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Nutrient Transportation Associated With The Migrations Of Atlantic Salmon (*Salmo salar* L.).

Keith Williams

CANDIDATE'S ID NUMBER	0232860
CANDIDATE'S LAST NAME	Williams
CANDIDATE'S FIRST NAME(S)	Keith Leslie

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For

Keith Vivian Williams 1941-2002

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Contents

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Chapter 1

Introduction

Nutrients in Freshwater Ecosystems

Nutrients are essential in order that living matter can grow and reproduce successfully, and of particular importance are carbon (C), nitrogen (N) and phosphorus (P) (Stockner and Ashley 2003). C and N have a gas phase and are often readily available in freshwater ecosystems. P, however, does not have a gas phase, cannot be renewed and as such is often regarded as the element in shortest supply in most freshwater environments (Stockner and Ashley 2003). It should be noted, though, that other nutrients, for example silica, are also often of importance in freshwater ecosystems and that nutrients can be co-limiting in terms of primary production (Toetz 1999).

Production in freshwater systems can broadly be categorised as originating from two sources. Firstly, autochthonous production relies on the uptake of dissolved nutrients via photosynthesis by autotrophs such as periphyton (Waters 1993). Secondly, allochthonous production utilises nutrient inputs that originated outwith the stream in question. Typically, this may take the form of leaf litter and woody debris from riparian forestry that will be recycled by functional groups of invertebrates (termed shredders) that specialise in consuming this food source. Murphy (1998) notes that autochthonous production provides a more nutritious food source than allochthonous sources and that production from this source occurs over a shorter timescale. Vannote *et al.* (1980) proposed that in many river systems the relative importance of the two forms of production will vary longitudinally, a situation he termed the 'river continuum concept'. Put simply, in upper, heavily forested portions of the catchment it is likely that allochthonous production via leaf litter, woody debris etc will be more important than autochthonous production (which will itself be reduced due to the lack of light induced by the presence of dense forest). As stream order (the number of tributaries a stream has) is increased, however, the relative importance of autochthonous production also increases. Gradually, the dominance of allochthonous production in upper catchments will yield to the importance of autochthonous production further downstream as the physical characteristics of the waterbody alters.

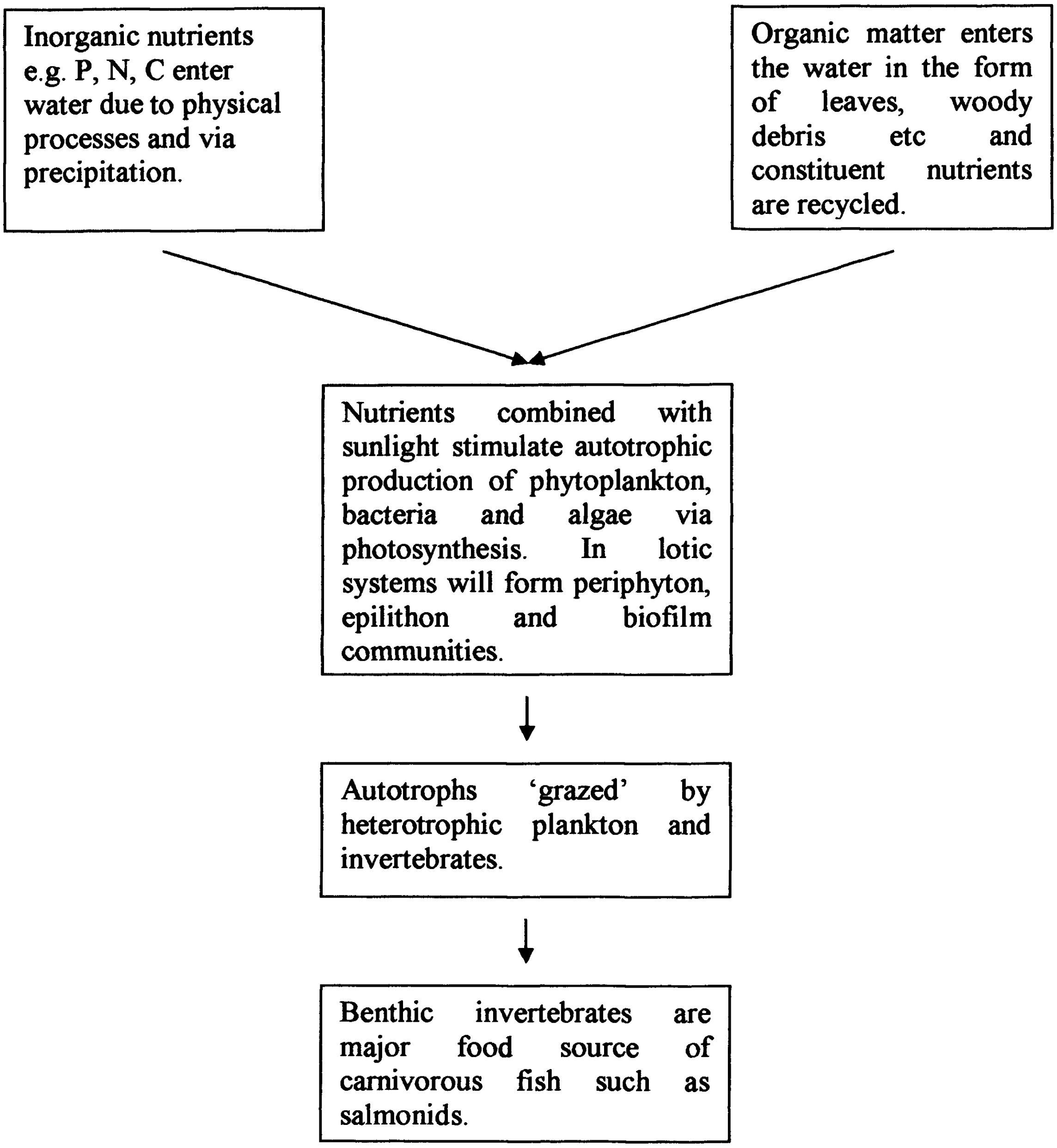
Primary production in freshwater ecosystems is likely to be dependent on a number of interacting factors such as light, nutrient availability, temperature, presence of herbivores, the physical characteristics of the stream and frequency of periodic flow episodes (Murphy 1998). Bisson and Bilby (1998) identified a number of broad categories of freshwater autotrophs that include vascular plants (largely aquatic angiosperms), bryophytes (mosses and liverworts), periphyton and phytoplankton (green and red algae), bacteria (principally blue-green algae) and protoists (diatoms, yellow-brown algae and euglenoids). Diatoms are considered to be of special importance due to the fact that they are a prime food source for herbivores and are usually favoured in the presence of filamentous and gelatinous algae (Murphy 1998). Abundance of invertebrate functional groups such as scrapers and collector-gathers will largely depend on the availability of these autotrophic food items. Benthic autotrophic production tends to display two annual peaks in production, the first occurring in spring and the second in autumn (Murphy 1998).

The availability of nutrients, especially N and P, has been shown to potentially be the most important limiting factor in the primary production of rivers and lakes (e.g. Perrin *et al.* 1987; Bothwell 1988, 1989; Morris and Lewis 1988; Perrin and Richardson 1997; Toetz 1999). In turn, levels of primary production are likely to influence the abundance of fauna at higher trophic levels, including species that may have commercial importance such as salmon and trout (*Oncorhynchus* spp. and *Salmo* spp). For example, Murphy *et al.* (1986) observed a causal positive relationship between juvenile coho salmon (*Oncorhynchus kisutch*) abundance and algal biomass on a river in North America. Additionally, Plante and Downing (1993) observed a relationship between overall trophic status and salmonid production within lacustrine environments. However, an excess of such nutrients (eutrophication) resulting from anthropogenic intervention can have what are perceived to be deleterious effects on aquatic communities and has thus been the focus of much research and attempts at remedial action (McClain *et al.* 1998). Inputs of nutrients from anthropogenic sources have the potential to radically alter species composition and diversity within ecosystems. At its most extreme, eutrophication can even result in fish kills due to removal of oxygen from waterbodies.

The process known as oligotrophication, or loss of nutrients, and concomitant reduced potential for biological productivity has in contrast received little research priority until recent times (Stockner and Ashley 2003). The productivity of watersheds, or parts of watersheds, already lacking in nutrients due to natural factors such as underlying geology may be further lowered by anthropogenic influences. Stockner *et al.* (2000) include changes in land use, forestry practices, impoundment of rivers, barriers to fish migration, habitat loss, over-harvesting of anadromous species and climate change as possible components in a process they term 'cultural oligotrophication'. Artificial impoundments, for example, may act as nutrient traps on some systems (Pieters *et al.* 2003).

Consideration of the factors affecting the abundance of commercially important freshwater fish species thus requires a thorough understanding of relevant trophic webs. For example, the availability of benthic invertebrates is believed to set the potential upper limit of salmonid productive capacity in many streams (Richardson 1993). Dislodged or migrating benthic invertebrates may form part of the downstream 'drift' that is an important source of prey for juvenile salmonids. The standing crop of benthic invertebrates is itself a function of a series of biotic and abiotic factors, however, that will include the availability of its own food sources. Figure 1 represents a highly simplified schematic of the nutrient pathways leading from primary production to salmon species in the lotic environment. It should also be noted that the recycling of organic nutrients will be achieved via a combination of microbial action and consumption of organic matter by some functional groups of invertebrates. The latter may also form a food source for juvenile salmonids. In reality, many interactions and feedback loops between trophic levels will exist and, for example, increased abundance of autotrophs may boost populations of both herbivorous heterotrophs and fish species which in turn are a source of food for both predatory invertebrates and carnivorous fish species. Abiotic factors that may also strongly influence each trophic level (e.g. light, river flow rates and dissolved oxygen availability may be highly important in periphyton production) are also omitted for simplicity.

Figure 1. Inputs of nutrients in lotic systems leading to Atlantic salmon production.



It should be noted, though, that the relative contribution of primary production in regulating overall biological productivity may vary widely between individual rivers and within rivers. For example, in some upland river systems allochthonous inputs in the form of leaf litter or woody debris may be highly important and the direct consumption of such items by detritivore invertebrates may effectively bypass the importance of primary production process within the river. In terms of salmonids, terrestrial invertebrates that fall into rivers can constitute an important source of prey, particularly older age classes of juveniles as noted by Mills (1964). Terrestrial invertebrates can also be considered to be an allochthonous input to freshwater systems (Bridcut 2000).

Fish as Sources of Nutrients

As fish grow they assimilate nutrients from their surrounding habitat. However, fish constitute prey items for a host of aquatic, avian and terrestrial predators and thus also represent a source of nutrients within food webs. Similarly, bodies of fish that succumb to disease or old age will be eaten by scavengers, broken down by bacteria or weathering processes and the nutrients they contain thus released and recycled. Many species of fish are highly migratory and thus act as vectors of nutrient transport within and between ecosystems (Murota 2003). Anadromous fish species accumulate much of their body mass in the relatively nutrient-rich marine environment but return to fresh water to spawn and as such have the potential to redistribute nutrients from the former to the latter. As such the nutrients assimilated in the marine environment can be considered to be potential allochthonous inputs to freshwater production.

A growing body of evidence suggests that Pacific semelparous (death occurs shortly after spawning) salmonids may play an important role in the distribution of marine-derived nutrients, via carcasses, gametes and the excretion of nitrogenous compounds, to the headwaters of rivers and lakes that are oligotrophic in nature (Schuldt and Hershey 1995; Cederholm *et al.* 1999; Gende *et al.* 2002; Naiman *et al.* 2002; Stockner and Ashley 2003). In turn, such nutrients are utilised at various trophic levels and, ultimately, juvenile salmonid production may itself be partly dependent on the annual influx of such nutrients, giving rise to the concept of the 'feedback loop' in assessments of Pacific salmon production in oligotrophic systems (Cederholm *et al.* 1999). Thus Pacific salmon have been afforded the status of keystone species from the viewpoint of some ecologists (Willson and Halpuka 1995).

The possibility of commercial overfishing of Pacific salmon stocks and the concomitant nutrient deficit that this may cause has led to a reappraisal of fishery management techniques in some regions (Larkin and Slaney 1997; Gresh *et al.* 2000;

Bilby *et al.* 2001; Knudsen *et al.* 2003). Thus, it has been suggested that spawning escapement levels for rivers should take into account the numbers of adult salmon required to produce adequate levels of nutrients for future salmon production rather than simply the number of adults needed to produce enough offspring to populate the system. In order to attempt to compensate for the lack of delivery of nutrients from returning salmon, fertilisation programmes utilising a variety of different techniques have been employed in both lacustrine and riverine environments (e.g. Griswold *et al.* 2003; Wilson *et al.* 2003). Achord *et al.* (2003) also note that density-dependent mortality may impinge on even depressed levels of Pacific salmon due to a reduction in the carrying capacity of habitat resulting from human perturbation of natural processes i.e. the reduction in returning salmon and hence nutrients due to overfishing, dam construction etc.

Stable isotope analysis has been employed in order to demonstrate the degree of utilisation of some marine-derived nutrients (especially C and N) by riparian flora and fauna and is an area of active research. Marine organisms typically display elevated levels of $\delta^{13}C$ and $\delta^{15}N$ compared to freshwater organisms, allowing the movement of marine-derived nutrients through trophic pathways to be traced Kline (2003). Using this approach Kline *et al.* (1990, 1993) and Bilby *et al.* (1996, 2001) have demonstrated the effects of spawning salmon on periphyton, epilithon and invertebrates in aquatic environments. Hicks *et al.* (2005) studied the effects of enrichment engendered by naturally occurring and artificially introduced salmon carcasses and eggs in beaver ponds in Alaska and concluded that enrichment was detectable in aquatic vegetation, invertebrates and fish – including salmon.

Similarly, the extent to which nutrients derived from salmon are incorporated into terrestrial trophic pathways has been highlighted and includes riparian soil, vegetation and insects (Helfield and Naimen 2001, 2002; Bilby *et al.* 2003; Reimchen *et al.* 2003; Bartz and Naimen 2005; Wilkinson *et al.* 2005), wolves (*Canis lupus*) (Darimont and Reimchen 2002), bears (*Ursus arctos*) (Hildebrand *et al.* 1996) and mink (*Mustela vison*) (Ben-David *et al.* 1998). The use of wood sample cores from trees has allowed assessment of the historical contribution of salmon to the productivity of the riparian zone (Reimchen *et al.* 2003). In addition to the use of stable isotope analysis, observers have noted the utilisation of salmon carcasses by a host of terrestrial and aquatic animals (e.g. Jaquet *et al.* 2003).

The importance of nutrients derived from salmon carcasses and gametes to the productivity of individual river systems has not been universally accepted, however. Rand *et al.* (1992) state that phosphorus is not a limiting factor on the production of introduced Pacific salmon from tributaries of Lake Ontario, arguing that light is the most important limiting factor. This is largely because the streams are already fertile: P is thus readily available for primary production. The authors do note, though, that P from carcasses does represent over 50% of the total daily discharge of phosphorus from streams during some periods in the spring. Interestingly, the study produces an historical model to simulate the effects of Atlantic salmon carcass decay in presettlement (i.e. oligotrophic) conditions with large numbers of spawning salmon in a stream now utilised by the introduced pacific salmon. The results suggest that these carcasses would have contributed an average of 5.4% to the total export of phosphorus in the stream under examination – a figure not considered to be a significant contribution by the authors. A model simulating nutrient loading of Redfish Lake, Idaho, by Pacific salmon reached similar conclusions (Gross *et al.* 1998). It would therefore appear that the importance of nutrients derived from marine-derived sources is likely to be location specific and may be of little significance in river systems not characterized by low ambient nutrient status.

Despite extensive research, transport pathways and storage mechanisms of marine-derived nutrients within freshwater and terrestrial ecosystems are as yet poorly understood (O'Keefe and Edwards 2003) and some possible vectors of nutrients have only recently been investigated. A study on Lynx Creek in Alaska, for example, has suggested that nutrients, particularly P, from spawning sockeye salmon (*O. nerka*) may be stored during the winter period in riparian hyporheic zone (subsurface saturated areas) sediments and heterotrophic biota and may subsequently become available to boost primary production within the stream (O'Keefe and Edwards 2003). Perhaps crucially, the substrate chosen by spawning salmon is also considered ideal for hyporheic flow.

Whilst much of the focus of research into nutrient transport has centred on Pacific salmon species, other anadromous species have also been examined for potential importance. Durbin *et al.* 1979; Garman and Macko 1998; Close *et al.* 2002, for example, have examined the nutrient contributions of the pacific lamprey (*Lampetra tridenta*) and clupeids such as alewife, shad and blueback herring (*Alosa* spp). Stable isotope analysis has also been utilised to trace the utilisation of marine-derived nutrients from such sources in trophic pathways. Thus, Macavoy *et al.* (2001) noted that the consumption of anadromous clupeids by a piscivorous freshwater catfish (*Ictacurus furcatus*) in Virginia resulted in the signature of ^{34}S and ^{13}C shifting towards its marine signal.

Assessment of the potential importance of anadromous fish in nutrient transport requires close consideration of the life history of the individual species in order that the spatial and temporal aspects of the movement are fully accounted for. For example, adult anadromous rainbow smelts (*Osmerus mordax*) are an important forage fish for commercially important species such as landlocked Atlantic salmon (*Salmo salar*) in eastern North America and return to fresh water to spawn in late spring (March-May), a time when many fish species are increasing feeding after the winter period and associated low water temperatures (Buckley 1989). Mortality after spawning varies between 25-75% depending upon location. After hatching, juveniles quickly drop downstream to the sea. Due to this limited rearing time in fresh water, returning adult smelts represent a large subsidy of nutrients to the freshwater environment. In contrast, Atlantic salmon may spend many years in fresh water prior to migration to the sea (Youngson and Hay 1996) and the nutrients assimilated during that time are exported from their natal river to the sea. Hence the net effect of Atlantic salmon migrations requires that the nutrients returned by adults to the freshwater environment are balanced against the nutrients removed by migrating juveniles.

Nutrients and Atlantic Salmon

There would appear to be a general paucity of information regarding the role of nutrients in the production of wild Atlantic salmon. Attempts to establish a relationship between riverine nutrient status and Atlantic salmon production has proved problematical. Bergheim and Hesthagen (1990) assessed production in various sections of the Kvassheimsåna in Norway, the lower sections of which received nutrient inputs via agricultural land use. No relationship between these inputs could be established, however, perhaps due to the relatively high ambient nutrient status of the river. However, some studies have suggested that nutrients may play an important role in the productivity of individual river systems. Kennedy *et al.* (1983) reported a correlation between increases in the growth of salmonids and the use of agricultural fertilisers in the vicinity of the River Carnowen, Northern Ireland. Gibson and Colbo (2000) reported what they termed 'exceptional rates' of growth and overall biomass of brown trout (*Salmo trutta*) and Atlantic salmon in sections of the Waterford River in Canada believed to result from the anthropogenic introduction of nutrients within urban areas. Overall, though, evidence of a relationship between riverine nutrient status and Atlantic salmon production is unsatisfactory.

With the major exception of an analysis of nutrient pathways leading to Atlantic salmon in the Miramichi system in Canada, stable isotope analysis appears to have been little used for investigations involving Atlantic salmon, especially compared to Pacific salmon (Doucett *et al.*1996). However, the use of such analysis has great potential for tracing the movements of Atlantic salmon and revealing trophic pathways and as such is likely to be increasingly used in the future. Pioneering use of such techniques has been used on tributaries of the River Conon, however, to trace the movement of marine-derived nutrients through trophic levels that include periphyton, invertebrates and salmonids (Keith Nislow, personal communication).

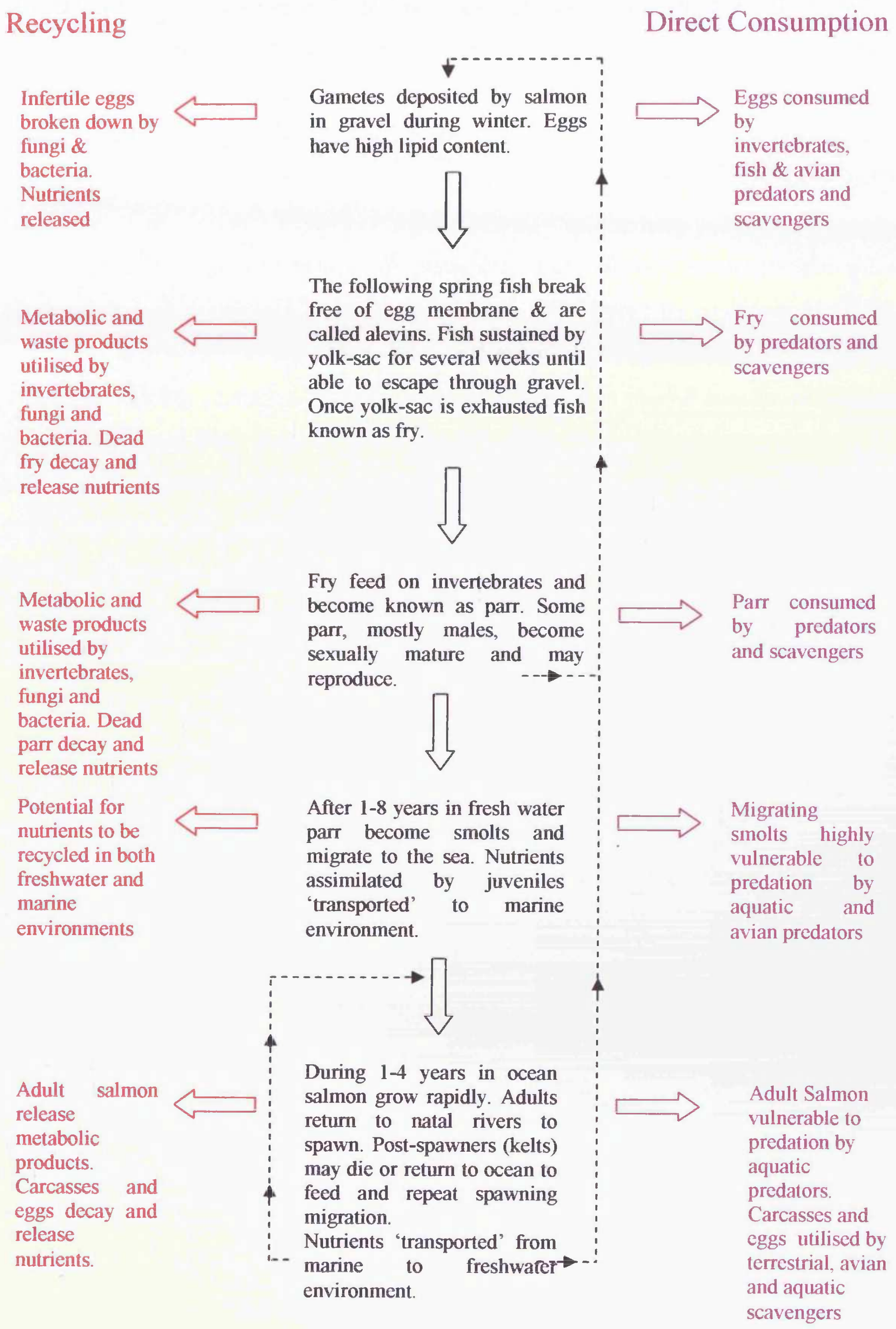
Perhaps due to their iteroparous life cycle (i.e. the ability to reproduce more than once) and lower abundance, the importance of Atlantic salmon in the nutrient flux of river systems has not been as thoroughly studied as their Pacific counterparts. Consideration of the movements of nutrients associated with salmon migrations requires a thorough understanding of the life history of the species under consideration. The reproductive strategies of Atlantic salmon display a high degree of plasticity throughout their range and as such meaningful assessments often have to be made at the level of individual river systems (Fleming 1996).

A simplified synopsis of the life cycle of Atlantic salmon and associated implications for nutrient transport is represented by Figure 2. The definition of the term fry and parr appears to be somewhat arbitrary and many authors are equivocal as to the precise point at which an individual transforms from a fry to a parr. For simplicity, in the present study fry will refer to individuals that are young-of-the year while the term parr will refer to all other age classes.

It should be noted that not all Atlantic salmon populations are characterised by anadromous behaviour and many salmon successfully complete their life cycle in fresh water. Indeed, so-called landlocked populations are endemic to North America, Scandanavia and Eastern Europe (Youngson and Hay 1996). Landlocked salmon have also been introduced in a number of regions in both the northern and southern hemispheres. In many of these populations large lakes are utilised by the adult salmon. Additionally, even within ostensibly anadromous populations a proportion of male parr will mature in fresh water and engage in spawning activities. Some of these will die after spawning but others may successfully undergo smoltification and migrate to the marine environment.

The ability of Atlantic salmon to successfully spawn on more than one occasion also varies greatly between populations (Mills 1984). Cunjak (1998) notes that a variety of factors are likely to influence the ability of salmon to recover from the rigours of spawning and return to the marine environment. Of particular importance are the physical characteristics of the river and associated availability of suitable overwintering habitat and also water temperature. High water temperatures are likely to have deleterious effects on survival rates and thus there are likely to be latitudinal differences between river systems. Genetic factors are also likely to play an important role. Overall, though, the post-spawning behaviour of Atlantic salmon appears to have received scant research attention.

Figure 2. Nutrient dispersal pathways from Atlantic salmon.



Murota (2003) notes that the 'nutrient shadow' cast by returning Atlantic salmon historically penetrated far inland in both North America and Europe. Migrations to tributaries of Lake Ontario and the headwaters of the Rhine, for example, entailed inland journeys of around 1000km. Some studies have suggested that returning adult Atlantic salmon may in fact make an important contribution to the availability of nutrients, particularly in those watersheds, or parts of watersheds, in which such nutrients are otherwise scarce (Jonsson and Jonsson 2003). If correct, this would have important implications for fishery management – particularly those engaged in restoration/enhancement schemes. In particular, many fishery managers currently plant salmon eggs or stock juveniles in habitat that cannot be easily accessed by migrating adults (above waterfalls, other natural obstruction or dams) in order to avoid introducing juveniles to areas already stocked by natural means. Migrating smolts from areas that cannot be easily reached by returning adults thus may represent a loss of P and other nutrients to that area in that they transport nutrients obtained via the consumption of invertebrates and vertebrate fauna to the sea (Nislow *et al.* 2004a). Similarly, Cunningham *et al.* 2002 suggest that restoration efforts on Scottish rivers with depleted migratory salmonid runs may be hampered by the lack of marine-derived nutrients, in particular P, hitherto available from the carcasses of post-spawned salmon and sea trout.

Estimates have been produced for the flux of marine-derived nutrients to some rivers in north-east England (Elliott *et al.* 1997; Lyle and Elliott 1998) and the River Imsa in Norway (Jonsson and Jonsson 2003). The former study highlights the fact that migratory salmonids may represent a net influx of such nutrients to river systems - but that when compared to the overall annual river loads of nutrients the percentage represented by the influx are very small (0.09-0.24%). However, the authors note that such calculations represent only an estimate of the total flux passing the river mouth. Given that the majority of salmon spawn in the upper reaches of rivers, the impact of such nutrients being deposited in these relatively small areas is not assessed by this type of study. Nislow *et al.* (2004a) highlight the importance of upland areas as rearing habitat, particularly for the early-running components of salmon stocks that are currently under pressure. This study, conducted on the River Bran in Scotland, represents the most comprehensive review currently undertaken of nutrient flux (in this case P) caused by Atlantic salmon migration in that downstream as well as upstream movements are modelled. Jonsson and Jonsson (2003) suggest that migratory fish provide the only direct source of marine-derived nutrients to the headwaters of rivers. The Imsa study states that the average annual flux resulting from salmon migration was in the order of 0.6% for nitrogen and 5% for phosphorous, and that these figures were high compared to those from the north-east of England due to the general nutrient load of the river being low. The authors suggest that the influx of these otherwise scarce elements may play an important role in the structure and dynamics of riparian ecosytems.

Since the potential importance of Atlantic salmon carcases and gametes with regard to sources of nutrients is contentious, empirical studies are required. Youngson and Hay (1996) for example, note that salmon 'parr eat substantial numbers of eggs' produced by adults and that the lipid content of eggs consumed may subsidise survival during periods of non-feeding in the low water temperatures of winter. Cunjak (1998), however, has suggested that this aspect of juvenile salmon feeding requires further investigation due to the absence of empirical data. Perhaps the most important contribution to the understanding of the role of decaying Atlantic salmon carcasses in freshwater ecosystems has been the use of stable isotope analysis on the River Blackwater, part of the Conon system in Northern Scotland. Enrichment of periphyton, invertebrates and juvenile fish by marine-derived nutrients was observed up to 400m downstream of individual carcasses (Keith Nislow, personal communication). Figure 3 shows a pre-spawned adult Atlanic salmon carcass removed from the River Carron, Sutherland, Scotland, by a predator or scavenger. The orange egg mass has become separated from the carcass and is visible on the gravel beside the fish.

Figure 3. Adult Atlantic salmon found by a river bank. The abdomen of the fish has been opened by a predator or scavenger.

To date, few documented attempts to manipulate nutrient levels of Atlantic salmon rivers appear to have been undertaken. A study of two tributaries of the Sainte-Marguerite River, Quebec, by Weng *et al.* (2001) utilised drip-fed phosphoric acid to assess the impact of fertilisation on periphyton, benthic invertebrates and Atlantic salmon and brook trout (*Salvelinus fontinalis*). A large flood prevented much of the experiment continuing but recovery of periphyton and in turn other trophic levels was quicker in enriched sections of rivers than in their unenriched counterparts (1.73-2.06 mg chlorophyll $a.m^{-2}.day^{-1}$ in enriched sections compared to 0.24-0.26 mg chlorophyll $a.m^{-2}.day^{-1}$ in unenriched sections). The authors conclude that the addition of nutrients may therefore be a useful tool in the restoration of rivers that are nutrient poor. Mills (1969) describes how Allt a'Chomair (part of the River Conon system in northern Scotland) was fertilised in April and June 1966 by the addition of calcium superphosphate in hessian bags. The standing crop of juvenile salmon was found to have increased by 10% on the previous year, but due to the absence of experimental controls this cannot be simply ascribed to the addition of fertiliser. The author also notes that experiments undertaken to fertilise a loch on the system produced better results than direct fertilisation of a stream.

