A Pioneer

of

Fisheries Research

Frank Buckland 1826-1880

The Buckland Lecture for 2005

Conservation of Atlantic Salmon Habitat

John D. Armstrong

Buckland Occasional Papers; No. 12

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One of a series of Occasional Papers providing a permanent record of the annual lectures maintained by bequests from Frank Buckland in 1880 and Fred Smith in 1997.

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C/O The Clerk
3 Woodside Avenue
Bridge of Weir
PA11 3 PQ

Tel/Fax 44(0) 1505 610972
Email jramster@lineone.net

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FRANK BUCKLAND AND THE BUCKLAND FOUNDATION

The Buckland Foundation was endowed by Frank Buckland, a sometime surgeon, natural historian, fisheries scientist and government inspector of salmon fisheries, but above all an inveterate communicator of the period 1860-80. People flocked to hear him talk and he never let slip any opportunity to make people aware of the importance of the fisheries and their problems in particular and of natural history in general.

Buckland trained as a surgeon and took a commission in the Life Guards in 1854 but from the outset began to write popular articles on natural history. These were published in 1857 to great acclaim as a book entitled *Curiosities of Natural History*: this grew to four volumes and appeared in 15 editions. His success increased demands upon him as a writer and lecturer and he resigned his commission in 1863.

He had become interested in fish culture, then regarded simply as the rearing of fish from the egg, and an exhibit he had in the office-window of *The Field* magazine on The Strand in London proved to be so popular that it stopped the traffic on occasion. He gave a successful lecture on the subject in 1863 at the Royal Institution, subsequently published as *Fish Hatching*, and was struck by the intense interest that it aroused. One consequence of it was that he set up a small aquarium at the South Kensington Museum, the forerunner of the Science Museum, and by 1865 had collected there a range of exhibits which were to form the nucleus of his eventual "Museum of Economic Fish Culture". This aimed to inform the public about the fish and fisheries of the British Isles and for the rest of his life he laboured, in part, to develop this display. At about the same time (1867) he was appointed to the office of Board of Trade Salmon Inspector; he also set up the weekly magazine *Land and Water*.

Britain's growing population in the last century created many problems of food supply. The sea fisheries offered a cheap source of abundant first-class protein and, as a result of the latent demand and the growth of railways, the North Sea fisheries grew spectacularly. Little was known about sea fish: no statistics of fish landings were available, at least in England, and there was little formal research. Buckland sat on four Commissions that looked at Fish and Fishing between 1875 and his death in 1880. In the same period a number of public fisheries exhibitions were held abroad and he tirelessly pressed for something similar to be staged in the United Kingdom. At all times he was concerned to explain, to teach and, most particularly, to make the general public aware of the importance of the fisheries and the need to protect and develop this great national asset. "Buckland's voice," says Geoffrey Burgess, his most recent biographer*, "remains the only one consistently calling for research into fishery problems, publicising the activities of the industry, drawing attention to the national importance of fish in the diet, and acting as a focus for those in the industry and elsewhere who were interested and concerned about its proper commercial development."

Something of the flavour of his views is given by the following quotations from his reports and articles.

- *"A greater cry should more properly be established against those which deter or kill the fish by noxious materials which they pour into public waters for their private use and Benefit ... - The above mentioned individuals and companies reap no inconsiderable profits from their individual operations, but while endeavouring to* *increase their own profits, they treat with indifference the welfare of the public, and an important source of food not only to themselves, but to the public in general".*

- *"What objection can be reasonably argued against the employment of revenue cruisers for the accommodation of naturalists, appointed by government ... in order that they make a thoroughly practical examination of the dark and mysterious habits of food fishes. The trawl and tow net, we firmly believe, if judiciously and persistently employed over an extended area of the sea, by men able to identify what the nets drag up and entangle, would do more to bring to light what is now hidden and unknown than all the evidence collected by the Sea Fisheries Commission. It is a government question, and not one of private or individual research. We feel confident that the time is not far distant when properly-equipped naturalists will be sent by government to investigate the habits of deep sea fish."*

- *"We want also samples of the surface water itself under peculiar conditions, for instance, what is the meaning of the wonderful white appearance of the sea which took place last autumn in nearly all the waters of the northern coast of England? What is the meaning of the occasional red appearance of the sea for many square miles? Again, how are we to devise a mesh of net that shall let go the small soles and undersized fry of other sea fish, and keep marketable fish only?"*

Frank Buckland died in December 1880. A few days before his death he signed his will. His wife was to have a life interest in his estate but on her death £5,000 would be used to establish a trust fund to support 'A professorship of Economic Fish Culture, to be called The Buckland Professorship'. The money became available in 1925 and in 1930 the first Buckland Lectures were given. It is clear that Frank Buckland intended the term 'Fish Culture' to be widely interpreted and to cover much more than fish hatching and the rearing of fry.

