

Chapter 7

Fish migration and passage in forested watersheds

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Introduction

Fish migration, and the physical, physiological and behavioural necessities to permit passageway through inland waters are all essential to maintenance of many fish populations in forested watersheds. Various conditions associated with deforestation may cause severe difficulties in migration or passage. Migratory behaviour itself has the potential to make fish populations vulnerable to passageway problems (Groot 1982). Evidence supporting these views has been mounting for decades in salmonid fishes in North America and Europe, but now is becoming recognized in freshwater fish populations of South America, the Antipodes and elsewhere (Northcote 1998).

Our purposes here are to (1) define the process of fish migration in inland waters, (2) outline the types and patterns of fish migration with examples from temperate and subtropical or tropical areas, (3) discuss briefly the sensory mechanisms involved in migration, (4) review the physiological capabilities, behavioural tactics and energetics of fish in migration, and (5) discuss the difficulties for fish in surmounting passageway problems, upstream and downstream, resulting from natural and forestry-related obstructions and barriers.

Fish migration defined

There are four essential features of fish migration: (1) individuals cyclically alternate between at least two separated habitats (spawning and feeding) and often three or even more (see Fig. 1 in Northcote 1997); (2) the alternation between habitats occurs with a reasonably predictable sequence; (3) a large fraction of any given population participates in the migratory stages of the life cycle; (4) at some stage the migration occurs as an active, directed movement although it may occur as a passive drift downstream for other stages. The most common migratory phases can be categorized as trophic migrations to feeding habitats, refuge migrations to survival habitats used during periods of severe environmental conditions (e.g. overwintering or oversummering in temperate or arctic regions), and reproductive migrations to spawning habitats. Together they complete the migratory cycle, given elsewhere in more detail (Northcote 1978, 1984, 1991, 1997: Fig. 1).

Types and patterns of migration

Interest in the descriptive aspects of fish migration has produced a plethora of terminology, some of which must be presented before delving into more fundamental features relevant to fish-forestry interactions. Much of it hinges around the origin, destination and direction with respect to water current where the migration occurs. If the migration is between inland waters and the sea then the term applied is *diadromy*, which in turn has two related forms: *anadromy* – ‘up-running’, involving at one stage a migration from marine waters up rivers or streams to reproduce in freshwater, and *catadromy* – ‘down-running’, involving at one stage a migration down streams or rivers to reproduce in the sea. If the migratory cycle occurs solely within flowing inland waters, regardless of its direction with respect to current, it is called *potamodromy*. Lake-dwelling fishes which enter tributary streams and rivers to reach spawning habitats are said to make *adfluvial* migrations. Other terms exist but need not be dealt with here.

Lucas & Baras (2001) reviewed migratory behaviour of arctic, subarctic, temperate and tropical freshwater fishes for 44 taxonomic groupings. Some 36 groups of fish, probably representing over 350 species, show well-documented migrations in inland waters (Table 7.1). Over 64 of these species (mainly sharks, rays, mullets and gobioids) are diadromous, over 84 (mainly lampreys, sturgeons, anchovies etc., northern smelts and salmonids) are anadromous, and over 25 (mainly freshwater eels) are catadromous. Potamodromy occurs in over 169 species and no doubt this form of migration is greatly underestimated in minnows, characins and catfishes. Twenty-nine of the 36 groups of fish (81%) have migrant species in temperate inland waters, 15 in subtropical (42%) and 10 (28%) in tropical inland waters. Clearly migratory behaviour seems much more common for temperate inland waters, but detailed information is only available for a small fraction of all freshwater fish, of which there are some 10,000 species (see Table 1.2 in Chapter 1).

Diadromy is said to occur in about 230 species of fish (McDowall 1988), many of which may make only short or brief excursions into estuaries or freshwater. The proportion of freshwater fish species exhibiting diadromy within an area seems to vary with length of coastline relative to land mass and also with latitude (McDowall 1996). For example, in some large insular areas such as New Zealand over half of the freshwater fishes are diadromous and in some such as Newfoundland (Hammar 1987) or Hawaii (Kinzie 1991), all species follow that type of migratory behaviour. Along the Atlantic coast of North America (25–61° N latitude) the number of diadromous species peaks just under 20 (about a third of the freshwater species in the region) at about 45° N. Along its Pacific coast (25–71° N) it peaks at 20 (again nearly a third of the total freshwater species in the region) at just over 60° N, and ranges in New Zealand from nearly 90% of its freshwater fish fauna at 34° S latitude to about 70% at 46° S latitude (McDowall 1996). Diadromy facilitates invasion of new or reinvasion of formerly perturbed inland waters (McDowall 1996), but is also a behavioural feature that can create difficulties for species attempting to gain access to former habitats that become obstructed naturally or anthropogenically (Northcote 1998).

