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How well do we understand the migratory habitats and needs of freshwater fish?

Mark Everard considers the importance of river, lake and wetland connectivity for freshwater fish migration.

Maybe the term 'migratory fish' conjures images of the weir-leaping salmon or the ocean-wandering tuna.

Amongst British and European freshwater fish, in vernacular but also in some other, more expert, discourse, salmonids have historically been considered migratory with most coarse fish generally overlooked and implicitly assumed not to migrate.

Migration is defined as deliberate, temporally predictable translocation in space. On that basis – spoiler alert – virtually *all* freshwater fish migrate!

Night and day

Many smaller freshwater fish exploit different habitats on a diel (24-hour) basis, adapting to changing conditions. One such example of 'small fry' (young fish rarely longer than 12 cm) is the stone loach (*Barbatula barbatula*), a species of temperate rivers and lakes that tends to live under stones and woody debris by day, emerging to forage for food by night. Studies have shown that foraging activity in stone loach remains significantly higher during the night compared to twilight and daytime even when fish were experimentally starved, and all daytime foraging ceased when a predator was introduced.[1] This diurnal pattern balances feeding requirements with predation risk, especially important for benthic (bottom-dwelling) species with low swimming speeds and therefore low potential to escape faster-moving predators.

Different diurnal habitat use is also observed in larger and more agile coarse fish species. One example is the dace (*Leuciscus leuciscus*), a shoaling, rheophile, lithophile cyprinid fish of moderate size (rarely longer than 30 cm). Radio-telemetry studies of dace recorded diel movements between different, clearly defined daytime and night-time habitats in the summer, with individual dace returning, predictably, to previously occupied locations at dawn and dusk suggesting differential habitat suitability related to light intensity similar in some respects to roosting behaviour in birds.[2] Pike (*Esox lucius*), the principal fish predators of dace, are also known from tracking experiments to migrate on a predictable cycle making use of different habitats by day and night.

Seasonal migrations

It has been widely and long known that many riverine benthic invertebrates with aerial adult life stages undertake upstream flights on emergence, prior to breeding, partially compensating for the downstream drift of eggs and larvae.[3]

It should not then be surprising to learn that many coarse fish also undertake upstream migrations prior to spawning. This may also be to access suitable spawning habitat, such as gravels and vegetation flushed by stronger flows that may be less favourable for the needs of these fish during the rest of the year. Studies on freshwater fish species from a range of families – including roach (*Rutilus rutilus*), perch (*Perca fluviatilis*) and pike – found varying degrees of upstream spawning migrations in rivers or in more favourable locations in lakes, ranging from tens of metres to several kilometres or, in some cases, hundreds of kilometres. Access to better-oxygenated waters that may tend to warm faster than deeper reaches downstream can enable earlier spawning and shorten the hatching time of eggs, resulting in higher survival of resultant juveniles compared to those of fish that spawn lower down in catchments.

Seasonal migrations relate not only to spawning but also to predator evasion. An extensive field telemetry study found that tagged roach commonly migrate from lakes to streams during winter, and that this confers a significant survival benefit from predation by piscivorous birds, specifically cormorants (*Phalacrocorax carbo* spp.), based on recovery of transponder tags found at communal cormorant roosts derived from the fish that these birds had consumed.[4] In this study, roach were found to significantly reduce predation risk from cormorants by migrating into streams; the probability that they were preyed upon by cormorants was positively related to the time individuals spent in the lake during winter.

Fish such as dace and roach are also known to move downstream in autumn and winter, forming aggregations in deeper and slower reaches, even into tidal sections, apparently to evade strong spate flows and to conserve energy in maintaining station in the river.

Lateral migration

The rivers of Britain and lowland Europe, as indeed much of the world, are very far from natural. The lowland rivers in which many fish species evolved would not only naturally meander within wider corridors but, in the absence of widespread human channel reinforcement and floodplain drainage, would evolve as braided systems. As trees fall obstructing existing channels, perhaps through the actions of Eurasian beavers, diverted water would form new channels also sweeping clear floodplain landscapes kept open for some time by the grazing activity of aurochs and other herbivores, though subject to successional processes. Over time, braids would form, reticulating the river corridor with channels of varied flow regimes and creating diverse wetland types. Whilst this type of dynamic, wild landscape may not be fully attainable as a conservation goal in today's highly populated and exploited world, it does nonetheless reflect the needs of fish and other organisms that evolved in landscapes with those characteristics.