When considering the artificial fertilisation of river systems, interspecific interactions at various trophic levels must also be taken into account. Mookerji *et al.* (1999, 2004) suggest that Atlantic salmon may be able to respond more rapidly to changes in the abundance of grazing invertebrates (themselves responding to increases in periphyton production) compared to sympatric populations of brook trout. This is a result of juvenile salmon being largely benthic feeders and brook trout consuming more insects of terrestrial origin. Studies of the stomach contents of salmon and brown trout on the River Bran by Mills (1964) suggests some overlap in prey species, although salmon diet consisting largely of benthic invertebrates and brown trout consumed more items of terrestrial origin. There was also a degree of temporal variation in the extent of this overlap. Similar partitioning of prey items between salmon and brown trout was reported by Bridcut (2000). It should also be noted that interspecific competition within invertebrate communities may result in reductions in abundance of some species of insects. In an extensive analysis of the effects of P fertilisation on the ecosystem function of the Kuparuk River, Peterson *et al.* (1993) observed reductions in the populations of blackflies (*Stegopterna mutate* and *Prosimulium martini*), probably as a response to interspecific competition with caddisflies (*Brachycentrus americanus*). The size of Arctic grayling (*Thymallus arcticus*) increased post fertilisation suggesting that blackflies were not an important component in the diet of this fish species, or the loss of such insects was compensated for by increases in abundance of other species also used for food. Gibson and Colbo (2000) also note a reduction in the diversity of invertebrate taxa in enriched sections of a river. These studies highlight that attempts to increase the abundance of a given species of commercial importance, e.g. salmon, must take into account the complexities of interactions within food webs.

A review of the literature with regard to Atlantic salmon and marine-derived nutrients reveals large gaps in available knowledge, particularly in comparison with Pacific migratory salmonids (Nislow *et al.* 2004a). Because Atlantic anadromous salmonids are iteroparous, much of the relative importance of the nutrients they contain will depend on the degree of retention of carcasses within the key nursery areas of river systems. Kelts (salmon that have spawned) attempting to return to the sea may die in the lower reaches of rivers or the sea itself, with the nutrients they contain thus being lost from upland, oligotrophic parts of the system. Kelt carcasses may also be washed into lochs during periods of high winter flow. Therefore these lakes may act as an important nutrient sink on some river systems. Similarly, the ability of invertebrates to sequester nutrients from carcasses during their passage downstream and the role of terrestrial and aquatic predator and scavenger communities in distributing nutrients from Atlantic salmon may be of importance. Knowledge on the temporal importance of nutrients derived from salmon within food webs is also lacking.

Aims of this Study

The aim of this study is to close gaps in knowledge regarding Atlantic salmon and nutrients in a number of key areas and test the hypothesis that returning adult salmon can contribute important nutrients to freshwater ecosystems. The particular aims of this project are:

- Conduct a nutrient manipulation experiment to investigate the relationship between inputs of nutrients and production of juvenile salmon.
- Assess the temporal and spatial aspects of adult salmon mortality in an upland, nutrient poor location and improve the accuracy of the model of nutrient flux resulting from salmon migrations on the River Bran developed by Nislow *et al.* (2004a).
- Assess how the presence of natural features e.g. a loch may alter the nutrient status and hence productivity of riverine habitat.
- Assess if anthropogenic or natural factors that occur in fresh water may impinge on marine survival of salmon and in turn affect the input of marine derived nutrients to freshwater systems.

Chapter 2

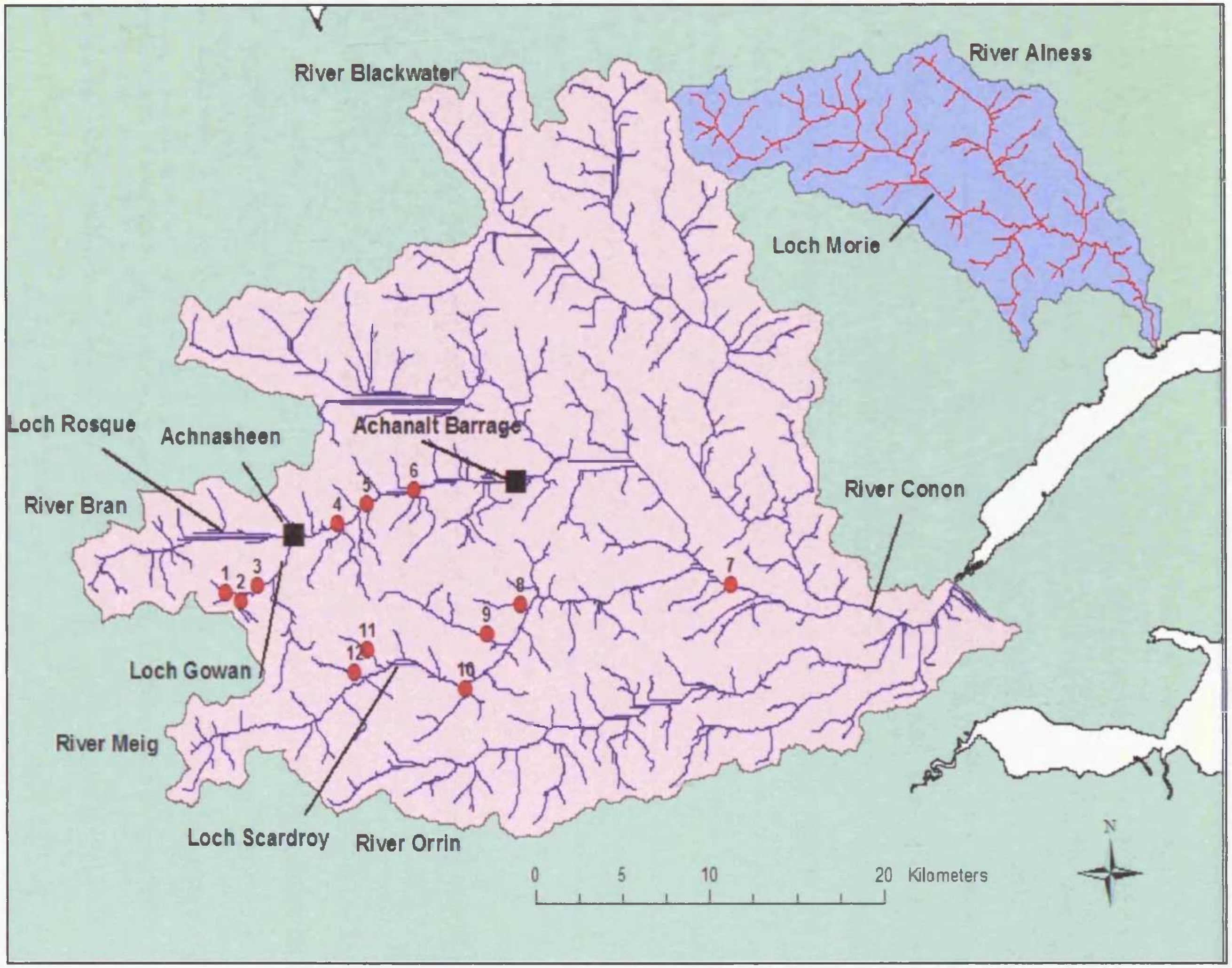
River Conon as a Study Area

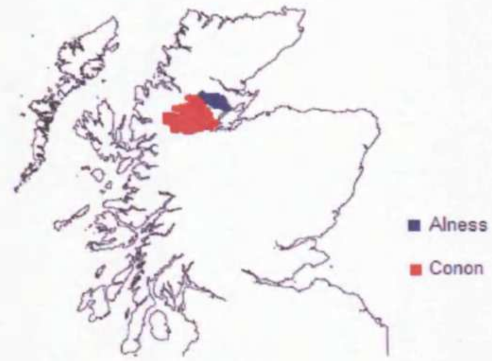
General Description of River Conon Catchment

The majority of the investigations undertaken in the present study were conducted within the catchment of the River Conon. The exception was the inclusion of the River Alness for one investigation. The River Conon is located in the Northern Highlands of Scotland and drains a catchment of approximately 625km^2 (Grimble 1908). There are a number of important tributaries within the River Conon system, in particular the River Blackwater, the River Bran, the River Meig and the River Orrin (see Figure 4).

The River Conon catchment has been heavily modified by anthropogenic influences. In particular, the harnessing of much of the watershed for the provision of hydroelectric power radically altered the flow regime and the ability of migratory fish to access parts of the river system. The system was first utilised for hydroelectric production in the 1920's with the installation of a small-scale scheme at the Falls of Conon (Anon 2005). Between 1946 and 1961, however, extensive development of the system was undertaken that utilised all the major tributaries as well as the mainstem of the Conon itself (Payne 1988). Thus a total of nine dams and seven power stations were installed and over 1000km of pipe were utilised in the development of the scheme. The harnessing of the system for the production of electricity has altered the hydrological and sediment regime of the Conon and its tributaries due largely to the presence of artificial reservoirs and flow regulation (Anon 2000) and has also radically altered the areas available to be utilised by adult and juvenile Atlantic salmon (Payne 1988). For example, the River Bran was historically inaccessible to salmon due to the presence of an impassable falls but these were circumvented by the provision of a fish ladder. In contrast, historically important nursery areas of the River Blackwater are currently inaccessible due to the lack of fish passage facilities.

Figure 4. Map of the Conon and Alness catchments showing the important study areas.





Red dots represent the study burns used in the carcass addition study.

1 Gharagain
2 Luib
3 Coire a Ghormachain
4 Chamasaidh
5 a Chomair
6 Chaiseachain
7 Garrimatic
8 t-Straithain Mhoir
9 Gleann Meinich
10 Gleann Chorain
11 Scardroy
12 Coire a Bhuic

The river Conon catchment provides a wide variety of habitat. The catchment has been described by Anon (2000) as 'a typical Scottish highland glen with rugged mountains in the headwater areas and glaciated valleys containing active gravel beds feeding into a lowland floodplain'. The latter was once characterised by bog and alluvial woodland and whilst much of the floodplain has been the subject of drainage schemes in order to provide land for agricultural use, important remnants of riparian woodland remain (Anon 2000). Much of the upper catchment was once characterised by native woodland below an altitude of 450m, especially in the riparian corridor, with heath and moorland dominating at higher altitudes (Anon 2000). Much of this woodland has been removed due to agricultural practices and demand for wood to be used as a source of fuel. However, parts of the systems have also been the more recent focus of commercial forestry planting which have largely utilised non-native conifer and spruce species. The changing land use and deforestation and reforestation practices are likely to have impacted on the flow, sediment and nutrient regimes on the River Conon (Anon 2000). For example, trees provide protection to soils from rainfall and in particular tree roots are important in binding soils and preventing erosion. Removal of canopy cover is thus likely to have increased rates of soil erosion, lowered ability of soils to store rainfall and hence increased peak discharges of the river. However, canopy cover is likely to have had other impacts on the hydrological regime of the catchment as native woodland effectively intercepts much rainfall during summer months and can delay snowmelt during the winter and spring periods (Anon 2000). Assessment of the overall effects of removal of the original native woodland and the more recent introduction of non-native species in the form of commercial plantations is likely to be highly complex.

The flow regimes in the system are likely to be heavily influenced by the bedrock geology of the catchment. The upper parts of the system are dominated by the presence of hard rocks such as granite and schist whereas the lower altitude parts of the catchment consist largely of soft rocks such as sandstone. The thin soils, hard bedrock and steep gradients of the upper catchment facilitates rapid surface runoff in contrast to the floodplain (Anon 2000). In contrast, base flows in the upper part of the catchment are considerably lower than on the floodplain. The presence of hydroelectric impoundments in the lower reaches is also likely to have lessened the likelihood of extremes of flow conditions. Nutrient flux of P, N and sulphur in rivers are strongly positively related to discharge levels, although actual concentration levels of the nutrients are less predictable and responses to changes in discharge may vary depending upon the season McClain *et al.* (1998).

Many of the upper parts of the catchment are characterised by low ambient nutrient status, particularly with regard to P (Nislow *et al.* 2004a). Additionally, there are few population centres in the upper regions of the watershed which lowers the likelihood of significant anthropogenic inputs of nutrients into the rivers in these areas. Urban centres often contribute large amounts of nutrients to the overall loading of waterbodies for example via sewerage outflows. As such the upper portions of the Conon catchment offer an ideal location to conduct nutrient manipulation experiments.

Research Potential of the Conon System

Despite, or perhaps because of, the large anthropogenic influence on the River Conon, the system has been the focus of a considerable amount of research particularly with regards to salmonids. For example, a number of pioneering studies with regard to the ecology of salmon and in particular their relationship with their environment and interactions with predators and competitors were undertaken in the period following the extensive alterations of the system due to hydroelectric development. Mills (1964) produced an extensive study of the ecology of introduced juvenile Atlantic salmon in the River Bran. More recently, Gowans *et al.* (2003) utilised telemetry to study the movements and behaviour of returning adults with regard to the fish ladders and fish passes in various locations in the catchment.

Traps have been extensively employed within the Conon system for both research and management purposes. On the River Blackwater, a trap at Loch na Croic captures adult salmon on their upstream spawning migration and provides broodstock for the large-scale hatchery operation conducted annually. The hatchery has a capacity in excess of three million eggs and as such constitutes one of the largest wild-fish hatcheries currently in operation in the United Kingdom (Simon McKelvey, personal communication). Stocking on the Conon catchment is conducted exclusively on the tributaries of the system and takes the form of producing artificial redds (nests) for eggs, unfed fry, fed fry and small quantities of smolts. The purpose of stocking is to mitigate for the adverse effects of the hydroelectric schemes on the salmon population. Many studies on juvenile salmon ecology require copious quantities of juveniles to be stocked in order to be successful. At Achanalt Barrage, on the River Bran, another trap captures smolts migrating downstream each spring. In order to facilitate successful migration of returning adult salmon to the upper reaches of the catchment some of the dams have inbuilt Borland fish passes (Gowans *et al.* 2003). These are fitted with automatic fish counters that register fish movements in both an upstream and downstream direction. Historically, traps were also positioned on the River Meig and at Tor Achilty dam on the mainstem of the Conon and important data in respect of survival of adult salmon after spawning was garnered from these facilities.

The combination of these features allows research to be conducted regarding salmon ecology at a number of key stages of their life cycle. For example, since 1996 numbers of smolts have been captured by electrofishing in tributaries of the River Bran and tagged with passive integrated transponders (PIT). Those that survive downstream migration are recaptured at the Achanalt smolt trap facilitating research into such factors as speed of migration and survival rates. Similarly, smolts have also been tagged at this location and released further downstream in order for factors influencing marine mortality to be assessed. The PIT tags are placed in the body cavity of the smolts and the tags in the returning adults are detected automatically by aerials placed within fish passage facilities. The presence of such features has enabled long-term data sets to be established which provide an ideal means of examining trends in salmon survival and salmon management (e.g. Nislow *et al.* 2004a).

Chapter 3

Response of Juvenile Atlantic Salmon to Carcass Additions

Introduction

Water chemistry is likely to have an important bearing on the productivity of salmonid streams (Binns and Eiserman 1979; Egglishaw and Shackley 1985). Thus Binns and Eiserman (1979) include nitrate nitrogen in a model of factors explaining production of various salmonid species in a number of different river systems in Wyoming, U.S.A. Assessment of the relative importance of water chemistry in terms of salmonid production within an individual stream is problematical, however, given that a host of other factors are also likely to influence production, for example water temperature and substrate type.

Atlantic salmon producing rivers are likely to have experienced considerable alteration to their physical and chemical characteristics as a result of anthropogenic activity (Elliott *et al.* 1998). In particular, it is likely that many river systems have been subjected to forest clearance and river flow regulation, both of which may have serious implications for the nutrient dynamics of a given river. Whilst juvenile salmon production is related to nutrient status, returning adults themselves have the ability to alter nutrient availability in their natal streams via excretion of metabolic products, gametes and carcass decay (Chaloner *et al.* 2004). Little information with regard to the ecological effects of nutrients made available by the return migration of adult Atlantic salmon is available although the recent pioneering use of stable isotope analysis to assess the effects of carcass decay on periphyton, invertebrate populations and fish within the River Conon catchment has suggested that significant effects may accrue (Keith Nislow, personal communication). In addition, a considerable and growing body of evidence from North America is available regarding the importance of marine-derived nutrients from returning Pacific salmon to riparian ecosystems (Naimen *et al.* 2002). Attempts to counter oligotrophication via nutrient additions, including the use of salmon carcasses, have been undertaken on various river systems in North America (Stockner and Ashley 2003).

The direct and indirect effects of adult Pacific salmon carcasses on the ecology of riparian, riverine and lacustrine environments have been extensively studied (e.g. Kline *et al.* 1990, 1993; Schuldt and Hershey 1995; Bilby *et al.* 1996, 2001; Wipfli *et al.* 1998,1999; Minakawa and Gara 1999; Wold and Hershey 1999; Chaloner *et al.* 2002a, 2002b, 2004; Minakawa *et al.* 2002; Ito 2003; Jauquet *et al.* 2003; Nakajima and Ito 2003; Quamme and Slaney 2003, Heintz *et al.* 2004; Bartz and Naiman 2005). Many of these studies utilise mesocosm or natural stream experiments, or a combination of the two, in order to ascertain trophic responses to carcass-derived nutrients. It should also be noted that spawning salmon also provide a number of other important ecological functions such as making benthic invertebrates available to predators during gravel excavation (Minakawa and Gara 1999). Responses to the introduction of nutrients have not proved to be universally positive, however, as attempted manipulation can be mitigated by other limiting factors e.g. light (Rand *et al.* 1992; Ambrose *et al.* 2004; Chaloner *et al.* 2004). Zhang *et al.* (2003) also report that the presence of salmon carcass material in a mesocosm study retarded the decomposition of leaf litter.

Although many river systems in Pacific North America have large numbers of salmon spawning annually, Wold and Hershey (1999) state that even small levels of nutrients can have important effects at a local level on nutrient limited streams. Similarly, Schuldt and Hershey (1995) reported increased periphyton biomass, nitrogen and phosphorus levels after the introduction of only twenty-four chinook (*O. tsh*awytscha) carcasses to Lake Superior tributary streams. This may have implications for the study of similar responses in Atlantic salmon rivers where numbers of spawning adults are likely to be much lower than in many Pacific salmon producing systems. It should also be noted that many other factors play an important role in making nutrients available from carcasses, for example river flow and predator activity (Ben-David *et al.* 1998).

The relationship between autotrophic and invertebrate production and the availability of food for juvenile Pacific salmon has led to fishery managers instigating fertilisation programmes on a number of commercially important Pacific salmon fisheries. In addition, experiments have been conducted to study the trophic interactions engendered by fertilisation on both a large and a small scale. Both organic (e.g.

salmon carcasses from the canning industry) and inorganic (e,g. high concentration liquid fertilisers based on ammonium polyphosphate and urea-ammonium nitrate) sources of nutrients have been utilised in these programmes and experiments (Perrin *et al.* 1987; Stockner and MacIsaac 1996). The latter are often spread by helicopter or fixed–wing aircraft in remote regions. Roni *et al.* (2002) also note that slow-release fertiliser pellets have been utilised for enrichment of streams.

Stockner and MacIsaac (1996) describe the results of over twenty years of lake enrichment in British Columbia stemming from initial trials conducted in 1969. Fertilisation of twenty lakes occurred weekly from 1976 onwards, with some lakes receiving twice weekly fertilisation from 1983 onwards. Results indicted a positive response at every trophic level with a doubling of bacteria abundance, a 50-60% increase in autotrophic picoplankton and phytoplankton biomass and a doubling of primary production and zooplankton biomass. Juvenile sockeye salmon weight in turn increased in excess of 60%. Smolt size is an important factor in determining adult sockeye salmon survival rates (Koenings *et al.* 1993). Many of the lakes in British Columbia fertilised in the programme are remote and reliable figures for post-fertilisation stocks of returning adults are limited. However, Stockner and MacIsaac (1996) suggest that fertilisation of the Barkley sound nursery lakes included in the programme have increased returns from annual levels of less than 100,000 prior to fertilisation to 300,000-1.5 million after the programme commenced.

Other fertilisation studies have also demonstrated positive results. Edmundson *et al.* (1997) note that sockeye smolt production of Coghill lake rose from an estimated pre-enrichment average of 263,604 (1989-1993) to an estimated enrichment average of 940,411 (1994-1996). Juvenile sockeye salmon were also observed to increase in size on Redfish Lake after fertilisation (Budy *et al.* 1998). Kyle (1994) observed a 25% increase in the ability of Bear Lake, Alaska, to produce coho salmon (*O. kisutch*) biomass, with an accompanying increase in the proportion of juveniles undergoing smoltification after just one year. Estimates of increased production after nutrient enrichment should be treated with caution, however, as many other factors must be taken into consideration. Changes in marine survival or natural climatic factors, for example, could account for some or all of the differences in adult returns or smolt production. Not all studies utilise experimental control areas to quantify the effects of nutrient manipulation. Some fertilisation experiments are ongoing, for example attempts to increase numbers of kokanee (landlocked coho salmon) salmon in Arrow Lakes reservoir (Pieters *et al.* 2003).

Whilst fertilisation of lakes may appear to increase juvenile numbers of sockeye salmon in most cases, trophic interactions may reduce such effects over time in some circumstances. Reduced *daphnia* levels in Packers Lake, Alaska, resulting from heavy predation by juvenile sockeye in turn resulted in declines in average size of salmon despite continued fertilisation (Mazumder and Edmundson 2002). The efficacy of fertilisation programmes should thus be considered to be site specific rather than generally applicable, as increases in production from 'bottom up' effects may be negated by 'top down' controls by predators.

Roni *et al.* (2002) report that direct fertilisation of riverine habitat has been utilised less often than fertilisation of lacustrine environments. Experiments have been conducted on river systems e.g. the Keogh, however, in order to ascertain the effect of additions of inorganic nutrients at various trophic levels (Perrin *et al.* 1987; Slaney *et al.* 2003; Ward *et al.* 2003). Increased periphyton accrual was observed in stretches of river that received inorganic fertiliser (Perrin *et al.* 1987). Elevated levels of growth of both steelhead (*O. mykiss*) and coho salmon were also observed in response to additions of inorganic fertiliser in a separate study, the authors suggesting that production in the Keogh system was phosphorus limited (Johnston *et al.* 1990). Ward *et al.* (2003) observed increased juvenile abundance and size of steelhead and coho salmon in response to additions of nutrients and habitat structures in the Keogh watershed compared to the Waukwaas which was untreated.

The use of stable isotope analysis has highlighted the fact that juvenile coho salmon and steelhead consume the products of artificially introduced carcasses both directly and indirectly, and that in more general terms carcasses may provide an important source of food during a period when other sources of nourishment are largely unavailable (Bilby *et al.* 1998). The capacity of rivers to retain nutrients from salmon carcasses may in part rest on the availability of small organic debris, for example tree branches, that prevent the movement of such carcasses downstream during periods of high flows (Cederholm and Peterson 1985). Similarly, the retention of nutrients within a river system can occur via biotic retention engendered by consumption of carcasses by macroinvertebrates and fish feeding directly on carcasses (Cederholm *et al.* 1999).

Protocols for the artificial application of nutrients to both riverine and lacustrine waterways have been established by Ashley and Stockner (2003). Initially, the trophic status of each stream or lake should be assessed to ascertain which, if any, nutrients are limiting. Levels of soluble reactive phosphorus of <1μg/L and <2-3μg/L total dissolved phosphorus during the growing season suggest that phosphorus is limiting. Similarly, levels of dissolved inorganic nitrogen of <20 μg/L in streams or <30μg/L in lakes (spring epilimnetic concentrations) suggest that nitrogen is limiting. The authors then delineate seven key variables for enrichment programmes:

1. Desired concentration of nutrients
2. Nutrient formulation of fertiliser
3. Seasonal timing of application
4. Frequency of nutrient addition
5. Location of application sites
6. Dissolved inorganic nitrogen: total dissolved phosphorus ratio to be added
7. Application technique.

As such, detailed physical, chemical and biological data is required prior to the commencement of fertilisation. In particular, discharge patterns of streams and residence times of nutrients within lakes are very important. Such care must be taken when considering the addition of nutrients due to the potential for possible deleterious effects resulting from over-enrichment.

Problems regarding the application of liquid fertiliser via automatic feeder systems has led to the development of slow-release fertiliser briquettes (Sterling *et al.* 2000; Sterling and Ashley 2003). These have been designed to release predetermined concentrations of nutrients over a period of four months, thus negating the need for periodic fertilisation during the growing season. Weighing 9g, these briquettes release both phosphorus and nitrates. Without the latter, nitrogen can become limiting in some circumstances.

Many experiments attempting to ascertain trophic responses to fertilisation in streams and rivers have utilised mesocosms in order that the many variables that can affect production can be controlled or more readily observed. Controlling such factors in actual river experiments presents difficulties and many field studies contain caveats in relation to the low power of the statistical analysis employed and the problem of psuedoreplication. As such some of the results of these experiments should be viewed as indicative of biotic processes rather than presenting statistically robust findings. Many studies appear to adopt a combination of both mesocosm and natural stream experiments to ascertain if similar patterns emerge from both types of study.

Groups of streams believed to have similar physical characteristics are often used in experiments designed to observe trophic response after enrichment by organic or inorganic inputs (Chaloner *et al.* 2002a). Weng *et al.* (2001) sampled 100m areas within 1km enrichment and control stretches on two tributaries of the Atlantic salmon producing Sainte-Marguerite River. Other experiments, however, utilise sites within one river (Perrin *et al.*1987; Peterson *et al.*1993; Wipfli *et al.*1998, 1999; Minakawa and Gara 1999). Controls may take the form of areas above obstacles impassable by anadromous fish (e.g. waterfalls or culverts) or may simply be stretches of stream above enriched areas. The latter is especially, though not exclusively, used in those rivers that do not have runs of migratory fish. This control system was utilised by Peterson *et al.* (1993) in recording the trophic response to phosphorus fertilisation of a stream containing Arctic grayling. Levels of inputs of phosphorus (and eventually nitrates) to sites were varied over the course of the experiment to facilitate analysis of production at various trophic levels. Some reaches did not receive inputs in certain years in order to assess 'recovery' of post-enrichment sites.

Comparison of the experiments undertaken reveals little consensus in the timing of additions of nutrients. While chemical and physical variables are recorded in many studies (e.g. water flow and temperature, light and levels of dissolved nutrients) this is not always the case. Similarly, protocols for the length of stream chosen for study sites appear to vary between experiments. Examples of fertilisation experiments in natural streams that include analysis of responses in fish populations are summarised in Table 1.

Table 1. Summary of fertilisation experiments (order as in table: Peterson *et al.*1993; Slaney *et al.* 2003; Bilby *et al.* 1998; Wilson *et al.* 2003; Weng *et al.* 2001; Wilzbach *et al.*2005).

River System(s)	Year	Fish Species Studied	Method of Fertilisation	No. of Study Areas Including Control(s)	Length of Study Areas	Controls
Kuparuk	1983-6	Arctic grayling	Phosphoric acid via drip system	Varied during experiment	Varied during experiment	Reaches upstream of fertilisation
Keogh and Salmon rivers	Keogh 1983-6	Coho salmon Steelhead	Liquid fertiliser/ slow release fertiliser	4	No details given	Reaches upstream of fertilisation
	Salmon 1989	Steelhead	Liquid fertiliser/ slow release fertiliser	No details given	No details given	No details given
Chehalis and Willapa watersheds	1994-5	Coho salmon Steelhead	Carcass addition	4	500m	Different tributaries used for treatment and controls
Big Silver and Adam Rivers	1994-1997	Rainbow trout Mountain whitefish (*Prosopim williamson -i*)	Liquid fertiliser	6	3-8km per section	Reaches upstream of fertilisation
Sainte-Marguerite	1996	Atlantic salmon Brook trout	Phosphoric acid via continuous drip system	4	1km Sample stretches of 100m	Reaches upstream of fertilisation
Smith and Klamath Rivers	2001-2003	Rainbow trout Cutthhroat trout (*O. clarki*)	Carcass Addition	6	100m	Reaches upstream of fertilisation

The purpose of the present study is to assess the response of juvenile Atlantic salmon to the introduction of salmon carcasses in tributaries of the River Meig and River Bran, both part of the River Conon system in Scotland. Six tributary streams on each river were utilised in the study. Studies of the response of aquatic communities conducted on natural streams in North America have often suffered from a lack of genuine replication (Wipfli *et al.* 2004; Wilzbach *et al.* 2005), thus the present study attempted to encompass as many streams as possible in order to facilitate statistical analysis. The streams utilised in the study are characterised by low nutrient status, particularly P (total P below detection levels of $4\mu gl^{-1}$, soluble reactive P below detection levels of $5\mu gl^{-1}$ (K.Williams, unpublished data)). Whilst P is considered to be the key limiting nutrient in upland systems (e.g. Bradford and Peters 1987), limitation is location specific and may change as nutrients are added. It became apparent during the course of this study that testing for P with detection levels comparable to those routinely used in North America was not available in the United Kingdom.

Salmon carcasses were the preferred means of nutrient introduction for the present study in order that each study stream received a range of both macronutrients and micronutrients (Ashley and Stockner 2003). In addition, the use of carcasses circumvents the attention of regulatory authorities who regard the introduction of nutrients in their chemical form as at best highly unorthodox and at worst a form of pollution best avoided. A large-scale trapping and broodstock holding programme that is conducted annually on the Conon system afforded an opportunity to collect large numbers of carcasses for this purpose.

Desired rates of carcass loading in Pacific salmon fisheries has been established via the use of stable isotope analysis (Bilby *et al.* 2001) and has facilitated the formulation of guidelines for the introduction of carcasses that is dependent on the species targeted for enhancement. Guidelines suggest that maximum loading rates are: Chinook 0.39 $kg.m^{-2}$ bank full width; pink (*O. gorbuscha*), chum (*O.keta*) and sockeye 0.78 $kg.m^{-2}$ bank full width; coho, steelhead and cutthroat 0.15 $kg.m^{-2}$ bank full width (Ashley and Stockner 2003). In the present study, logistical consideration of the amount of carcasses available from hatchery operations set an upper limit to addition levels. However, the maximum input utilised in this study equates to approximately 0.2 $kg.m^{-2}$ wetted area which is broadly similar to those suggested for coho, steelhead and cutthroat.

Whilst the use of carcasses allows inputs of a range of nutrients into the watercourse in a manner analogous to a naturally occurring event, i.e. salmon dying after spawning, it should be noted that there is a paucity of spatial and temporal data regarding mortality of Atlantic salmon particularly over small spatial scales. Thus the experiment does not attempt to replicate known densities of carcasses that occur after spawning but rather attempts to assess response over a range of inputs. However, the approach adopted in this study provides an insight as to how changes in the overall nutrient status of Atlantic salmon producing streams due to natural or anthropogenic factors may have impinged on juvenile productivity or, indeed, how alterations in nutrient availability that may take place in the future may affect salmon production.

Materials and Methods

Study Area

The Rivers Bran (57° 35 ′ N, 5°W) and Meig (57° 31 ′ N, 4° 59 ′ W) are tributaries of the River Conon, Scotland (see Figure 4, Chapter 2). Both are situated above extensive hydroelectric schemes. Fish assemblage in the study areas is dominated by salmon, although brown trout and minnow (*Phoxinus phoxinus*) were also captured in some of the study areas. Details of the streams used in the study are illustrated in Table 2. Ambient P levels in the study streams were below detection levels of 4μgl^{-1} for total P and 5μgl^{-1} for soluble reactive (K.Williams, unpublished data). Obtaining testing with detection levels below this in the UK proved impossible.

