et al.*, 2014). Similarly, studies on anadromous clupeids also show evidence of nutrient subsidies (Browder & Garman, 1994; Walters *et al.*, 2009; Hanson *et al.*, 2010). Ecosystem responses to nutrient transfers by iteroparous fishes are poorly documented, but the example provided by semelparous salmon provides ample motivation for further research.

A broad range of consumers benefit from fish migrations either through direct consumption of migrants or indirect dependence on the productivity arising from ecosystem subsidies. Bald eagles have greater reproductive success when nesting near rivers with spawning migrations (Gerrard *et al.*, 1975). Bear populations, which transfer salmon nutrients far into terrestrial ecosystems (Hilderbrand *et al.*, 1999), are sensitive to decreases in salmon availability (Levi *et al.*, 2012). Even the abundance and diversity of songbirds increase in the presence of salmon migrations as they capitalise on the salmon subsidy indirectly via increases in the emergence of aquatic insects (Christie & Reimchen, 2008). In large neotropical rivers, migrations of juvenile fish from productive nursery habitats to oligotrophic streams help to support piscivorous fishes (Winemiller & Jepsen, 2004).

In addition to providing nutrients and energy, migratory fish can alter material processing. *Prochilodus* and their relatives are major iteroparous migrants in most river systems of South America, and they play a key role in ecosystem dynamics by fastidiously consuming sediment from the bottom. Their feeding alters algal and invertebrate assemblages on rocky substrates (Flecker, 1996), dramatically affects several

dimensions of carbon cycling (Taylor *et al.*, 2006) and contributes substantially to nitrogen and phosphorus recycling (McIntyre *et al.*, 2007). On the tropical island of Puerto Rico, dams frequently block access to streams for migratory fishes and shrimps, which leads to substantially higher biomass of algae, detritus and invertebrates upstream (Greathouse *et al.*, 2006). These examples underscore the strength and variety of ecosystem-level effects of losing migratory fishes (Flecker *et al.*, 2010).

Ultimately, the conservation of major freshwater fish migrations should be seen as a necessary component of protecting the integrity of aquatic ecosystems, rather than being a purely fish-centric effort. An extensive web of species depends on the material subsidies and activities of migratory fishes, and this has been well demonstrated for various anadromous species as well as a few potamodromous counterparts. Coverage of catadromous species from an ecosystem perspective is distinctly lacking, which raises interesting questions about whether certain marine ecosystems are meaningfully fertilised by the spawning activities of mullets or anguillid eels.

11.3.3 Human consequences of lost migratory fisheries

Freshwater fisheries are gaining increasing recognition as an anthropocentric reason to conserve migratory fishes (Beard *et al.*, 2011). Migratory species constitute a large proportion of inland fish catch in many regions of the world, the loss of which can have significant nutritional, economic and social consequences. Reliable global data on the magnitude of fishery catches is lacking for potamodromous and amphidromous species, but 360,000 T of diadromous fishes were caught in 2010 (~5% of total inland catches; FAO, 2012). Riverine catches of diadromous species represent the bulk of reported harvest for many temperate nations: > 80% each for the USA, Canada and Russia. Diadromous catches are lower in tropical nations where rivers are the more productive habitat, peaking at ~10% for Bangladesh and ~7% for India. Although limited data quality precludes any strong conclusions, tropical diadromous species – most of which are catadromous or amphidromous – may simply not produce enough biomass from any single river to support a major fishery. Low catadromous fish catches could also reflect historical overfishing. In the case of anguillid eels, for example, culinary traditions in many cultures motivate continued fishing pressure even as eel populations become increasingly endangered (Crook, 2010).

Available data from select inland fisheries indicate that potamodromous species comprise a large proportion of catches. For instance, 40–70% of the fish biomass harvested from the Mekong River basin is believed to be migratory species (Barlow *et al.*, 2008; Baran & Myschowoda, 2009), most of which are potamodromous. With the Mekong's annual fishery valued between $4.3 and $7.8 billion on retail markets (Hortle, 2009), the loss of these migrations would be economically devastating. Moreover, river fisheries provide up to 80% of animal protein consumed by people in the lower Mekong; hence, declining migrations could create a crisis in food security. These Mekong data highlight the high stakes involved in migratory fish conservation even from a strictly human perspective, and additional examples exist throughout the world (Limburg & Waldman, 2009; Welcomme *et al.*, 2010; Beard *et al.*, 2011).