Anadromy is a very common form of migration in salmonids, especially in the salmon, trout and char, but also occurs in whitefish and some grayling populations.

Members of this family of freshwater fish are widely distributed in forested regions of North America and Eurasia (see Scott & Crossman (1973) for a map of their native world distribution). Salmonids have been introduced into forested regions of Central and South America, Africa, India, New Guinea, New Zealand, Australia and some major nearshore as well as smaller offshore oceanic islands. Salmonids commonly migrate into and spawn in forested watersheds. They are the most studied group with respect to fish-forestry interactions, which in many regions of the world have been going on for decades. Furthermore they support important food, commercial and recreational fisheries.

In many salmonids the marine migratory legs of anadromy can be very long – thousands of kilometres are not uncommon. They are usually short and coastal in whitefish and in some grayling populations (Scott & Crossman 1973; Reist & Bond 1988; Bond & Erickson 1992, 1997). In the large (seventh order) glacial Taku River (Canada, Alaska), some of the Pacific salmon (*Oncorhynchus* spp.) juveniles remain in Alaskan lower reaches which then must be carefully considered as rearing habitat for whole-river management purposes (Murphy *et al.* 1997). In anadromous Atlantic salmon (*Salmo salar*) young the freshwater movements increase in distance over the first several years up to the late smolt stage (McCormick *et al.* 1998). Anadromous salmonid populations of the far north, such as the Arctic char, may need freshwater habitat for overwintering so the sea resident period can be no longer than 2 months (Gulseth & Nilssen 2000). The anadromous migratory patterns followed by lacustrine and fluvial forms of Dolly Varden char, as proposed by Armstrong & Morrow (1980), now seem even more complex than previously thought, given that up to 58% of the lacustrine forms overwinter in the sea near Juneau, Alaska, rather than in lakes (Bernard *et al.* 1995). Both anadromous and non-anadromous but still migratory forms of inconnu (*Stenodus leucichthys*) occur in the Mackenzie River system of northern Canada, so these differences have to be accounted for in their management (Howland *et al.* 2000).

Catadromous migrations are much less common than anadromous ones. They occur in 15 species of freshwater eels in inland waters and seas of eastern North America, Europe, northern and southeastern Africa, India, China, Korea, Japan, some of the major islands of southeast Asia, New Zealand and Australia. Catadromy occurs in a few galaxid fishes from southern South America, southernmost Africa, New Zealand, New Caledonia and Australia. It also occurs in some gobies, often the most abundant fish in freshwater of tropical and subtropical oceanic islands (Nelson 1994), and in a few other groups (Table 7.1). Young eels of the elver stage move from marine waters into river systems to freshwater feeding habitats. Later at maturity eels move downstream and out to sea; some species and stocks move long distances offshore. Galaxids and gobies generally move over shorter distances both in freshwater and marine legs of their migrations.

Potamodromy in river-dwelling whitefishes, graylings and other salmonids includes trophic, refuge and reproductive migratory stages (Northcote 1997). The riverine distribution pattern for Arctic grayling, wherein the larger and older fish inhabit upstream reaches, can be explained by differential migrations upstream and downstream between fast and slow growing fish (Hughes 1999). Juvenile downstream migration in

Table 7.1 Type, extent and general location of well-documented migratory behaviour^a in 36 major groups of fishes frequenting inland waters of the world

| Fish group | Number of species showing migratory behaviour ^b | | | | General location |
|--------------------------------------|--|----------|-----------|--------------------------|----------------------------------|
| | Diadromy ^c | Anadromy | Catadromy | Potamodromy ^d | |
| Lampreys | | 9 | | 2 | temperate ^e |
| Sharks, rays | 10 | | | | subtropical, tropical |
| Sturgeons | | 10 | | 3 | temperate |
| Paddlefishes | | | | 2 | temperate |
| Gars | | | | 2 | temperate |
| Osteoglossids | | | | 3 | temperate, tropical |
| Tarpons | 1 | | | | subtropical |
| Freshwater eels | | | 15 | | temperate, subtropical, tropical |
| Anchovies, shads, herrings, menhaden | 1 | 22 | | 2 | temperate, subtropical, tropical |
| Milkfish | 1 | | | | tropical, subtropical |
| Carp, minnows | | | | >33 | temperate, subtropical |
| Suckers | | | | 19 | temperate |
| Loaches | | | | 2 | temperate, subtropical |
| Characins | | | | >31 | subtropical, tropical |
| Catfishes | | 1 | | 11 | temperate, subtropical, tropical |
| Pikes, mudminnows | 1 | | | 4 | temperate |
| Smelts (northern) | | 7 | | 1 | temperate |
| Noodlefishes | | >1 | | | temperate |
| Smelts, graylings (southern) | | 1 | | 1 | temperate |