Table 2. Location of study streams and level of carcass addition.

	Location	Study Area Mean Width(m)	% of Maximum Addition	Carcasses Added
River Bran				
Luib	57° 33 ′ N, 5° 08 ′ W	4.00	0	0
Gharagain	57° 33 ′ N, 5° 07 ′ W	8.00	20	11
Chamasaidh	57° 35 ′ N, 5° 02 ′ W	5.50	40	15
Chaiseachain	57° 36 ′ N, 4° 57 ′ W	3.50	60	14
a Chomair	57° 36 ′ N, 5° 00 ′ W	4.50	80	24
Coire a Ghormachain	57° 33 ′ N, 5° 08 ′ W	3.00	100	20
River Meig				
Garrimatic	57° 34 ′ N, 4° 39 ′ W	3.00	0	0
Gleann Chorain	57° 31 ′ N, 4° 55 ′ W	8.75	20	12
Scardroy	57° 31 ′ N, 4° 49 ′ W	2.50	40	7
Gleann Meinich	57° 32 ′ N, 4° 52 ′ W	6.75	60	27
Coire a Bhuic	57° 31 ′ N, 5° 00 ′ W	3.75	80	20
t-Srathain Mhoir	57° 33 ′ N, 4° 51 ′ W	3.25	100	22

Experimental Design

In each study stream a 100m stretch was selected for carcass addition with a reference section of 100m also identified upstream of the addition site. Sites were stocked with salmon fry reared at the Conon and District Salmon Fishery Board hatchery, Contin, Ross-shire in 2003 (25/4/03 for Bran sites and 23/5/03 for Meig sites) and 2004 (29/4/04 to 14/5/04 for Bran sites and 18/5/2004 to 19/5/2004 for Meig site) at a density of 10 fry m^{-2}. Male salmon carcasses (typically 3kg on the Conon system, S McKelvey personal communication) were collected from Loch na Croic salmon trap in November and December 2003 and frozen in preparation to being placed in study areas in 2004. Salmon carcasses were placed in cages made of wire mesh (Figure 5), positioned in study areas and partially covered with rocks to prevent removal by spates or scavenging animals. Cages were placed at four locations within each study area at intervals of 25m, the first located at the upstream extent of the treatment study area.

Figure 5. Salmon carcasses being prepared and placed in study area. Partially defrosted carcasses are firstly placed on wire mesh (A), securely enclosed within mesh envelope by means of cable ties (B) and placed in location within study stream with rocks placed on top to prevent removal by spates and scavenging animals (C) whilst still allowing for a throughput of current.

A.

B.

C.

The maximum input of carcasses was one per $15m^2$ wetted area, with inputs of 80%, 60%, 40%, 20% and 0% of the maximum value also utilised. Introduction of carcasses was completed between 1/5/04 and 15/5/04. Study sites were electrofished between 19/7/04 and 8/8/04 using a backpack system (Electracatch International, Killiney, Dublin, Eire) Upstream and downstream stop nets were utilised. In each study area a minimum 10m length of riffle habitat was electrofished with three passes per section. In addition, a similar length of riffle habitat was electrofished upstream of the treatment area to provide reference data. Captured fish were anaesthetized in an immersion bath (Benzocaine, 40 mg l^{-1} as per Laird and Oswold 1975) and fork length and weight of each salmon captured was recorded. Juvenile densities were obtained using Remove software (Institute of Freshwater Ecology, Dorset, UK) using the Zippin method (Zippin 1958). Where the software was unable to calculate a value for density due to low numbers, a minimum population estimate was obtained by dividing the area fished by number of fish captured. Values for missing weights of fish were obtained by using linear regression to derive a length/weight relationship from the data obtained in the study (ln Weight = -0.798 + 0.0328, R^2 = 98.7%, P= <0.001). Examination of histograms of the lengths of all captured individuals within each river was utilised in order to designate individuals as fry or parr. Biomass estimates were calculated and log transformed (common log of biomass + 1) to satisfy the assumptions of simple linear regression (Zar 1999). Difference of logged biomass at treatment sites from corresponding reference sites was regressed against percentage of carcass inputs using Minitab (Minitab Inc, USA) with α =0.05. Data for Chamasaidh was excluded from statistical analysis due to the presence of a deer carcass within the study area which is likely to have represented a large input of additional nutrients to the treatment site area.

Results

A total of 901 juvenile salmon were captured in the study. Tables 3a and 3b summarise biomass estimates of fry, parr and combined salmon biomass. Statistical analysis of logged biomass data suggests a positive linear relationship between level of carcass addition and differences of biomass from corresponding reference densities in terms of overall salmon biomass (Sb) with R-Sq =38.4% and $p < 0.05$. The relationship between addition level and response for Sb is graphically represented in Figure 6. Analysis in respect of individual year classes (fry biomass and parr biomass) did not yield statistically significant relationships ($R-Sq = 18.5\%$, $p=0.187$ and $R-Sq = 30.5\%$, $p = 0.078$ respectively).

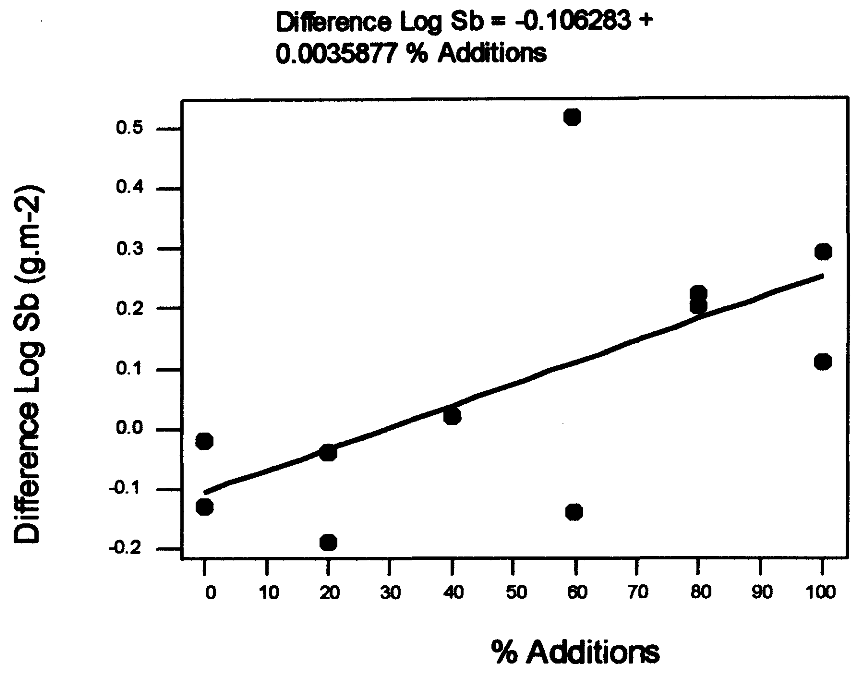
Table 3.a Salmon density estimates per square metre for treatment sites and corresponding upstream reference sites. Combined values refer to the total of fry and parr density. SE = standard error. * denotes minimum density estimate, no SE available.

Stream	Treat Fry	SE±	Ref Fry	SE±	Treat Parr	SE±	Ref Parr	SE±	Treat Combined	Ref Combined
River Bran										
Luib	0.24	0.00	0.22	0.00	0.33	0.00	0.22	0.00	0.57	0.44
Gharagain	0.67	0.34	0.77	1.76	0.56	0.08	0.51	0.18	1.23	1.28
Chamasaidh	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Chaiseachain	1.85	0.41	1.17	0.27	0.66	0.00	0.11	0.00	2.51	1.28
a Chomair	1.91	0.40	1.02	1.88	0.26	0.00	0.15	0.00	2.17	1.17
Coire a Ghormachain	1.44	0.34	1.35	2.65	0.41	*	0.04	*	1.85	1.39
River Meig										
Garrimatic	0.94	0.30	1.08	0.26	0.18	*	0.18	*	1.12	1.26
Gleann Chorain	1.30	0.74	0.66	1.02	0.09	*	0.40	0.00	1.39	1.06
Scardroy	2.19	0.34	1.96	0.66	0.27	0.00	0.19	0.00	2.46	2.15
Gleann Meinich	0.30	0.05	0.07	*	0.49	0.10	0.72	0.25	0.79	0.79
Coire a Bhuic	3.03	1.39	0.60	0.30	0.35	*	0.30	0.00	3.38	0.90
t-Srathain Mhoir	0.87	0.12	0.44	0.00	0.10	*	0.07	0.00	0.97	0.51

Table 3.b Salmon biomass ($g.m^{-2}$) estimates for treatment sites and corresponding upstream reference sites. Combined values refer to the total of fry and parr biomass.

Stream	Treat Fry	Ref Fry	Treat Parr	Ref Parr	Treat Combined	Ref Combined
River Bran						
Luib	0.16	0.26	1.60	1.61	1.77	1.87
Gharagain	0.40	0.49	3.56	3.90	3.96	4.39
Chamasaidh	NA	NA	NA	NA	NA	NA
Chaiseachain	2.28	1.14	6.42	0.78	8.70	1.92
a Chomair	1.21	0.69	1.79	0.73	3.00	1.42
Coire a Ghormachain	0.95	0.92	2.17	0.21	3.12	1.13
River Meig						
Garrimatic	0.76	1.08	1.21	1.93	1.97	3.01
Gleann Chorain	1.37	0.65	0.89	3.37	2.25	4.02
Scardroy	1.75	1.67	2.92	2.70	4.68	4.37
Gleann Meinich	0.31	0.06	2.83	4.70	3.14	4.77
Coire a Bhuic	1.97	0.39	3.14	2.43	5.11	2.82
t-Srathain Mhoir	0.39	0.28	1.17	0.72	1.56	1.00

Figure 6. Fitted line plot of relationship between salmon biomass and level of carcass additions.



Discussion

The results of this study reveal a positive relationship between juvenile salmon biomass and nutrient addition. At the maximum input used in the study, the model derived predicts an increase in juvenile salmon biomass of 78.85% from reference levels. Given a typical weight of 3kg per carcass, the maximum level of carcass input utilised in this study equates to approximately 0.20 $kg.m^{-2}$. In terms of input of P, the most likely limiting nutrient in upland streams, the introduction of 200g of carcass approximates to a potential treatment of 0.94$g.m^{-2}$ (Lyle and Elliot 1998) which using the mean of reference salmon biomass in the study (2.79$g.m^{-2}$) in turn results in an increase in biomass of 2.20$g.m^{-2}$ and of P held in the form of juvenile salmon biomass of 0.01$g.m^{-2}$. However, some of the phosphorus and indeed other nutrients contained within the carcasses - especially in the form of bones – will have persisted well beyond the study period. Visual inspection of the remains of carcasses at the end of the study period suggests a degree of variability of decomposition rates between study sites.

It should be noted that the calculations only assess the response to additions within the study area and almost certainly underestimate the total effects of carcass addition given that effects can be detected a considerable distance downstream of addition sites. Evidence from stable isotope analysis suggests that marine derived nutrients can be detected up to 400m downstream of an Atlantic salmon carcass (Keith Nislow, personal communication). In North America, stable isotope analysis has been utilised to obtain δ^{15} N saturation curves for juvenile salmonids and in turn protocols for maximum levels of carcass inputs have been obtained. These vary between 0.15kg and 0.78 $kg.m^{-2}$ depending on species (Ashley and Stockner 2003). Similar information is not available for Atlantic salmon but the present study suggests that juveniles may respond to relatively low levels of nutrient inputs.

Variation in the magnitude of response to nutrient inputs between the streams used in this study may have been the result of a number of factors. Little information is available regarding the ambient nutrient status of the streams utilised. In the present study, reference levels of salmon biomass on the River Meig were generally higher than the River Bran and in the latter there appeared to be more of a response to biomass additions. However, it is not known if the Bran has lower ambient nutrient levels than the Meig. Thus the response for a given input of nutrients may vary between streams due to differences in their background nutrient status. A response to additions of nutrients by juvenile Atlantic salmon requires the response of biotic communities at lower trophic levels e.g. an increase in benthic invertebrates arising from an increase in periphyton due to the greater availability of nutrients. Therefore trophic level interactions allied to abiotic factors are likely to be important influences in determining the level of response. For example, even if benthic invertebrate production is elevated this may not necessarily translate to increased availability of food for salmonids as substrate characteristics or stream flow regime may prevent ready utilisation of the food source (Richardson 1993).

Decomposition rates of introduced carcasses may also have differed between streams thus introducing nutrients at differential levels between sites and over time. Mass loss of salmon carcasses is likely to be a function of stream discharge, dissolved oxygen content and water temperature (Chaloner *et al.* 2002b) and may have varied between streams. Whilst attempts were made to match habitat between addition sites and their corresponding upstream reference sites as closely as possible, even small differences in habitat quality could have also introduced variation to the data.

Direct comparison of results from this study with nutrient manipulation experiments that have been undertaken in North America is problematical due to the wide variety of treatment methods, fish species and response criteria utilised. Examination of experiments that have utilised salmon carcasses as nutrient inputs, however, reveals that higher levels of inputs have generally been employed in comparison to the present study. Bilby *et al.* (1998) describe how the availability of 0.56 and 0.71 $kg.m^{-2}$ of coho carcasses in two Washington streams increased densities and condition factor of juvenile coho salmon and steelhead although this was over a relatively short time-scale due to the migratory nature of juveniles. A number of studies have utilised artificial channels in order to assess the impact of different levels of carcass treatment on juvenile salmonids (e.g. Wipfli *et al.* 2003, 2004; Heintz *et al.* 2004). Additionally, a natural stream is often also used in conjunction with such channels in order to assess if similar responses can be observed. Wipfli *et al.* (2003) employed treatments of 0, 1.9, 3.7, 5.6 and 7.4 $kg.m^{-2}$ of pink salmon carcasses in such channels to demonstrate increased body mass and fork length of introduced coho juveniles. However, the authors note that incremental increases sharply diminished above levels of 1.9 $kg.m^{-2}$. Carcasses added at a density of 0.54 $kg.m^{-2}$ to a nearby stream resulted in increased growth of cutthroat trout and Dolly Varden (*Salvelinus malma*). High levels of carcass addition do not guarantee responses at even the lowest of trophic levels, however. Ambrose *et al.* (2003) note the lack of response of periphyton to carcass introduction and manipulation of canopy cover. Wipfli *et al.* (2004) note that stream shading can reduce the effects of carcass introduction in terms of lipid responses in salmonid populations. Wilzbach *et al.* (2005) state that salmonid density and biomass responded to canopy removal as against carcass addition in a study carried out on six streams although the lack of replication within the experiment may explain the inability to detect a response to carcass addition. In the present study seven of the study streams had no canopy cover and five had partial shading suggesting that light availability did not play an important role.

Other manipulation experiments have used direct chemical inputs to increase salmonid productivity, often on a much larger spatial scale than carcass addition experiments. This method has the advantage of being able to maintain target levels of N and P over entire growing seasons. A long-term study of response to river fertilization (P) by Arctic grayling on the Kuparuk river in Alaska between 1985-90 resulted in 1.4-1.9-fold increases in size of 0+ grayling, 1.5-2.4 increase in weight gain of adults and 1.3-3.4 increase in neutral lipid storage by adults compared to controls (Deegan and Peterson 1992). Slaney *et al.* (2003) describe how mean weights of steelhead and coho fry on the Keogh (British Columbia) were 1.4-2.0-fold higher than controls and mean weights of steelhead parr 30-130% higher. Target nutrient levels were reduced by a third on the Salmon River compared to the Keogh but the authors still describe 2-3 fold greater mean weights and biomass of steelhead in fertilized zones compared to controls. Increased abundance of rainbow trout (average four-fold increase over four seasons) and mountain whitefish were also reported as a result of fertilization of Big Silver Creek and Adam River (Wilson *et al.* 2003).

The present study was conducted over a relatively short timescale and the importance of the timing of additions could not be addressed. This may be of particular importance when density-dependent mortality of juveniles is at its highest levels – likely to be in the early stages of fry development (Milner *et al.* 2003). Nislow *et al.* (2004b) reported evidence in support of the Critical Period Concept of salmon survival (the critical period being 'the transition from dependence on maternally-derived yolk reserves to independent feeding'). Thus the introduction of nutrients targeted to provide Atlantic salmon fry newly emerged from spawning gravels with an abundance of prey items may help overcome a major 'bottleneck' in productivity. No information is available from the present study with regard to the temporal variation in food supply to juveniles resulting from the input of nutrients. Additionally, fry stocked in the tributaries of the Meig had been fed at the hatchery prior to release. This may have effectively bypassed this critical period of survival. The effects of inputs on food availability at different stages of juvenile development should thus be addressed in future research. The input of nutrients in chemical rather than carcass form may aid such analysis given the greater ease with which target levels of nutrient concentration for individual nutrients can be achieved via the former method. The response of juvenile Atlantic salmon to a greater range of nutrient inputs should also form a key component of future research given that the present study utilised carcass addition levels below those utilised for many of the experiments conducted in North America.

The importance of Pacific salmon carcasses to aquatic and riparian ecosystems has been extensively studied and many nutrient pathways identified (e.g. Reimchen *et al.* 2003). It is unlikely that Atlantic salmon play as important a role due to their ability to repeatedly spawn, lower overall abundance and the likely lack of retention mechanisms for carcasses in Atlantic salmon producing regions. However, studies have demonstrated that the direction of nutrient flux due to Atlantic salmon migrations can be positive on a number of river systems (Lyle and Elliot 1998; Jonsson and Jonsson 2003). In areas that are inherently nutrient poor the direction of the nutrient flux may be of critical importance as even losses of a small magnitude may have significant impacts over a long timescale. Nislow *et al.* (2004a) note that many fishery managers utilise areas above obstacles that are impassable for returning adults for stocking juvenile salmon. The lack of returning adults may lead to a gradual diminution in the nutrient status of such locations as a result of such policies unless nutrient remediation measures are concurrently implemented. The most direct form of nutrient transfer from adult Atlantic salmon to juveniles is likely to take the form of the consumption of eggs and the importance of this requires further study.

The streams utilised in this study are likely to have been the subject of many of the processes identified by Stockner *et al.* (2000) as leading to cultural oligotrophication. These include the loss of connectivity due to the installation of hydroelectric schemes, removal of native riparian woodland, human depopulation in the most remote areas and changes in wild and domestic animal assemblage. For example, the lack of availability of large woody debris due to deforestation is likely to have reduced the ability of the study streams to retain nutrients from salmon carcasses. Anon (2000) notes that the upper portions of the Conon catchment, such as those used in the present study, are likely to have experienced considerable deforestation. It is also possible that the lack of diversity in predatory and scavenging animals due to persecution and even extinction of a number of species has also lowered the capacity for retention of nutrients. The removal of wild and domestic grazing animals for slaughter also effectively transports the nutrients they have sequestered during their life outwith the area, although during their life such animals may well have aided the transport of nutrients within the catchment.

In order to aid the restoration of Atlantic salmon nursery habitat that has potentially suffered degradation in its nutrient status further research is required in order to close gaps in knowledge. In particular, assessments are required to ascertain the overall magnitude (if any) of nutrient decline in upland catchments and detailed investigation of nutrient fluxes on a relatively small spatial scale should also be prioritised.

Management Implications

The present study highlights that oligotrophic systems can respond to relatively low inputs of nutrients and production of salmon may significantly increase after nutrient addition. An increase in the numbers of returning adults resulting from such nutrient additions will in itself increase levels of marine-derived nutrients in upland areas, thus establishing a positive feedback loop. In terms of the overall nutrient status, it is suggested that fishery managers be cognisant of the potentially important role that nutrients may play in the productivity of rivers. Care must be taken to assess any proposed alterations in respect of land use, particularly activities such as deforestation, with regard to their implications for the quantity of nutrients entering the system.

Many sections of the upper parts of catchments in Scotland may have once been characterised by extensive forestry and in turn allochthonous inputs of nutrients from leaf litter etc may have been more important in terms of the productivity of these areas relative to primary production derived from autochthonous sources. The removal of canopy cover due to deforestation practices may well have increased the importance of primary production in these areas over time and thus any reduction in dissolved nutrients available may have deleterious consequences for salmon populations. Similarly dams have the potential to cause what Vannote *et al.* (1980) termed 'reset' i.e. cause nutrient status to be lowered back to levels associated with areas upstream of the dam in question. Nutrient addition may therefore be more justifiable in regulated rivers rather than unregulated ones.

Caution must be exercised, however, in the use of nutrient inputs for management purposes. Interactions within food webs may negate any perceived beneficial advantages. In addition, the effects of accelerated growth on stock composition achieved via this mechanism are not fully understood. Many early-running salmon stocks in Scotland, for example, originate in high altitude, nutrient poor areas of catchments and have been under considerable pressure in terms of abundance (Nislow *et al.* 2004a). A better understanding of the effects of food availability on individual components of Atlantic salmon stocks is required before nutrient addition is used as a tool where there is a wide diversity in stock composition.

The European Union Water Framework Directive suggests that heavily modified watercourses such as those subject to hydroelectric schemes are restored to a status of 'good ecological potential' and the management of the nutrient status of upland catchments is an important challenge in implementing the Directive's edicts (Anon 2002). In North America, conflict has been reported between fishery scientist who wish to add nutrients to boost fish stocks in a river and regulatory authorities who are concerned that nutrient levels already exceed quality standards (Compton *et al.* 2006).

Chapter 4

Mortality of Atlantic Salmon After Spawning

Introduction

Anadromous Atlantic salmonids are iteroparous and some individuals are able to repeat spawning migrations on a number of occasions. Little consideration has been given to the potential role of Atlantic salmon in nutrient transport between marine and freshwater environments in comparison to Pacific salmon (Milner *et al.* 2003). A mass-balance approach has been employed, however, to assess the movements of nutrients represented by juvenile Atlantic salmon migrating downstream to the sea and adult salmon returning upstream to their natal rivers for a number of systems (Elliott *et al.* 1997; Lyle and Elliott 1998; Jonsson and Jonsson 2003; Nislow *et al.* 2004a). Whilst such studies provide a useful assessment of overall nutrient flux resulting from Atlantic salmon migrations, the authors note that spatial and temporal considerations of the associated nutrient transfer are not adequately addressed by this approach.

Spatial factors may be of particular importance given that salmon spawning locations are often situated in upland, nutrient poor areas of catchments. For example, the amount of P represented by adult salmon returning to their natal river may appear modest in terms of the overall annual P load of the river - but overall P load may include large amounts of anthropogenically introduced nutrients from urban habitation that occupies only a relatively small proportion of the catchment. Often such urban conurbations are situated in the lowland, coastal regions of catchments that are likely to be more inherently nutrient rich than the upland portions of the watershed. Thus a longitudinal gradient of nutrient status can theoretically exist for a given river, with the possibility of the problems of oligotrophication and eutrophication occurring concurrently in different areas of the same catchment. (Stockner *et al.* 2000).

Nislow *et al.* (2004a) utilised extensive data from traps and fish counters to model P flux resulting from Atlantic salmon migrations on the River Bran in Scotland, an oligotrophic upland tributary of the River Conon system. Estimation of P represented by smolts migrating downstream was extrapolated from annual counts of smolts captured at a trap on the system and numbers of adult salmon returning upstream were available from fish counter information available from the fish pass facilities at the hydroelectric dams on the system. Since not all Atlantic salmon die after spawning, however, the nutrients they are transporting will not necessarily remain in the River Bran. Little information was available to the authors with regard to the mortality of the River Bran salmon after spawning and the retention of kelt (post-spawned salmon) carcasses within the study area, thus introducing uncertainty into the P budget predictions produced by the study.

Some information regarding salmon survival after spawning has been obtained via scale-reading studies (Mills 1984). The presence or absence of spawning marks (caused by the reabsorption of scales during residency of adult salmon in fresh water) allows an assessment of the proportion of a given population that are repeat spawners or die after spawning. Such studies have revealed wide geographical variation in the ability of Atlantic salmon to spawn on more than one occasion. In general, it would appear that survival is highest in northern latitudes with low ambient water temperatures and lowest at the southern extremes of the range of the species. However, other factors such as the physical characteristics of a river and the genetic makeup of the population under examination are also likely to be important given that survival rates can differ greatly between adjacent rivers that are ostensibly similar (Cunjak *et al.* 1998). Knowledge of mortality rates from this source yields only limited information in terms of nutrient flux, though, given that it cannot provide an assessment of the location in which mortality occurred. Mortality may occur shortly after spawning in the headwaters of a system thus allowing nutrients from a carcass to be dispersed at that location, for example, or an individual may successfully return to the marine environment before succumbing to a predator thus depriving the freshwater ecosystem of the associated nutrients.

More spatially specific insights into mortality can be gleaned from data obtained from traps or counting fences that include numbers of fish making upstream migration and then successfully returning downstream after spawning. Fleming (1996) summarises published information of the survival of Atlantic salmon that has been obtained via this method (Table 4). While useful, trap and counting fence data only gives information in respect of a fixed point: little information is likely to be available regarding the final location or timing of death of individuals that migrated upstream of the trap in question but did not successfully return downstream.

Table 4. Percentage survival of Atlantic salmon garnered from traps and counting fences. ND= no data available. (Order as in table: Jonson *et al.* 1991; Mills 1984; Anon 1990; Baglinière *et al.* 1990, 1991; Chadwick *et al.* 1978).

River System	Female	Male	Combined
Imsa (Norway)	85.3	64.5	74
Conon (Scotland)	ND	ND	26
Burrishoole (Eire)	ND	ND	40
Oir (France)	16.7	1.2	9
West Arm Brook (Canada)	ND	ND	63

The degree of retention of salmon carcasses in a given area is likely to be influenced by a number of factors. Cederholm *et al.* (1989, 1999) identify the availability of large woody debris (see Figure 7) that trap carcasses and prevent them being flushed downstream, activity by predatory and scavenging animals and the preponderance of floods as being of particular importance. The role of animals in sequestering and making nutrients from salmon carcasses available within the riparian zone has been extensively studied in Pacific salmon producing systems but has been less extensively studied in Atlantic salmon producing systems (Murota 2003). However, some studies of the utilisation of Atlantic salmon carcasses by terrestrial and avian predators and the movement of individual carcasses in Scotland, particularly on the River Dee system, have been undertaken (Hewson 1985, 1995; Carss *et al.* 1990). In particular these studies demonstrate that otters (*Lutra lutra*) predate heavily on salmon in the spawning period and beyond with up to 80% of diet of individual otters being from this source during November-January (Carss *et al.* 1990). Removal of living and dead salmon from the watercourse by otters in order to facilitate easier consumption of their prey also increases the availability of carcasses to a range of terrestrial and avian scavengers that includes badger (*Meles meles*), fox (*Vulpes vulpes*), heron (*Ardea cinerea*), buzzard (*Buteo buteo*), great black-backed gull (*Larus marinus*), merganser (*Mergus merganser*), moorhen (*Gallinula chloropus*) and crow (*Corvus corone*).

Although some of the nutrients contained within the carcasses may be removed initially from the waterbody and riparian zone by the activity of animals, some will remain via the decomposition of carcass remnants and some will also be returned to the area via faeces and urine of the predatory and scavenging animals. This fertilisation of the riparian zone vegetation is likely to feed back into beneficial effects to juvenile salmonid populations given that such vegetation can provide cover, act as a source of the input of terrestrial invertebrates which are a source of food for fish and may provide allochthonus inputs to rivers via leaf litter and woody debris (Naimen *et al.* 2002). Hewson (1995) estimated that in the study area utilised in his investigation on the River Dee carcass deposition was in the order of 6.7-36 $kg.km^{-1}$ with the largest amounts being available at the downstream extent of the area of the catchment he studied.

Figure 7. Skull of salmon entangled in a tree branch. The picture was taken in April on the banks of the River Carron, Sutherland, Scotland after a large spate.

Radio-tracking studies have been employed to observe many aspects of adult Atlantic salmon behaviour and a number studies have utilised this technique to ascertain salmon spawning locations as this may have important implications for fishery management (e.g. Hawkins and Smith 1986). However, most studies have not continued tracking salmon after the spawning period and as such there is a general dearth of information regarding post-spawning behaviour. Exceptions do exist, however, with Baglinière (1990, 1991) tracking both male and female salmon during their spawning migration and subsequent post-spawning period. In this study, conducted in France, mortality of tracked individuals was total and occurred relatively quickly after spawning, probably due to high water temperatures and concomitant elevated susceptibility of individuals to disease. The small number of individuals tagged in this study and single study area, however, make it unwise to extrapolate results into a general assessment of post-spawning Atlantic salmon behaviour and mortality. Hewson (1995) also tagged salmon carcasses on the River Dee and its tributaries in order to assess their movement in relation to predator activity and flood episodes on the system.

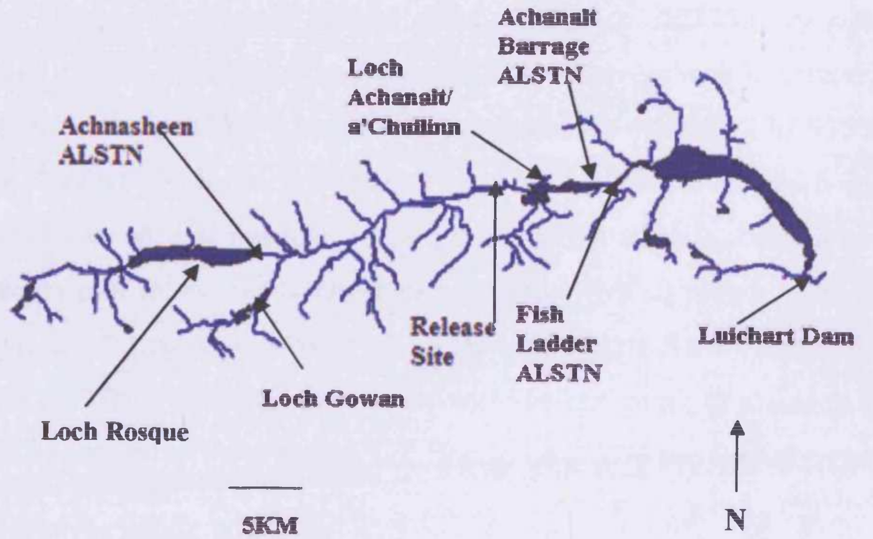
The purpose of the present study is to utilise radio telemetry in order to assess the post-spawning behaviour and, in particular, mortality rate of adult Atlantic salmon in the River Bran, an upland, nutrient poor area of the Conon catchment. A model budget for P movement embodied in salmon migration to and from the River Bran was produced by Nislow *et al.* (2004a). The model allowed for assessment of P flux under a wide range of different scenarios. However, knowledge regarding a key component of the model, namely retention of salmon carcasses in the study area, was lacking. The primary purpose of this investigation is to test if the assumed rates of carcass retention utilised by the model are realistic.