The invitation to deliver the Buckland Lectures is made by the Trustees of the Foundation: one representing the Department of the Environment, Food and Rural Affairs (Defra) and two the Department for Education and Employment, the direct descendents of the Board of Education and the Ministry of Agriculture and Fisheries respectively in 1925. Down the years they have sought to ensure that the lectures are not only of interest and relevance to as broad a section of society as possible but also are of value to those who depend for their livelihood on some aspect of fish and fishing. Most of the lectures have been printed either as developed texts or full-length books and the Foundation ensures that the sets of Buckland Books in the libraries of the Fisheries Laboratories at Aberdeen and Lowestoft and the marine science libraries at the Marine Biological Association in Plymouth and at the Southampton Oceanography Centre are as complete as is possible. It also offers a Buckland Summer Studentship each year which supports a university student for ten weeks during the summer vacation in a research project supervised by a scientist from one of the government-supported research laboratories in the UK and Ireland. The Trustees hope that by continuing to keep alive the memory of a man who dedicated his life to the improvement of the commercial fisheries of the British Isles they help, in their turn, improve people's understanding of current problems in the commercial fisheries and the aquatic environment.

Further Reading

Burgess, G.H.O., The Curious World of Frank Buckland, London, John Baker 1967.

List of Buckland Lectures

1930	Frank Buckland's Life and Work	W.Garstang
1931	Salmon Hatching and Salmon Migrations	W.L.Calderwood
1932	The Natural History of the Herring in Scottish Waters	H Wood
1933	The Natural History of the Herring in the Southern North Sea	W.C.Hodgson
1934	The Hake and the Hake Fishery	C.F Hickling
1935	Oyster Biology and Oyster Culture	J.H.Orton
1936	The Nation's Fish Supply	E.Ford
1937	Fish Passes	T.E.Pryce Tarrant
1938	Hydrography in Relation to Fisheries	J.B.Tait
1939	Rational Fishing of the Cod in the North Sea	M.Graham
1947	The Stock of Salmon, its Migrations, Preservation and Improvement	W.J.Menzies
1948	Sea Fisheries	G.T.Atkinson
1949	The Plaice	R.S.Wimpenny
1950	River Pollution	H.D.Turing
1951	Fishery Hydrography	J.R.Lumby
1952	River Purification	F.T.K.Pentelow
1953	Irish Salmon and Salmon Fisheries	A.E.J.Went
1954	Inshore Fisheries	H.A.Cole
1956	The Haddock	B.B.Parrish
1957	Plankton (Published as the Fertile Sea)	A.P.Orr
1958	Lemon Sole	A.R.Bennett
1959	Fish Capture	R.Balls
1960	Historical Background of International Organisations for Regulating Fisheries, their achievements so far, and prospects for the future	R.J.H.Beverton
1961	The Stocks of Whales	N.A.Mackintosh
1963	British Freshwater Fishes	M.E.Varley
1964	Developments in the Handling and Processing of Fish	G.H.O.Burgess
1965	The Lobster - its biology and fishery	H.J.Thomas & A.C.Simpson
1966	Sonar in Fisheries - a forward look	D.G Tucker
1967	The Artificial Cultivation of Shellfish	P.R.Walne
1969	Ocean Currents and their Influence on Fisheries	A.J.Lee
1970	Fish, Nets and Men - An Underwater Approach to Fisheries Research	C.C.Hemmings
1971	Behaviour and the Fisheries	F.R Harden Jones
1974	Exploitation of the Salmon Stocks	K.A.Pyefinch
1977	The Edible Crab and its Fishery	E.Edwards
1979	Maximum Use of British Aquatic Food Resources	J.J.Connell & R.Hardy
1980	Scallop and Queen Fisheries in the British Isles	J.Mason
1981	Marine Pollution and its Effect on Fisheries	A.Preston & P.C.Wood
1982	Engineering, Economics and Fisheries Management	G.Eddie
1983	A Story of the Herring	G.Buchan