| | | | | | | | |
|----------------------|-----|-----|--|-----|--|------|----------------------------------|
| Galaxids | | | | >1 | | | temperate |
| Salmonids | 1 | >3 | | | | 34 | temperate, subtropical |
| Trout-perches | | 21 | | | | 1 | temperate |
| Cods | 14 | 1 | | | | 1 | temperate |
| Mullets | | | | | | 1 | temperate, subtropical |
| Silversides | | | | | | 3 | temperate, tropical |
| Sticklebacks | | 3 | | | | | temperate |
| Cottids | | | | 1? | | | temperate |
| Snooks | 2 | | | | | | temperate, subtropical |
| Moronid basses | | 2 | | 1 | | | temperate |
| Percichthyid perches | | | | 1 | | 3 | temperate |
| Perches | | 2? | | | | 4 | temperate |
| Tigerperches | | | | 1 | | 2 | subtropical, tropical |
| Jungleperches | | | | >2 | | | tropical |
| Sandperches | | | | | | 1 | temperate, subtropical |
| Gobioids | >33 | 1 | | >1 | | >3 | subtropical, tropical |
| Flatfishes | | | | 2 | | | temperate, subtropical, tropical |
| Totals | >64 | >84 | | >25 | | >169 | |

^aInformation mainly from text in Lucas & Baras (2001); other inputs from Northcote (1997) and McDowall (1988, 1996).

^bSame species within a group may be recorded in more than one migratory type.

^cHere includes amphidromous fishes whose larvae migrate to sea soon after hatching; see Lucas & Baras (2001).

^dHere includes a fluvial migrations from lakes into tributary spawning habitats.

^eHere and below may include a few species also found in arctic inland waters.

tributaries by adfluvial cutthroat trout to a Utah reservoir occurs mainly at night and shortly after emergence (Knight *et al.* 1999), similar to that of underyearlings for several lake-dwelling but inlet spawning populations of trout (Northcote 1969). Several species of salmonids make regular seasonal use of small tributaries during riverine residence, so their passageway into and out of such important temporary habitat is critical to their production (Hartman & Brown 1987; Bramblett *et al.* 2002). Information on potamodromous migrations, which occur in the many other groups of fishes (Table 7.1), is provided by Lucas & Baras (2001). The important concept of core area use in rivers and streams for seasonal habitat occupation, along with associated movement to and from such areas, is now emerging from radio-tagging studies in several groups of fishes such as sturgeon (Knights *et al.* 2002), bull trout (K. Bray & P. Mylechreest, pers. comm.), brook trout (Curry *et al.* 2002) and Atlantic salmon (Hiscock *et al.* 2002).

In lakes, some salmonids (especially sockeye and kokanee *Oncorhynchus nerka*) undertake extensive and regular diel vertical migrations (Northcote 1967; Narver 1970; Levy 1990, 1991), even under ice in winter (Steinhart & Wurtzbaugh 1999). They occur as a complex compromise to optimize feeding, growth and predator avoidance. These migrations, especially in their near-surface portion, can bring the fish into direct contact with various forestry activities and also their environmental effects (see Chapter 14).

Many non-salmonid fishes make extensive and multidirectional migrations (see Table 7.1). These include anadromy in smelts, clupeid shads (McDowall 1996; Blaber 1997) and sturgeon (Veinott *et al.* 1999; Fox *et al.* 2000), and potamodromy in paddlefish (Lein & De Vries 1998), galaxids (Richardson *et al.* 2001) and cyprinids (Lindsey & Northcote 1963; Tyus 1990; McAda & Kaeding 1991; Osmundson *et al.* 1998). For the latter group, precise reproductive homing has been documented in roach (*Rutilus rutilus*) by L'Abe'e-Lund & Vollestad (1985) and in *Leuciscus cephalus* by LeLouarn *et al.* (1997). Cyprinids in some African lakes have spawning migrations much like trout in temperate lakes (G.F. Hartman, pers. comm.). Schindler (1999) has developed a model to examine the lake onshore-offshore diel migratory strategies of minnows. Catostomids may migrate into lake tributaries to spawn and their young move back to lakes at a young stage (Geen *et al.* 1966). For non-salmonid tropical freshwater fishes, Blaber (1997) has reviewed both anadromous and potamodromous migratory patterns.

Several groups of fish exhibit what has been termed 'partial migration' (Jonsson & Jonsson 1993), i.e. where a particular population can be composed of both migratory and resident individuals, the latter often being dwarfs compared with the migratory forms. This phenomenon is common in at least nine species of salmonids and two species of smelts (see Table 1 in Jonsson & Jonsson 1993).