Despite their dire consequences for migratory fishes (e.g. Agostinho *et al.*, 2008), new dams are under development for the mainstem and large tributaries of rivers that support many of the world's greatest freshwater fisheries (Kareiva, 2012). Even as dam removals begin to outnumber dam construction projects in North America and Europe, many additional large dams are proposed for rivers in Asia, Africa and South America where migratory species represent a major portion of the fish fauna (e.g. Ziv *et al.*, 2012; Finer & Jenkins, 2012). For example, channel obstruction by the Three Gorges and Gezhouba dams on the Yangtze River in China is blamed for endangerment of the anadromous Reeve's shad, Chinese sturgeon, Yangtze sturgeon and the now-extinct Chinese paddlefish (Dudgeon, 2010). Estimates from a variety of tropical rivers suggest that the contribution of potamodromous species to fisheries is disproportionately high compared to their richness (Welcomme, 1985; Carolsfeld *et al.*, 2004; Ziv *et al.*, 2012). Unfortunately, reliance of local people on fish migrations as a low-input, low-cost source of protein sometimes seems to be overlooked in evaluating proposals for new dams.

Reservoir fisheries are often cited as compensation for the adverse impacts of dams on riverine fishes (e.g. Costa-Pierce, 1997), but losses of migratory fisheries caused by dams may rival or exceed the reservoir yields that have been gained. For example, average diadromous catches reported by FAO for the last 10 years (FAO, 2012) exceed aggregate yields estimated for reservoirs in India, Russia and many other Asian and European countries, signifying that all of these reservoir fisheries together could not compensate for loss of diadromous catches (Reidy

Liermann *et al.*, in preparation). Unfortunately, our ability to quantify the human consequences of lost migratory fisheries is limited by lack of high-resolution catch data, especially in developing nations (Welcomme *et al.*, 2010). Despite recent calls for economic and nutritional valuation of inland fisheries (Beard *et al.*, 2011), lack of worldwide mapping and valuation of migratory fisheries precludes understanding of the full ramifications of their loss.

11.4 SOCIETAL DIMENSIONS OF CONSERVATION

Keeping in mind the diverse rationales for conserving migratory fishes, we now turn to the societal considerations that influence conservation actions. Some of the most complex decisions involve weighing the costs and benefits of dams and road crossings, which directly serve human interests. Spatial prioritisation methods (see Moilanen *et al.*, 2009) can be used to balance conservation and societal needs when selecting dam and road crossing remediation projects as well as the placement of new structures. In contemplating barrier removals, decision makers must also account for legitimate ecological costs arising from species invasions and chemical pollutants. Finally, conservation approaches developed for one taxon or environmental setting are often applied much more broadly, sometimes with disappointing or even negative results. We conclude this section by discussing the importance of tailoring conservation efforts to the local migratory fauna.

11.4.1 Managing dams – old, new and impending

After millennia of dam construction to serve societal needs (Chapter 4), two contrasting outlooks have emerged among nations of the world, each having distinct implications for conserving migratory fishes. In countries that had built many large dams by the mid-twentieth century, there is an accelerating trend towards decommissioning and removing dams that is driven by financial, safety and environmental concerns (Stanley & Doyle, 2003). Many of these dams have reached an age at which maintenance costs rival or outweigh costs of removal (Doyle & Havlick, 2009). Amplifying cost issues are regulatory shifts; for instance, the European Union's Water Framework Directive mandates sustainable management of river networks, including free passage of migratory fishes and environmentally sensitive flow regimes (Acreman & Ferguson, 2010). In the USA, the Federal Energy Regulatory Commission (FERC) is

increasingly addressing obstruction of migrations for endangered species, even requiring complete dam removal in a few cases. For instance, in 1997 FERC mandated removal of a 160-year-old dam at the mouth of the Kennebec River in Maine with the goal of restoring habitat access for seven species of anadromous fishes, including the endangered shortnose sturgeon (Bowman, 2002). Shortnose sturgeon numbers are now rising in the Kennebec River (Bain *et al.*, 2007), and FERC has subsequently required the removal of two large dams on the Elwha River in Washington to restore breeding habitat access for endangered anadromous salmon (Brenkman *et al.*, 2012). The wave of dam removals in North America and Europe is likely to expand in the coming years (Chapter 4).

