# MIGRATION IN FISHES

Animal migration is an amazing phenomenon that has fascinated humans for long. Many freshwater fishes also show remarkable migrations, whereof the spectacular mass migrations of salmonids from the spawning streams are the most well known and well studied. However, recent studies have shown that migration occurs in a range of freshwater fish taxa from many different habitats.

We now know that migration is a ubiquitous feature in the life cycle of an extremely diverse range of animals, from microscopic crustaceans to large, sea-dwelling mammals. Migration in freshwater fishes was previously thought to be relatively rare, as most fish species were considered to be largely sedentary and showing only limited local movement. Notable exceptions to this historical view are of course the salmonids, many of whom make spectacular and highly visible migrations from the sea to their natal habitat, leaping up waterfalls, and congregating in great numbers to spawn in mountain streams. The migratory behaviour of salmon is also the best-studied example of freshwater fish migration.

Evidence now shows that fishes from almost all freshwater habitats and from all ecological niches make migratory movements at a range of spatial and temporal scales. Understanding patterns of freshwater fish migration is also pertinent in fisheries management, as many commercially important fishes, such as salmonids, are migratory. Furthermore, fish are major players in aquatic ecosystems, and hence, the synchronized movements of often thousands of individuals between habitats can potentially have profound impacts upon ecosystem dynamics

**Types of migration**

Migratory strategies in nature are diverse, and perhaps especially so among the fishes. Migratory diversity can be addressed in a number of ways, and one can categorize types of migration by function, habitat, and temporal scale or by patterns of movement of the animals themselves. In previous reviews, migration in fishes has mostly been categorized by function, whereby fish migrate to spawn, take seasonal refuge from predators or adverse environmental conditions, or to feed. Spawning migrations are seasonal and most likely evolved in scenarios whereby the optimal habitat for growth and survival differs between juveniles and adults. Many freshwater fish undertake spawning migrations, for example, the nase (*Chondrostoma nasus* that migrates from rivers into tributaries to spawn. There are also examples in the literature of refuge migrations, where individuals migrate to reduce the risk of predation, often at times of the year when growth potential is reduced. Fish can also migrate to refuge from seasonally adverse environmental conditions, such as low temperature or oxygen. Finally, feeding migrations are common when food resources fluctuate in a predictable manner across time and space.

A second way to classify fish migration is by habitat. Many fishes migrate between freshwater and marine habitats, which is known as “diadromy”. Diadromy can be further divided by whether a fish migrates from freshwater to marine habitats ("anadromy"), or from marine to freshwater habitats ("catadromy"). Anadromy is thought to be more common than catadromy and is widespread in well-studied groups such as salmonids, which migrate as juveniles from streams to the ocean, returning to spawn often in the same stream where they were born. A classic example of catadromy is the European eel (*Anguilla anguilla* (L., 1758)), which migrates from its natal habitat in the Sargasso Sea to spend its adult life stages in the rivers and lakes of Europe, before making the return journey to reproduce and then die . Migration between two freshwater habitats is known as "potamodromy" and is less well studied. Potamodromous fishes may migrate from lakes to streams, as is the case with roach, common bream (*Abramis brama*, and white bream (*Blicca bjoerkna* , or may make migrations to different areas of river habitats, as do predatory pikeperch (*Sander lucioperca* Finally, fish that migrate between marine habitats are known as "oceanodromous" migrants. While these latter migrations are both fascinating and increasingly studied, they are beyond the scope of our review and we direct interested readers to other reviews on this subject.

Migrations can also be classified according to the temporal scale over which migratory cycles occur. Most freshwater fish migrations are "seasonal", and population movements occur in response to changes to seasonal shifts in food availability, predation risk, or to spawn in habitats optimal for juvenile growth and survival. However, a number of fish species perform migrations at a much smaller temporal scale. "Diel vertical migration", where fish migrate up and down the water column has been shown to occur in a number of freshwater fish species. For example, juvenile Bear Lake sculpin of <30 mm in length spend the day at the bottom of lakes and then vertically migrate 30–40 m to the surface waters during the night. Furthermore, many fish species perform a "diel horizontal migration", where they migrate from the littoral zone of lakes into offshore areas at dusk and then return to the littoral zone at dawn.

A final way of categorizing migratory behaviour in fishes is based upon describing migratory variation between individuals from the same population. "Differential migration" refers to cases where individuals within populations differ in their migratory behaviour in some way, such as in their destination or direction of movement, in their timing, or in their propensity to migrate. For example, it has been shown that male and female salmon differ in the timing of their migration to the sea, and some males may even stay the whole life cycle in the natal stream, adopting an alternative life-history strategy. Variation in the destination of migratory fish has been shown in populations of roach migrating seasonally from shallow lakes into connected streams during winter. Migratory roach from Lake Krankesjön in southern Sweden migrated into different streams, and for many individuals their destinations were consistent over a number of years. There are also many examples of fish populations that do not migrate in their entirety, a phenomenon known as "partial migration". Recent reviews highlighted that partial migration is widespread in freshwater fishes and that many populations are composed of a mixture of migrant and resident individuals.