Materials and Methods

Study Area

The River Bran (57° 35 ′ N, 5°W) is a tributary of the River Conon, Ross-shire, Scotland with a catchment of 191km^2 (Mills 1964). The Conon system was the subject of extensive hydroelectric schemes between 1941 and 1961 (Payne 1988) which included the installation of seven major dams and seven power stations. Prior to the hydroelectric schemes, an impassable falls downstream of what is now Luichart Dam prevented adult salmon from accessing this area of the catchment. The falls (Conon Falls) was circumvented via the construction of a fish ladder and adult salmon are thus able to access Loch Luichart. The purpose of opening up access to the River Bran was to mitigate for the loss of spawning habitat in other areas of the Conon catchment caused by the construction of hydroelectric facilities (Mills 1964). Further upstream of Loch Luichart, however, other hydroelectric installations are in place and of particular importance in this study are Achanalt fish ladder and Achanalt Barrage (Figure 8). For the purposes of this investigation, the region upstream of Achanalt Barrage was considered to constitute the study area. Achanalt Barrage represents the furthest inland hydroelectric structure within the River Bran catchment. Gowans *et al.* (2003) noted that hydroelectric structures are likely to cause delays in migration or even prevent successful migration of adult salmon.

Figure 8. Location of Study Area and Automatic Listening Stations ALSTNs.



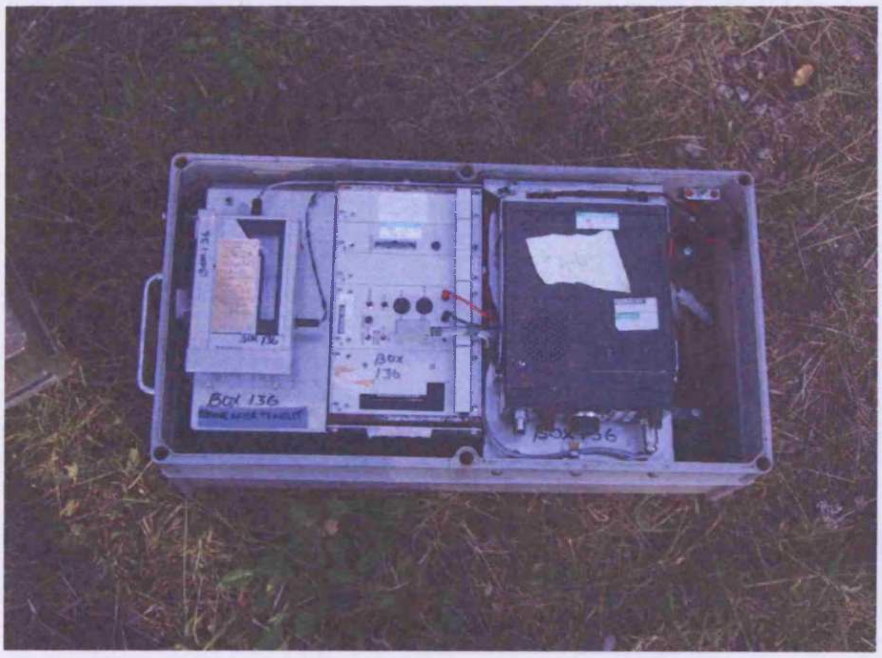
Radio Tagging and Tracking

The header pond at Conon Falls fish ladder, immediately below Luichart Dam, was dewatered on 30/10/03 and adult salmon were captured using a fyke net attached to the outlet pipe at the downstream end of the header pond. Loch Luichart is located at the downstream end of the River Bran catchment and migrating adult salmon attempting to obtain access to the Bran via fish passes situated at the dam are know to be delayed at the header pond (Gowans *et al.* 2003). A total of 18 salmon (11 female and 7 male) were captured and transported by road to a site upstream of all hydroelectric structures on the River Bran. Examination of the female salmon suggested that all fish contained eggs and that spawning had not commenced. Fish were transferred to an anaesthetic immersion bath (Benzocaine, 40 mg l^{-1} as per Laird and Oswold 1975) via dip net. A radio tag (Sal3, HS Electronics, UK) was inserted into the stomach of the fish via the oesophagus using a perspex tube (Figure 9).

Combinations of tag frequencies (173.861-173.904 MHz) and pulse rates (26-40 pulses per minute) were employed to allow identification of individual fish. Tags were 54mm in length, 16mm in diameter and weighed 14g in air. Fork lengths of individual fish were recorded and a uniquely numbered T-bar anchor tag (Floy Inc, USA) inserted into the dorsal region. Tagged salmon were released in the River Bran at Chaiseachain Bridge (Ordnance Survey Grid Reference 223200 860800). A combination of manual tracking using Yaesu FT290R receivers with bi-directional H-Adcock antennas and MAFF-type automatic listening stations (ALSTNs) was employed to establish the location of fish (Figure 10). Attempts to locate fish were conducted on a minimum of a weekly basis except during adverse weather episodes. Ordnance Survey grid references of locations of salmon were recorded. ALSTNs were located at Achanalt Barrage, Achanalt Fish Ladder and Achnasheen Village. ALSTNs were removed on 1/6/04 and tracking ceased with the exception of a search for tags conducted by a boat on Loch a'Chuilinn and Gowan on 8/6/04 and 9/6/04.

Figure 9. Sal3 radio tag.

Figure 10. Automatic listening station.



The process outlined above was repeated in the autumn of 2004 when 20 salmon (10 female and 10 male) were captured, tagged and released on 8/10/04 using identical methods to 2003 with the exception of the use of TW3 radio tags manufactured by Biotrack, UK, (frequencies 173.704-173.795, pulse rates 25-40 pulses per minute). Tags were 52mm in length, 16mm in diameter and weighed 15g in air. Tracking ceased on 1/6/05 and searches using boats were subsequently conducted as per 2004. It was assumed that all salmon that remained in the study area were dead by at the end of the tracking period.

Not all salmon remained in the study area in the period immediately after release. It is likely that some of the fish captured below Luichart dam were in that location in an attempt to gain access to the River Meig rather than the River Bran. This is due to the presence of a diversion tunnel immediately above Luichart Dam that pipes water from the Meig into Loch Luichart. Gowans *et al.* (2003) observed that the olfactory cues from this source may entice salmon destined for the Meig to that location despite the actual confluence of the River Meig and the mainstem of the River Conon being approximately 1km downstream. Tagged salmon that left the study area within 15 days of release or were not located after 15 days of release were excluded from data analysis. Fish recorded on Achanalt Barrage/Achanalt Fish Ladder ALSTNs and not subsequently located upstream were deemed to have left the study area. Fish that were unable to be located on the River Bran but were not registered on either of the Achanalt Barrage or Achanalt Fish Ladder ALSTNs were deemed to have remained in Lochs Achanalt/a'Chuilinn/Gowan. Data was analysed using Minitab 13.20 (Minitab Inc, USA) and SPSS 12.0 (SPSS Inc, USA) with α =0.05.

Results

A total of three fish left the downstream boundary of the study area within 15 days of release (fish 4 in 2003 and 20, 22 in 2004) and were excluded from the study. In addition, fish 26 was not located outwith the 15 day period after and was similarly excluded. A two-sample Kolmogorov-Smirnov test showed no significant difference in the timing of fish leaving the study area in the two years ($Z=0.732$, $p=0.658$) thus data from both years was pooled for further analysis. Multiple logistic regression utilising fork length, maximum observed upstream distance travelled and gender as regressors did not reveal a statistically significant relationship in terms of ability to successfully leave the study area after the spawning period (p=0.481, p=0.866 and p=0.340 respectively).

Upstream movement after release was observed for each of the remaining fish with the exception of fish 29 and the study area was extensively utilised. Overall, twelve fish (35%) successfully vacated the study area after the period in which spawning was likely to have taken place, twelve (35%) remained in riverine habitat and ten (30%) remained in lacustrine habitat. Details of individual fish, including the maximum observed upstream distance from the release site that the fish was located, distance between final location of fish/tag on river and maximum observed upstream location and date of leaving the study area are summarised in Table 5.

Of the 18 female salmon included in the analyses 8 (44.44%) were successfully able to leave the study area compared to only 4 (25%) of the 16 males. In contrast, 16.67% of females remained in lacustrine habitat compared to 43.75% of males. Riverine habitat accounted for 38.89% of females and 31.25% of males respectively.

The study area was extensively utilised by the tagged salmon in this investigation with the exception of the area west of Achnasheen. Only one individual (fish 9) is known to have penetrated the system above Loch Gowan and was located on several occasions in Coire a Ghormachain a small tributary with a mean width of 3m. The tag was located at the end of the 2003/4 study period at the head of Loch Gowan. Several fish were located above the Achnasheen ALSTN and fish 36 was detected on hand-held tracking apparatus in Loch Rosque, west of Achnasheen. This individual and all other individuals known to have accessed this part of the study area were subsequently located downstream of the Achnasheen ALSTN. Little stocking of juvenile salmon takes place above Loch Rosque and so it is possible that relatively few adult salmon return to this area (Simon Mckelvey, personal communication).

Table 5. Details and fate of tracked salmon. * denotes assumed location.

No	Sex	Fork Length (mm)	Upstream Max (km)	Upstream Max-Final Location (km)	Date Left Study area	Fate
2003						
1	M	710	9			Loch
2	F	625	6		2/3/2004	Left
3	F	660	6			Loch*
4	F	660	NA	NA	NA	NA
5	M	621	9			Loch*
6	F	640	8		28/11/2003	Left
7	F	620	9.25	1.25		River
8	F	651	9		25/1/2004	Left
9	M	588	14			Loch
10	M	565	7.5	11.75		River
11	M	635	9		27/11/2003	Left
12	F	651	3		8/12/2003	Left
13	F	602	8.75	0		River
14	M	620	2.75	4		River
15	M	572	7.25			Loch*
16	F	628	9			Loch
17	F	630	2.75	2.25		River
18	F	578	5.5	10		River
2004						
19	M	669	10			Loch*
20	M	704	NA	NA	NA	NA
21	M	610	9	12.5		River
22	F	605	NA	NA	NA	NA
23	M	600	9.75	3.75		River
24	M	575	9	13.75		River
25	M	670	6			Loch*
26	F	830	NA	NA	NA	NA
27	F	540	7			Loch*
28	F	613	10		5/12/2004	Left
29	F	724	0		5/11/2004	Left
30	F	605	6.25	5.25		River
31	M	709	3		29/11/2004	Left
32	F	588	9.25		23/11/2004	Left
33	F	720	2.75	3.75		River
34	F	748	8		9/11/2004	Left
35	F	690	3	5.75		River
36	M	588	10.25		3/12/2004	Left
37	M	638	7			Loch
38	M	534	3		11/12/2004	Left

Figure 11 illustrates the known final location of fish that remained within the study area. Red dots represent fish tagged in 2003, green triangles fish tagged in 2004. Numbers correspond to the fish identification number as per Table 5.

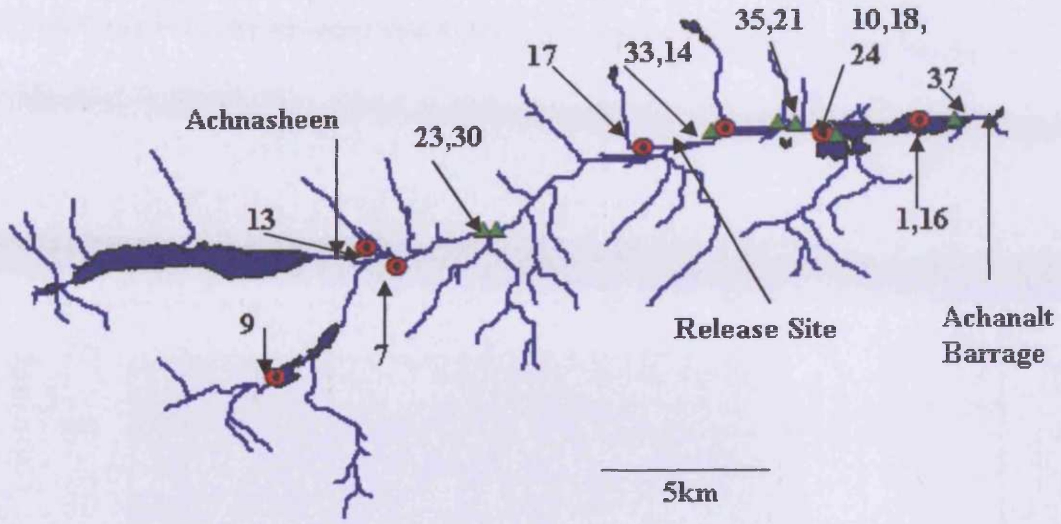


Figure 11. Final location of fish tagged in 2003 and 2004.

Areas particularly favoured during the spawning period were often in the vicinity of the confluence of small tributaries and the mainstem of the River Bran. In particular areas adjacent to the mouth of Chamasaidh and Allt a Chomair were heavily utilised. Although fish were never actually located in these tributaries by manual tracking it is likely that some spawning took place in them during periods of high water or perhaps under the cover of darkness. Examination of data obtained from Achnasheen ALSTN suggests that extensive movement of individuals took place in crepuscular and nocturnal periods and it is possible that much of the spawning activity took place during this time and was not observed in this study. Additionally, favoured areas included the vicinity of the confluence of Avon a Chomair with the River Bran and Achnasheen Burn. Chamasaidh, Allt a Chomair, Avon a Chomair, Achnasheen Burn and Coire a Ghormachain are stocked with fry annually by the Conon District Salmon Fishery Board (Simon Mckelvey, personal communication). Figure 12 shows the percentage of tagged fish located within 250m of Chamasaidh, Allt a Chomair, Avon a Chomair and Coire a Ghormachain 10, 30 and 60 days after release in each of the two years of the study. It should be noted that other fish were also located in the vicinity of the numerous unstocked small tributaries located in the Achnasheen area during the period in question. It should be further noted that the release dates were different in the two years in question (30/10/03 and 8/10/04) so care should be taken when comparing results between years.

Figure 12. Percentage of tracked salmon within 250m of specified tributaries.

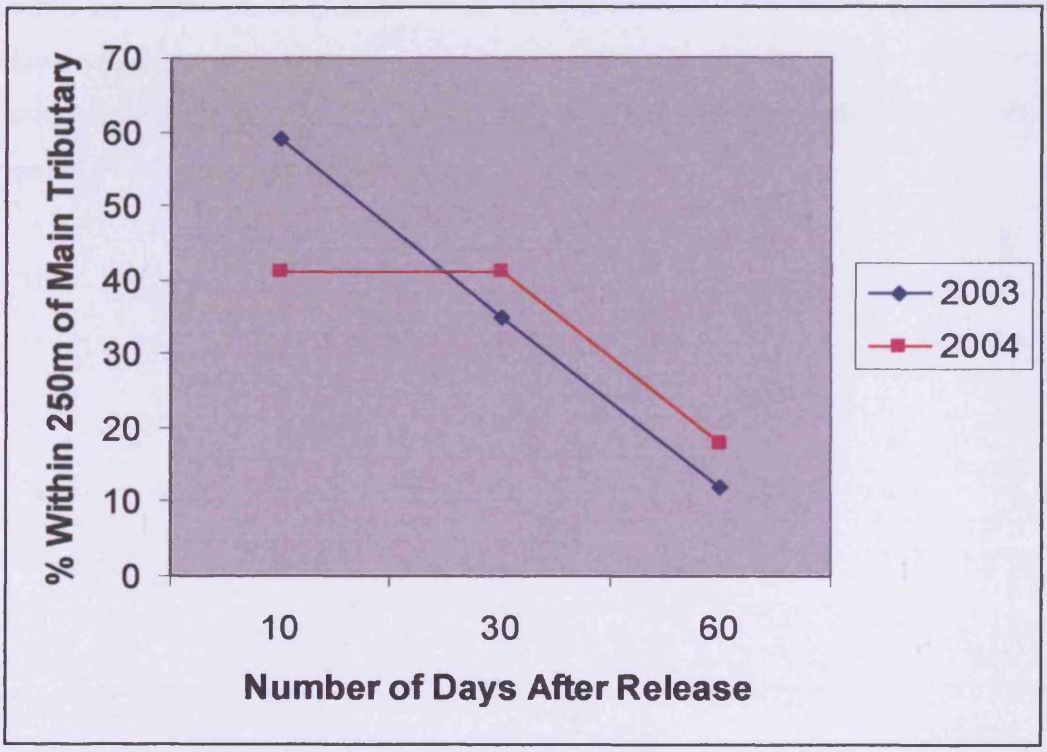
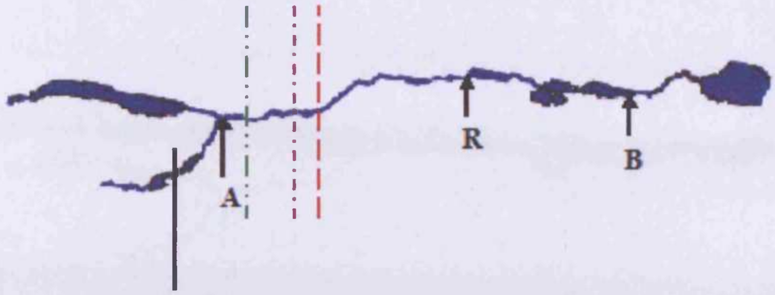


Figure 13 illustrates the utilisation of the study area as the spawning period progressed in each of the two years of the study. Vertical lines represent percentiles (25,50,75 and 100%) respectively with the 25% percentile, represented by the red line, being the furthest downstream in each case and the 100% percentile, represented by the black line being the furthest upstream. Thus, for example, the red line shows that 25% of the tracked fish were downstream of the position of the line at that point in time. The 50, 75 and 100% percentile are illustrated by the purple, green and black lines respectively. For illustrative purposes, the position of fish that were known to have left the study area after spawning was deemed to be Achanalt Barrage. The diagram illustrates that in the period immediately after release the majority of fish occupied the region upstream of the release point with percentile lines being tightly clumped. However, as the study period continued, the area downstream of the release site was more intensively occupied – presumably by post-spawned individuals – and the percentile lines become wider spread.

Figure 13. Utilisation of study area by tracked salmon. Red line = 25%, purple=50%, green=75% and Black=100% percentile.

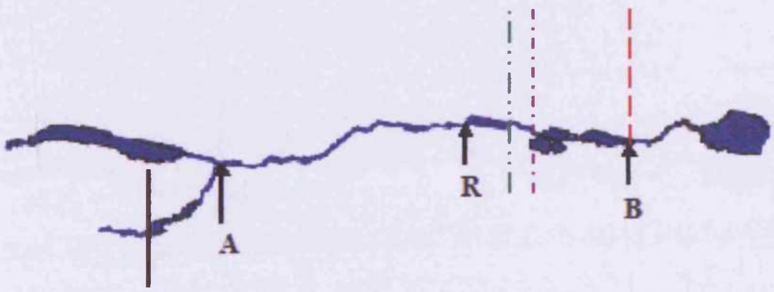
2003/4 10 days after release. A=Achnasheen, R=Release site, B=Barrage.



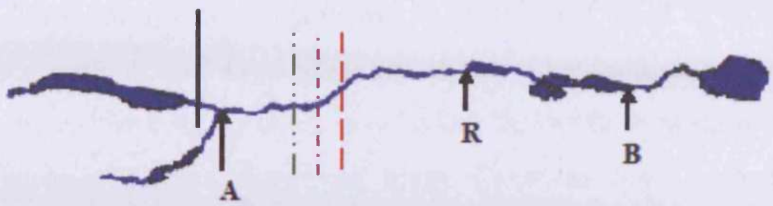
_________ 5km

2003/4 30 days after release.

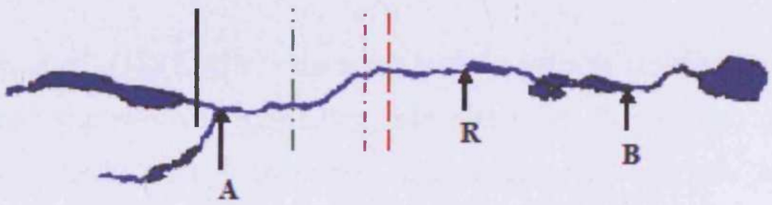
2003/4 60 days after release.



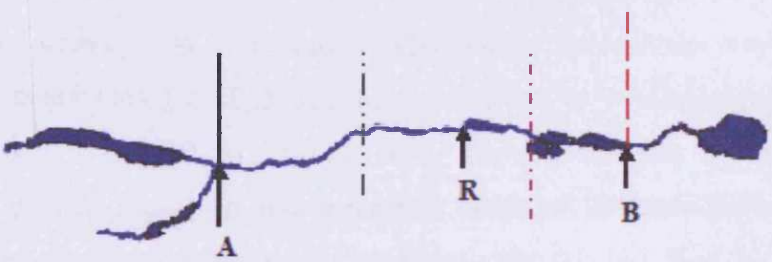
2004/5 10 days after release. A=Achnasheen, R=Release site, B=Barrage.



2004/5 30 days after release.



2004/5 60 days after release.



Discussion

Post-spawning survival rates of Atlantic salmon vary widely between individual river systems and are likely to be a function of a number of biotic and abiotic factors. A summary of post-spawning survival data by Fleming (1996) cites survival rates varying between 9% on the River Oir, France (Baglinière *et al.* 1990, 1991) and 74% on the River Imsa, Norway (Jonsson *et al.* 1991). Cunjak *et al.* (1998) suggest that water temperature and the availability of lacustrine habitat or deep pools that afford winter shelter for kelts on rivers may be key factors in explaining differential survival rates between systems. However, many Canadian rivers experience ice episodes during the winter months and habitat preference of kelts may be largely a response to the presence of ice. Male salmon are believed to have greater post-spawning mortality than females as a result of aggressive behaviour during spawning and associated increased susceptibility to disease and infections (Fleming 1996, 1998). Whilst mortality of males in the present study was higher (75%) than females (55.66%) no statistical association between fate and gender could be detected.

Jonsson *et al.* (1991, 1997) demonstrated an inverse relationship between size and post-spawning survival suggesting that metabolic factors may play a key role in survival. Similarly, the energetic costs associated with the extent of upstream migration may be expected to influence survival given that individuals are not able to feed to replace lost energy reserves. In the present study, however, no relationship between either fork length or observed maximum upstream distance travelled and survival could be detected. The relatively limited size range of salmon available for this study (534-748mm) and the limited size of the study area may be a possible explanation for the lack of relationships in this investigation. In addition, overall levels of activity and thus energy expended by individuals may not correspond to upstream distance travelled and no information is available regarding the energy expended by individuals prior to their capture for this investigation. Available evidence with regard to the metabolic costs of Atlantic salmon migrations and spawning behaviour appears to be equivocal (Hendry and Beall 2004).

Trap data from the River Conon system garnered over a six year period suggests the proportion of kelts descending after the spawning period averaged 26% (range 20-36%) of the total that had migrated upstream (Mills 1984). Thus the survival of 35%

of tagged fish in this study appears reasonable. The overall retention rate of 65% observed in this study is in excess of the maximum level of 60% utilised by Nislow *et al.* (2004a) in presenting a mass balance P model for the River Bran. The estimate of 60%, however, took into account the advective transport (downstream movement) of some P from carcasses and metabolic products. Overall, this study suggests that retention of P from returning adult fish on the Bran is at the upper end of the estimates utilised in the model, with associated implications in terms of the strength and direction of nutrient flux resulting from salmon migrations. It should also be noted that some kelts may have perished downstream of the study area, thus the values observed in this study may be viewed as minimum estimates for overall mortality.

Several features of the River Bran as a study area may suggest that mortality in other river systems could be even higher. For example, numbers of returning adults are relatively low (200-300 annually, Simon McKelvey, personal communication) and thus there may be a lower level of competition between individuals for mates and spawning locations than on systems with higher numbers. Elevated competition could possibly increase the incidence of injuries for an individual, increase the energetic costs of spawning and may result in a higher probability of mortality. Historically, no salmon were present in the River Bran and the current population are present due largely to an annual stocking programme. Returning adults to the River Bran are dominated by grilse (salmon that have spent a single year in the marine environment) and few multi-seawinter (MSW) salmon salmon return annually (unpublished data). There is evidence from Norwegian fisheries that populations consisting predominately of MSW salmon will experience greater levels of mortality than those consisting largely of grilse due to the higher metabolic costs of spawning experienced by the former (Jonsson *et al.* 1991, 1997).

Data obtained from traps give no insight into the location of the kelt carcasses that remained upstream of the trap. In terms of the present study, the fate of kelt carcasses is especially significant given that the Bran system contains both riverine and lacustrine environments. Carcasses retained within the latter may be less important in terms of nutrients being biologically available within juvenile salmon rearing habitat. Twelve fish/carcasses remained in riverine habitat. Of these, seven were located in the section between the release site and Loch Achanalt. Mills (1964) describes this reach as sluggish with a gradient of only 1 in 750 and pool depths of 1.3-2.7m. The upper half of this section does contain some stretches of shallow, turbulent water with suitable substrate for juvenile salmonids, however.

The preponderance of carcasses in the lower section may be explained with reference to two factors. Firstly, studies in Canada have demonstrated that kelts utilise lacustrine habitat to overwinter and may quickly drop downstream into such areas after spawning (Lèvesque *et al.* 1985). Whilst the section in question is riverine, the low gradient and sluggish flows may approximate to the physical conditions favoured by post-spawned fish, although a number may ultimately succumb to disease or exhaustion. Tracking studies in France have shown that mortality after spawning can be quick (all fish dying in less than two weeks) and is likely to take place in the vicinity of spawning areas (Baglinière 1990,1991), probably due to relatively high water temperatures resulting in elevated metabolic costs of spawning and increased susceptibility to *Saprolegnia* spp. infections (Cunjak *et al.* 1998). In the present study, distances between upstream extent of migration and final position in the river of up to 13.75km were recorded and a number of fish were successfully able to migrate from the study area suggesting that post-spawning behaviour and survival differs from that observed in the French studies. Hewson (1995) noted the lack of salmon carcasses in the spawning tributaries of the River Dee in comparison to the mainstem of the river and hypothesised that post-spawned individuals are likely to drop downstream of small tributaries in which they have spawned. It should also be noted that the deposition of gametes by spawning adults in small tributaries is in itself a potential source of nutrients in those areas and the clustering of adults in the vicinity of the confluence of small tributaries and the mainstem of the River Bran observed in the present study suggests that such tributaries may well have been utilised. Secondly, retention of carcasses of perished fish is affected by a number of factors, particularly flow rate, the availability of woody debris that trap carcasses and the presence of terrestrial and aquatic predators (Cederholm *et al.* 1989). Downstream displacements of radio tagged carcasses of up to 20km were recorded on the mainstem of the River Dee resulting from spates (Hewson 1995). Carcasses in the waters of the River Dee were typically found in backwaters or in locations were they had become snagged on woody debris. The author further notes that carcasses in the tributaries and narrower sections of the mainstem were less likely to be moved as a result of spate activity (typically less than 1km). In the present study, carcasses could therefore have been flushed into the lower section from higher gradient sections further upstream in periods of high flow. If the tag becomes separated from the carcass, due to decomposition, the tag is unlikely to be flushed any great distance (Webb 1990).

No information is available with regard to the amount of woody debris present within the Bran system and in particular how this compares with other river systems. This highlights the importance of site-specific studies regarding the retention rates of carcasses. Cederholm *et al.* (1989) has suggested that a reduction in the availability of woody debris is likely to have occurred in many river systems as a result of anthropogenic influences. The role of woody debris in the retention of carcasses in Atlantic salmon producing systems appears to have been less extensively studied in comparison to their Pacific salmon counterparts.

In contrast to previous tracking studies undertaken on the Conon system and on catchments elsewhere in Scotland no tags were retrieved from the river bank and there was no evidence of activity by predators or scavengers. Gowans *et al.* (2003) observed patterns of damage on dead tagged salmon consistent with attack by otter during a tracking study on the mainstem of the Conon and lower River Bran. On the Ewe catchment, a number of tagged salmon were believed to have been killed by otters and a number of scavengers e.g. pine martin (*Martes martes*) were observed in the vicinity of carcasses (Cunningham *et al.* 2002). Hewson (1995) undertook an extensive appraisal of the activities of predators and scavengers in relation to salmon carcasses on the River Dee. Otters were shown to play an important role in removing salmon/carcasses from the water and making them available to terrestrial and avian scavengers. Carss *et al.* (1990) and Hewson (1995) note that male salmon are particularly vulnerable to attack by otters. This is likely to result from the increased length of residency in spawning areas in comparison to females. The activities of predators and scavengers have been shown to play a key role in the distribution and retention of nutrients from salmon carcasses in riparian ecosytems (e.g. Jauquet *et al.* 2003).

A total of six fish were assumed to have remained in lacustrine locations as the individual tags could not be located within the study area and had not been detected by the ALSTNs positioned at the downstream extent of the study area. Whilst Loch

Achanalt has a maximum depth of less than 2m, Loch a'Chuilinn and Loch Gowan contain regions in excess of these depths (Mills 1964). Attempts to locate tags identical to those used in the study at a variety of depths in Loch Luichart were made utilising the same receiving equipment employed for manual tracking of salmon. With the aerial placed directly above the location of the tag, reduction in signal strength was noticeable when the tag was allowed to sink to depths in excess of 6.5m and at depths in excess of 8m no signal was detected unless the aerial was directly above the tag. Loch a'Chuilinn has a maximum depth of 13.7m and Loch Gowan 17.7m (Mills 1964) and this would suggests that tags/fish may have been located in areas too deep to allow detection by the equipment used. It was assumed that all fish had died by the end of the study period.

This study suggests that a significant proportion of Atlantic salmon may die in the upper reaches of a catchment thus contributing important nutrients to oligotrophic areas. Assessments previously conducted with regard to the overall direction and strength of the nutrient flux resulting from migratory Atlantic salmonids have often assumed relatively high rates of retention. The results of this investigation suggest that such estimates are not unrealistic.

Chapter 5

Productivity of Juvenile Atlantic Salmon Upstream and Downstream of Lochs

Introduction

Abundance of juvenile salmon varies extensively both between rivers and within a given river system (Milner *et al.* 2003). The productivity of a given area of river is likely to be strongly dependent on the quality of habitat, and in reviewing published data Armstrong *et al.* (2003) highlight water depth and velocity, substrate type, availability of instream cover, water temperature and oxygen availability as being of particular importance. In addition to these variables, it is likely that at a (local level at least) other factors such as levels of riparian vegetation, pH and food availability may play an important role in determining productivity (Gibson 2002; Johansen *et al.* 2005a, b). Many of these variables have been incorporated into models that attempt to predict the productive potential of habitat Armstrong *et al.* (2003). Efficient models are useful tools in terms of fishery management as they allow managers to gauge the likely effects of habitat manipulation.