Most developing countries exhibit a very different outlook on dam projects; new hydropower dams are seen as essential for meeting projected electricity and irrigation demands as their populations and standard-of-living increase. In many of these regions, new hydropower generation is likely to impose high costs on diverse assemblages of migratory fishes (Chapter 4). For example, dams in China's Yangtze River have eliminated access to over 99% of the historical spawning grounds of the anadromous Chinese sturgeon, which is critically endangered (Wang *et al.*, 2012). Proposed dams in Brazil and Southeast Asia would carve up the two most species-rich rivers on earth, the Amazon (Finer & Jenkins, 2012) and the Mekong (Ziv *et al.*, 2012), where migratory species are both diverse and essential for fisheries.

There is emerging consensus within the conservation community that successfully protecting and restoring freshwater fish migrations will require adaptive management, using lessons learned from previous dam projects to inform those currently underway (Beck *et al.*, 2012; Kareiva, 2012). In most developed nations, decades of research provide guidance on best practices and needed regulations; acting on this knowledge could allow protection and recovery of many migratory fishes. Unfortunately, in the tropical rivers that are home to many more species, we generally lack a full accounting of the number and biomass of migratory fishes, let alone an understanding of their lifelong habitat needs, migration phenology and contribution to human food security. Without such data, the full consequences of dams for migratory fishes are difficult to predict beyond the basic generalisation that losses are likely. Nonetheless, incomplete information does not justify overlooking the societal and environmental implications of new dams; while some projects will deservedly pass muster, environmental impact assessments

should be required to account for lost migrations and fisheries, useful lifetime of reservoirs and long-term maintenance costs.

11.4.2 Prioritising restoration and conservation efforts

In this era of simultaneous barrier removals and construction, efforts to safeguard migratory freshwater fishes while giving due consideration to sociopolitical and economic issues can benefit from quantitative tools that identify cost-effective strategies. Spatially explicit prioritisation methods (Moilanen *et al.*, 2009) can be tailored to identify locations where removing dams or road culverts would maximise gains in fish habitat access throughout a river network, or where the placement of new barriers would have minimal effects on habitat connectivity. For both removals and additions of barriers, prioritisation analyses should consider economic costs, site-specific social and political factors, and the distribution of resident and migratory species (Kuby *et al.*, 2005; Kemp & O'Hanley, 2010; Null & Lund, 2012). Such multifactor decision-making scenarios are complex, and realistic recommendations often require more input data than are available (e.g. Kuby *et al.*, 2005). Nonetheless, decision support software is becoming ever more accessible and powerful, reducing the logistical barriers to exploring quantitative prioritisation approaches (Chapter 14).

As with other aspects of migratory fish conservation, data availability is a major constraint on the prioritisation of barrier management strategies. For large river basins, lakes or coastal regions, mapping the locations of dams and road culverts can be daunting because georeferenced data are often unavailable or require labour-intensive collation and refinement (Januchowski-Hartley *et al.*, 2013). Even after locating all potential barriers to migrations, assessing their passability to particular species can be a challenge (e.g. Pepino *et al.*, 2012). Bridges (fully passable) and tall dams (completely impassable without specialised passage structures) are end-members of the passability spectrum, and most small dams and road culverts are somewhere in between. In many cases, detailed field surveys are required to determine whether particular fishes can move through these smaller structures. The passability of a structure depends on its size and construction details (e.g. baffles to create low-flow zones), the local environmental context (e.g. stream gradient), hydrological conditions during the migration season, and the fish's swimming abilities (Kemp & O'Hanley, 2010). With data from a representative subset of barriers, it is possible to calibrate models that

predict the passability of additional structures based on readily derived variables such as landscape slope and stream size (Januchowski-Hartley *et al.*, 2014).

To supplement data on the location and passability of each structure, quantifying the amount of upstream habitat and the costs of alternative barrier removal actions can facilitate restoration prioritisation (Kuby *et al.*, 2005; Kemp & O'Hanley, 2010). Spatial data on the distribution of historical and present-day habitats both up- and downstream and the ecological condition of these habitats can be difficult to find. However, coarse spatial data on landscape stressors or other proxies can be substituted for field data on actual stream habitat condition when necessary (e.g. Hermoso *et al.*, 2011; Linke *et al.*, 2012). Explicit consideration of economic costs and political constraints will, in most cases, yield more cost-effective recommendations than prioritisation analyses that do not account for these real-world issues (e.g. Carwardine *et al.*, 2008; O'Hanley, 2011). Unfortunately, data on economic and political constraints are usually even scarcer than ecological data. Thus, methods for estimating these factors and incorporating them into spatial prioritisations and conservation planning remain a growing area of research. Even if truly comprehensive analyses are not possible, accounting for at least a subset of the factors outlined above can boost conservation effectiveness compared to *ad hoc* selection of remediation projects (Kuby *et al.*, 2005; Kemp & O'Hanley, 2010).