Mechanisms of fish migration in freshwater

The control of diadromous migration in fishes involves a complex and hierarchical series of mechanisms. This has long been recognized (McCleave *et al.* 1984), as has the importance of olfactory imprinting and other controls in the precision of reproductive homing (Døving *et al.* 1974; Hasler & Scholtz 1983; Smith 1985; Groot *et*

al. 1986). Multiple mechanisms are used in the homing phenomenon of migration in rivers (Northcote 1984) and in lakes (Hodgson *et al.* 1998). The olfactory organ of lake salmonids may discriminate among different intensities of various freshwater odours (Sato *et al.* 2000). Olfaction also plays an important role in homing and estuarine migration of the catadromous eel (Barbin 1998). A suite of guidance cues may be integrated through the sensory capabilities used by fish (visual, olfactory and others). These may be regulated by genetic control, by previous experience and learned behaviour as young, and by past as well as present environmental conditions (such as water temperature, light and photoperiod, water currents). Among salmonids, each species may have different strategies of homing migration (Northcote 1978, 1998) and use different sensory abilities affected by hormonal states (Ueda 1998).

Although home stream odours may be imprinted by learning as juveniles and remembered by returning adults several years later, there has been continuing research to identify just when and how such imprinting occurs. Experimental work on coho salmon juveniles suggests that imprinting only occurs during the short period of parr to smolt transformation (Dittman *et al.* 1996). Nevertheless, under wild rearing conditions young salmon can learn site-specific home odours long before reaching the smolt stage. Several species of salmonids that leave freshwater rearing areas as young fry are able to reproductively home with high precision. The field is still under active research by several groups (Barinaga 1999). Because of the importance of 'home stream' olfactory cues, imprinted as young and used by returning adults several years later, it is not difficult to see the implications of changing stream odours by various human activities, including forestry.

Physiological capabilities, behavioural tactics and energetics

Physiological capabilities

Species vary in their physiological capabilities to migrate. Natural selection has resulted in some species or stocks having superior migratory abilities. These capabilities, however, have costs in fecundity, morphology, or other aspects of fitness associated with maintaining them (Crossin 2002).

There are two fundamental types of swimming, sustained and burst. Their magnitude and duration vary among stocks and species in relation to underlying physiological factors and particular environmental features. Sustained swimming is the slowest class of speeds and can usually be maintained indefinitely without causing fatigue. Burst swimming is the fastest class and when elicited usually causes fatigue in less than 1 minute. An intermediate class of speeds, termed 'prolonged', reflects a zone of transition between sustained and burst, and may be the most common one used by upstream migrating individuals (Beamish 1978).

At the physiological level, swimming capabilities are governed by muscular, enzymatic and metabolic factors. Fish swimming musculature is made up of two types, 'red' and 'white' muscle (Gill *et al.* 1989). In red muscle, glucose is converted to energy in the presence of oxygen (aerobic metabolism). This function can go on indefinitely

provided that oxygen and glucose are present in the blood. Red musculature is used for day-to-day routine activities (e.g. sustained swimming). White muscle also converts glucose, via glycogen, to energy but it does so without oxygen (anaerobic metabolism), and is only used when blood oxygen is lacking and aerobic swimming is not possible, for instance when fish try to ascend fast stretches of rivers (e.g. burst swimming). However, anaerobic metabolism is much less efficient for conversion of glucose to energy than is aerobic metabolism and its byproduct, lactic acid, can itself impair swimming, leading to fatigue if it cannot be eliminated quickly. In some circumstances, blood lactic acid can accumulate to such high levels during hyperactive swimming that blood acidosis causes mortality (Black 1958). Thus, species or stocks with relatively high proportions of white muscle, and good abilities to eliminate lactic acid and recover from strenuous exercise, may be able to migrate more successfully through fast water. However, high proportions of white muscle will be disadvantageous for steady cruising activities, which may be required for feeding or other behaviour. Trade-offs in relative proportions of muscle types may depend on more than just migratory constraints in a fish's life history (Gill *et al.* 1989).