The presence of lacustrine habitat is believed to enhance the productivity of Atlantic salmon producing watersheds (Gibson 2002). In both Europe and North America, lakes can constitute important habitat for Atlantic salmon parr – particularly for older age classes (e.g. Dempson *et al.* 1996). Utilisation of lacustrine habitat by juvenile Atlantic salmon has been observed in Newfoundland, Canada (Hutchings 1986), Iceland (Einarsson *et al.* 1990), Ireland (Matthews *et al.* 1997), Finland (Erkinaro *et al.* 1995) and Norway (Halvorsen and Jørgensen 1996). There would appear to be a dearth of information with regards to the use of such habitat by Atlantic salmon in Scottish river systems, however. In addition to providing potentially important habitat for juveniles, lakes are likely to modify a number of abiotic factors that may in turn affect the production of juveniles in adjoining riverine habitat. Gibson (2002) states that temperature and hydrology regimes of outflowing riverine habitat are stabilised by lakes, resulting in elevated levels of productivity in lake outlets. The author further notes that the length of river influenced by the lake will depend upon the size of the lake and its characteristics. Richardson and Mackay (1991) note that in addition to alteration of temperature and flow regimes, lakes alter sediment and turbidity profiles.

In particular, lake outlets are a rich source of seston which in turn boosts the population of filter feeding invertebrates. Given that the theoretical upper limit for salmonid production is believed to be set by the availability of benthos (Richardson 1993) and that there is evidence of a relationship between juvenile Atlantic salmon density and invertebrate density (Johansen *et al.* 2005) then elevated levels of such invertebrates are likely to result in increased juvenile salmon biomass.

Gibson (2002) notes that, in general terms, lakes act as nutrient traps. However, river systems are individual and nutrient regimes for a given system will depend on a number of complex factors (Hendricks and White 2000). Given that many salmon carcasses are likely to be flushed into lochs or salmon kelts may perish in such locations then migrating salmon may contribute to the nutrients trapped in their sediments. An extensive literature exists relating to assessment of nutrient profiles of systems that include both riverine and lacustrine habitat often as a result of long term studies. Whilst lakes may for the most part retain nutrients and reduce levels of nutrients available downstream, periodically such stored nutrients may be released from sediments due to their disturbance as a result of hydrological or climatic factors. The timing of the delivery of pulses of nutrients to the riverine sections may be important with regard to salmon production given that fluvial primary production peaks in spring and autumn and may thus heavily influence the amount of food available for invertebrates and in turn juvenile salmon (O'Connor 2002).The relationships between trophic levels are complex and remain poorly understood, however.

Water chemistry is often cited as being an important factor with regard to salmonid production in streams e.g. Egglishaw and Shackley (1985). A relationship between lake trophic status and salmonid production has been demonstrated by Plante and Downing (1993), but examination of the primary literature suggests that no counterpart for fluvial habitat exists. Fluctuations in juvenile Atlantic salmon populations have been ascribed to anthropogenically introduced nutrients in a number of studies (Mills 1969; Kennedy *et al.* 1983; Gibson and Colbo 2000). However, such studies provide no statistically robust evidence of a relationship, causal or otherwise, between nutrients and juvenile productivity.

Armstrong (2005) notes that the most commonly adopted approach with regard to models of how habitat affects the production of juvenile salmon attempt to correlate the former with the latter. While such models provide useful tools in explaining variation in abundance, the author notes that successful models are required to incorporate factors such as food availability and distribution of suitable spawning areas. The latter is of particular importance if the year classes of juveniles under consideration includes fry as there is strong evidence that there is only limited dispersal away from the redds (nests) in which eggs were deposited e.g. Webb *et al.* (2001). Thus the distribution of juveniles within streams is likely to be strongly clumped, at least initially (Armstrong 2005). Failure to recognise this may result in assessment of juvenile densities reflecting proximity to spawning locations rather than yielding insights into the underlying productivity of a particular area of nursery habitat. Ideally, assessment of juvenile densities would be undertaken in areas of rivers that are known to have received large numbers of eggs but such knowledge is often not available. In order to circumvent this problem, the stocking of either eggs (deposited in artificial redds) or hatchery reared fry is often utilised to ensure that experimental areas have sufficient juveniles to fully utilise any habitat that may be available (e.g. Kennedy and Strange 1986a). However, this approach may still be undermined by catastrophic events that may occur after stocking has taken place e.g. large spates may damage artificial redds or remove juveniles from a given area (Weng *et al.* 2001).

The habitat requirements of juvenile Atlantic salmon vary during each phase of their life history. In broad terms, density of young-of-the-year juveniles has been shown to be negatively correlated with water depth, deeper areas being favoured by older age classes, although this relationship may be modified due to intra-specific and inter-specific competition (Kennedy and Strange 1986a,b). Thus individuals may be required to change location on numerous occasions in order to secure suitable habitat. As such, knowledge of the habitat requirements and dispersal patterns at various stages of the life cycle of juveniles is vital when considering the productivity of habitat (Armstrong 2005).

The purpose of the present study is to compare density and size data of juvenile Atlantic salmon from riverine sites upstream and downstream of lochs on the River

Conon and neighbouring Alness system. In particular, the hypothesis that habitat in loch outlet streams affords enhanced growth and survival prospects relative to ostensibly similar physical habitat located in inlet streams is to be investigated. Nutrients realeased in pulses from lakes may, amongst other factors, be responsible for such enhanced growth and survival and salmon carcasses in lochs may contribute to those nutrients released. Particular emphasis was placed on young-of-the-year (fry) in this study as all areas utilised in this investigation on the Conon system had been stocked with fry or eggs in order to negate as much as possible potential differences in natural spawning success. In contrast, sites on the River Alness system were selected outwith stocked areas as only high altitude areas of the system are routinely stocked.

Materials and Methods

Study Area

The Rivers Bran (57° 35 ′ N, 5°W), Abhainn Dubh (57° 34 ′ N, 5°W), Abhainn a' Chomair (57° 34 ′ N, 5° W), Allt Gharagain (57° 32 ′ N, 5° 07 ′ W) and Meig (57° 31 ′ N, 4° 59 ′ W) are tributaries of the River Conon. The Alness catchment abuts the Conon catchment in a northerly direction. The location of the Conon and Alness systems and the individual study sites are detailed in Figure 14. All the study areas on the Conon system were located in regions upstream of hydroelectric structures. The River Alness has not been harnessed for the production of electricity but the flow out of Loch Morie (57° 44 ′ N, 4° 25 ′ W) can be controlled due to the construction of a small-scale dam, primarily to allow freshets to be released in low water conditions to facilitate improved angling conditions. Fish assemblage in the study areas is dominated by salmon, although small quantities of brown trout and minnow (*Phoxinus phoxinus*) were also captured in some of the study areas.

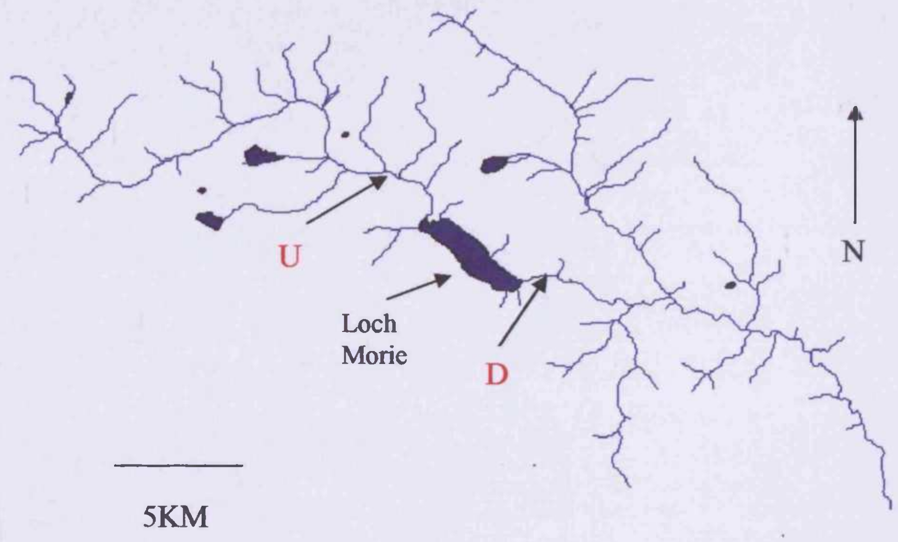
Stocking

Areas for electrofishing were selected above and below three lochs on the Conon system (Rosque, Gowan and Scardroy) and one on the neighbouring Alness system (Morie) as illustrated in Figure 14. Each study area in the outlet streams was selected to be the first suitable riffle habitat available (i.e. in closest proximity to the loch). On the Conon system, stretches selected as potential experimental areas were stocked with juveniles reared by the Conon and District Salmon Fishery Board hatchery, Contin, Ross-shire between 21st April and 25th May 2003 at a density of 10 fry m^{-2}. The exception to this was Abhainn Dubh which, due to its remote location, could not be stocked with fry. On 15th February 2003 artificial redds containing eggs from the hatchery were constructed in the experimental area. All fish were the progeny of broodstock captured at Loch na Croic on the River Blackwater tributary of the River Conon. The sites selected on the Alness were outwith stocked areas in order that a comparison between stocked areas (Conon) and unstocked (Alness) could be obtained.

Electrofishing

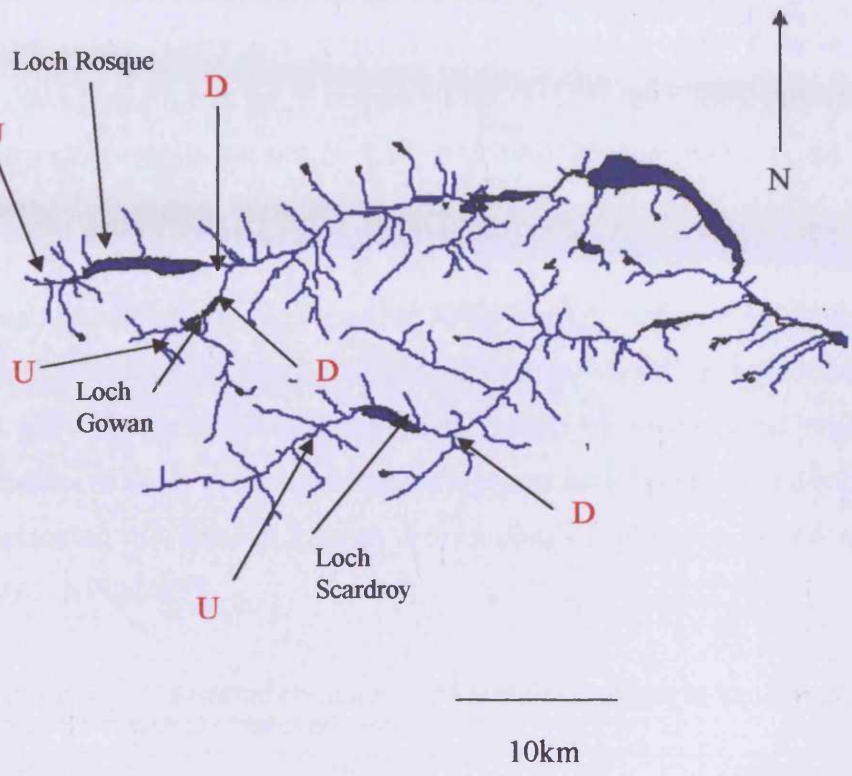
Treatment sites were electrofished between 19/7/03 and 8/8/03 using a backpack system (Electracatch International, Killiney, Dublin, Eire) Upstream and downstream stop nets were utilised. In each study area a minimum 20m length of riffle habitat was electrofished with three passes per section. Captured fish were anaesthetized in an immersion bath (Benzocaine, 40 mg l^{-1} as per Laird and Oswold 1975) and fork length of each salmon was recorded. Juvenile densities were obtained using Remove software (Institute of Freshwater Ecology, Dorset, UK) using the Zippin method (Zippin 1958). Weights of salmon were not recorded as Baum *et al.* (2004) have demonstrated a strong correlation between length and weight in juvenile salmon. Separation of year classes was accomplished via inspection of the length data and is consistent with known stock structure on the Conon system from historical electrofishing data and scale readings (Simon Mckelvey, personal communication). Data was analysed using Minitab 13.20 (Minitab Inc, USA) with α =0.05.

Figure 14. Location of Alness and Conon catchments and individual study sites. U = Upstream site, D= Downstream site.



Alness Study Sites

Conon Study Sites



Results

Estimates of salmon density in each of the study area are summarised in Table 6. Fry density downstream of lochs was higher with the exception of the Scardroy pairing where the reverse was the case. Density of parr downstream of lochs was higher in two pairs but lower in two pairs. Overall salmon density was also higher in two pairs and lower in two pairs. There was no statistical difference between density found upstream and downstream of lochs in respect of fry ($t=1.29$, $p=0.266$), parr ($t=0.24$, $p=0.829$) and overall juvenile density ($t=0.95$, $p=0.396$). Median fork lengths of fry were significantly different in each pairing (all $p=<0.01$). However, median values were higher in the upstream locations in two pairings and lower in two pairings illustrating a lack of consistency in the results. With respest to parr, only the Rosque and Morie pairings were significantly different (both $p=<0.01$. In both cases the median values were higher in the upstream sites. Details of median fork length (fl) values and statistical analysis of each pairing are represented in Table 7a and substrate details are represented in Table 7b. Length distributions of salmon captured at each site are illustrated in Figure 15.

Table 6. Estimated density of salmon/m^2 N= actual number of fish captured at site, D = Zippin estimate of density, SE = standard error of estimate.

Pair	Location	River	Fry			Parr			Combined Density
			N	D	SE±	N	D	SE±	
Rosque	D/stream	Bran	42	0.318	0.084	23	0.156	0.028	0.474
Rosque	Upstream	Dubh	17	0.251	0.036	17	0.237	0.064	0.488
Gowan	D/stream	Chomair	103	0.669	0.214	54	0.453	0.337	1.122
Gowan	Upstream	Gharagain	56	0.543	0.124	37	0.391	0.156	0.934
Scardroy	D/stream	Lower Meig	30	0.212	0.185	12	0.051	0.000	0.263
Scardroy	Upstream	Upper Meig	13	0.278	0.289	18	0.211	0.053	0.489
Morie	D/stream	Alness	95	1.131	0.192	48	0.496	0.037	1.627
Morie	Upstream	Kildermorie	10	0.076	0.019	29	0.206	0.019	0.282

Table 7a. Median fork lengths of salmon captured at each site. * denotes statistically significant difference in lengths between upstream and downstream fork lengths in each pairing. AAD = average absolute deviation.

Pair	Location	River	Fry fl	AAD	P	Parr fl	AAD	P
Rosque	D/stream	Bran	48	3.45	<0.01*	87	5.74	<0.01*
Rosque	Upstream	Dubh	64	3.59		108	7.2	
Gowan	D/stream	Chomair	52	7.15	<0.01*	85	7.61	0.8179
Gowan	Upstream	Gharagain	43	2.59		85	13.57	
Scardroy	D/stream	Lower Meig	55	2.53	<0.01*	84	7	0.5393
Scardroy	Upstream	Upper Meig	49	3		79	10.89	
Morie	D/stream	Alness	48	3.46	<0.01*	92	11.93	<0.01*
Morie	Upstream	Kildermorie	61	1.8		108	3.72	

Table 7b. Width, depth and substrate details of study sites

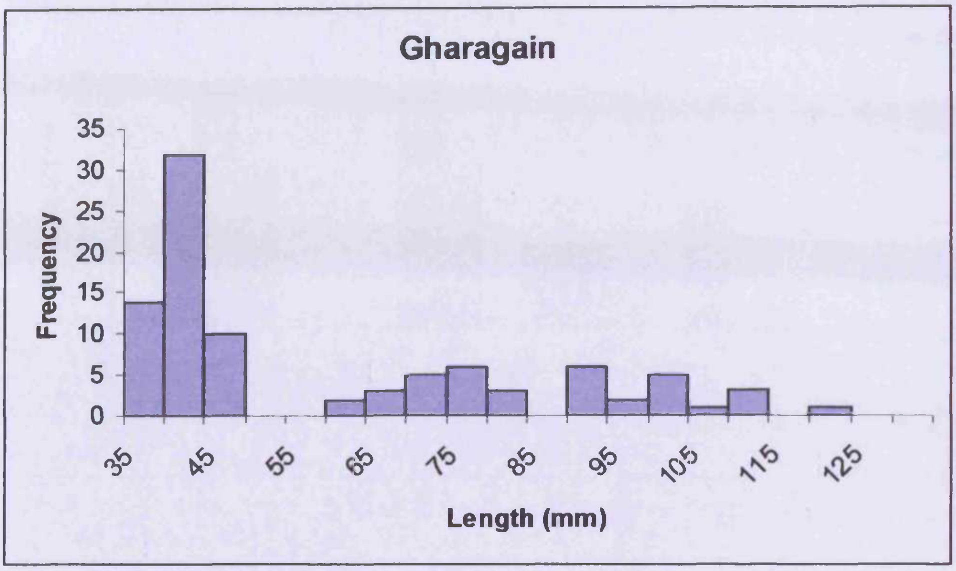
Pair	Location	River	Mean Width (m)	Depth (%)						Substrate (%)					
				<10cm	11-20cm	21-30cm	31-40cm	41-50cm	>50cm	Sand	Gravel	Pebble	Cobble	Boulder	Bedrock
Rosque	D/stream	Bran	7	20	30	30	20	0	0	0	10	15	60	15	0
Rosque	Upstream	Dubh	4	5	90	5	0	0	0	0	0	5	75	20	0
Gowan	D/stream	Chomair	11	10	80	10	0	0	0	0	0	10	70	20	0
Gowan	Upstream	Gharagain	7	30	60	5	5	0	0	0	0	5	80	15	0
Scardroy	D/stream	Lower Meig	12	10	20	40	10	10	10	0	0	10	80	10	0
Scardroy	Upstream	Upper Meig	4	10	70	15	5	0	0	0	5	20	60	15	0
Morie	D/stream	Alness	5	10	80	19	0	0	0	0	15	35	40	20	0
Morie	Upstream	Kildermorie	7	5	10	70	5	5	5	0	5	5	25	65	0

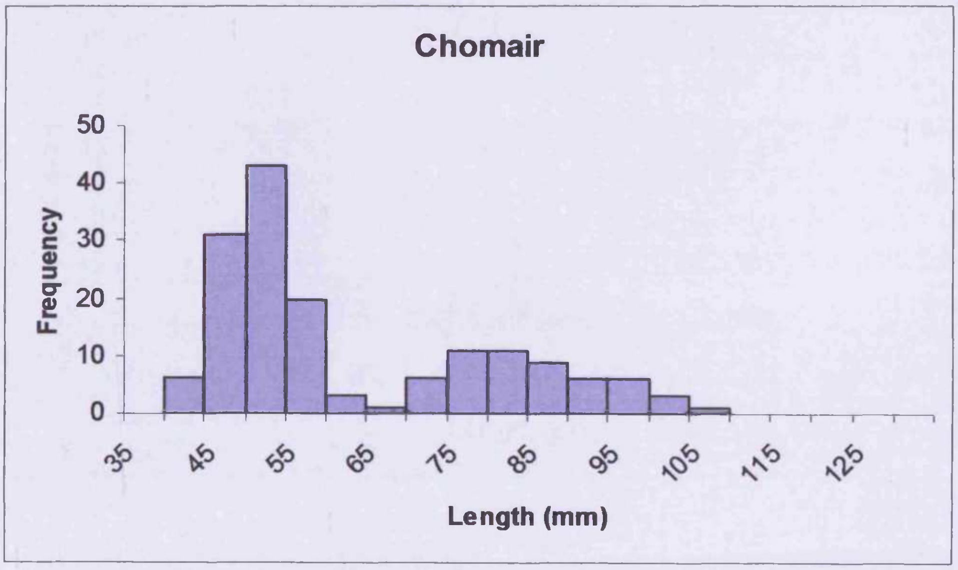
Substrate Definitions:

Sand <2mm
Gravel 2-16mm
Pebble 16-64mm
Cobble 64-256mm
Boulder >256mm
Bedrock = continuous rock surface

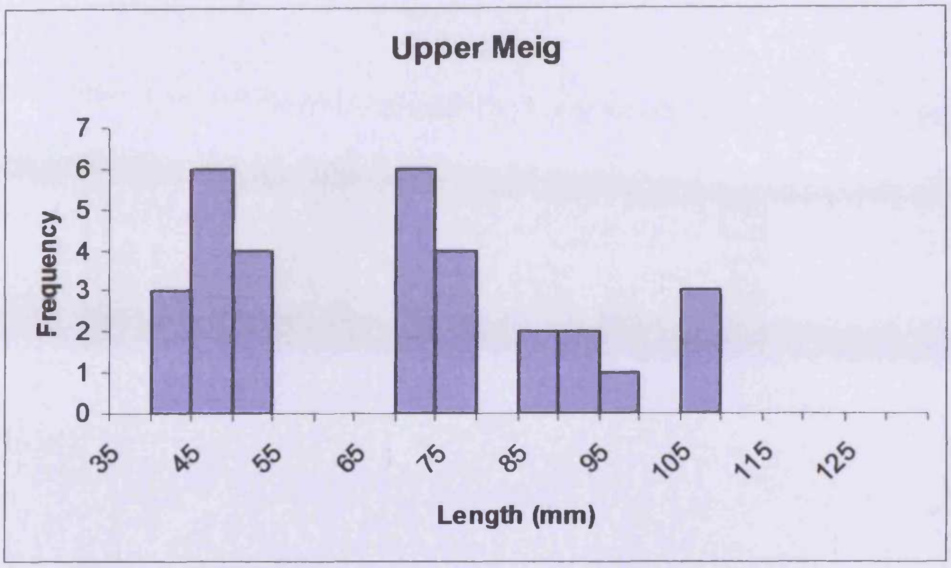
Figure 15. Length distributions of salmon captured at each site.

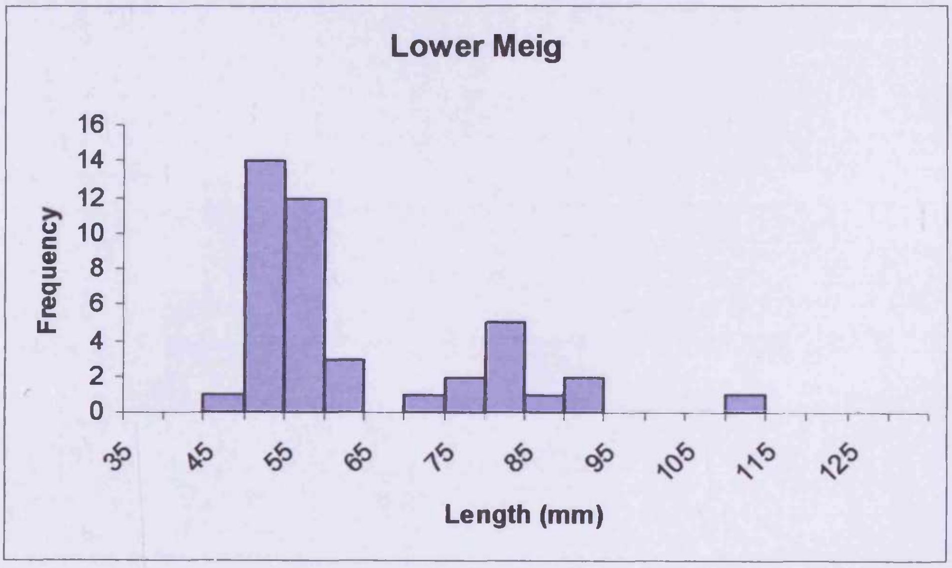
Gowan Pairing



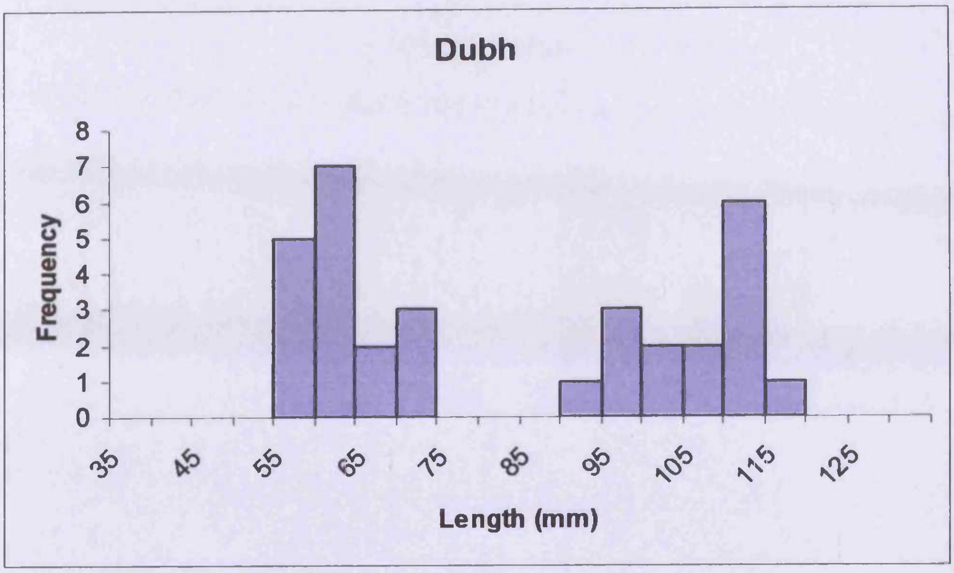


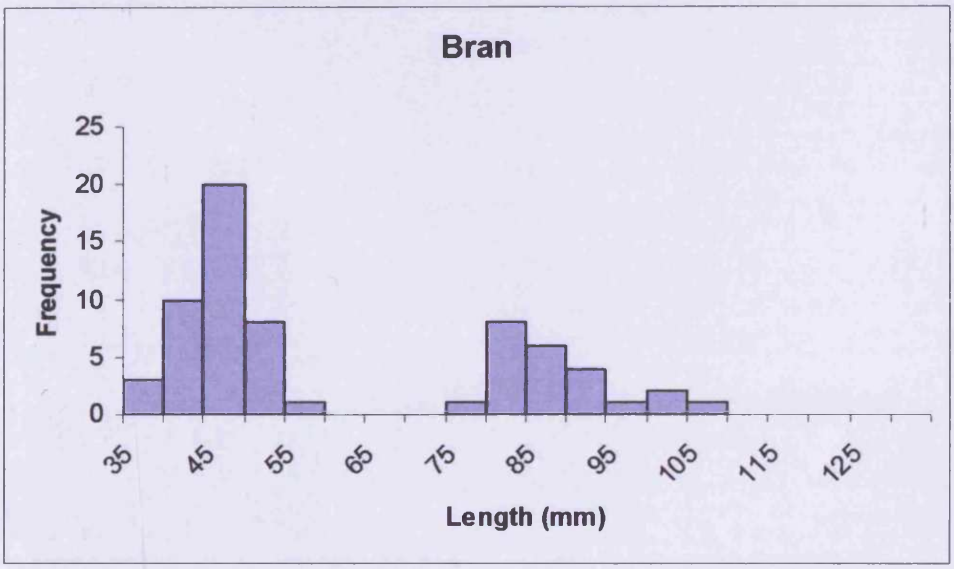
Scardroy Pairing

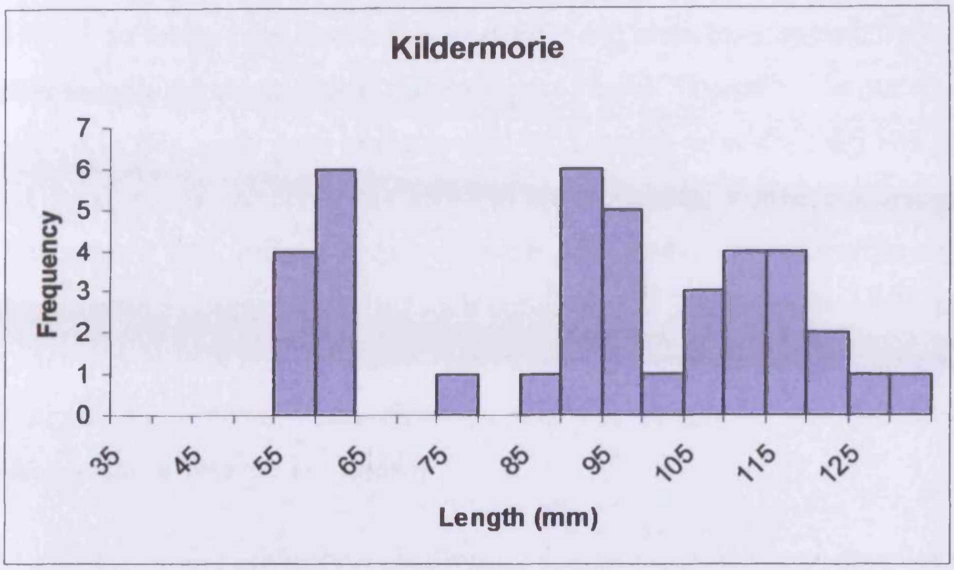


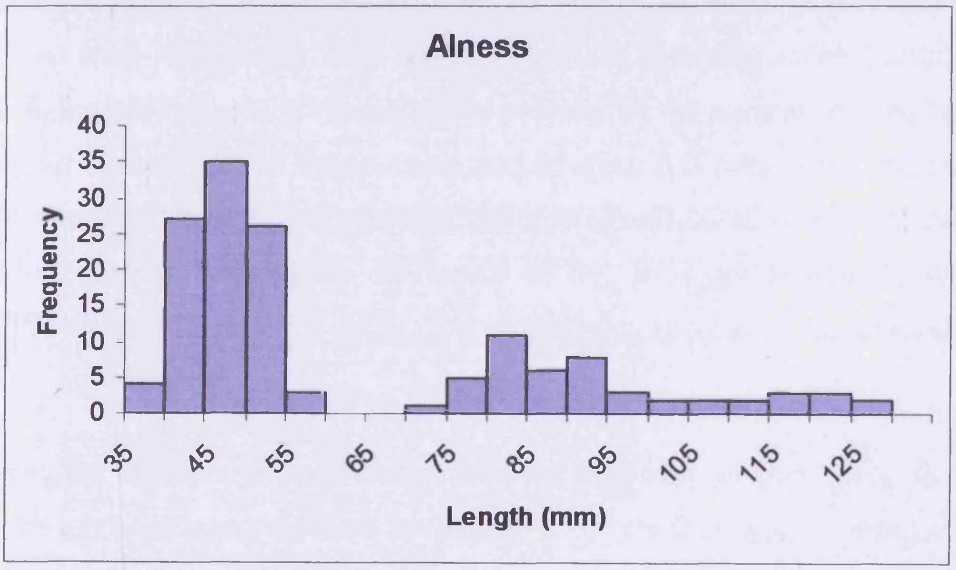


Rosque Pairing






Kildermorie
Frequency
7
6
5
4
3
2
1
0
35
45
55
65
75
85
95
105
115
125
Length (mm)


Alness
Frequency
40
35
30
25
20
15
10
5
0
35
45
55
65
75
85
95
105
115
125
Length (mm)

Discussion

No statistically significant difference in the density estimates obtained from sites above and below lochs was observed in this study. Suitable study areas proved difficult to locate both on the Conon system and elsewhere, especially with regard to sites suitable for elecrofishing downstream of lochs. Typically, the outlets of the lochs utilised in this study were characterized by a stretch of wide, deep and slow-moving habitat that was unsuitable for efficient electrofishing. Whilst the first suitable area downstream was utilised in every case in this study, this was often some distance downstream from the start of the loch outlet stream. The extent to which the effects of an individual loch may influence factors such as temperature and nutrient status may diminish in a downstream direction and the effects of the positioning of the electrofishing sites are not known.