For migratory fishes, the value of spatial prioritisation analyses derives from the facts that there are typically more potential barrier remediation projects than society can pay for, the costs and benefits of individual projects vary widely, and gains from each project are contingent on other projects undertaken within the same river network (Chapter 14). Initial efforts could focus on barriers that no longer serve any identifiable purpose for society (low social cost) or are cheap to remove (low economic cost), as these targets often engender minimal trade-offs (Stanley & Doyle, 2003; Doyle & Havlick, 2009). However, low-cost projects may not be worth including in an overall restoration portfolio if they only make a small amount of habitat accessible. For example, there may be little habitat gain from removing dams or culverts lying above or just below a large dam. Moreover, a series of dams, weirs and road culverts along a river channel can collectively block most migratory fishes even if each structure is partially passable when considered alone (O'Hanley, 2011; Neeson *et al.*, 2015). Spatial prioritisation models can be designed to account for these fish-oriented factors while also balancing economic

costs, political complexity, diverse management objectives and stake-
holder attitudes toward both fishes and barriers (Johnson & Graber,
2002). As a result, prioritisation models have become an invaluable tool
for selecting portfolios of restoration projects that could conserve migra-
tory fishes in a cost-effective way (e.g. Kuby *et al.*, 2005; Null & Lund,
2012; Ziv *et al.*, 2012; Neeson *et al.*, 2015).

11.4.3 When not to remove barriers: containing invasive species and pollution

River networks are managed for many values other than fish migra-
tions, and even from a conservation perspective there are sometimes
ecological reasons to retain existing barriers despite their detrimental
effects on migrations (Stanley & Doyle, 2003; Jackson & Pringle, 2010;
McLaughlin *et al.*, 2012). Foremost among these are cases where bar-
riers prevent the movement up- or downstream of invasive species
that have arrived at the site after the barrier was put in place. Potential
invaders are sometimes migratory species themselves, as in the case of
potamodromous sea lampreys in the North American Great Lakes or
anadromous Atlantic salmon that have escaped from aquaculture facil-
ities on the Pacific coast of Chile. In such situations, creating facilities
where all migrating fishes are trapped and then invaders can be culled
may be a feasible – albeit costly – option. This approach relies on swim-
ways or lift systems to route fish into a holding area where screening
allows passage of only the desirable species. The US Fish and Wildlife
Service has used such 'trap-and-sort' facilities to control sea lampreys
for decades in tributaries of the Great Lakes (Klingler *et al.*, 2003), and
lift systems have become common at hydropower dams on large rivers
worldwide even though their effectiveness at native fish passage is ques-
tionable (Brown *et al.*, 2013). Automated sorting has not yet been feas-
ible, but might one day facilitate selective upstream passage, although
the challenge of downstream passage for adults and fry would remain.

In specific cases, semipermeable barriers can enable upstream
migrations by select fishes while blocking unwanted species. The sea
lamprey control programme in the Great Lakes again exemplifies this
approach; seasonal barriers have been used at some sites, while others
use permanent low-head dams to block lampreys but allow salmonids
to pass (Lavis *et al.*, 2003). The latter approach embodies a very specific
value system; exotic Pacific salmon are able to leap small dams readily,
while both invasive sea lampreys and a wide variety of native migratory

fishes (catostomids, percids, esocids) are denied access (Velez-Espino *et al.*, 2011). Interestingly, eel-ladders designed to enable catadromous anguillid eels to overcome barriers are now being tested as another selective means of trapping invasive sea lampreys (Lavis *et al.*, 2003).

Perhaps more common are situations where anthropogenic barriers limit range expansions by non-migratory invaders, giving management agencies pause when assessing restoration projects (McLaughlin *et al.*, 2012). Invasive species are often talented dispersers, and removing a dam or other barrier may open up a large amount of new habitat to them. The feared invader usually occurs downstream, where it is poised for upstream expansion into a river network upon removal of a barrier (e.g. Fausch *et al.*, 2009). Problematic invaders include more than just fishes; parasites and diseases may also be of concern when barrier removals would open new routes for infection to spread (McLaughlin *et al.*, 2012).