1984	Mackerel – its biology, assessment and the management of a fishery	S.J.Lockwood
1985	Aquaculture	R.J.Roberts
1986	No appointment	
1987	The Norway Lobster	C.Chapman
1988	North Sea Cod	C.T.Macer
1989	Atlantic Salmon	W.M.Shearer
1990	Pollution and Freshwater fisheries	R.Lloyd
1991	The Common Fisheries Policy: Past, Present and Future	M.J.Holden
1992	Industrial Fisheries, Fish Stocks and Seabirds	R.Bailey
1993	Marine Protected Areas and Fisheries	S.Gubbay
1994	Deep-Sea Fisheries: a new resource?	J.D.M.Gordon
1995	Bivalve Cultivation in the UK: structuring influences	B.E.Spencer
1996	Protecting the seas: using science for a better environment	J.S.Gray
1997	Global Change in the Coastal Zone - implications for fisheries	P.Holligan
1998	The Deep Ocean: Use and Misuse	M.Angel
1999	The European Eel	C.Moriarty
2000	Integrated fisheries management – a challenge for the Common Fisheries Policy	D.Symes
2001	Plankton and Fisheries	C.P.Reid
2002	Fish Conservation and the design of fishing gear	R Ferro
2003	Fishing and Fish Farming - are they conflicting or complementary industries?	J Goodlad
2004	Science and the management of the United Kingdom's Crab Fisheries.	J Addison
2005	The conservation of Salmon habitat	J.D.Armstrong
2006	Regional Advisory Councils and the future of fisheries policy.	B Deas
2007	Climate Change and Scottish Fisheries	W Turrell
2008	Aquaculture: the Blue Revolution?	M Beveridge

Most of the lectures have been published in book form; many are still in print. For more information as to their availability and also for a list of Buckland Occasional Papers please contact: John Ramster, Clerk to the Buckland Foundation, 3 Woodside Avenue, Bridge of Weir, PA11 3PQ. Phone/fax 01505 610972, email jramster@lineone.net

Foreword

The Atlantic salmon, *Salmo salar* (L.), is one of the more advanced members of a group of relatively primitive bony fishes, called salmonids, which are thought to have split from the fishes which gave rise to the smelt family of today some 100 million years ago. Smelts are estuarine creatures that spawn in fresh water just above the head of tide. Estuaries are rather productive habitats that can support the rapid growth of those fishes able to cope with the large changes in salinity that take place where a river meets the sea. Fresh waters are usually much less productive but they harbour fewer predators and so are good places in which to spend the earliest stages of life.

Most members of British salmon populations take this so-called "anadromous" life cycle a step further by using entire river systems for spawning and juvenile development and then growing to adulthood in the exceptionally productive waters of sub-arctic seas. The result is that the returning adults are able lay larger numbers of larger eggs than if they had stayed behind in the river. However there is a price to pay in that there is only so much food and space in the river to support the production of the young salmon. That is why wild Atlantic salmon have never been common fishes. It follows, therefore, that the conservation and, where possible, the improvement of their spawning and nursery habitats in fresh water is one of the corner stones of salmon management. In this Occasional Paper, Dr. John Armstrong, who was the Buckland Professor in 2005, provides a straightforward account of the scientific basis for this important work.

Richard Shelton
Chairman
The Buckland Foundation
July 2008

The Conservation of Atlantic Salmon Habitat

The Buckland Lecture 2005

John Armstrong

Introduction

The Atlantic salmon can follow an anadromous life cycle, in which fish start life in fresh water but migrate to sea before returning to the river to spawn. Not all individual salmon migrate to sea and in UK waters it is common for males to mature as "parr" of typically 8-13cm long. These fish may spawn successfully and never leave their natal stream or they may spawn again having undergone seaward migration and return. However, for much of the population, and nearly all the females, migration to sea occurs before first spawning. It is the anadromous component of the population that supports the fisheries.

Marine migrations may take the fish several hundred kilometres from their home river. On the high seas they largely inhabit the surface zone, making occasional dives to depths of 100m or more. Their food comprises primarily the surface plankton and nekton, including crustaceans and small fish. Their survival and growth in the marine phase can be expected to be influenced by how the physical and chemical environments affect the biomass of this plankton and nekton. There is currently concern that changes in global climate are influencing the thermal characteristics of the main feeding areas used by some stocks of salmon from UK on the high seas and driving a decline in the survival and condition of these fish. In particular, declines in number are being noted in those stocks of fish that spend several years at sea, as opposed to those returning after one winter at sea as "grilse". Furthermore, there is also concern that grilse have been in relatively poor condition in some recent years. These changes may be linked in that poor salmon body condition after one year may result in death within two years at sea.

Salmon are a small, but important component of the vast ecosystems that are under threat of global climate change. The modifications to climate required to restore marine conditions experienced by migrating salmon might only be brought about by international efforts to ameliorate the detrimental influences of humans. Such changes are not likely to be specifically targeted at any particular animal, but a product of massive adjustments in the way that fuels and other chemicals are used by man. However, there may be scope for some action at sea targeted at salmon; for example, through control of fisheries and predation on salmon in coastal zones and estuaries. The pre-requisite in considering control of predators is a good understanding of the likely scale of their impact.