Maximum sustained speeds vary considerably among sizes and life stages within species, and among taxa. Within a species, larger fish generate greater tail thrust and can attain higher absolute swimming speeds than smaller fish. Yet relative to body size, small fish are better fitted to sustained swimming. For example, 8-cm sockeye salmon (*Oncorhynchus nerka*) have sustained swimming speeds of 6.7 Ls⁻¹ (lengths per second) but 60-cm sockeye can only sustain 2.1 Ls⁻¹ (Brett & Glass 1973). Maturation stage can also affect swimming performance, irrespective of body size. For instance, 13-cm Atlantic salmon smolts have a maximum sustained speed of 114 cm s⁻¹ whereas that for the same sized parr is 82 cm s⁻¹ (Peake *et al.* 2000). Some differences among taxa in maximum sustained speeds can be attributed to differences in body shape and fin position, features that affect their ability to generate power and overcome drag (Webb 1984, 1995). Adult salmonids, with their fusiform bodies and medially positioned pelvic fins, can attain high sustained swimming speeds. These reach 178 cm s⁻¹ in sockeye salmon, 138 cm s⁻¹ in brown trout (*Salmo trutta*) and 122 cm s⁻¹ in brook trout (*Salvelinus fontinalis*). In adult fishes with more laterally compressed body shapes and anteriorly positioned pelvic fins they are lower (e.g. 118 cm s⁻¹ in smallmouth bass (*Micropterus dolomieu*) and 67.9 cm s⁻¹ in walleye (*Stizostedium vitreum*)) (Brett & Glass 1973; Peake *et al.* 1997, 2000; Bunt *et al.* 1999).

Maximum sustained swimming speeds are governed by water temperature. Fish body temperature is usually the same as surrounding water temperature, and standard metabolism (the energetic costs of respiration) increases exponentially with increasing water temperature. Maximum sustained swimming speeds also increase with increasing temperature, peak at a temperature specific for species and size, and decline with further increases in temperature. Thus, the temperature where sustained speeds are maximal may be different, even for closely related species (Brett 1995).

Temperature also affects prolonged swimming speeds, the transition speeds that involve both aerobic and anaerobic metabolism. Provided that temperatures are within a species' thermal tolerance, warmer temperatures permit higher speeds before fatigue ensues (Brett 1967; Mesa & Olson 1993). Although larger fish swim faster than small

fish and may exhibit higher prolonged speeds, in relation to their size, larger fish tend to fatigue at slower speeds than small fish (Brett 1967; Mesa & Olson 1993). Fatigue velocities (c. 15–65 cm s^{-1}) of young flannelmouth suckers (*Catostomus latipennis*) increased with temperature and fish size over a tested range of 10–20°C and 25–115 mm total length (Ward *et al.* 2002).

Maximum burst speeds are periodic high acceleration sprints and last for only a few seconds. Bainbridge (1958) was the first to rigorously examine 'voluntary' burst swimming. He quantified adult sprint speeds for dace (*Leuciscus leuciscus*; 220 cm s^{-1}), trout (*Salmo irideus*; 330 cm s^{-1}) and goldfish (*Carassius auratus*; 88 cm s^{-1}). Relative to their body size, dace and trout can reach burst speeds of 10–12 L s^{-1} and goldfish 8–10 L s^{-1} . Webb (1995) predicted that adult salmonids could sprint at speeds up to 10 L s^{-1} , and juveniles up to 25 L s^{-1} . Adult sockeye salmon migrating upstream have been observed by telemetry to regularly attain speeds of over 9 L s^{-1} and occasionally up to 12 L s^{-1} (Fig. 7.1) (Hinch *et al.* 2002). However, sprint speeds remain inadequately studied for