Downstream and upstream movement of chemical contaminants is another major ecological concern when considering barrier removals (Jackson & Pringle, 2010; McLaughlin *et al.*, 2012). In industrialised countries, the most common worry is downstream release of sediments contaminated with toxic chemicals (e.g. metals, polychlorinated biphenyls) as a legacy of historical pollution. In addition, trapping sediment behind dams can foster nitrogen removal through denitrification, thereby alleviating nitrogen-loading in agricultural landscapes (Powers *et al.*, 2013). Moreover, migratory fishes have a unique capacity to serve as an upstream vector for contaminants. For instance, salmon bioaccumulate toxic chemicals while feeding in the ocean and the North American Great Lakes, and subsequently boost concentrations of these toxins in stream biota when they die after spawning (e.g. Baker *et al.*, 2009; Janetski *et al.*, 2012). Thus, fish migrations themselves can complicate contaminant containment strategies by carrying pollution against the current, particularly when semelparous species are involved.

How should we balance these concerns against the benefits of restoring fish migrations when considering barrier removals? The negative effects of dams and road culverts on migratory species have often been deemed less pressing than the benefits of preventing the spread of invasive species or contaminants, particularly when no gamefish species are at stake. In reality, these are complicated scenarios that involve multiple hypothetical elements and implicit value judgements that are rarely discussed fully and openly. Thus, it is understandable that the spectre of spreading invasive species and contaminants could trump the potential benefits of restored fish native fish migrations, favouring

the maintenance of existing barriers. For a case study of a structured decision-making approach to this type of scenario, we recommend the US Fish and Wildlife Service's pilot analysis of barrier removal options in the Bad River, a tributary of Lake Superior (Patronski *et al.*, 2009). In that example, the status quo of barrier maintenance was favoured after considering a wide variety of alternatives. Unfortunately, we are not aware of any quantitative analyses at regional (or larger) scales for which data were available on both conservation benefits (e.g. Northeast Aquatic Connectivity Project; Martin & Apse, 2011) and conservation costs of barrier removals, let alone an analyses that also incorporates economic and social management objectives at large scales.

11.4.4 Clarifying our values: what species are we managing for?

Designing sensible conservation strategies for migratory fishes must begin with specifying what species we are managing for, because the benefits of particular restoration or protection efforts will vary among species. In rivers, lakes and oceans with numerous freshwater migratory species, a broad range of life-history strategies, migration phenologies and habitat needs are invariably present. Despite this diversity, management usually focuses on a subset of species that have high commercial and recreational value. This tacit value judgement is rarely discussed openly, yet it can direct barrier management, technological research investment and field assessments towards these select species, potentially to the detriment of other migrants.

In North America and Europe, the bias has often been toward salmonid-centric management of barriers unless endangered status gives special priority to other taxa. For instance, the largest dam removal projects in the USA have focused on coastal rivers where Pacific salmon (Elwha River, Washington) or Atlantic salmon (Kennebec River and Penobscot River, Maine) are the focal beneficiaries, although other diadromous species may also profit (Limburg & Waldman 2009). Operators of large dams have made modest shifts in many countries toward 'environmental flows' that better replicate the timing of high and low flows during an annual cycle (Bunn & Arthington, 2002; Poff *et al.*, 2007), but major experiments in restoring natural flow regimes have rarely targeted migratory fishes explicitly.

Mitigating the impacts of dams on migratory fishes often focuses on development of passage structures, but this substantial literature deals primarily with salmonids (Roscoe & Hinch, 2010; Katopodis &

Williams, 2012). Unfortunately, the design parameters of fishways for salmon, which are unusual in both their athleticism and semelparity, are a poor match to the needs of other migratory species found in the same rivers (Stuart & Mallen-Cooper, 1999; Agostinho *et al.*, 2007; Mallen-Cooper & Brand, 2007). In the Columbia River basin, declines of the once-abundant anadromous Pacific lamprey reflect the incompatibility of their anguilliform swimming mechanics with the fast, turbulent flows that attract salmon (Moser *et al.*, 2002). Failures of salmon-oriented fishways have been so profound for American shad, which were once a dominant anadromous migrant in eastern North America, that dam removals have been suggested as the only viable restoration approach (Brown *et al.*, 2013). Despite these shortcomings, salmon passage technology has been used in many rivers where no salmon – or even ecological analogues of salmon – are present (e.g. Figure 11.3), leading to a variety of failures worldwide (Mallen-Cooper & Brand, 2007). Comparatively high migratory biomass, species diversity, variable hydrology and floodplain extent in tropical rivers distinguish their fish passage challenges from those of temperate coastal rivers (Oldani & Baigún, 2002; Pelicice & Agostinho, 2008; Baumgartner *et al.*, 2011). Addressing all of these issues using a single structure for upstream and downstream passage represents a formidable challenge (Godinho & Kynard, 2008), but is essential as major new dams are being planned for many tropical rivers.