A further important approach for addressing the problems that salmon face at sea is to focus closely on fresh water. This is because the number of returning adult salmon is proportional to the number and quality of smolts, the stage at which salmon metamorphose from fresh- to salt-water forms, leaving the river. Therefore, there is potential for increasing the returns of adults, or at least offsetting losses during the marine phase, by ensuring that the habitat in fresh water is conserved, enhanced and restored. Attention to freshwater habitat is particularly important because it is accessible, relatively well understood and provides potential for real value in terms of making positive changes to salmon-population strength. However, this potential is contingent upon an adequate understanding of the factors that influence the number and quality of salmon smolts produced in a river system.

There is a large body of information concerning salmon habitat, which has been reviewed in components of the scientific literature, some of which is a product of this Buckland study, and listed at the end of the text. These lecture notes provide a summary of some of the key aspects of salmon habitat and give some insights into how the fish use their local environment.

Adults and eggs

In some cases, salmon enter the river up to a year before spawning, which occurs in autumn and winter. It is still not clear why they may spend such a long period of time in the river, where they do not feed but burn up energy that otherwise may have been used to produce more eggs. Certainly the behaviour is not simply required to allow time to traverse the river to reach their spawning grounds. It is possible that the right type of freshwater habitat provides a degree of security from predators that cannot be realised at sea and is worth the sacrifice of the loss of precious energy while waiting to spawn. Deep pools are the essential habitat for salmon to over-summer in rivers; indeed it is mainly in the longer rivers with good pool habitat that fish enter well before spawning time. Relatively low water temperatures are likely to be important in moderating energy depletion of over-summering salmon. Appropriate water-discharge regimes coupled with good access are crucial for facilitating the upstream migration of adults.

Salmon are believed to need very specific habitat for spawning and tend to use cobble-sized stones at the tails of pools where the water accelerates through the gravel. The female lays eggs in one or a series of nests, which she covers with gravel. The eggs are fertilised by an attendant anadromous male and often also by one or more of the male parr that compete among themselves for access to the female. Nests may be deposited in an adjacent sequence progressively upstream to form a redd. It is possible that eggs are also deposited in other contexts, such as small pockets of gravel among boulders. Such possibilities have yet to be evaluated fully; there is a tendency to focus on large redds because they are so easily identified. Mortality of eggs can result from the excessive intrusion of fine particles that reduce water flow, and low-quality ground water seeping up through the redd. Throughout the life of the fish, good water quality with high oxygen and low levels of pollutants is beneficial.

Fry and parr

Young salmon hatch in spring as alevins and may start to feed while still fuelled primarily from a yolk-sac containing the remnants of food provision from the mother. They emerge as fry in synchronised groups and at night. The fish must quickly find shelter and are particularly vulnerable to predators at this time. Nocturnal emergence provides some cover due to low light, and the large number of salmon emerging together probably swamps predators, since they can only digest so many fry at a time. Perhaps the most dangerous predators at this time are those such as the bullheads, commonly found in England and a few waters in the south of Scotland, that live among the cobbles where the salmon themselves seek shelter as they disperse. This is a crucial stage for the salmon as it has very low energy reserves, is in an unfamiliar area and can hold station to feed only in relatively slow water currents. In some stream systems, the availability of suitable areas of slow water flow can determine the number of surviving fry and ultimately the number of smolts produced. In other systems it is a bottleneck in suitable habitat later in life, such as for over-wintering of pre-smolts, that determines final smolt production.

Dispersion of young salmon from the redd is usually strongly biased towards movement downstream and may be quite limited in extent such that even at the end of the second summer of growth, densities are high only within approximately 50m of the redd. Therefore, unless spawning substrate is abundant and well distributed throughout the stream, subsequent dispersal may limit the numbers of salmon locally. Dispersal is not generally continuous but tends to occur soon after fry emerge from the gravel and during the autumn and winter months.

Salmon fry and parr i.e. the older established pre-anadromous fish, can be very aggressive to one another and vigorously defend favoured areas of stream bed that provide them with good shelter and food availability. They are not distributed in fixed territories but move among different patches of habitat within overlapping home ranges. The reasons for such movements are not yet clear, but are not simply related to responses to change in local food and water flow. It is clear, however, that good sheltering and feeding positions may be spatially remote from one another, requiring changes in position depending on the needs at any one time for food and protection from predators.