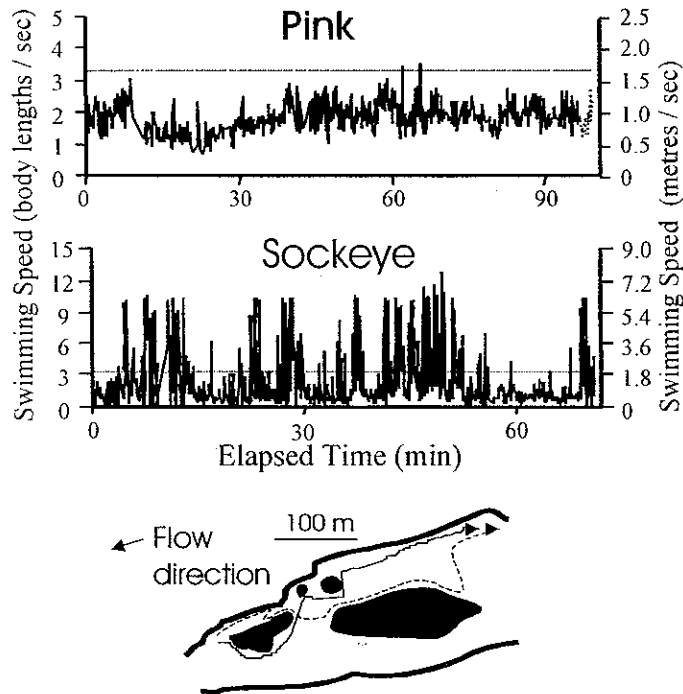


Fig. 7.1 Plots of instantaneous swimming speeds (upper two panels), estimated from EMG transmitters surgically implanted into main swimming muscles, for an adult pink and sockeye salmon to pass through a 400-m reach in the Fraser River canyon (lower panel). Speeds are given in absolute (m sec^{-1}) and relative ($\text{body lengths sec}^{-1}$) measures. The horizontal lines on upper two panels indicate transition zones between low-cost aerobic metabolism and high-cost anaerobic metabolism. This reach contains four islands, white water rapids and multidirectional currents. The lines on the reach diagram (lower panel) represent the upstream trajectory of a pink (broken) and a sockeye (solid) salmon through the reach. Arrowheads indicate direction of fish migration. Additional details in Hinch *et al.* (2002).

most species, despite their importance for understanding migration energetics and passage success. Temperature does not seem to affect maximum burst swimming speeds in fish (Peake *et al.* 2000), but more research is needed.

Behavioural tactics

Physiological capabilities set the stage upon which swimming behaviour acts. This is particularly evident in spawning migrations of salmon, although field studies linking adult fish migration tactics, swimming abilities and energetics have focused on only a few stocks of salmonids. Energy must be conserved for gamete production, development of secondary sexual characteristics, and spawning activities. Where spawning migrations are energetically expensive (e.g. high water temperatures and high water velocities) and with cessation of feeding (as generally occurs in upstream migrating salmonid adults), energy conservation should be under strong natural selection. These adult migrants should be energy-efficient wherever possible. There are several behavioural tactics that migrants could use to conserve energy. The limited field studies suggest that adults may invoke most of these, and switch among them depending on local conditions. Migrants could swim in low speed or reverse-flow current paths (Hinch & Rand 2000) or, where possible, utilize upstream tidal transport (Levy & Cadenhead 1995). In these instances, migrants use sustained speeds and avoid burst swimming. This is a predominant tactic used by adult pink salmon (*O. gorbuscha*) (Fig. 7.1) (Hinch *et al.* 2002).

Paradoxically, under some circumstances, burst swimming can be energetically efficient if alternated with coasting. Such 'burst-then-coast' swimming could be up to 60% more efficient than swimming at sustained speeds (Weihs 1974). Sockeye salmon appear to occasionally invoke this behaviour (Fig. 7.1) (Hinch *et al.* 2002). Another tactic to save energy is to swim in configurations, such as schools, which enable fish to receive locomotory benefits from conspecifics via a reduction in incident water velocity (Weihs 1975).

A final tactic for conserving energy involves steady swimming at sustained speeds, but speeds that are constantly being adjusted to minimize the total energy expended in moving mass through unit distance. Termed swimming at hydrodynamically (Weihs 1973) or metabolically 'optimal speeds' (Ware 1975), this behaviour has recently been documented in migrating salmon, but seems prevalent only at sites where the current speeds encountered are relatively slow ($<25 \text{ cm s}^{-1}$) (Hinch & Rand 2000). Analogous studies on adults of other species, or on juvenile migrants, are lacking.

Energetics

Much more is known about the energetics of adult spawning migrations than those of juveniles. This is particularly the case in adult anadromous fish for whom body energy analyses are simplified because they rarely eat and only use reserve energy to fuel their upstream migration. Across stocks and species, typically 50–70% of initial energy is used to complete such migration (Brett 1995; Jonsson *et al.* 1997; Leonard

& McCormick 1999). Energy use is accelerated when migrants encounter elevated temperature, elevated flow rates, or river constrictions. The latter two usually result in higher encountered water velocities (Hinch & Rand 1998; Rand & Hinch 1998). Energy exhaustion is believed to be a factor causing pre-spawning mortality in some stocks (Rand & Hinch 1998; Leonard & McCormick 1999). In iteroparous stocks (spawning several times over lifespan), post-spawning survival rates are negatively related to energetic losses during spawning (Jonsson *et al.* 1997). Bernatchez & Dodson (1987) reviewed energy use studies of both iteroparous and semelparous (spawn only once over lifetime) species and summarized energetic costs of 15 anadromous spawning stocks that migrate upriver distances ranging from 30 to 1200 km. Short distance migrants (<100 km; river lamprey (*Lampetra fluviatilis*), cisco (*Coregonus artedii*), shad (*Alosa sapidissima*) and alewife (*A. pseudoharengus*)) were the least efficient in energy use (all <20 kJ kg⁻¹ km⁻¹), whereas long distance migrants (>1000 km; chinook salmon (*O. tshawytscha*), sockeye salmon and chum salmon) were most efficient (all <6 kJ kg⁻¹ km⁻¹). This pattern of increasing energy conservation with increasing migratory difficulty has also been observed in a multi-stock examination within one species and one watershed (Fraser River sockeye salmon; Crossin 2002).