In addition, it was difficult to obtain pairs of streams above and below lochs that were suitable for stocking with fry due to logistical factors in respect of remote geographical location. Whilst study areas in systems that had natural spawning only and had not experienced stocking were available, densities of juveniles obtained in those areas may simply have reflected previous spawning success rather than yield insights into the underlying productive potential of the study areas. The Morie pairing (River Alness) utilised sites outwith stocked areas. It is noteworthy that the difference in densities between the upstream and downstream sites was most marked in the Morie pairing, particularly in respect of fry. It is not known, however, if this difference is the result of initial rates of spawning success or the survival of fry after they have hatched.

Weights of captured individuals were not recorded as they were in the carcass addition experiment outlined in Chapter 3. In previous studies strong relationships between length and weight have been observed for Atlantic salmon and (Baum *et al.* 2004) therefore it was assumed that such a relationship existed in the present study. Nutrient manipulation experiments focussing on Pacific salmon, however, have shown that condition factor may alter in response to nutrient additions (Wipfli *et al.* 2003) and therefore both length and weight should perhaps be included in future studies.

Few studies appear to have compared densities and size of juvenile Atlantic salmon in inlet and outlet streams of lakes. An exception is a study of three Norwegian watercourses by Halvorsen and Svenning (2000). This study utilised otolith data from fish captured in inlet streams, outlet streams and the lakes themselves in order to compare growth rates and size-at-age in the different locations. Temperature recording was also undertaken in the study areas. Density of parr in the outlet stream was similar to the inlet stream in one watercourse, but 1.5 times and 2.0 times higher respectively in the other two watercourses. Density information was not available for fry. Lacustrine parr were larger than fluvial parr across all age classes but not all differences were statistically significant. Comparison of size of parr from inlet and outlet streams revealed more nebulous results, however. There was no significant difference in size of parr from the inlet and outlet in one watercourse despite large differences in temperature regimes but were significantly longer and heavier in the outlet compared to inlet in another (excepting parr aged 3+ years). The reverse was the case in the final watercourse, as fry and 1+ parr were significantly longer in the inlet stream than in the outlet. The latter would appear to be the only watercourse for which comparison of fry size was possible. Overall the study concluded that temperature alone could not explain the variation in growth between either fluvial and lacustrine parr or inlet and outlet parr. In addition the differences in growth appeared less pronounced in older age classes. Baum *et al.* (2004) have noted that whilst density-dependent growth was important in terms of young parr (1+) this was not evident in the older age classes occupying similar reaches of tributaries of the River Spey.

Similar results were obtained in the present study in that no clear pattern was discernable although in terms of fry, inlet and outlet fork lengths were significantly different in every pairing. Of the three pairings that had been stocked, fry were significantly larger in the outlet streams in two cases (Gowan and Scardroy pairings) even though density was also higher in the outlet stream in the Gowan pairing. The largest median values of fry were observed at Abhainn Dubh (Rosque pairing) and may possibly be explained by the low density of fry at that location (i.e. density-dependent growth). This section also was stocked with eggs whereas the corresponding outlet section (Bran) was stocked with fry. Similar results were evident in the Morie pairing where no stocking had taken place in the locality of the study areas with a relatively low density of larger fry being found in the inlet.

There was no significant difference in parr size in the Gowan and Scardroy pairing but the Rosque and Morie pairings revealed larger parr in the inlet study areas, despite parr density also being higher in the Rosque inlet stream. Scale samples were not taken in this study to ascertain the age of parr, therefore it is possible that more than one age class of parr was present in some study areas, although on the Conon system the majority of fish smolt after two years in fresh water (Simon Mckelvey personal communication). More volatile temperature regimes in the inlet streams may inhibit growth, thus delaying seaward migration and causing differences in age structure which are reflected in the parr fl data. Parr are also likely to be more mobile than fry and it is likely that increasing size will lead to migration in order to obtain suitable habitat (Armstrong *et al.* 1994; Johansen *et al.* 2005 a,b). Thus it is possible that some or all parr captured in an inlet stream have spent a portion of their lives as fry in outlet streams or other areas and may retain competitive advantages from increased growth at earlier stages of their life history. Thus size of a parr captured at a given location may reflect not only the productivity of the area it currently occupies but also the productivity of all previous areas that it has occupied. Movements of parr tend to be seasonal in nature and extensive upstream and downstream movements have been noted in a number of studies particularly in late summer and autumn. Interestingly, Johansen *et al.* (2005a,b) observed that older age classes of parr tended to inhabit the uppermost reaches of the Tana system in Norway in the growing season, with younger age classes often being absent. Similar observations were noted by Erkinaro and Niemelä (1995). Studies in streamside channels have also demonstrated a positive relationship between parr size and tendency to explore new areas (Armstrong *et al.* 1997). Lacustrine habitat is also important for parr in many other regions, but the importance of lacustrine habitat in Scotland is poorly understood. However, on the Conon system juvenile salmon are known to pass upstream through lochs in order to utilise inlet streams (Simon Mckelvey personal communication) and are known to pass downstream through lochs in March-June (personal observation).

Grant and Imre (2005) synthesised the results of 16 studies in order to assess patterns of density-dependent growth in fluvial salmonids. In the majority of cases the relationship between growth and density was best described by a negative power curve. In addition, there is strong evidence from a ten year study of the growth of fry on the Catamaran Brook in Canada that the importance of density-dependent growth is most marked at low densities (Imre *et al.* 2005). This is attributed by the authors to exploitative competition (i.e. the removal of food by competitors) rather than interference competition from territoriality. Grant and Imre (2005) suggest that if patterns of density-dependent growth in juvenile salmon observed by Imre *et al.* (2005) are correct, then populations may be regulated by two mechanisms. Firstly, at high densities space is limiting and density-dependent mortality and emigration are likely to be observed as proposed by Grant and Kramer (1990). Secondly, at high densities the likelihood of observing density-dependent growth diminishes as proposed by Keddy (1989).

Gibson *et al.* (1993) and Gibson (2002) have noted that high juvenile density and high growth rates occurring concurrently are often associated with sites enriched with nutrients, often from anthropogenic sources. Care must be taken with drawing such conclusions, however, as physical habitat features, water temperature etc must also be taken into account. In the present study higher fry density and increased fl were observed in the outlet stream of the Gowan pairing. In the inlet stream of the Rosque pairing, parr were both larger and at a higher density than in the outlet.

Velocity of current is an important habitat criterion, and optimal levels are likely to vary at different stages in the life history of Atlantic salmon (Armstrong *et al.* 2003). The frequency and severity of high current velocity due to flood episodes may impact the population of juveniles directly and indirectly. Heggenes *et al.* (1999) noted that newly emerged Atlantic salmon utilise areas of low velocity. Armstrong *et al.* (2003) suggests that mortality of trout fry due to displacement in spates has been observed in trout fry but not salmon fry. However, Weng *et al.* (2001) observed a large reduction in the density of fry on two tributaries of the Sainte-Marguerite River, Quebec, after a large flood. The authors further note that the numbers of one year old parr the following season was similarly depressed. Larger juvenile salmon are likely to be able to tolerate higher flow conditions. The presence of a Loch on a river system tends to moderate extremes of velocity and might therefore be expected to promote enhanced survival and growth especially in fry. Flood episodes may also exert an indirect effect on salmon populations as they may lower the abundance of periphyton which may in turn lower the abundance of invertebrates that are important food sources for salmon (Waters 1993). In the present study this was not be observed.

In an extensive study of twenty tributaries of the Tana system in Northern Norway twelve environmental variables were tested in order to explain parr density (Johansen *et al.* 2005b). Positive relationships between density and stream width and the amount of overhanging riparian vegetation resulted. Negative relationships between density and water velocity and pH were also observed. Only limited vegetation cover was evident in the present study, with most bankside vegetation being dominated by moorland grasses. Values for pH and water velocity were not obtained in the present study.

Temperature is likely to affect productivity of habitat and the growth of salmonids (e.g. Elliott 1993). More stable temperature regimes would be expected in the outlet sections utilised in this study (Gibson 2002). Strong evidence of a negative relationship between size (length and weight) of salmon parr and altitude on tributaries of the River Spey has been proffered by Baum *et al.* (2004). Lower temperatures in the upper reaches of rivers may lower potential for growth. No data is available in the context of the present study with regard to the differences of temperature profiles between sites. Given the mixed results obtained in the present study, however, temperature differences alone are unlikely to supply an adequate explanation for the variation in size observed.

Assessment of the abundance of a particular year class of Atlantic salmon in relation to habitat variables alone is problematical due to the potential for intra-specific and inter-specific competition. In experiments that utilised the stocking of individual year classes Kennedy and Strange (1996a,b) observed that the presence of trout and parr can modify the behaviour and abundance of salmon fry. Few trout fry were captured in the present study although the occasional relatively large trout was captured. The effects of the presence of trout on the density and growth of salmon fry and parr and the effects of the size and abundance of salmon parr on the density and growth of salmon fry in the present study are unknown. De Leániz *et al.* (2000) note that predation by larger salmonids on salmon fry is frequent in the early stages of their development. Milner *et al.* (2003) suggest that, generally, evidence for the phenomenon of intra-specific and interspecific competition is contradictory and inherently difficult to establish.

Milner *et al.* (2003) note that the resources in terms of space and food required by an individual juvenile salmon will increase as the fish grows. If such resources are, theoretically, regarded as constant then density of fish is likely to decrease as average weight increases, a process termed as self-thinning. As such a self-thinning curve represents the theoretical carrying capacity of a given area of habitat. Armstrong (2005) notes that the elevation of the thinning curve in the model he describes will reflect the quality of habitat. Thus practical use of such theoretical concepts would require accurate assessment of physical habitat quality, often routinely monitored by fishery managers, as well as other factors such as food availability which appears to receive much less attention in Atlantic salmon systems by both fishery scientists and managers.

Overall, a host of factors e.g. substrate type or the presence or absence of vegetation may enhance or negate the positive effects on salmon production of the presence of a loch. In particular, the effects of lakes on the nutrient profile and hydrological regime of outlet streams are highly complex and are likely to be location specific. Additionally, the interactions between age classes of salmon are complex and the migratory nature of individuals may also confound the use of simplistic field experiments.

Chapter 5

Marine Survival of Damaged Smolts

Introduction

Stock assessment of anadromous Atlantic salmon is complex due to the migratory nature of individuals, and in particular the fact that an individual is likely to reside in both marine and freshwater environments during its life. Thus fishery scientists and managers are required to utilise a holistic approach in order to seek explanations as to variations in abundance. The precipitous decline in total declared catches of Atlantic salmon, particularly evident from the 1980's onwards, has led to increasing emphasis on determining the factors responsible for lower abundance (Hutchinson and Mills 2000). In order to monitor long-term trends in abundance during both the freshwater and marine phases of their life cycle, index rivers are utilised in order that the population of a single river can be extensively scrutinised (Potter and Crozier 2000). Trapping and tagging techniques are often employed in order to facilitate such monitoring. Potter and Crozier (2000) note that that there is a general paucity of such long-term data sets and that evidence as to the relative importance of mortality in the freshwater environment compared to mortality in the marine environment is often contradictory. For example, low abundance in the freshwater phase of a cohort can be offset by a higher survival rate in the marine phase.

The picture is further complicated by the fact that adult salmon may remain in the ocean for different amounts of time before commencing their return to their natal rivers, often expressed in terms of sea winters (SW). Thus different patterns of mortality in the marine phase may be observed for 1SW fish compared to their 2SW counterparts from the same river. As such, Potter and Crozier (2000) conclude that the causes of the decline in overall salmon abundance are likely to be caused by factors operating in both phases of the life cycle and meaningful explanations for such declines will thus require examination of all phases of the life cycle simultaneously.

Obtaining data from the marine phase of the life cycle of salmon is inherently logistically difficult – and expensive – due to the huge spatial scales involved and the relatively low density of salmon in the ocean. However, evidence of a relationship between sea-surface temperature and salmon abundance has been obtained by Reddin and Shearer (1987); Friedland and Reddin (1993); Friedland *et al.* (1998). It is not known whether this is a result of temperature being directly important to salmon survival or indirectly important i.e. via the abundance of food favoured by salmon. Other factors that may affect survival include predation pressures in the marine environment, the presence of aquaculture facilities in the estuaries of salmon-producing rivers and by-catch from pelagic fisheries that are targeting species such as mackerel but which coincide with the migration routes of post-smolt salmon travelling to the feeding grounds in the North Atlantic (Hutchinson and Mills 2000; Holst *et al.* 2000).

As previously noted, however, the ocean phase of the life cycle of salmon cannot be satisfactorily examined without reference to previous stages of the life history. For example, factors that did not necessarily affect the survival of an individual in the freshwater environment, or were sub-lethal in their extent, may impinge on the ability of that individual to survive the rigours of the marine environment. For example, there is evidence that water quality encountered in fresh water by juveniles may have a bearing on the success of individuals in the ocean. In particular, anthropogenically induced acidity in fresh water has been shown to subsequently lower the survival of Atlantic salmon in the marine environment (e.g. Magee *et al.* 2003). Whilst such mortality may only become apparent in the ocean, in reality the factor that actually led to mortality occurred in fresh water. It is likely that the presence of other contaminants in both the marine and freshwater environments will have similar effects (Mills 2000). Therefore, it is vital that a thorough understanding of both phases of the life history is available in order to properly apportion the sources of mortality.

The above highlights the interconnectedness of the freshwater and marine phases of the life cycle of Atlantic salmon. In the context of the present study, a reduction in the numbers of returning adults to their natal rivers represents an interruption in the feedback loop of nutrients in the form of carcasses, gametes and metabolic products that have been accrued largely in the ocean but are delivered to often nutrient-poor inland areas. In the Pacific salmon fisheries the loss of this marine subsidy due to natural and anthropogenic factors is thought to have had serious consequences for both terrestrial and riverine ecosystems (Stockner *et al.* 2000). Thus progressive reductions in the numbers of returning adults not only has the potential to reduce the number of offspring produced but may also lower the productivity of the environment in which the juveniles may develop: in essence a 'downward spiral' may be established. In Pacific salmon fisheries located within nutrient poor regions in which only remnant runs of salmon remain or have been extirpated, restoration efforts can include the artificial introduction of nutrients in order to circumvent this 'downward spiral' (Budy *et al.* 1998).

Atlantic salmon smolts migrating to the sea undergo a range of physiological, behavioural and morphological adaptations and are believed to be particularly vulnerable to predation by a wide range of avian and aquatic animals (McCormick *et al.* 1998). Indeed, the shoaling behaviour often exhibited by smolts is likely to be a strategy to reduce the chances of mortality of a given individual i.e. a positive density-dependence effect (Milner *et al.* 2003). The timing of entry of smolts to the marine environment is believed to be of critical importance, leading to the concept of the 'smolt window' (McCormick *et al.* 1998). Predation that occurs at this stage of the life cycle may be of particular significance for fishery managers in that density-dependent factors that may have facilitated compensation for predation within the population at earlier stages of juvenile development may no longer operate once the smolt stage has been reached (Marquiss *et al.* 1998). Density- independent factors are believed to be more important in the marine environment compared to density-dependent factors in the freshwater environment. (Jonsson *et al.* 1998).

The majority of studies that have investigated interactions between salmon and predators have concentrated on direct mortality and the indirect consequences of such interactions have often been ignored. However, pioneering studies have identified evidence of damage inflicted by predators on adult salmon in both Scottish and North American fisheries, in particular studies by Harmon *et al.* (1994) and Thompson and Mackay (1999). In the latter study, conducted on the River Conon, protocols for the classification of damage observed on adult salmon were established. In addition, damage has been observed in other fish species. Reimchen (1998) observed injuries on giant sticklebacks (*Gasterosteus aculeatus*) and similar injuries to fathead minnows (*Pimephales promelas*) were noted by Smith and Lemley (1986). Generally, however, there would appear to be a dearth of information regarding the prevalence of predator damage in wild fish (Hislop and MacDonald 1989).

In addition to interactions with predators, migrating smolts may also incur damage from collision with both natural and man-made structures. This is particularly likely in the case of rivers harnessed for the production of electricity, as dams, weirs and turbines etc are common features of such systems (Kostecki *et al.* 1987). Such features may also increase the likelihood of predation given that they are known to delay the migration of smolts (McCormick *et al.* 1998).

Damage incurred by smolts due to the attention of predators or from anthropogenic sources may result in elevated levels of susceptibility to disease and vulnerability to further attention from predators (Carss and Marquiss 1992; Mesa *et al.* 1994; Handeland *et al.* 1996; McCormick *et al.* 1998). Experimental exposure of smolts to sea water have demonstrated that loss of scales, removal of protective mucus and puncture wounds may result in elevated levels of osmotic stress which may prove fatal. Osmotic stress is believed to play an important role in antipredator responses of smolts (Järvi 1989,1990; Gadomski *et al.* 1994; Handeland *et al.* 1996). Given that healthy smolts require 4-6 days to fully acclimatise to marine conditions (Prunet and Boeuf 1985) and predators are believed to aggregate in estuaries (e.g. Hvidsten and Møkklegjerd 1987; Hvidsten and Lund 1988; McCormick *et al.* 1998) any delay in estuaries in order to complete acclimatisation is likely to render individuals more susceptible to predation. It should be noted, however, that evidence with regard to predators aggregating in estuaries for the express purpose of intercepting the smolt run is equivocal. Some authors have suggested that the aggregations are more likely to constitute a response to peaks in abundance of other prey species particularly sandeels (*Ammodytes* spp.) rather than migrating smolts (Greenstreet *et al.* 1994; Svenning *et al.* 2005a,b).

Smolts that perish in estuaries or in the ocean represent a loss of nutrients to the freshwater environment. Thus the nutrients that the individual has accumulated from consumption of food items during its residency in its natal stream cannot be returned by the individual in the form of its carcass, gametes or metabolic products. The mortality of a proportion of individuals in the marine environment is, of course, inevitable. As such, a mass balance approach is often utilised in order to assess the net direction and magnitude of nutrient transfer represented by salmon migrations for an individual river system (Nislow *et al.* 2004a).

In a study conducted on the River Conon system in 2001, protocols for the classification of damage observed on smolts captured at a trap were established (Williams 2001). In addition, the fork length of individuals and numbers of smolts captured in the trap on a daily basis were recorded. Statistical analysis suggested a significant positive relationship between the size of smolt and the incidence of damage, a negative relationship between numbers of smolts captured and the incidence of damage and an increased likelihood of damage being observed at the latter stages of the smolt run. Seven individual categories were also used to classify the types of damage observed in the study but statistical analysis conducted using the same variables as used with the overall incidence of any damage was more nebulous. Although some categories of damage displayed a significant relationship with one or more of the variables, no category had a significant relationship with all three variables. A number of damaged smolts were tagged with passive integrated transponders (PIT) in order to facilitate an assessment of the survival of individuals. However, results were not available at the time the 2001 study was completed. PIT tags, each having a unique code, are inserted into the abdominal cavity of fish and require no internal source of power thus reducing the overall size of the tag. Tags can be read by either small portable receivers or by antennas that are usually placed in fish passage facilities. Such technology has been extensively utilised for monitoring Pacific salmon fisheries (e.g. Ferguson *et al.* 2006).

The purpose of the present study is to repeat the monitoring of damage observed on smolts captured within the Conon system over a period of several smolt runs. This will establish if the relationships observed in 2001 in relation to smolt size, date, numbers of smolts captured in the trap and the incidence of damage are consistent or whether there is variation in these relationships between years. In addition, results from PIT tag returns will be used to test the hypothesis that damaged and undamaged smolts will exhibit different return rates from the marine environment.

Materials and Methods

Study Area

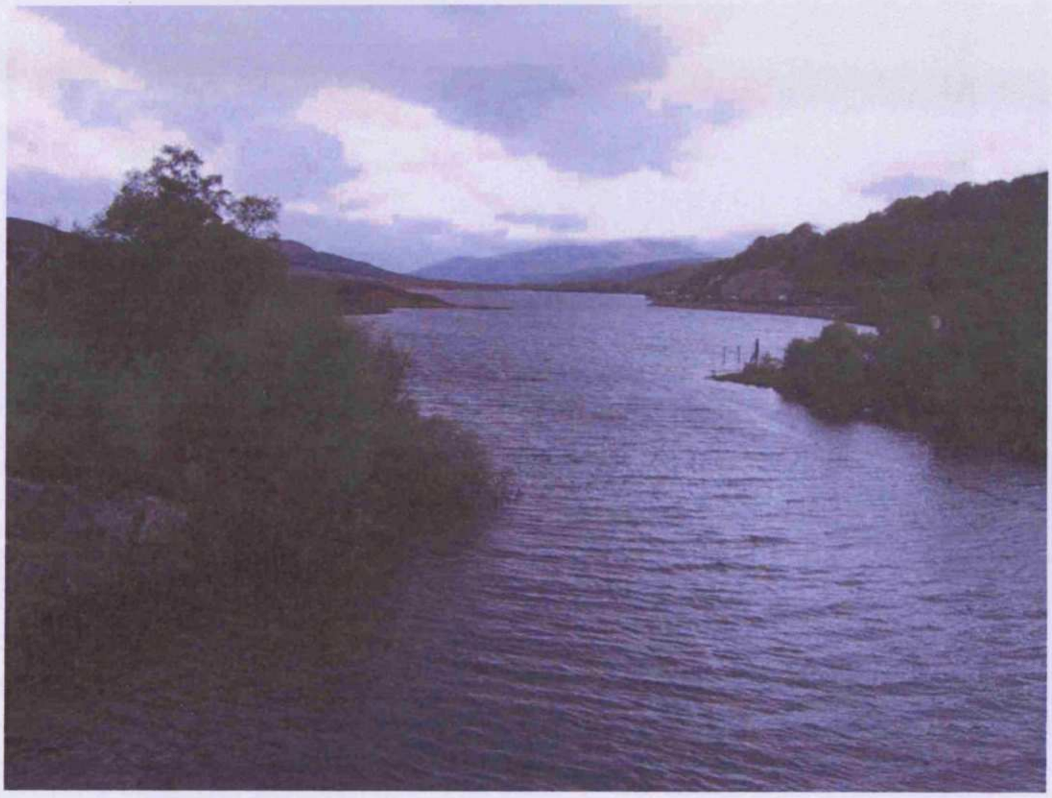
The present investigation took place at the Achanalt smolt trap in April-June 2002-2004. The smolt trap is situated at Achanalt Barrage at the downstream end of Loch a'Chuilinn, part of the River Bran which is a major tributary of the River Conon (see Figure 13, Chapter 4). An impassable falls on the River Conon prevented access of salmon to the River Bran until the advent of hydroelectric schemes in the 1950's. Fish passes were installed at Conon Falls and in all upstream hydroelectric facilities in order to facilitate upstream access to migratory fish. A series of stocking experiments were initiated in order to establish a population of salmon in the River Bran, as described by Mills (1964). Abnormally high levels of mortality were observed, however, and stocking of juveniles ceased. It is believed that migrating smolts are unable to locate the entrance of the fish pass at Loch Luichart, further downstream of Loch a'Chuilinn, probably due to a lack of flow and are thus unable to leave this part of the system (Simon McKelvey, personal communication).

Since the 1990's stocking of salmon in the River Bran and its tributaries has recommenced. In order to circumvent the problems smolt encounter downstream of Loch a'Chuilinn, a Wolf trap has been constructed at Achanalt Barrage, and smolts captured at this location are transported by road to be released on the mainstem of the River Conon. Release sites are located downstream of all hydroelectric structures on the system, thus allowing open access to the sea.

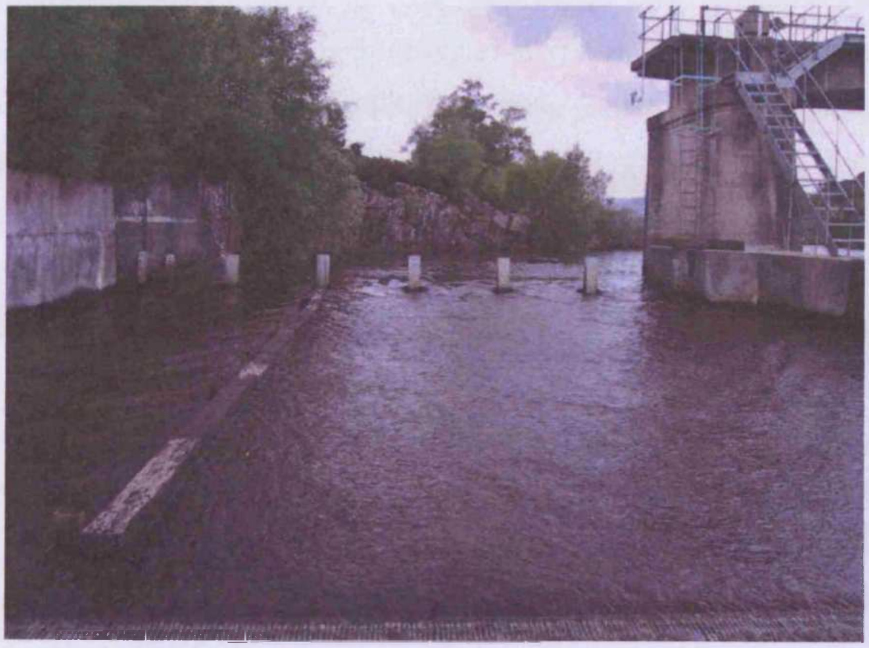
The catchment area of the River Bran system to the intake of Achanalt power station is 191 km^2 (Mills, 1964). The smolt trap consists of a concrete raceway by which smolts descend onto a grid by which they are, in effect, "sieved" out of the main flow of water. Smolts are then deposited into a narrow channel of flowing water and are hence delivered into a holding cage. In order to remove smolts from the trap, the inflow of water to the holding cage can be stopped, and the water level within the cage lowered via the use of a valve. It should be noted, however, that smolts can gain access to areas below Achanalt Dam if the barrage is lifted for operational reasons: subsequent counts of numbers of smolts reaching the smolt trap may therefore be underestimations of the true figure. Figure 15 shows Loch Achanalt and the smolt trap facilities.

Figure 15. Views of Achanalt Barrage smolt trap showing: A Loch a 'Chuilinn as seen from the barrage; B.the raceway leading to the trap; C smolts being removed from the holding facility at the trap.

A



B



C

An extensive study into the ecology of juvenile salmon in the Bran catchment by Mills (1964) revealed the extensive range of potential predators in the system. More specifically, the following potential predators of juvenile salmon were identified: trout, pike (*Esox lucius*), perch (*Perca fluviatilis*), eels (*Anguilla anguilla*), goosanders (*Mergus merganser*), cormorants (*Phalacrocorax carbo*), black-headed gulls (*Larus ridibundus*), common gulls (*L. canus*), greater black-backed gulls (*L. marinus*) and black-throated divers (*Gavia artica*). Also present in the Bran system are Arctic charr (*Salvelinus alpinus*), but these were not considered to be predators of juvenile salmonids. Larger charr are known to be piscivorous in some regions, however (L' Abée-Lund *et al.* 1992, 1996; Amundsen 1994). Otters (*Lutra lutra*) are also known to predate on both juvenile and adult salmon (Carss *et al.* 1990) and are present on the Conon system (Gowans *et al.* 2003). In addition, mergansers (*M. serrator*) and herons (*Ardea cinerea*) are also present and are known to consume salmonids on the system. Marquiss *et al.* (1998) note that the proportion of salmon recorded in the stomachs of mergansers shot on the River Conon system is unusually high.

Fish Sampling and Tagging

In order to assess return rates of salmon leaving the system, a proportion of smolts captured in Achanalt trap are routinely PIT tagged. PIT tags are small glass covered devices that contain a capacitor, antenna coil and microchip. Tags are placed in the abdominal cavity of fish via a small incision. Tags used in this study were manufactured by UKID Systems Ltd, UK, and measured 11mm in length. Each tag has a unique code which allows future identification of individual fish. PIT tags have the advantage of requiring no internal power source and can be detected either automatically by antennae placed in fish passes, traps and similar facilities or manually by the use of handheld receivers. The latter is particularly useful in identifying fish captured in commercial or recreational fisheries.

Smolts were removed from the holding facility using a small hand-held dip net. Prior to PIT tagging, smolts were placed in an anaesthetic immersion bath containing Benzocaine (40 mg l^{-1} as per Laird and Oswold 1975) in fresh water. All smolts selected for PIT tagging were examined visually for evidence of damage. In addition to undamaged smolts, those found to be damaged were subsequently PIT tagged unless the extent of the damage prevented the insertion of the PIT tag.

All smolts undergoing PIT tagging were weighed and fork length measurements also recorded. Details of any damage observed were noted. In previous studies of adult salmon, acetate sheets have been placed over fish in order that patterns of damage may be recorded (Thompson and Mackay, 1999). Due to the extremely delicate condition of juveniles undergoing smoltifiacation, and in particular the risk of inflicting further scale loss, such methods were not deemed appropriate in this instance. As such, digital images of the majority of smolts were also recorded using a Canon Ixus AiAf, Canon, Japan, camera in order to facilitate a more considered analysis of damage. All images were recorded against a scale.

Digital images of individual fish were examined and damage observed assigned to categories according to the protocols established by Williams (2001). The various categories are defined as per Table 8 below. It should be noted that categories are not mutually exclusive i.e. damage observed on an individual fish may fall into a number of categories. Smolts observed to have scale loss that fulfilled the criteria for categories I and/or II, however, but that also had other general areas of scale loss were not also additionally assigned to category VII unless other injuries were also evident. Images of actual fish with each type of damage are illustrated in appendix I.

Table 8. Description of the 7 categories used to classify damage to smolts.