Salmon parr form dominance hierarchies, which are sometimes also referred to as pecking orders. The most dominant, high-ranking fish can gain priority access to food and shelter but must pay the sustained energy cost of a high metabolic rate. It is not yet clear why resting metabolic rate is highest in dominant fish, but it is likely that these individuals maintain a high state of physiological readiness to digest food quickly. Dominant parr adopt a bold, stripey appearance whereas subordinates are more drab, with colouration that provides good camouflage. These fish tend to occupy marginal positions near cover where they feed by short-range bursts.

Even when free from the constraints of dominant fish, individual salmon parr use the local space in different ways. Some fish tend to feed predominantly on benthos, food crawling on the substratum, whereas others feed on insect larvae drifting downstream and may hold position by swimming actively in the water column. The relatedness of parr influences their use of space on the streambed. "Dominant" salmon aggressively repel invaders from favoured areas unless those fish are its kin, in which case it allows them to feed. Hence the quality of a local patch of habitat is related to both its physical properties and the way that they are used by the particular fish that occupy the space. It is likely that different families of salmon use the habitat in slightly different ways. Local densities of salmon parr are highest when the population comprises mixtures of families, presumably because they can then use the available habitats most fully.

Salmon use their habitat in different ways at different times of the day. The focus of attention to date has been on the daytime, when the fish are easily observed. However, it is becoming increasingly clear that by preference salmon emerge from shelter under the cover of darkness, regardless of season. It is likely that the rules of engagement among competing fish are quite different at night when it is perhaps more difficult for individuals to gauge the status of the fish they are up against. There is currently little information regarding the role of social structure in nocturnal feeding. However, it is well established that smell plays an important part for salmon in distinguishing one from another and this sense may be particularly important at night and under turbid conditions when visibility is reduced.

Salmon need less food in winter than in summer so that in cooler months habitat that offers good sheltering opportunities becomes of overriding importance. There may be a change in the spatial distribution of fish during autumn reflecting a move to regions with high abundance of interstitial spaces or water depths that provide shelter and avoid the risk of becoming trapped within the gravel by ice. During winter, sheltering kin tend to avoid one another, perhaps reducing the risk of an entire family being destroyed in a local catastrophe.

It is evident that there is a wide range of ways that salmon use their habitat and therefore a need for a range of habitat types within the river. In general, parr tend to use deeper, faster-flowing areas with larger substratum particles as they grow. To an extent, this shift reflects the increased swimming capabilities of the fish as they get larger. However, small parr may also be excluded from their preferred areas by larger fish. Shallow areas with fine gravel substratum may provide young parr with refuge from such competition because there is an absence of shelter suitable for the larger, older fish.

Water chemistry is important for salmon. Good oxygenation is essential as are low levels of metals, such as aluminium, and more complex compounds such as organic pesticides. Nutrients, principally phosphates and also possibly nitrates in some systems, are required at intermediate levels. Low levels of phosphates or other limiting nutrients in upland regions result in low production of invertebrate food whereas high levels of phosphates and nitrates in agricultural regions can cause streams to choke with algae. The principal components of physical habitat are depth, flow rates and the nature of the stream bed, which together influence food and shelter for the fish. A mixture of boulder and cobble with abundant low-velocity niches and occasional pools is a highly productive habitat.

Crucially important too is the biotic habitat. This comprises the community of plants and animals that include prey, predators and competitors. To an extent, the biotic, physical and chemical habitats are linked, in that certain types of animal and plant are associated with particular chemistries, flows and substrates. However, many factors beyond the local environment influence the presence and abundance of predators, such as otters and fish-eating birds, and competitors. The last of these may include, perhaps, the invasive signal crayfish, which can out-compete salmon for shelter and may affect salmon populations in some habitat types.

Trout frequently occupy areas of stream used by salmon and being a more dominant, aggressive species have been considered to be major competitors for food and space. However, recent work suggests that the presence of trout reduces aggression by dominant to subordinate salmon parr with a potential overall benefit for the salmon population. It remains to be seen how the balance of positive and negative effects of trout on salmon responds to their range of population sizes in wild habitats.

The complexity of factors that influence the position chosen by each individual fish is illustrated in Figure 1, which summarises the range of biotic - the plant and animal community and abiotic - the physical and chemical - habitats.

Recruitment, growth and "carrying capacity"

The number of salmon of a given size that can be supported in a patch of space depends on its chemical, physical and biological characteristics, the natures of the occupying fish and the season. This number may be termed the "carrying capacity".

The actual number of salmon in a local area of stream at a given time depends on how many eggs were deposited there, how many fish have immigrated and the subsequent mortality and emigration of those fish in the intervening period. If the local population is at its carrying capacity then the habitat can be said to be saturated.