In contrast with adults, relatively little is known about energetic costs of juvenile fish migrations. Unlike most adults during spawning migrations, juveniles do feed during their migrations (e.g. Brett 1995). Increasing (or at least not losing) weight is extremely important for maximizing chances of survival by juveniles when entering their new environments. Energetic state is an important determinant of migration initiation in juvenile salmon. A survey of juvenile Atlantic salmon populations revealed that local environmental conditions, specifically water temperature and day length, were good predictors of smoltification (Metcalfe & Thorpe 1990). These conditions reflect changes in growth opportunity and the potential for large energetic gains by migrating to a new environment. For instance, energy availability to young anadromous brown trout was 10% greater than same-aged non-anadromous residents (Jonsson & Jonsson 1998).

However, environmental conditions can be detrimental if anthropogenically altered. For example, when stream temperatures increased in Carnation Creek, British Columbia, following logging, coho (*O. kisutch*) and chum (*O. keta*) salmon emerged several weeks earlier than normal, entering the ocean at a time when coastal survival rates were poor – thus the number of returning adults was negatively affected by the juvenile migratory response to temperature (Hartman & Scrivener 1990). Presumably the energetic costs of juvenile downstream migrations are low as these fish can seemingly move passively, except where lakes or reservoirs are encountered. Indeed, river flow speeds positively correlate with travel times of downstream salmonid smolts (Berggren & Filardo 1993). Yet juveniles are not ‘involuntarily’ carried downstream. The prolonged swimming speeds of juveniles often exceed the slowest current speeds of the rivers they migrate in (Peake & McKinley 1998). Moreover, juveniles are capable of swimming upstream in rivers with strong currents by using reverse-flow fields near the river banks (McLaughlin & Noakes 1997), similar to the tactic used by adult migrants (see above).

Migration obstructions and barriers

Obstructions (features that slow a migration) and barriers (those that stop a migration) occur both naturally and anthropogenically. Natural fluctuations in turbidity, dissolved oxygen, temperature and discharge can create minor obstructions and cause slight delays in migrations (reviewed by Bjornn & Reiser 1991). However, most stocks have evolved under these varying natural conditions and may not be seriously affected by modest levels of obstruction. Because upstream spawning migrations occur at discrete and precise times each year, more substantial delays could affect proper timing of reproduction, or impair spawning by depleting energy reserves (see above), increasing stress, or increasing susceptibility to disease. Natural barriers, such as waterfalls, rapids or in some cases debris jams, may prevent upstream migratory access, but such barriers are often species- or season-specific (Bjornn & Reiser 1991). There are few natural barriers to downstream migrations. This is particularly true for most juvenile migrations in temperate regions, which are timed to coincide with spring runoff when water temperatures are usually modest and stream flows adequate for passage. Nevertheless, there may be many man-made obstructions even to downstream migration caused by hydroelectric and other types of dams.

All of the natural obstructions listed above can be affected by forestry practices (Chapter 13). For instance, logging can increase stream turbidity, reduce dissolved oxygen, increase stream temperature and reduce apparent summer stream flows and water velocities. Reduction in the latter two could facilitate a spawning migration if it means that energy can be saved because current speeds are reduced. In some cases, streams can become entirely dewatered due to logging-induced landslides and bank erosion, thereby eliminating migration routes and spawning areas. Furthermore, small bridges and road culverts – if partially plugged with debris – can impede fish passage upstream and downstream.

Perhaps the greatest environmental impact of forestry on fish migration is that caused by stream crossings. These can have a variety of effects, but most importantly for migrations, they can create water velocity obstructions or barriers. The scope of these problems can be appreciated when one considers the number of crossings in existence. In British Columbia alone there are over 225,000 stream crossings with 10,000 new ones being installed each year (Harper & Quigley 2000). The most common crossing types used in a forestry context are round or oval corrugated metal pipes (the standard culvert), open/natural bottom structures made of logs, metal or concrete (open box culvert), variants of these with 'baffles' or other forms of surface 'roughness' (Bates & Powers 1998), and bridges. In some regions, slab and ford crossings (roads built through the stream) are also present (Warren & Pardew 1998). Pipe culverts are by far the most common extant crossings, and because they are the cheapest of structures, they are still the ones most frequently being installed today.

Structures that constrict the channel and accelerate water speeds can cause barriers for migrations by creating water velocities that exceed fish maximum speeds or endurance. By scouring out the streambed at the downstream end of the structure thereby 'perching' it with drops to the pool below often well over a metre, access by fish can

be prevented. Pipe culverts are notorious for creating these barriers. In recent surveys, 25% of pipe culverts in British Columbia were impassable by salmonids (Harper & Quigley 2000), and in Arkansas, USA, pipe culverts acted as barriers to the movements of nine different fish species (mostly cyprinids, catostomids and fundulids; Warren & Pardew 1998).