A parallel overgeneralisation of salmonid results to other migratory fishes may apply to concern about contaminant transport. Most of the published papers on this topic address semelparous salmonids as vectors. While salmon are indeed ideal bioaccumulators by virtue of their large body size, piscivorous diet and lipid-rich tissues, they are also unusual among migratory species in being semelparous. Iteroparous migrants are less likely to introduce substantial quantities of bioaccumulated chemicals to their breeding grounds, both because they do not die after spawning and because they are generally lower in tissue lipids and create smaller eggs (which can concentrate lipophilic compounds) than salmonids. Thus, the evidence supporting fears about the delivery of toxic chemicals by migratory fishes applies primarily to coastal drainages where semelparous salmonids are native, as well as the introduced ranges of Pacific salmon in the North American Great Lakes, southern South America and New Zealand (Correa & Gross, 2008) and Atlantic salmon in western Canada, Chile and Tasmania (Thorstad *et al.*, 2008). Further research is needed to determine whether contamination

Figure 11.3 Pak Moon Dam fish ladder in Thailand. Spanning the Mun River just 5 km upstream of its confluence with the Mekong River, the Pak Mun Dam has been named among the world's most ecologically and socially damaging hydropower projects. To bypass the dam, fish must swim through a minimum of 44 baffles, which requires a climb of 15 vertical metres across a 92-m horizontal distance (i.e. a 16% grade). Few potamodromous species have been reported to successfully traverse the ladder, which was modelled after ladder designs for anadromous salmon. Photo: Aaron A. Koning.

concerns apply equally to the iteroparous species that constitute the majority of the world's migratory fishes.

We believe that a broader value system is requisite to conserving migratory freshwater fishes. If management and conservation efforts focus primarily on species with direct economic value derived from recreational and commercial fishing, we are likely to see continued erosion of the world's ichthyofaunal diversity even if priority fisheries remain stable. Low economic value should not be equated with low conservation value as we attempt to manage new and old barriers, minimise degradation of water quality and quantity (Vörösmarty *et al.*, 2010; Carpenter *et al.*, 2011) and limit overfishing (Allan *et al.*, 2005). Rather, conservation strategies should be designed to meet the requirements of all migratory species in an area. The resulting efforts are unlikely to conflict with the needs of non-migratory species, and applying a more

inclusive value system to migratory fish conservation efforts will ultimately benefit most freshwater species through greater habitat protections and improved analytical tools (Kemp & O'Hanley, 2010).

11.5 FUTURE RESEARCH DIRECTIONS

Much work remains for both researchers and practitioners interested in conserving migratory freshwater fishes around the world. While successes may not always be cheered by the public at large, our review indicates that fish migrations provide diverse benefits to species, ecosystems and humanity. The metapopulation structure of migratory species means that conserving each local population also contributes to species persistence at larger spatial and temporal scales, as well as buffering regional fishery potential (Schindler *et al.*, 2010). The future of migratory fishes and their contributions to ecosystem functioning and human well-being will depend on forward-looking policies as well as management informed by past lessons and ongoing research.

We conclude by touching on four issues that we believe are especially important for advancing conservation research on migratory freshwater fishes. First, it is imperative that the development of fish-passage technologies – ladders, lifts, bypass channels, and the like – address a wider range of fish species and background hydrologies (Roscoe & Hinch, 2010; Baumgartner *et al.*, 2011), as well as tackling downstream passage in addition to upstream access. We must avoid unthinking extrapolation of lessons from one region or taxon to others. Instead, a concerted effort is needed to engage the hydropower industry, water users, government regulators and conservation organisations in testing fish-passage methods in each region where new dams are contemplated or existing ones fail to demonstrate adequate passage. Developing efficient passage structures for a diversity of migratory fishes will surely be challenging and expensive (Lucas & Baras, 2001; Bunt *et al.*, 2012; Thiem *et al.*, 2013), and will require engineers to 'think like a fish' to match their approaches to the traits of the migratory fauna at a given site (Williams *et al.*, 2012). After commissioning, the ability of these structures to effectively pass migrants should be evaluated against a standard of maintaining viable populations of all migratory species (da Silva *et al.*, 2012; Pompeu *et al.*, 2012). This approach could encourage local adaptive management at a particular dam as well as fostering the transfer of effective designs to projects elsewhere in a judicious manner (Bunt *et al.*, 2012; Katopodis & Williams, 2012).