Growth rates of salmon can vary with local population density. It can be the case that at high densities, fish are sufficiently stunted in size that they suffer high mortality at some later life stage, perhaps during over-wintering due to low fat levels. Therefore, the carrying capacity may be an optimum density which, if exceeded, leads to reduced numbers of smolts being produced. It is clearly apparent then that artificially elevating densities by stocking, even using stock with appropriate gene constitutions, can be damaging.

In general, as fish grow, their demands for food and space increase and the total number that can be supported within a patch of space at carrying capacity decreases. This process is termed self-thinning and is analogous to the concept of necessarily thinning out vegetable seedlings to enable a crop of full grown plants to develop. Although self-thinning due to a limit on food demands occurs in some cases, in others, the availability of suitably sized shelters may be the main factor that determines carrying capacity. For example, a fine-gravel substratum may be good habitat for small fry but **a** poor habitat for large parr because it provides only small shelters.

Spatial variations in density, size and habitat saturation

The consequence of dispersal, growth and self-thinning patterns is that unless spawning areas are abundant and well dispersed, substantial variation can be expected in the number and size of salmon found independent of local habitat quality. Fish near a redd tend to be at high densities but small whereas those further downstream are at lower density but larger. Progressing downstream from a redd, habitat may be saturated by different combinations of size and density until a point where, although the fish grow fast, they never fully use the available resource. Such patterns of dispersal and population processes help us to understand why substantial variation in numbers of fry and parr occur that may not be explained by local habitat characteristics. From a management perspective, the first consideration when finding low local densities of fish is an assessment of how available is the habitat needed by the earlier development stages, particularly for spawning. This process can establish where the bottleneck is in production of smolts so that appropriate remedial or conservation action can be targeted at the specific habitat that is limiting.

Leaving the river: smolts and pre-smolts

Some of the salmon from upper tributaries may leave their home stream in autumn, before smolting and going to sea the following spring. These fish need a secure habitat downstream of their natal area during winter, but as yet we do not know what this comprises or how far they have to go to find it. It is possible that these parr are particularly vulnerable to predators in the main river channel because immigrant parr are usually out-competed for space by residents, a phenomenon termed "prior-residence advantage".

Smolts aggregate into shoals as they migrate downstream in spring. For predators they are a dense food supply that is predictably available and easily exploited. Losses of smolts are particularly high in hydro-electricity reservoirs where they can be ambushed by fish and bird predators. Ideal habitats are those that allow rapid exit from the river, minimise disorientation and avoid bottlenecks where fish are funnelled through narrow gaps.

Hierarchies of scale

Local habitat for salmon in a section of stream is influenced by land-use within the stream catchment, which in turn is influenced by the regional geology and climate. This tendency for small-scale processes to be influenced by those occurring at larger spatial and temporal scales is termed a "hierarchy of scales" and has been found to be particularly appropriate to the biology and habitat of salmon-parr. An important implication is that the relationships between populations of salmon and their local habitat in any one catchment do not necessarily apply in all others. This expectation is realised in the variation in models to link habitat and salmon parr densities among regions of Scotland.

Habitat juxtaposition and connectivity

The location of different habitat types relative to one another (juxtaposition) at any given life stage can be expected to determine the amount of daily movement required by fish and hence their vulnerability to predators and their expenditure of energy. Furthermore, juxtaposition of habitat requirements for successive life stages is important because it determines the likelihood of fish migrating successfully to new habitats as they grow. Streams with mixtures of pool, riffle and glide areas with a wide range of substratum sizes offer the necessary habitats for a range of life stages with minimum need for movements. However, there may also be benefits in having discrete sections of more homogeneous habitats if this arrangement minimises competition among year classes. This is an important area of interest that requires further consideration and investigation.

Movement between habitat patches is possible only if they can easily be accessed through good connectivity. Natural waterfalls can impede connectivity as can man-made structures, such as weirs and dams.

Conclusions and applications

This summary of the biology of salmon in relation to freshwater-stream habitat indicates that many of the details of the lives of salmon in fresh water and their habitat requirements are well established although much remains to be learned regarding the larger main sections of rivers and of lochs. Conversion of the knowledge we have into practical management is required to improve or restore habitat and therefore increase the output of smolts. Scaling up from small scientific studies to river -management exercises while accounting for uncertainties in the process is not easy. Therefore, it is particularly important to monitor the success, or otherwise, of management initiatives by comparison between modified (treated) and unmodified (control) areas. Future actions can then benefit from past experience and be refined on the basis of the results of earlier trials. It is through this process of adaptive management that the entire management community can benefit and improve its knowledge base over time.