An understanding of species- and size-specific prolonged and burst swimming speeds is required as a starting point to predict whether fish can pass upstream through a culvert that is not perched. Indeed, we know a considerable amount about prolonged speeds for several species and size classes (e.g. Jones *et al.* 1974; Scruton *et al.* 1998; Toepfer *et al.* 1999). Moreover, numerous equations have been developed by engineers to understand and predict water velocities and discharges from culverts with differing size and shape characteristics (e.g. Bates *et al.* 1999). Thus, with a basic understanding of hydraulics and swimming performance, it should be possible to design and install culverts of dimensions that will not generate velocities that exceed the swimming endurance of the species and size of concern. As highlighted by the recent culvert surveys described above, this has turned out to be much more difficult than was once believed.

With few recent exceptions (e.g. Belford & Gould 1989), most swimming performance experiments used to predict culvert swimming abilities are conducted in swimming tunnels (tubes, flumes) where fish swim in the light against water that is propelled past them. These apparatuses are designed to have no channel turbulence and no gradient, and are a poor mimic of a long dark corrugated culvert. In addition, fish that choose to not swim in a trial are normally removed from the study. Standard corrugated culverts have considerably more surface roughness, boundary layers and turbulence than swimming tunnels and these features can affect passage success (Bates & Powers 1998). Small fish may be able to utilize boundary layers for passage but turbulence could also overpower them (Bates & Powers 1998). Large-scale river turbulence is believed to cause confusion in adult migrants (Hinch & Rand 1998).

New culvert designs include baffles or bed material embedded into their bottoms. The belief is that these designs aid passage by 'weak-swimming' fish, those with naturally low prolonged or burst swimming speeds, and enable 'strong-swimming' fish to utilize lower swimming speeds and thus conserve energy (reviewed in Poulin & Argent 1997). However, little biological evaluation has been made of these culvert modifications, and in general, we know very little about how turbulence influences fish swimming performance. We also know very little about burst swimming in fish, which they no doubt use frequently to pass through standard pipe culverts. Thus we must be more cautious when applying laboratory-derived swimming criteria to culvert design and selection – the approach that most management agencies have adopted (e.g. Poulin & Argent 1997). These criteria should be set very conservatively. There have been surprisingly few rigorous studies (except see Belford & Gould 1989; Bates & Powers 1998; Warren & Pardew 1998) that have examined swimming abilities of fish through actual or simulated pipe culverts, and many more are needed. Until then, the most 'risk-adverse' approach in culvert choice to minimize chances of creating a migratory obstruction would be to use natural bottomed culverts that span the entire channel width or else bridges (Harper & Quigley 2000).

Concluding comments

Freshwater fish migration, a cyclic alternation between two and often three or more essential habitats – spawning, feeding and survival (under severe conditions) – normally occurs at particular life history stages with regular seasonal and annual timing. It usually involves a large fraction of any given population, although not necessarily all individuals. And the cycle commonly includes energetically demanding and directed movement upstream against current at one stage along with downstream less demanding movement or even drift at another stage. Overall, however, the cycle is key to survival of the species that engage in this remarkable behaviour. Sometimes the complete cycle occurs over thousands of kilometres, but distance is no measure of importance to the populations involved, so migrations of a few kilometres or even a few tens of metres can be just as vital to their long-term survival.

Two groups of freshwater fishes, salmonids and eels, are universally recognized to be phenomenal migrants. Both are abundant and important in forested watersheds over many regions of the world. Even with these groups there is still much to be learned about their migratory behaviour, the many mechanisms used in completing their migratory cycle, their energetic capabilities and tactics, and particularly the effects of forestry practices on their migrations. We are now becoming aware that migration is an important feature in the life history of nearly 40 different groups of freshwater fishes, a number of which occur in arctic, subarctic, temperate, subtropical and tropical areas of the world, often forested or partially so. For many of these fishes we only have rudimentary knowledge of their migrations, surely not enough to effectively prevent their severe loss resulting from forest removal taking place over much of their inland habitats.

The need for more relevant migratory research is great and this will be featured along with other needs in the concluding chapters (Part VIII) of this book. The message must be effectively presented to government agencies locally, nationally and internationally, and to the forest industry. Furthermore the problems and means for their solution also need to be given clearly to relevant professionals, and those in training, in both forestry and fisheries. Together, with appropriate knowledge and funding, they will work out the ways to maintain the many important migratory fish populations in forested watersheds of the world.

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