A key feature of such a natural historic landscape is connectivity of diverse habitats, including different flow regimes across and between braided channels but critically also laterally to wetlands of various types upon which, in particular, the spawning needs of many species and their juvenile life stages most depend. Yet lateral connectivity not only to rich channel edge habitats but with linked floodplain wetland systems is a rarity in our much drained, farmed, built and otherwise encroached-on floodplains. Many things can be done to soften river edges and floodplains, informed by the spawning, nursery, feeding and refuge needs of fishes. Such changes would also yield wider societal benefits such as enhanced flood and drought buffering, water purification, nutrient and carbon cycling, aesthetic enhancement, and habitat provision for many types of wildlife.[5]

The ultimate canary in the coalmine of the loss of lateral connectivity is the burbot (*Lota lota*), once native to eastern-flowing rivers in England from the Skerne and Esk in the north, down to smaller Norfolk and Suffolk rivers in the south but extinct since around 1970 (the last verified specimen was captured in 1969). A curious fish, the burbot is the only freshwater member of the Gadiformes (the order of cod-like fish), spawning in the cold water of winter. A lazy assumption is that climate change is to blame for its demise, but this is to ignore the ecology of the genetic strain of burbot of small lowland European rivers. The closest genetic match to the extinct British population is with the extant burbot populations in western European rivers. Although burbot are widely distributed across cool freshwaters of the northern hemisphere from Alaska, Canada and some northern states of the USA, across Northern Europe and Northern Asia many of these fish are of larger genetic strains inhabiting still waters and spawning under ice.

Western European fish are not only smaller, but largely riverine and occur where ice lakes are absent, inhabiting lower river reaches as well as upstream trout-type habitat. This smaller, riverine western European genetic strain of burbot consequently spawns in inundated floodplains in midwinter, sometimes migrating up to hundreds of kilometres upstream and then laterally into floodplain wetlands. Typical of other cod-like fish, burbot release a very high abundance of tiny non-sticky eggs – large females can release up to 3.5 million eggs – that then settle in the near-static waters of riparian wetlands. The hatching larvae enter the plankton to grow before metamorphosing into juveniles that embark on a benthic lifestyle that continues into their adult life. To complete their life cycle, riverine burbot need suitable floodplain wetlands that are inundated for at least two months in the winter. It is exactly this landscape that has been virtually expunged from lowland Britain and much of lowland Europe starting from Roman times but completed under aggressive land drainage programmes driven by the overriding food security policy priority following the Second World War.

Fenland, formerly a landscape of around 1,500 square miles that was neither fully wet nor fully dry, now contains just a few hundred hectares of remnant fen. It is no coincidence that burbot also went into precipitous decline in these rivers after long-term decreases in numbers that were also far from coincidentally proportionate with previous land drainage. It is also no coincidence that salmon and sea trout were also lost from these rivers during the same period, although, of course, salmonids, unlike burbot, are able to repopulate from their sea-going phases. The 1950s–1970s was a cool cycle in the climate, further undermining the oft-repeated assumption that climate change was the major culprit.

River habitat restoration has played a key part in the successful reintroduction or recovery of the western European strain of burbot in Belgium, Germany and the Netherlands, at latitudes far further south than the eastern English rivers from which they were lost. There are almost no rivers left in lowland Britain in which floodplain habitats are diverse, connected and inundated for at least two months in winter, though one site is being investigated for a potential British reintroduction. (For more on the ecology and conservation of burbot, see Everard. [6])

In addition to physical survival, habitat loss and fragmentation can have severe impacts on the genetic diversity and, consequently, future population trajectories of freshwater fish.[7]

River connectivity for fish and people

There are costs to fish undertaking migratory behaviours, including energy expenditure in locomotion, reduced foraging opportunities and increased predation risk. Consequently, there must be evolutionary advantages. The 2008 book *Migration of Freshwater Fishes*[8] challenged previously held assumptions that many freshwater fish do not move between habitats based on spatiotemporal variations in their abundance and distribution. In fact, virtually all freshwater fish species regularly move on seasonal or other bases for spawning, feeding and refuge, in many cases in ways that are fundamental for the successful completion of life cycles.

River connectivity matters for all fish for their daily, seasonal, feeding, spawning, nursery, refuge and other needs. This includes both longitudinal connectivity (up and down rivers) as well as laterally (across channels and across the floodplain into connected wetlands). Whilst the EU Water Framework Directive is driving thinking about improving longitudinal connectivity – bypassing or removing weirs and other impoundments that serve no important purpose – lateral connectivity remains a regulatory blind spot. Yet, functional floodplains not only host wide biodiversity, including helping support natural regeneration and diversification of fish populations by catering for the temporally variable needs of their various life stages, but also provide a great richness of wider ecosystem services.[9] In that sense, catering for the migratory needs of fish is far from an altruistic measure; it is responding to an indicator of wider catchment functioning and the wealth of societal benefits that this provides.

We need to know more about the migratory habits and habitat needs of all fish. Most investment to date has been targeted at commercially important species, particularly trout and salmon[10] although there are also some studies of eels, shad and other recognised migratory fish. But, above all, we need to account for these fish in the ways we manage, regulate and incentivise rivers and landscapes as bioindicators of the viability of catchment functioning and the multiple benefits that this confers as a key building block of sustainable development.

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