Category	Description
I	Scales removed, including 'rake marks' / areas of parallel scale loss.
II	Scales removed, including converging lines or 'v'-shaped areas of scale loss.
III	Single small puncture wound.
IV	Single large puncture wound.
V	Multiple small puncture wounds.
VI	Multiple puncture wounds, including one or more large wounds.
VII	General scale loss or miscellaneous injuries.

Statistical Analyses

Data was analysed using SPSS (12.0.1) with α =0.05. Logistic regressions were used to assess the relationship of damage and individual categories of damage with smolt length, number of smolts captured (count) and date of capture. The data for all years, including that recorded in the 2001 study, was combined. In order to assess inter-annual variations in the factors influencing damage, year of capture was included as an independent categorical variable. The year 2001 was utilised as the reference category. A chi-square test was used to assess the relationship between survival and damage.

Results

A total of 5467 smolts were examined in 2001-4 of which 503 were found to be damaged. Not all damaged smolts were tagged, however. Table 9 illustrates the numbers of smolts tagged in each year and subsequent return rates

Table 9. Number of smolts captured and tagged during the study.

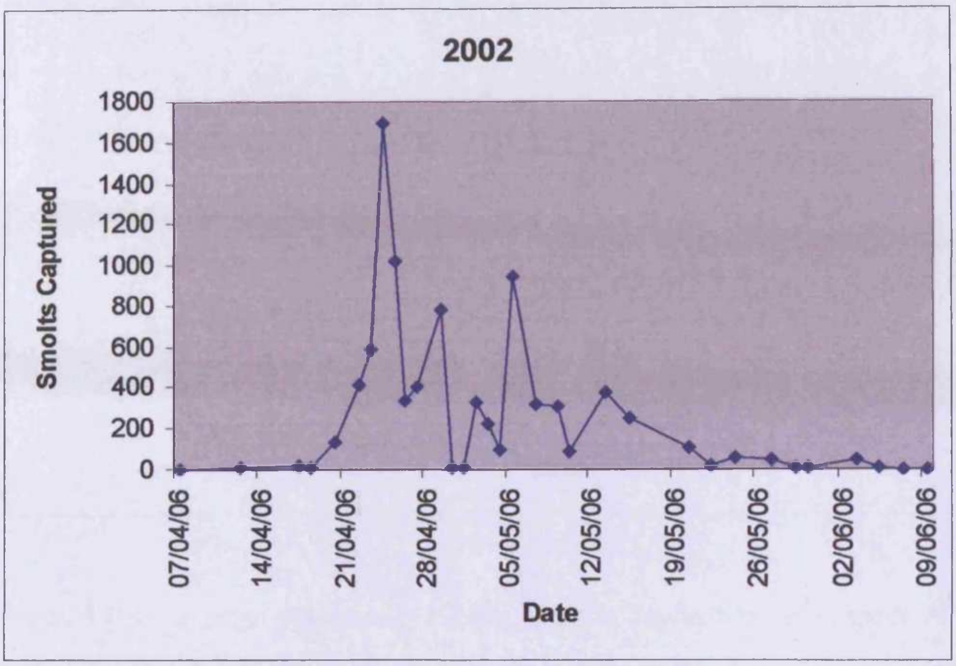
Year	No. Examined	PIT Undamaged	Undamaged Return	% Return	PIT Damaged	Damaged Return	% Return
2001	2069	1734	79	4.56	89	0	0
2002	1177	1081	20	1.85	96	1	1.05
2003	1124	1027	26	2.53	95	4	4.21
2004	1097	1010	34	3.36	83	0	0

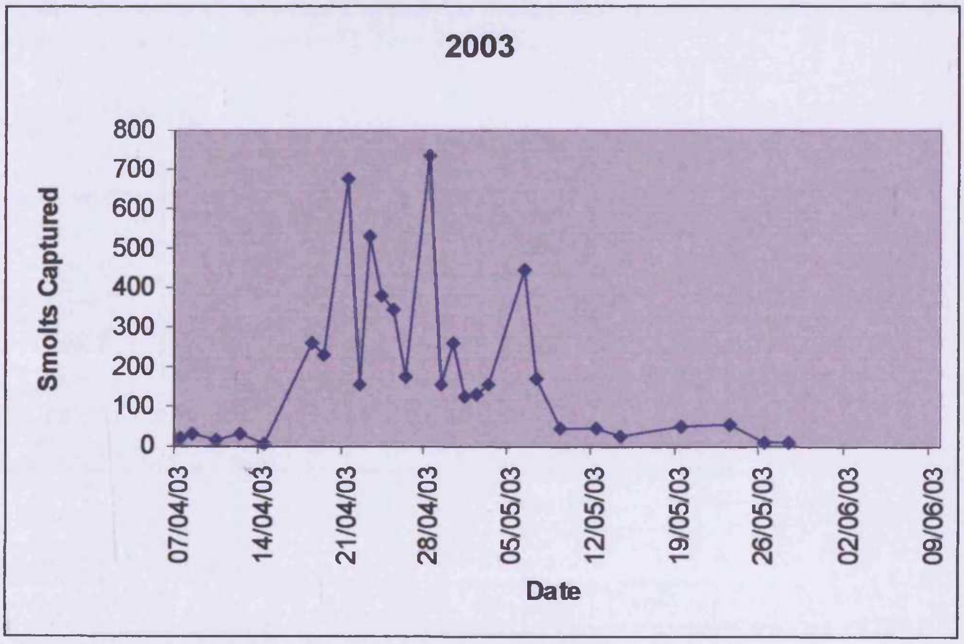
Numbers of smolts displaying each type of damage are illustrated in Table 10.

Table 10. Categories of damage.

Year	I	II	III	IV	V	VI	VII
2002	15	35	10	17	16	24	61
2003	20	43	6	16	39	43	97
2004	15	32	6	7	12	27	40

Figure 16. Graphical representation of numbers of smolts captured on a daily basis in each year.





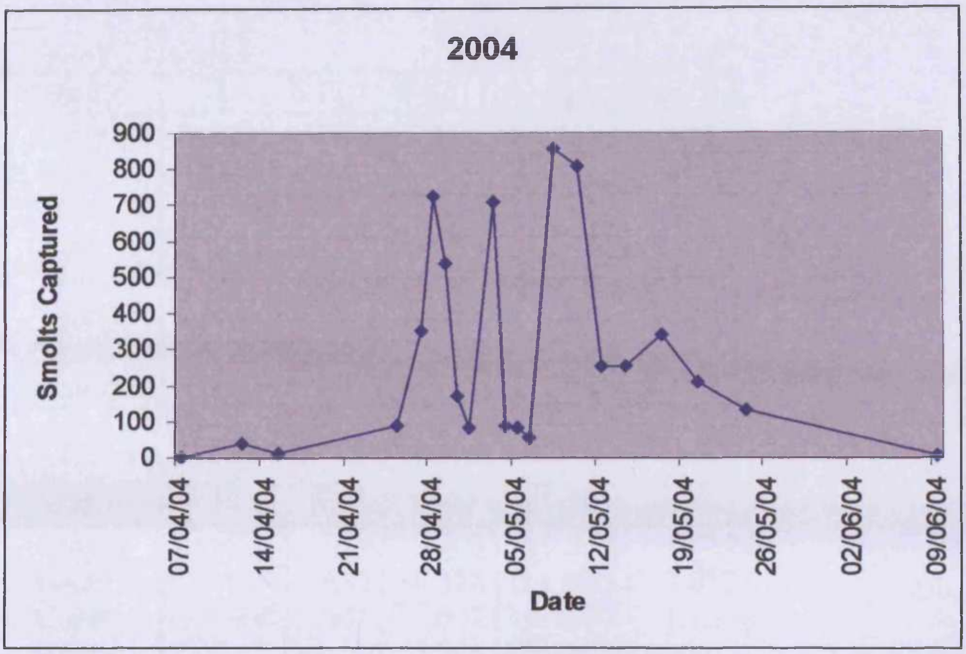


Table 12 summarise the results of the logistic regression in respect of the overall incidence of damage and each of the categories of damage described in Table 8.

Table 12. Results of statistical analyses for overall damage and individual categories of damage. Year 1 =2002, Year 2 =2003 and Year 3 = 2004.

Overall Damage

Variable	B	S.E.	Wald	df	Sig.	Exp(B)
Length	.013	.005	6.732	1	.009	1.013
Date	.031	.007	20.753	1	.000	1.031
Count	.000	.000	3.427	1	.064	1.000
Year			5.841	3	.120	
Year(1)	-.097	.144	.454	1	.501	.907
Year(2)	-.082	.144	.321	1	.571	.922
Year(3)	-.334	.139	5.726	1	.017	.716
Constant	-7.429	1.044	50.631	1	.000	.001

Category 1 Damage

Variable	B	S.E.	Wald	df	Sig.	Exp(B)
Length	.019	.012	2.641	1	.104	1.019
Date	.000	.016	.000	1	.986	1.000
Count	.000	.000	.445	1	.505	1.000
Year			1.185	3	.757	
Year(1)	-.207	.368	.317	1	.574	.813
Year(2)	.165	.334	.245	1	.621	1.180
Year(3)	-.086	.331	.067	1	.795	.918
Constant	-6.343	2.489	6.495	1	.011	.002

Category 2 Damage

Variable	B	S.E.	Wald	df	Sig.	Exp(B)
Length	.001	.008	.006	1	.938	1.001
Date	.020	.011	3.241	1	.072	1.020
Count	.000	.000	.011	1	.915	1.000
Year			2.688	3	.442	
Year(1)	.011	.240	.002	1	.962	1.011
Year(2)	.285	.230	1.545	1	.214	1.330
Year(3)	-.086	.225	.145	1	.703	.918
Constant	-6.000	1.721	12.160	1	.000	.002

Category 3 Damage

Variable	B	S.E.	Wald	df	Sig.	Exp(B)
Length	.021	.015	2.008	1	.156	1.021
Date	.055	.022	6.322	1	.012	1.057
Count	.000	.001	.007	1	.932	1.000
Year			2.255	3	.521	
Year(1)	.210	.436	.233	1	.629	1.234
Year(2)	-.306	.512	.356	1	.550	.736
Year(3)	-.494	.483	1.050	1	.306	.610
Constant	-14.186	3.356	17.870	1	.000	.000

Category 4 Damage

Variable	B	S.E.	Wald	df	Sig.	Exp(B)
Length	.014	.012	1.426	1	.232	1.014
Date	.047	.017	8.239	1	.004	1.049
Count	.000	.000	.016	1	.898	1.000
Year			6.110	3	.106	
Year(1)	.155	.335	.216	1	.642	1.168
Year(2)	.122	.347	.123	1	.726	1.129
Year(3)	-.895	.426	4.414	1	.036	.409
Constant	-11.798	2.544	21.505	1	.000	.000

Category 5 Damage

Variable	B	S.E.	Wald	df	Sig.	Exp(B)
Length	.016	.013	1.468	1	.226	1.016
Date	.039	.018	4.943	1	.026	1.040
Count	-.001	.001	2.895	1	.089	.999
Year			2.765	3	.429	
Year(1)	.630	.381	2.731	1	.098	1.878
Year(2)	.361	.393	.843	1	.359	1.435
Year(3)	.255	.383	.445	1	.505	1.291
Constant	-11.266	2.759	16.671	1	.000	.000

Category 6 Damage

Variable	B	S.E.	Wald	df	Sig.	Exp(B)
Length	.007	.009	.508	1	.476	1.007
Date	.037	.013	8.076	1	.004	1.038
Count	.000	.000	1.007	1	.316	1.000
Year			13.080	3	.004	
Year(1)	.466	.298	2.450	1	.118	1.594
Year(2)	.973	.271	12.855	1	.000	2.646
Year(3)	.500	.270	3.441	1	.064	1.649
Constant	-9.526	2.019	22.262	1	.000	.000

Category 7 Damage

Variable	B	S.E.	Wald	df	Sig.	Exp(B)
Length	.027	.006	18.583	1	.000	1.028
Date	.032	.009	12.795	1	.000	1.032
Count	.000	.000	2.803	1	.094	1.000
Year			8.966	3	.030	
Year(1)	.063	.185	.118	1	.732	1.065
Year(2)	-.302	.201	2.255	1	.133	.740
Year(3)	-.460	.194	5.646	1	.017	.631
Constant	-9.966	1.371	52.867	1	.000	.000

Marine Survival

The return rates of both damaged and undamaged smolts varied during the course of the study. Table 9 contains details of the returns for each year of the study. The majority of the returning adults were automatically detected at Tor Achilty Dam fish pass as they accessed the upper parts of the catchment. Additionally, a number of details were returned from fish captured on the rod fishery conducted downstream of Tor Achilty Dam. No damaged fish that were tagged in 2001 and 2004 respectively were registered as returnees. A single fish that was tagged in 2002 returned the following year. Four fish that were tagged in 2003 were recorded as returning, however, giving a return rate of 4.12 % which contrast to the return rate of only 2.53% with regard to their undamaged counterparts for that year. The study suggests that there is a relationship between damage incurred in freshwater and subsequent return rates χ^2= 4.001, d.f.=1, $p<0.05$. It should be noted, however, that the results in terms of return must be regarded as preliminary as there is the possibility that smolts tagged in 2004 may return in 2006.

The five damaged fish that were known to have successfully returned during this study displayed injuries in all categories with the exception of categories III (single small puncture wound) and VI (multiple puncture wounds including one or more large puncture wounds). Details of returning fish are summarised in Table 13. Two of the fish tagged in 2003 had managed to successfully complete their migration despite the presence of a single large puncture wound (IV) and varying types of scale loss (II and VII) in each case. The other two fish returning from the 2003 tagging had scale loss in varying categories (I, II and VII). The sole fish returning that had been tagged in 2002 displayed multiple small puncture wounds, in this instance two, as well as damage to its dorsal fin (VII). A picture of the damage incurred by two smolts is illustrated in Figure 18.

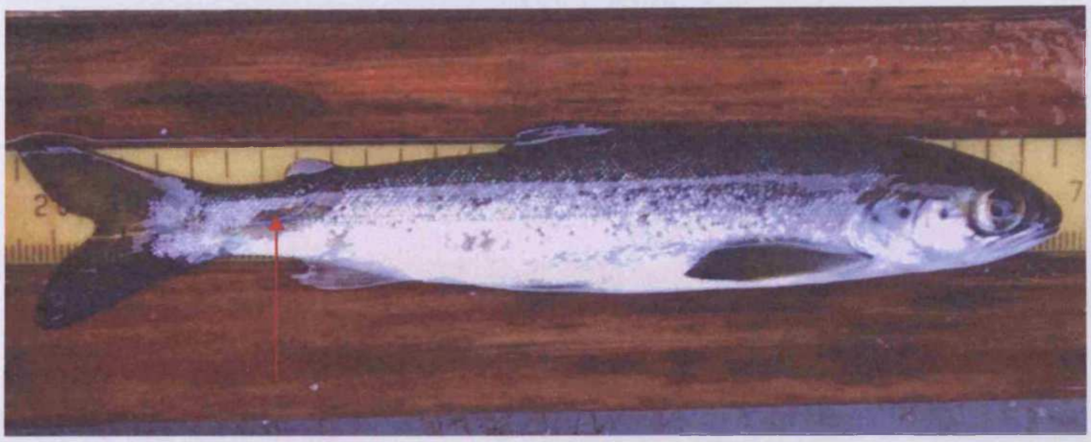
Table 13. Details of damaged fish that returned as adults to the Conon system.

Tagging Date	Fork Length	Category of Damage
15/5/02	136	V VII
23/4/03	113	I II
26/4/03	112	II IV
30/4/03	126	IV VII
6/5/03	136	VII

Figure 18. Fish A was tagged on 15/5/02. The white arrow points to a damaged dorsal fin. The red arrows point to two small puncture wounds. Fish B was tagged on 6/5/03 and displays general scale loss anterior to its caudal fin (red arrow).

A

B



Discussion

The study undertaken by Williams (2001) revealed statistically significant relationships in respect of the overall incidence of damage and length of smolt (positive), date (positive) and count (negative). Combining the data for the 2001 study with that obtained in 2002-2004 produces statistically significant positive relationships in respect of the overall incidence of damage and length of smolt and date of capture. No relationship in respect of the count of smolts in the trap could be detected, however. The addition of the categorical variable year yields a statistically significant term in the final year of the study, suggesting that there may well be annual variations in the factors influencing the incidence of damage.

Increased mortality of smaller size classes of smolts has been observed by Hvidsten and Lund (1988) and Feltham and MacLean (1996) have demonstrated that merganser and goosander tend to consume the smaller classes of salmonid prey available to them. Traditionally, however, assessment of prey preference has relied heavily on stomach contents of predators or retrieval of tags placed on smolts from nesting sites. Such analysis takes no account of unsuccessful attack by predators. Sanford and Harris (1967) note that larger items of prey are required to be manipulated by piscivorous birds in order that they may be eaten head-first. If the prey had been initially gripped posterior to the dorsal fin then manipulation was often unsuccessful and the fish escaped. Fish such as pike, perch and brown trout are also known to have to complete similar manipulation although the ability of prey to escape during manipulation is not known (Hart and Connellan 1984; L' Abée-Lund *et al.* 1996). Hislop and MacDonald (1989) observed that larger pelagic fish displayed more damage by sea birds in the Moray Firth. In addition, it is likely that larger smolts are better able to evade successful capture by predators due to elevated burst-speed (Taylor and McPhail 1985a,b) and sustained swimming ability (Peake and McKinley 1998) compared to their smaller counterparts.

The positive relationship between date and incidence of damage can possibly be explained with reference to a number of factors. Firstly, predators likely to inflict injury may have greater opportunity to attack smolts at the latter end of the smolt run. Youngson and Hay (1996) noted that movements by smolts on a Scottish river primarily occurred during periods of darkness at the start of the annual migration, presumably as a means of avoiding detection by predators. However, during later periods of the smolt run individuals would migrate during daylight even during periods of low river discharge, perhaps increasing vulnerability to attack by predators. Secondly, smolts captured during the latter part of the smolt run may be at more advanced stages of smoltification compared to those captured earlier in the run and may be more prone to scale loss due to interactions with predators or the trap apparatus itself. Thirdly, a more basic explanation may be that injured smolts have reduced ability to migrate because of their injuries and thus are delayed in reaching the trap. No information is available with regard to alterations in speed of migration caused by damage to smolts.

In the 2001 study, a negative relationship between count of smolts and the overall incidence of damaged was observed suggesting that the likelihood of observing damage was less when large numbers of smolts where migrating. Shoaling behaviour of fish is believed to largely be adaptive response to the threat of predation although others factors such as reproductive stimulus and obtaining food may also be important (Krause *et al.* 1998a,b). Krause (1998a) identified three potential benefits of shoaling. Firstly, shoals of fish may benefit from early predator warning compared to the ability of an individual to detect the presence of predators. Secondly, predators may become confused by the 'sensory overload' engendered by the presence of shoals of fish. Lastly, encounter-dilution effects may be of benefit if the likelihood of detection and attack by predators is not increased over-proportionately in relation to increasing shoal size. No such relationship could be observed for the pooled data, however, suggesting that the benefits of shoaling in terms of the incidence of damage do not always operate.

The statistically significant term for the year 2004 suggests that there may be inter-annual variation in factors affecting damage. The timing of smolt runs and the abundance and diversity of predators present may all vary over time. Numerous factors are believed to influence the initiation and density of smolt runs, for example water temperature, water flow, moon phase, cloud cover and social interaction (Thorpe and Morgan 1979; Hvidsten *et al.* 1995; Youngson and Hay, 1996; McCormick *et al.* 1998). Numbers of smolts captured at Achanalt tend to display several peaks during each smolt run with often relatively few numbers being captured between such peaks. In the 2001 study, the first peak occurred around the 8/9th May. However, in 2002 the first peak of the smolt run occurred on the 23/24th April, in 2003 21st April and in 2004 around the 27/28th April. The delayed smolt run in 2001 is likely a response to the extended period of low water temperatures in the winter and late spring of that year (Simon Mckelvey, personal communication). In the last three years of the present study, the numbers of smolts found to be damaged represented 8.16%, 8.62% and 7.93% of the total numbers examined in each year. In the 2001 study, however, 10.78% of the smolts were found to be damaged which suggests that 2001 may represent an unusually high incidence of damage.

Of particular importance to smolt survival and perhaps incidence of damage in a given year may well be levels of water discharge in the system. Hvidsten and Hansen (1988) reported elevated survival of hatchery-reared smolts released into a Norwegian river during periods of high flow. Possible explanations for this include increased turbidity in the river during periods of high flow affording protection from predators that rely on visual location of their prey. Additionally, smolts may migrate quicker during periods of high flow. Evidence as to whether smolts actively migrate, rely on passive displacement or utilise a combination of the two is contradictory (Aarestrup and Koed (2003). Difference in discharge may, however, be proposed as an explanation of variance in observed damage both in individual years and between years. Similarly, differences in water temperature may affect interactions between smolts and predators. For example, low water temperatures may render poikilothermic fish such as smolts more vulnerable to endothermic predators such as piscivorous birds.

Evidence suggests that timing of smolt migration may be influenced by the behaviour of those species likely to predate on smolts. For example, temporal overlap of smolt migration and the reproductive behaviour of predators may afford some protection for migrating smolts. Larsson (1985) has suggested that pike do not eat during their spawning period which typically lasts for around two weeks. Thus smolts migrating during this period may have less susceptibility to damage by pike and hence elevated survival prospects. Additionally, analysis of the diet of mergansers and goosanders on Scottish river systems suggests that the majority of juvenile salmon predation occurs in March and April i.e. at the earlier stages of the smolt run (Marquiss *et al.* 1998). However, it is likely that some predation can occur over a longer period if larger size-classes of salmonids such as smolts are available (Marquiss and Duncan 1993). The authors suggest that the inland migration of mergansers largely takes place in April and that incubation of eggs by females in May will likely reduce opportunities for predation at that time. Additionally, male mergansers may vacate inland areas in order to moult. With particular reference to the Conon system, however, mergansers and goosanders have been observed in the lower part of the system during the smolt run (personal observation). Studies of the behaviour of goosanders and mergansers by Sjöberg (1985, 1988 and 1989) have demonstrated a linkage between activity of the birds and their prey. In particular, a relationship between foraging behaviour and times when prey are most aggregated or are highly vulnerable has been observed.

In addition to the above named predators it is likely that the activities of a whole suite of other predators are likely to impact on the smolt run. These include heron, black-throated divers, various species of gulls, perch and brown trout. In the 1960's gulls shot on the River Bran contained tags that had been attached to smolts. It is not known, however, if the gulls had simply captured smolts rendered moribund by the tagging procedures (Mills 1964). Observations by Sjöberg (1989) and Armstrong (1990) suggest that gulls may simply be attracted to large aggregations of migrating smolts and are thus largely opportunistic in nature. Examination of the stomach contents of brown trout and perch captured by anglers on the Conon system also suggests that these species can consume migrating smolts.

In general there would appear to be a dearth of information with regard to predation on smolts by a number of potential predators. Particularly lacking in terms of predation on smolts is information with regard to temporal variation in the interactions of predators and prey. Care must be taken when assessing numbers of potential predators of salmonids and assuming that this will lead to elevated levels of predation, however, as the predators may simply be responding to the presence of another food source (Svenning *et al.* 2005a,b).

Category II damage (converging lines of scale loss) were particularly common in this study. 'V-shaped' areas of scale loss on salmonid species have been associated with interactions with avian predators in some studies (Carss 1990; Carss and Marquiss 1992). No statistically significant relationships in respect of Category 1 (parallel areas of scale loss) or Category II damage and the regressors were obtained. A significant positive relationship between all other categories of damage and date of capture was observed. Additionally, a positive relationship between length of smolt and the occurrence of most general category of damage, Category VII, was observed. Again, there appears to be inter-annual variation in the relationships as significant values for the year 2004 were observed in respect of category IV (single large puncture wound) and category VII and for 2003 in respect of category VI (multiple puncture wounds including one or more large wounds). Possible explanations for these significant terms mirror those postulated for overall damage.

Generally, however, most injuries did not correspond with known patterns of damage. This may be a result of the diversity of potential predators on the Conon system. Some of the damage observed in the study may have been the result of collision with apparatus in and around the trap at Achanalt. It is suggested that, in particular, some of the general scale loss observed in this study is likely to have been incurred from this source. The interaction of smolts with trap apparatus appears to be poorly understood.

This study suggests that the presence of damage may lower the ability of smolts to survive the rigours of the marine environment and return successfully to their natal rivers. However, some smolts did manage to survive injuries that included puncture wounds as well as areas of scale loss. There would appear to be a degree of inter-annual variation in the ability of smolts to survive such injuries as, surprisingly, in 2003 survival of damaged smolts exceeded that of their undamaged counterparts in percentage terms. Estuaries have been identified as key areas in terms of predation as smolts have to adapt to the physiological stress caused by entry to the marine environment while concurrently avoiding a increased suite of potential predators, for example sea fish (Hvidsten and Mokkelgjerd, 1987). It is suggested that assemblages of predators in estuaries and hence the interactions of predator and prey may vary between years. It is not known how quickly injuries to wild smolts heal in saline conditions and thus the length of any critical period of recovery is also indeterminate. In years with lower numbers of predators in the lower regions of rivers and in estuaries damaged smolts may have increased opportunity to evade capture and recover from injuries. Overall, though, it is likely that any injuries that delay migration will increase the likelihood of predation in estuaries.

Mesa *et al.* (1994) note that investigations with regard to interactions between predators and prey generally assume that the condition of prey is normal. In reality, however, this is unlikely to be uniformly the case – particularly in systems impacted by anthropogenic influences. In synthesising 37 studies available with regard to fish predator-prey interactions where the prey is in substandard condition, the authors note that 73% of the experiments concluded that substandard individuals were more likely to be preyed upon than control groups. These studies encompassed a wide variety of freshwater and marine species in both laboratory and field based studies, although there has been a strong bias toward tank-based studies. Categories of stressor include toxicants, thermal shock, physical stress (including descaling of salmonids), starvation, disease and prior lack of interaction with predators due to hatchery-rearing. Physical stress and damage resulting from prior interactions with predators does not appear to have been included in such experiments, however. With specific regard to salmonids, the results appear to be particularly mixed with affects of some stressors seemingly being undetectable in a number of studies. The authors note that there has been a general lack of field studies to corroborate the observations of laboratory experiments. In addition, many studies have been very limited in their temporal extent (often measured in hours or minutes) and have thus been unable to take into account the long-term implications of stressors.

McCormick *et al.* (1998) emphasised the importance of sub-lethal effects of a wide variety of stressors that may be of particular importance as individuals undergo smoltification. In particular, there is evidence from Norwegian rivers that exposure to acid water conditions during smoltification may reduce salinity tolerance of smolts and significantly lower survival in the marine environment (Staurnes *et al.* 1996). It has been suggested that other pollutants and stressors such as handling at trapping facilities and damage incurred when gaining passage at dams may exert similar negative responses in marine survival but overall there would appear to be a dearth of evidence to substantiate such claims (Carey and McCormick 1998; McCormick *et al.* 1998).

The existence of dams, weirs, fish traps etc on regulated rivers may cause delays in the migration of smolts, may increase the likelihood of interactions with predators and may inflict damage due to collision with man-made structures. It is believed that timing of entry into the marine environment is critical for the survival of smolts, a situation termed as the 'smolt window' by McCormick *et al.* (1998). In essence, the authors argue that two windows exist. Firstly, the smolts may be in an optimal physiological condition for entry into saltwater for a relatively short period, particularly in rivers experiencing high water temperatures (McCormick *et al.* 1998). Any delays in migration may lower the salinity tolerance of migrants. Secondly, there may be an environmental window in which conditions in rivers, estuaries and further offshore may be optimal for survival. An example of this is smolt arrival in the estuaries coinciding with boosts in productivity in that area and the influx of species important as food sources, such as sandeels. Survival is thus highest when the migration of smolts occur when optimal physiological windows and optimal environmental windows overlap. Delays in migration caused by injuries inflicted by predators or interaction with structures at dams may impinge on the ability of individuals to survive in the marine environment.

This study shows the importance of considering factors that occur in the freshwater environment when considering changes in mortality in the marine environment. Reductions in marine survival due to both natural factors and anthropognic influences are likely to have important consequences in both ecological and economic terms. Reduction in numbers of adults returning to their natal rivers reduces the availability of fish for both commercial coastal fisheries and recreational rod fisheries with the concomitant implications for regional economies. Fewer returning female salmon will also reduce the potential for egg deposition and may thus reduce recruitment in future years. Lower egg deposition may also lower the potential amount off eggs available to be scavenged by salmon parr and other fish and avian species. This is likely to be the most direct route in which nutrients derived in the marine environment are transferred to freshwater ecosytems by Atlantic salmon and eggs are known to be consumed by salmon parr (Youngson and Hay 1996). Eggs have a high lipid content and are available at a time of year when other sources of food are limited. During extended periods of low water temperatures in the winter months that are experienced in northern latitudes lipid reserves may play an important role in allowing parr to overwinter. A proportion of male parr are sexually mature and take part in spawning activities, incurring the associated energetic costs. Consumption of eggs may facilitate the recovery of this lost energy and may allow an individual to overwinter successfully and perhaps smolt the following spring. Overall there appears to be a paucity of information with regard to the importance, and particularly the temporal importance, of this potential source of food. The reduction in the number of returning adults will also likely lower the number of carcasses in the post-spawning period that are available for scavengers or that may decay and release the nutrients accumulated in the marine environment.

The increased marine mortality observed in this study resulting from the presence of physical injury represents a disruption in the positive feedback loop associated with Atlantic salmon migration. Of particular importance is the location in which such injuries were incurred i.e. in the upper section of the catchment. It would appear likely that a portion of the annual smolts run leaving the River Bran have already incurred injuries that will impinge on their ability to survive the marine phase of their life cycle. The importance of any sub-lethal injuries in terms of nutrient movement will depend on the location of any mortality that ultimately occurs. For example, predation of smolts in rivers by pike represents the recycling of the nutrients assimilated by the smolts within the freshwater environment. However, predation by cod in the estuary would represent a loss of assimilated nutrients to the freshwater environment.

Management Implications

On the Conon system, smolts have significant difficulties in locating the entrances to fish passage facilities at a number of dams thus increasing the likelihood of interactions with predators (Simon McKelvey, personal communication). If delays are of sufficient magnitude it is also possible that individuals will undergo 'de-smoltification' and lose the urge to migrate. This is likely to occur on the River Orrin within the Conon catchment. In order to circumvent these passage difficulties traps are often operated to capture the migrants. Often the smolts are then transported by road (or by barge on many Pacific salmon fisheries) and released further downstream. However, such procedures have the potential to induce delayed mortality via a number of mechanisms. Firstly, physical injuries may be inflicted on individuals due to collision with structures associated with the traps or are inflicted by personnel removing smolts from traps and placing them in transportation tanks. Secondly, stress can be inflicted on individuals due to the handling and transportation. It is therefore recommended that all fish traps be designed so as to minimise the risk of collision, and hence damage, as much as possible and that the minimum amount of handling and transportation stress is inflicted on individuals.