Second, major conceptual and practical challenges arise from the fact that many fish migrations encompass multiple ecological and political zones. Conserving migratory populations requires large-scale habitat protections and fishery regulations supported by coordinated actions, incentives and funding across agencies and interest groups (Alvarez-Romero *et al.*, 2011; Pracheil *et al.*, 2012). We must also recognise that the condition of key habitats is itself a reflection of numerous stressors, each of which may be driven by multiple human activities occurring across disparate spatial scales (e.g. Vörösmarty *et al.*, 2010). Thus, improving habitat quality for migratory fishes will often necessitate actions beyond the migration corridor itself. Attribution of responsibility for population declines is complicated by the triple-jeopardy nature of migratory life histories. For instance, low returns of chinook salmon from the Snake River compared to populations downstream have been attributed to mortality at hydroelectric dams during outmigration, but poor survival in the marine realm may in fact be responsible (Rechisky *et al.*, 2013). Identifying the bottlenecks that limit rehabilitation of migratory fish populations is an essential step, but causality is often contentious. Ultimately, successful conservation at appropriate spatial scales will often require interjurisdictional political agreements that account for the key details of species ecology, threats arising from diverse sources and social and economic considerations. As researchers, we must be prepared for long-term engagement in this complex process.

Third, we see an important role for basic research on the significance of the iteroparity–semelparity and diadromy–potamodromy life-history spectra for conservation strategies. For instance, no theoretical models or meta-analyses have addressed whether anthropogenic pressures more strongly affect species showing one life history compared to others. Natural selection favours semelparity when adult mortality is high but juvenile mortality is low (Crespi & Teo, 2002), whereas iteroparity is advantageous when adult survival is high but juveniles have low odds of survival. To the extent that migration barriers, fisheries and other factors boost mortality of adult migrants without affecting young fish, humans may be selecting for semelparous species or for maximal reproductive investment by first-time breeders within iteroparous species (Crespi & Teo, 2002). Conversely, if degradation of spawning or nursery habitats affects juveniles but not adults, then long-lived iteroparous species may perform best. With regard to migrations between freshwater and saltwater, landlocked populations of at least a few diadromous species have arisen due to

strong selection pressure by dams (e.g. Tsunagawa & Arai, 2009) and pollution (e.g. Bleackley *et al.*, 2009), and growing evidence of natural plasticity in migratory behaviour (e.g. Feutry *et al.*, 2012; Hogan *et al.*, 2014; Huey *et al.*, 2014) suggests that many diadromous species have the capacity to adjust their migration strategy. Anadromous salmonids also show fishery-induced evolution in a variety of traits (Hard *et al.*, 2008). Potamodromous species can experience reduced gene flow and population differentiation due to barriers between habitats (e.g. Wollebaek *et al.*, 2011) and intensive fisheries can drive large shifts in body size (e.g. Taylor *et al.*, 2006), and perhaps even favour loss of migratory behaviour (Theriault *et al.*, 2008). In each of these cases, elucidating differences among life-history strategies in their effect on susceptibility to anthropogenic stressors could help direct conservation efforts toward species and regions that are most at risk.