In some cases, management of habitat may require modest investment for large gain. Removing man-made obstructions to fish passage that can open up entire watersheds for production of salmon is a good example of this. In other instances, a substantial investment may be required, for example if seeking to change land-use and nutrient balance within a river catchment. In either situation, there is a reassurance that provided a suitable adaptive-management approach is in place, there can be real benefits derived for salmon populations irrespective of the less manageable factors affecting their survival on the high seas.

Appendix 1: summary checklist of some key points for managers

Water quality. Pollutant chemicals, such as heavy metals, may interfere with the normal biological functioning of fish, including the abilities to imprint to and respond to homing odours. They may also affect organisms that constitute food for salmon. Other chemicals, such as phosphates, nitrates and trace elements are essential for supporting the ecosystem that supplies food for salmon. These compounds are needed at intermediate levels since, when in excess, algal growth can choke streams.

Water quantity. Low flows (e.g. through abstraction) and prolonged high flows (e.g. through loss of water retention in the catchment) can be highly detrimental to all life stages and should be avoided where possible. Occasional high flow events may nevertheless be essential for maintaining low sediment intrusion in substrates.

Moderate temperatures. Juvenile salmon are physiologically geared to grow most rapidly at about 16°C. Warm temperatures during winter may be disadvantageous through increasing metabolic demands and consequently the need to feed and risk predation. Warm summer temperatures may facilitate rapid growth of parr, but may also increase the rate of energy loss in pre-spawning adults. High temperatures result in mortality.

Light. Bank-side vegetation may be beneficial in providing food of terrestrial origin and in stabilising stream banks. However, shading affects temperature regimes, which may be advantageous or disadvantageous depending on the local environment, and may reduce in-stream production of food by reducing the availability of light.

Good spawning habitat that is abundant and widely distributed. Areas of substratum of appropriate size are required. Excessive infilling with fine sediments may reduce survival and the emergence success of the early life stages.

Good nursery habitat. The period when fry emerge from the gravel is critical. They are particularly vulnerable to predators when aggregated and before establishing territories. At this stage the fish can feed effectively only at low water-flow rates and the availability of quieter patches of water, for example in the lee of boulders, is essential.

Good shelter. By choice, where food is sufficiently abundant, salmon parr stay in shelter during most of the daylight hours for protection from predators. Bouldery substrate is ideal in providing crevices that are secure from predators such as sawbill ducks, which can turn over smaller substratum particles. However, excessive boulder density can interfere with foraging and increase the risk of predation by forcing salmon parr into the water column to achieve the required field of view.

High food levels. Abundant food, primarily insect larvae, minimises the time that fish need to be out of shelter and vulnerable to predators, and increases the number of fish that can be supported in a given unit of space. Fast growth rates can also reduce the time taken to reach a size at which the fish can smolt and hence the number of competing year classes.

Moderate or low levels of predators. A degree of predation may be beneficial through thinning out populations to a density at which fish can grow sufficiently quickly. However, in many cases losses to predators beyond the early parr stages result in a direct decrease in the number of smolts produced. Furthermore, many smolts may be lost to predators as they migrate to sea.

Low levels of competitors. Competitors have the potential to decrease substantially the number of smolts produced. However, apparent competitors may also have beneficial effects through reducing aggression among salmon. Each case needs to be considered carefully.

Connectivity (access). There may be a need for the easing of obstructions and the provision of adequate water flows to enable the free movements of fish among habitat patches.

Appendix 2: further related reading in articles by the author.

These lecture notes are derived largely from a series of scientific reviews by the author and his colleagues. The full references to these sources are:

Armstrong, J.D., Grant, J.W.A., Forsgren, H.L., Fausch, K.D., DeGraaf, R.M., Fleming, I.A., Prowse, T.D. & Schlosser, I.J. (1999). The application of science to the management of Atlantic salmon: integration across scales. *Canadian Journal of Fisheries and Aquatic Sciences* 55, 303-311.

Armstrong, J.D., Kemp, P., Kennedy, G., Ladle, M. & Milner, N. (2003). Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fisheries Research* 62, 143-170.

Armstrong, J.D. (2005). Spatial variation in population dynamics of juvenile Atlantic salmon: implications for conservation and management. *Journal of Fish Biology* 67 (Supplement B), 35-52.

Armstrong, J.D. & Nislow, K. (2006). Critical habitat during the transition from maternal provisioning in freshwater fishes, with emphasis on Atlantic salmon and brown trout. *Journal of Zoology* 269, 403-413.

Armstrong, J.D. (2009). Variation in habitat quality for drift-feeding Atlantic salmon and brown trout in relation to local water velocity and river discharge. In: P. Kemp and D. Roberts. *Salmonid Fisheries: Freshwater Habitat Management*. Wiley-Blackwell.