## Which species migrate?

Migration has been increasingly documented in a diverse array of families of freshwater fishes. Besides the iconic examples of salmonid and eel migration, we now know that species from many other taxa also show migratory behaviour. Among the cyprinids, for example, a group that were until only recently thought to be mostly sedentary in their movements, migration between lakes and streams has now been reported in white bream, common bream, and roach. Anadromy has also been documented in this group. There has also been some geographical bias in studies of fish migration, meaning that most research focus has been directed to European and North American freshwater fishes. As studies proliferate in the tropics and in the southern hemisphere, the prevalence of migration in freshwater fishes becomes increasingly obvious.

Given that migration is so widespread among freshwater fishes, it appears that there are few phylogenetic constraints on the evolution of this fascinating behaviour. From an evolutionary perspective, migration has evolved as an adaptive strategy to maximize individual fitness, as individuals migrate to increase their growth, survival, or reproductive success. In the following section we discuss the ecological factors that play a role in the evolution of freshwater fish migration. We of course acknowledge that studies on salmonid migration have been instrumental in our understanding of migration in fishes and, hence, any review of the migration of freshwater fishes has to rely heavily on research performed on this group. However, we will try to add to the picture by also including studies on other taxa, to increase generality, but also because of our own research bias towards migration in cyprinids.

## Adaptations for migration

For a diverse array of animals, migration constitutes one of the most demanding events in the life cycle. To cope with the hardships during their arduous journeys, migrants parade an impressive suite of fine-tuned adaptations that act in concert to promote migratory behaviour. Many morphological, physiological, and behavioural traits correlated with migratory behaviour seem to be shared across migrants as diverse as birds, fish, and insects

### 3.1.Orientation

Many freshwater fishes show complex migration patterns, as described above. This can be exemplified by salmon that migrate to sea as juveniles and then return to freshwater habitats to spawn, in many cases to the exact stream, and even stretch within the stream, where they were born. The return to their native habitat may be regarded as an adaptive behaviour, as they return to a site where spawning obviously has been successful. Homing to native streams also results in low gene flow among neighbouring populations and this allow for the evolution of populations that are locally adapted to the specific environment of their home stream, resulting in, for example, population differences in body morphology. Also, migrating cyprinids show some degree of site fidelity, both during spawning migrations and during winter migrations, but whether this is due to local adaptation or simply individual behavioural consistency is yet unknown. The link between local adaptation and migratory site fidelity could, however, easily be imagined to be a general pattern for many types of fish migrations.

## The genetics of migration

A significant amount of the phenotypic variability in migratory traits in migrating animals is most likely under genetic control, but the genes involved are poorly understood. The classic approach to disentangle the genetic component of behaviours, i.e., local adaptations to specific selective environments, is by performing either translocation or common garden experiments. Such studies have also provided insight into the genetic component of migratory behaviour in freshwater fish. For example, in a translocation experiment migrating individuals of a cyprinid (roach) were moved to an unfamiliar habitat and their behaviour compared with the local population. The majority of fish in the translocated, nonlocal populations initiated their migration several weeks before the majority of the individuals of the local population, indicating a genetic component in the timing of migration in this species. Another example indicating the role of genetics in shaping interpopulation phenotypic differences in migratory behaviour comes from a study on Atlantic salmon.

The development of functional genomics has resulted in a new and powerful tool that could be used to study the genetics behind migratory behaviour. Studies on salmonids have already identified genes with different expression patterns between resident and migratory individuals pre-migration. Transaldolase 1 and endozopine are expressed at lower levels in potamodromous and anadromous individuals compared with resident individuals. In addition, Aubin-Horth et al. (2009) found differences in gene expression between Atlantic salmon males adopting different life-history strategies (for a recent review of alternative migratory tactics in salmonids. Sneaker males, i.e., males that are resident in the stream and become mature at an early age and smaller size, showed up-regulation of genes involved in the endocrine reproductive pathway and in genes associated with learning and memory. In migrating males, on the other hand, genes associated with regulation of thyroid hormones were up-regulated, which was suggested to be a preparation for the transition to the saltwater habitat. There were also differences in gene expression between early- and late-migrating males. Similar results have been found for anadromous and freshwater resident forms of three-spine stickleback. Further, studies on Pacific salmon (*Oncorhynchus* spp.) have suggested that clock genes are involved in determining the timing of spawning (and thus migration) among populations at different latitudes and that variation at this gene is shaped by selection. Gene expression studies can also be used to optimize management decisions as has been convincingly shown by Miller et al. (2011).