Finally, climate change research represents an essential frontier in the conservation of migratory fishes. Migrants may be strongly affected by climate change through shifts in phenology, habitat suitability and connections between habitats. Migrations are closely tied to seasonal environmental cues such as water temperature and discharge, which reflect regional climate. Shifts in migration phenology have already been attributed to climate change for a variety of species including shad, Pacific salmon (Quinn & Adams, 1996), Atlantic salmon (Juanes *et al.*, 2004), northern pike and smelt (Ahas & Aasa, 2006). Whether these phenological shifts reflect successful tracking of changes in the optimal timing of migrations, or instead turn out to be maladaptive, remains unclear. Migrations are timed to maximise resource availability or reduce mortality based on long-term averages of environmental conditions (Quinn & Adams, 1996); hence, the growth or reproductive success of migrants may be depressed when cues in one habitat that trigger the onset of migration become misaligned with the timing of optimal conditions in the destination habitat (Visser & Both, 2005). In some cases, the very existence of key habitats (e.g. floodplains) and the passability of corridors connecting them may be affected by altered precipitation patterns under climate change. For example, amphidromous Hawaiian gobies migrate from the ocean into streams whose hydrology fluctuates wildly between low baseflow and flood events (Radtke & Kinzie, 1996). Many of these streams already suffer reduced flow due to stream diversions for human use (Brasher, 2003), and recent and projected reductions in rainfall across the Hawaiian archipelago are likely to both reduce stream habitat and diminish migration corridors providing access to headwaters
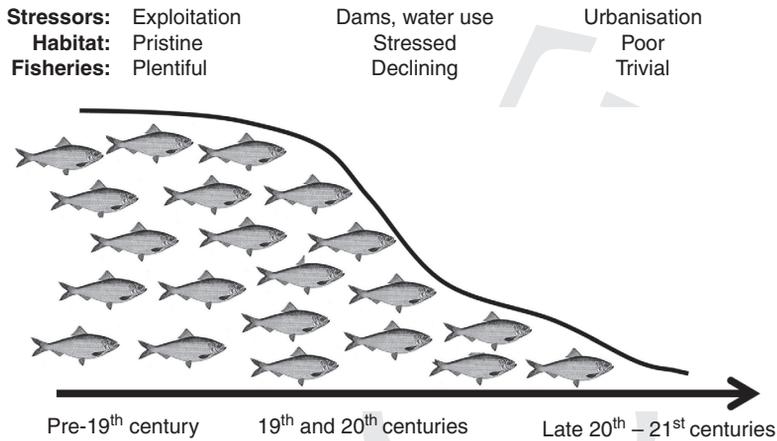
Stressors:	Exploitation	Dams, water use	Urbanisation
Habitat:	Pristine	Stressed	Poor
Fisheries:	Plentiful	Declining	Trivial

Pre-19th century   19th and 20th centuries   Late 20th – 21st centuries

Figure 11.4 Historical overview of declines in diadromous fishes of northeastern North America. Fisheries drove initial population declines, followed by habitat degradation and loss, and finally further habitat loss and climate change. Throughout this process, loss of institutional and societal memory about the past abundance and importance of migratory fish complicates setting conservation goals. This diagram is adapted from Limburg and Waldman (2009), with permission from Oxford University Press.

(Walter *et al.*, 2012). Taken together, shifts in migration phenology, habitat availability and connectivity under ongoing climate change are sure to complicate efforts to conserve migratory freshwater fishes, necessitating an adaptive approach to management (see Stein *et al.*, 2013).

As researchers and practitioners work together to resolve these and other challenges in conserving freshwater fish migrations, the perceptual problem of shifting baselines cannot be ignored (Humphries & Winemiller, 2009; Limburg & Waldman, 2009): remembering (or even imagining) the benefits of substantially larger fish migrations during a bygone era is difficult (Figure 11.4). This limitation of human perspectives undermines conservation efforts of all sorts, but neither decision makers nor the public can be faulted for it when we are frequently reminded that invasive species, habitat destruction, diseases and other changes make ecosystems of the past unrecoverable. To combat the shifting baseline challenge, we should continue to make use of iconic migratory fishes such as Pacific salmon as standard-bearers, but also doggedly highlight the fact that substantial fish migrations once occurred annually in rivers close to home for almost everyone. Broadening awareness of long-term declines, ecosystem importance and fisheries benefits of migratory fishes is essential for sustaining remaining migrations and

restoring those that have been lost. Overall, we are optimistic that the ongoing expansion of both public appreciation and scientific expertise will enable more effective conservation of migratory freshwater fishes worldwide.

11.6 DISCUSSION QUESTIONS

1. How many migratory fish species are in your area, and which major classes of migration do they represent?
2. Which is the most common barrier to fish migrations in your area: dams or road culverts?
3. Is it more problematic to inhibit adult fish from reaching upstream spawning grounds, or young fish from migrating back downstream?
4. When both desirable native fishes and harmful invasive species are migratory, which should have priority in management efforts?
5. How can we compare the ecological benefits of restoring migrations to the economic costs of removing barriers and improving habitats?
6. What would happen to sport fisheries if migratory fishes continue to be extirpated? How about subsistence fisheries?

11.7 ACKNOWLEDGEMENTS

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