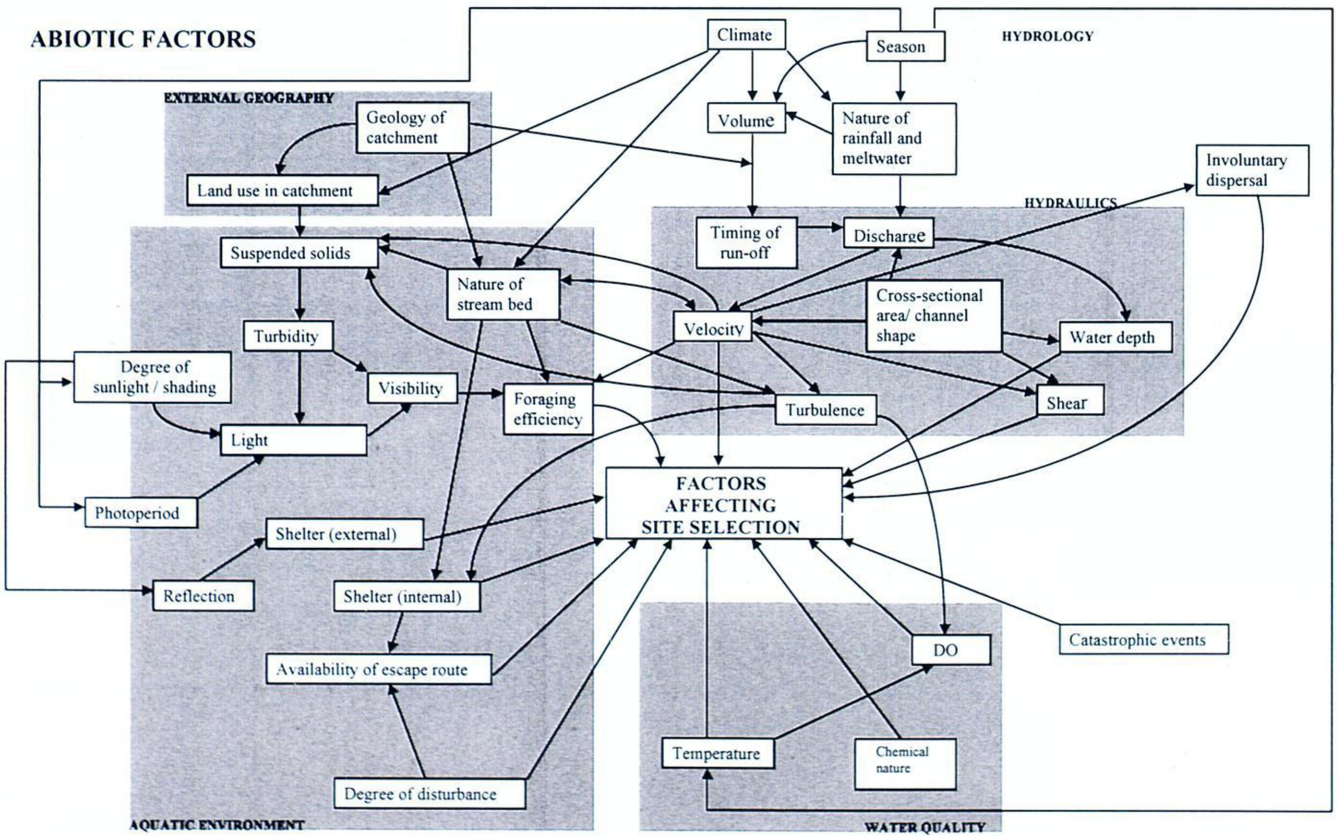
Höjesjö, J., Stradmeyer, L., Griffiths, S. W. & Armstrong, J.D. (2009). Effects of competing brown trout on habitat use by Atlantic salmon parr. In: P. Kemp and D. Roberts. *Salmonid Fisheries: Freshwater Habitat Management*. Wiley-Blackwell.

Nislow, K.H., Kennedy, B.P., Armstrong, J.D., Collen, P., Keay, J., McKelvey, S. (2009). Nutrient restoration using Atlantic salmon carcasses as a component of habitat management in Scottish highland streams. In: P. Kemp and D. Roberts. *Salmonid Fisheries: Freshwater Habitat Management*. Wiley-Blackwell.

Figure Legend

Fig. 1. The complexity of a) abiotic and b) biotic factors influencing local habitat choice in salmon parr (adapted from Armstrong *et al.*, 2003). (DO is dissolved oxygen).

ABIOTIC FACTORS



BIOTIC FACTORS