Injuries to, and mortality of smolts, also occur due to the presence of turbines in hydroelectric dams. When operating, the flows associated with turbines often attract smolts who attempt passage via this route even if fish passes are available to them. Attempts to minimise this sort of damage include the installation of turbine blades designed to minimise the risk of injuries, experiments designed to ascertain the optimum revolutions of turbines in terms of minimising damage and the use of a wide variety of screening devices to try and prevent smolts obtaining passage via the turbines. It is recommended that the prevention of this source of damage be maximised and that more research is targeted at easing the difficulties associated with the downstream passage of smolts.

The culling/scaring of various predators is often advocated in order to increase survival of juvenile salmon. In addition to reducing direct mortality of smolts, such an approach may reduce the incidence of damage and in turn reduce the likelihood of mortality of individuals in the marine environment. A better understanding of the species of predators likely to cause damage and the types of damage they cause would aid the appropriate utilisation of these techniques.

Chapter 7

General Conclusions and Recommendations

The Importance of Nutrients in Salmonid Production

The positive response of juvenile salmon to the introduction of nutrients (in this case in the form of adult salmon carcasses) within tributaries of the Conon system observed in this study provides strong evidence that the availability of nutrients should be regarded be a key component of assessment of the potential productivity of habitat. Interactions between the suite of factors that are likely to affect production render the formulation of accurate predictive models highly complex but it is suggested that availability of nutrients should receive more attention. Nutrient availability is also highly significant with regard to the abundance and diversity of other trophic levels, for example invertebrate communities, and salmon migrations are likely to play a key role at ecosystem level.

In order to gain a better understanding of the relationship between juvenile production and availability of nutrients it is suggested that a number of approaches should be adopted. Firstly, accurate assessment of the nutrient status of the most oligotrophic catchments or sections of catchments is required – particularly in regard to P. Assessment of nutrient levels in streams requires frequent sampling due to the relationship between nutrient flux and stream discharge. Currently, however, chemical analysis techniques commonly used in the British Isles have detection limits for P that are too high to constitute a useful tool in assessment of nutrient status for many oligotrophic regions. It is suggested that this is indicative of the paucity of interest in the positive role of nutrients in ecosystems and the apparent view of many regulatory authorities that nutrients are inherently 'bad'. This is understandable given that excessive anthropogenic inputs of nutrients can have obvious deleterious consequences in terms of biodiversity but more research is required into the potential negative alterations in ecosystems resulting from reductions of nutrient levels due to anthropogenic intervention. It became apparent during the course of the present investigation that North American research utilises chemical analysis that appears to have much lower detection levels of P than is commonly used in the British Isles. If practicable, these techniques should be adopted in order that a proper understanding of nutrient levels in the most nutrient poor areas is facilitated.

Gentle nutrient manipulation in areas that currently enjoy low nutrient status would, on the evidence of this study, appear to offer considerable potential as a tool for fishery managers to increase the abundance of juvenile salmon. Given that Atlantic salmon have high conservation status and recreational fisheries for the species have high economic value this would appear to be an appealing prospect particularly as abundance of adults is currently low in historical terms. However, there are a number of important caveats that are required to be considered before such an approach should be contemplated. For example, abundance of the early-running MSW component of stocks in the British Isles is currently believed to be most under pressure and in many systems these tend to originate from the highest altitude (and nutrient poor) portions of the catchments. There is evidence that the propensity to adopt this life strategy is linked to genetic factors but environmental factors may also play a role. In particular, short growing seasons and low water temperatures at high altitude may increase freshwater residency times and in turn this may influence the residency period of an individual in the marine environment. Inputs of nutrients in Pacific salmon fisheries have been shown to lower freshwater residency periods of juveniles but no information is available with regard to the likelihood of similar patterns resulting from the input of nutrients in Atlantic salmon streams. Research into residency times would be a prerequisite before attempting to introduce nutrients into habitat known to be utilised by early-running MSW salmon as there is the potential for such techniques to be counterproductive.

Additions of nutrients for fishery management purposes are likely to be perceived as highly unorthodox by regulatory authorities and are thus unlikely to be readily sanctioned. This view is likely to become further entrenched with the imminent implementation of the European Water Framework Directive. This legislation regards nutrients such as P as a source of pollution and as such sets upper limits that cannot be exceeded if a waterbody is to be regarded as having good ecological status. In North America, conflict has been reported between fishery scientist who wish to add nutrients to boost fish stocks in a river and regulatory authorities who are concerned that nutrient levels already exceed quality standards (Compton *et al.* 2006). Whilst salmon carcasses were used as the method of achieving enrichment in the present study, this method would not be practical for large-scale addition programmes in the British Isles. Other techniques such as the direct input of chemicals via drip-feed systems or artificial pellets would have to be employed and would require the consent of the relevant regulatory environmental agencies. Additionally, it is likely that in the future there will be an increasing tendency to manage the environment in order to maintain overall diversity rather than enhance one component of the ecosystem, however economically important that component is. In terms of nutrient addition, there is evidence from North America that overall species diversity of invertebrates can be lowered after artificial inputs although diversity within some functional groups can be enhanced and it is this type of effect that may attract objections from regulatory authorities and interest groups.

It is thus incumbent upon fishery managers to demonstrate that increasing the numbers of returning adult Atlantic salmon via this technique will in turn foster increased abundance and diversity of species at higher trophic levels. For example, increased spawning activity may increase the amount of eggs available for consumption by instream invertebrates, salmonid and non-salmonid fish species and various bird species. Likewise, increased numbers of spawning salmon and of carcasses of post-spawned salmon may have important implications for the populations of predators such as otters and of numerous species of scavengers. Spawning salmon can also have other important ecological effects such as making invertebrates available for consumption by predators via the displacement of gravel in the excavation of their redds. At the same time it is important to demonstrate that any negative effects of nutrient enrichment in terms of biodiversity are limited in extent and are reversible if enrichment ceases.

Justification for nutrient enrichment would perhaps be best achieved if it can be demonstrated that changes in land use (for example deforestation) has lowered the nutrient status of watersheds. Sediment cores from lakes are increasingly being employed in order to reconstruct changes in the nutrient profile of catchments over time (Bennion *et al.* 2004). These cores can be examined for the presence of both lotic and lentic diatoms, both of which are highly sensitive to changes in nutrient levels and are also an important source of food for higher trophic levels. Many of these studies utilise lochs that are known to have experienced eutrophication, however, and take the date for baseline conditions as being c1850. It is suggested that the use of sediment cores may shed more light on historical changes in nutrient profile if a broader range of lochs are studied and that nutrient profiles are studied from pre 1850 as well as post 1850.

Many sections of the upper parts of catchments in Scotland are likely to have been characterised by extensive forestry and in turn allochthonous inputs of nutrients from leaf litter etc may have been more important in terms of the productivity of these areas relative to primary production derived from autochthonous sources. The removal of canopy cover due to deforestation practices may well have increased the importance of primary production in these areas over time and thus any reduction in dissolved nutrients available may have deleterious consequences for salmon populations. Similarly dams have the potential to cause what Vannote *et al.* (1980) termed 'reset' i.e. cause nutrient status to be lowered back to levels associated with areas upstream of the dam in question. Nutrient addition may therefore be more justifiable in regulated rivers rather than unregulated ones.

The enrichment experiment undertaken in this study provides evidence for the potential importance of nutrients in terms of juvenile Atlantic salmon production but there remain large gaps in knowledge that will require a more refined approach to experimental design. For example, the present study has not addressed a number of temporal considerations. Carcasses will provide food for some functional groups of invertebrates directly as they are able to scavenge the flesh from the body. As the carcass decays and nutrients are released periphyton production is likely to boosted and in turn the invertebrates that rely on this food source are likely to benefit. The availability of invertebrates to salmon fry emerging from the gravel is likely to be an important factor in determining survival rates. The timing of peaks of periphyton biomass and hence the timing of nutrient inputs designed to boost this biomass and in turn invertebrate and juvenile salmon population is thus crucial. Investigations with regard to obtaining an improved understanding of the importance of timing of inputs are thus required. Carcass decomposition rates may vary between rivers and within rivers and carcass addition may be a crude way to attempt to investigate the relationships between various trophic levels. It is suggested that the use of direct chemical inputs into streams or experimental streamside troughs may provide better research opportunities to close this gap in knowledge. Similarly, this study essentially constitutes a 'snapshot' of the response of juveniles to nutrient addition and does not address any long-term effects. No information can be gained from this study with regard to the persistence of any effects of nutrient addition in terms of increases in salmon biomass. It is therefore suggested that future studies may benefit from greater longevity in study period and sampling on multiple occasions in order to ascertain the persistence of effects.

The present study demonstrated a positive causal relationship between nutrient additions and overall juvenile salmon biomass, but no satisfactory relationship within cohorts could be established. It is likely that this is a result of interactions between year classes and in particular it is possible that at least a proportion of parr populations in streams are sufficiently mobile enough to take advantage of an improved food source. An influx of parr responding to nutrient addition may in turn alter the behaviour and survival rates of fry. Fry survival is likely to represent a 'bottleneck' in salmon production and is thus likely to be of particular interest to fishery managers. In order to assess the influence that nutrient addition may have on the survival of fry it is suggested that further experiments be undertaken that assess the response of fry both in sympatry and allopatry with older cohorts. Such experiments may best be undertaken in areas of streams that are inaccessible to adult salmon due either to the presence of natural or manmade barriers further downstream. Difficulties can still arise in such experiments, however, due to inter-specific competition from other fish species, particularly brown trout. Use of artificial or semi-natural streamside channels in which the population of fish species present can be more readily controlled and monitored perhaps offers the best opportunity to investigate the effects of nutrient additions on different age classes of salmon.

Overall it is suggested that fishery managers be cognisant of the potentially important role that nutrients may play in the productivity of rivers. Care must be taken to assess any proposed alterations in respect of land use, particularly activities such as deforestation, with regard to their implications for the quantity of nutrients entering the system.

Atlantic Salmon as a Source of Marine Derived Nutrients

This study has provided strong evidence that Atlantic salmon that perish after spawning may be retained in the upper portions of catchments and can thus contribute to the nutrient dynamics of those areas. However, in the present study the final locations of the majority of fish that were tracked but did not successfully leave the study area were clustered in the lower gradient section of the study area. This area is characterised by relatively deep water and low velocity flows and is thus not likely to constitute important juvenile salmonid nursery habitat. During the spawning period itself, many of the tracked salmon tended to remain close to tributaries of the River Bran but were rarely located in them. Examination of data from the ALSTN's suggest that much movement occurred during crepuscular and nocturnal hours and it may well be the case that occupation of, and spawning activities within, small tributaries was largely restricted to the hours of darkness. If correct, this would suggest that few if any carcasses will remain in and contribute nutrients to small tributaries that may be important nursery areas. Adults may have sufficient energy reserves after spawning to leave tributaries and may actively seek areas of low flow velocity such as lochs, or carcasses of those individuals that perish may simply be flushed downstream into such areas.

The overall mortality rate observed in the study is at the top end of estimates utilised in the assessment of the P flux associated with salmon migrations on the River Bran by Nislow *et al.* (2004a). However, several features of the River Bran as choice of study area may suggest that mortality in other river systems could be even higher. For example, numbers of returning adults are relatively low (200-300 annually) and thus there may be a lower level of competition between individuals for mates and spawning locations than on systems with higher numbers. Elevated competition could possibly increase the incidence of injuries for an individual, increase the energetic costs of spawning and may result in a higher probability of mortality. Historically, no salmon were present in the River Bran and the current population are present due largely to an annual stocking programme. Returning adults to the River Bran are dominated by grilse with few MSW salmon present. There is evidence from Norwegian rivers that populations consisting predominately of MSW salmon will experience greater levels of mortality than those consisting largely of grilse due to the higher metabolic costs of spawning experienced by the former. It is therefore suggested that studies on a wide variety of river systems be undertaken in order to obtain a greater understanding of the differences in mortality between catchments of different physical characteristics and different stock composition. Specific attention should be paid to the fate of large MSW salmon. Trap data has historically been utilised in order to assess mortality rates but, whilst this provides some useful data, it yields no spatial or temporal information as to the fate of those individuals that die. Telemetry can provide this information and should be more extensively utilised, the expense of this method not withstanding. The relative importance of the contribution of migrating salmon to the overall flux of nutrients in a river is likely to vary greatly between systems and is probably of negligible importance in those catchments that are inherently nutrient rich. It is thus further suggested that any future research effort should be concentrated on the most oligotrophic catchments or areas of catchments.

In contrast to a number of other published studies, there was no evidence in the present study of interactions between spawning salmon and predators/scavengers. However, predators and scavengers are likely to play an important role in the distribution and retention of nutrients from salmon in the riparian zone. Such interactions remain relatively poorly understood and warrant further investigation as do other retention mechanisms such as the presence of large woody debris.

Nislow *et al.* (2004a) note that many fishery managers stock areas that are inaccessible to adult salmon (e.g. areas above waterfalls or manmade structures). This has the advantage of allowing managers to increase overall production of juveniles within a system while avoiding stocking areas in which wild juveniles are present. The present study has illustrated, however, that returning adult salmon may die in the upper parts of catchments with the nutrients they have transported from the marine environment therefore being released within oligotrophic areas. Fishery managers should therefore be aware that stocking areas inaccessible to wild salmon may have implications for the nutrient flux in those areas. Smolts migrating from such areas will transport the nutrients they have assimilated during their residency period in fresh water without any natural mechanism existing for the return of nutrients from the marine environment to compensate for the loss. In the long term this may contribute to a gradual diminution in the nutrient status of such areas. This problem can be overcome by the removal of barriers to upstream migration or the introduction of fish passage facilities. Alternatively, gentle nutrient addition to areas deprived of returning salmon may be utilised in order to maintain a balance in the nutrient flux associated with salmon migrations.

No attempt has been made in the present study to examine perhaps the most direct route in which Atlantic salmon can contribute nutrients from the marine environment into freshwater food webs i.e. eggs being available to a host of invertebrate and vertebrate communities. Salmon eggs have a high lipid content and are available at a time when few alternative sources of food are available. The temporal aspect of this input of food may be of especial interest to salmon fishery managers as consumption of eggs may contribute to the lipid reserves in parr that will be of crucial importance in determining overwintering survival rates. Research utilising stable isotope analysis and fatty acid analysis has been proposed by scientists from Fishery Research Services in Scotland in order to investigate the importance of this food source to salmon parr populations (Anon 2006). Should the importance of this source of food for parr populations be demonstrated then this may have implications for management techniques that incorporate the stocking of juveniles into areas of streams that are inaccessible to adult salmon. Juveniles stocked in these areas will by definition be deprived of this potential food source for as long as they remain in such areas. In the present study, the clustering of salmon in the vicinity of smaller tributaries of the River Bran suggests that many of these may have been in receipt of eggs from spawning females and will have thus received nutrients accumulated largely in the marine environment.

Productivity Above and Below Lochs

The present study highlighted the difficulty in making assessments of productivity in relation to a single factor i.e. in this case nutrients. Density and size of juvenile salmon in the present study was highly variable as is likely to be the result of a multitude of factors. The use of electrofishing techniques in streams that are very wide and deep is also problematical and other techniques such as mark and recapture are probably more appropriate and it is therefore suggested that their more widespread use be adopted in this type of location if meaningful data is to be obtained.

Assessment of juvenile salmon production is hindered by differences in the mobility of individuals at different stages of their life history. At the earliest stages of development there would appear to be only limited downstream movement from the location of the redd and very little upstream movement indeed. This renders the distribution of fry inherently patchy in nature and strongly dependent upon the numbers and spatial distribution of spawning salmon. Stocking of eggs or juveniles from hatcheries can help to circumvent this difficulty and it is suggested that these techniques may be utilised more in order to assess the factors affecting fry abundance and survival in relation to their environment.

Parr are known to be much more mobile, however, and their movements may confound a simplistic assessment of the factors affecting their abundance and survival. Much research has been undertaken with regard to the movements of juvenile salmon particularly in respect of autumnal movements of parr associated with individual males becoming sexually mature and also autumnal movements that are likely to be associated with juveniles undergoing smoltification the following spring. The migratory behaviour of smolts in freshwater has also been extensively studied. Generally, however, the movements of parr are poorly understood. Evidence exists that upstream as well as downstream movements in order to occupy habitat in small tributaries and in lakes is undertaken in Scandanavia and North America and examination of scales and otoliths has suggested that it is often the fastest growing individuals of a cohort that undertake such migrations. Research effort needs to be aimed at obtaining a better understanding of the mechanisms underlying this ontogenic niche shift. For example, further information is required in order to assess if there is a genetic basis to this type of behaviour and if different populations of Atlantic salmon have different propensity for migration within streams. Until more information is available with regard to salmon parr movements then attempts to assess the productivity of areas of habitat will be problematical. It is likely that the further development of techniques such as stable isotope analysis (particularly those that utilise salmon scales and otoliths) will advance knowledge of the movements of juvenile salmon in the freshwater environment (Kennedy *et al.* 2004).

Many fishery managers would like to be able to have a better understanding of the carrying capacity of juvenile salmon of the rivers that they are charged with managing. This would allow for more accurate assessment of the minimum spawning escapement required to fully populate the system and/or the stocking levels of juveniles. The concept of self-thining has been examined by fishery scientists in respect of juvenile Atlantic salmon and is a useful conceptual tool in this respect given that the self-thining curve corresponds with the carrying capacity of habitat. A thorough understanding of allometry of territory size and the metabolic requirements of individuals are required in order to improve the usefulness of this concept. It is likely that a better understanding of these concepts will require both laboratory experiments in controlled environments and field studies. The relationship between food availability, territory size and fish movement warrants particular attention. Of course, in reality the carrying capacity of a stream or section of a stream will vary temporally but more research into the underlying mechanisms that determine the productivity of streams can only benefit fishery management.

Fishery managers routinely obtain data with regard to the density of juvenile salmon at various locations in catchments and also often extensively map the quality of habitat available. Monitoring of the chemical composition of watercourses is often also undertaken by regulatory authorities as is monitoring of the density and diversity of invertebrate communities (due to them being sensitive to alterations in water quality and other environmental variables). It is suggested that greater integration of the data generated should be attempted in order to better understand the relationship between environmental variables and salmon production. In addition, the interactions between Atlantic salmon and invertebrate communities remain poorly understood and much more research is required in order to close important gaps in knowledge.

Marine Survival of Damaged Salmon Smolts

The present study offers strong evidence that sub-lethal injuries can impinge on the survival of salmon smolts in the marine environment. This may have important management implications in a number of areas – particularly in those systems that have been subjected to anthropogenic alteration. Any structures that delay migration of salmon smolts have the potential to alter the interactions between smolts and predators and there is some evidence from telemetry studies that dams, weirs, sluice gates etc may be a focal point of predation.

The interactions of smolts and their predators remain poorly understood and requires further investigation. There is a widespread perception that estuaries are a key zone in terms of predation but evidence to substantiate this is equivocal. It is therefore recommended that further research efforts be targeted at predator-prey dynamics in estuaries.

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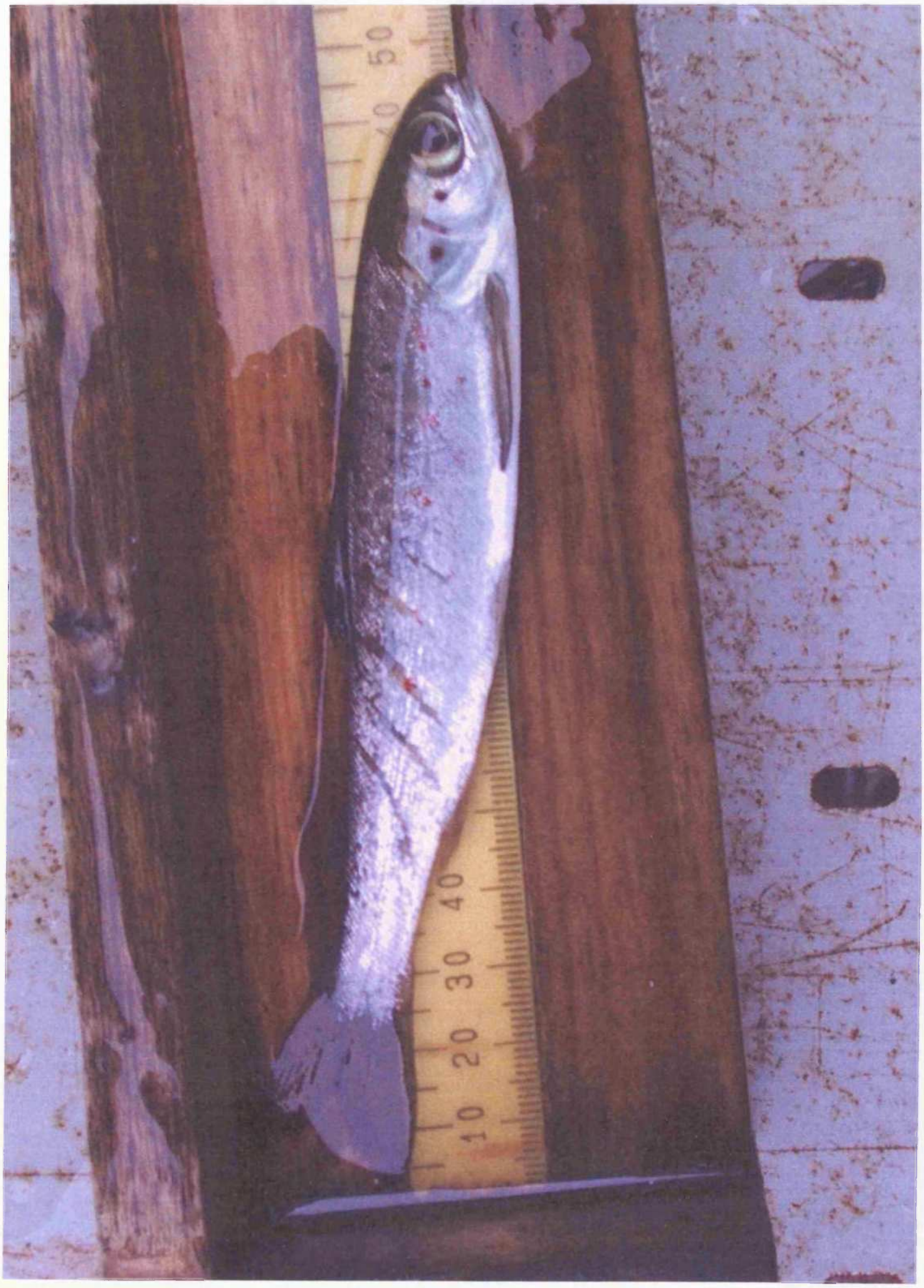
Appendix

Category I

This smolt displays parallel areas of scale loss between the dorsal fin and caudal fin.

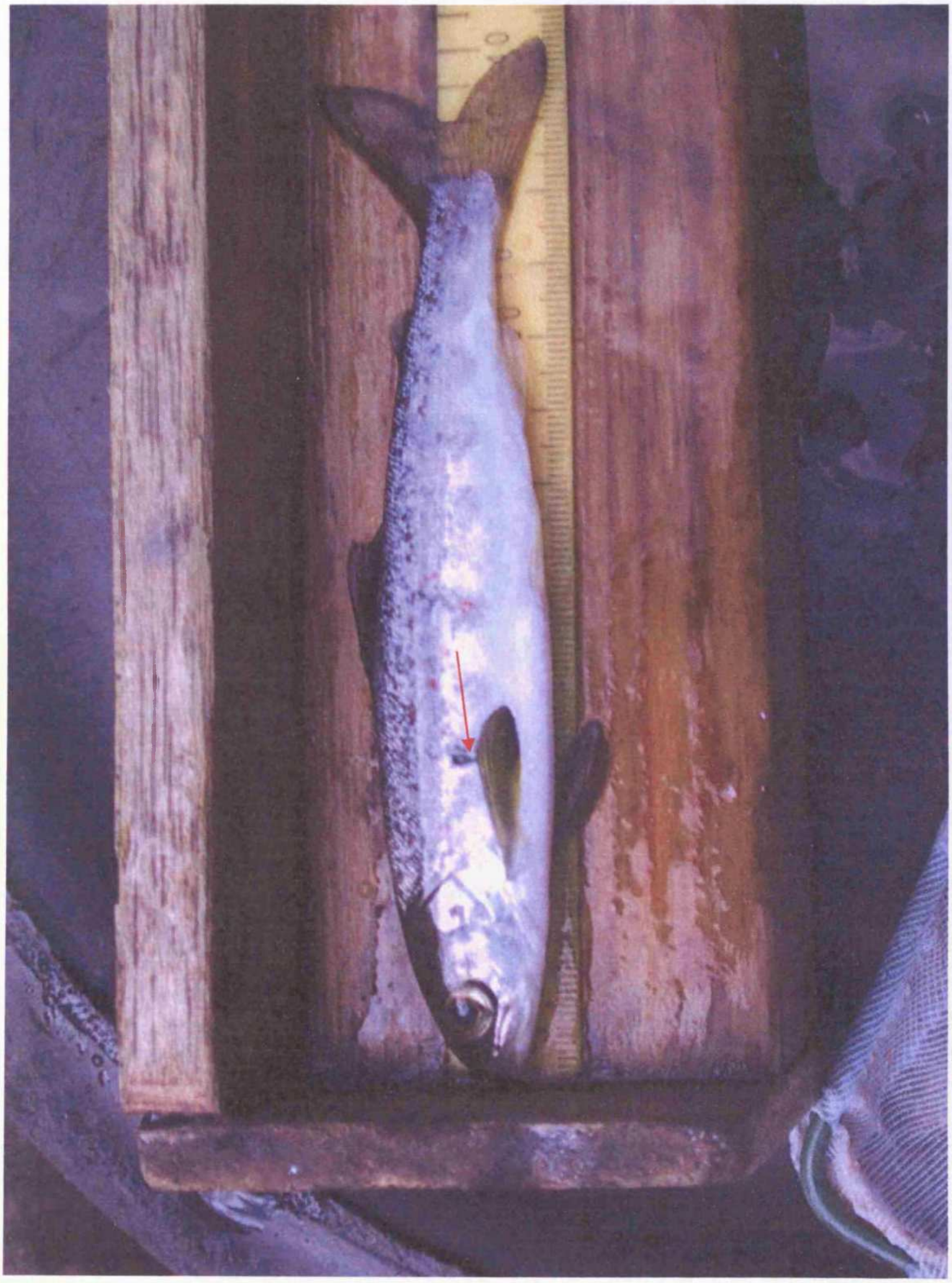


Category II

This smolt has large areas of scale loss, including many areas of converging lines and 'v' shaped areas of loss that are particularly noticeable posterior to the dorsal fin.

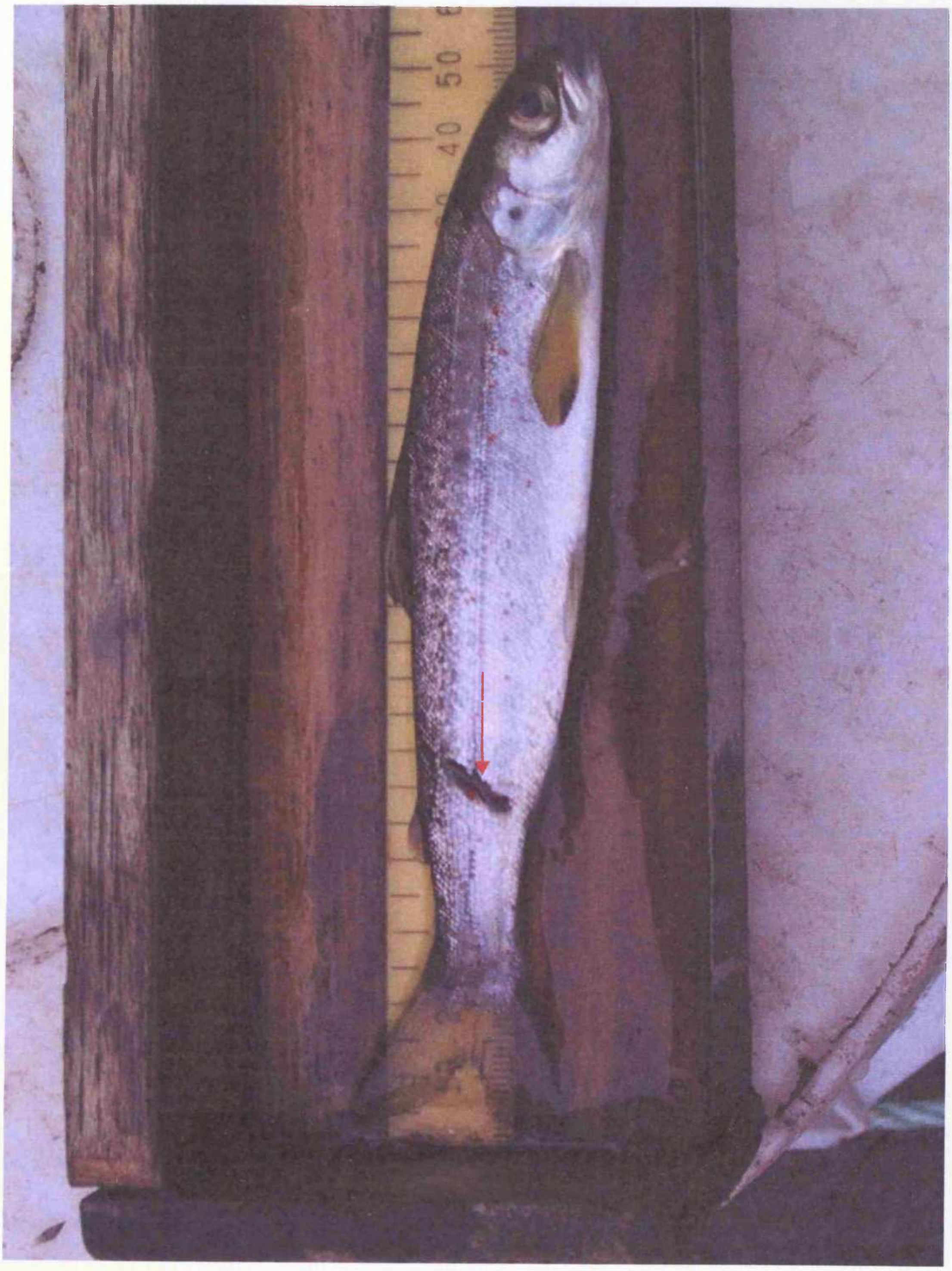
Category III

The red arrow points to a single small puncture wound above the pectoral fin.



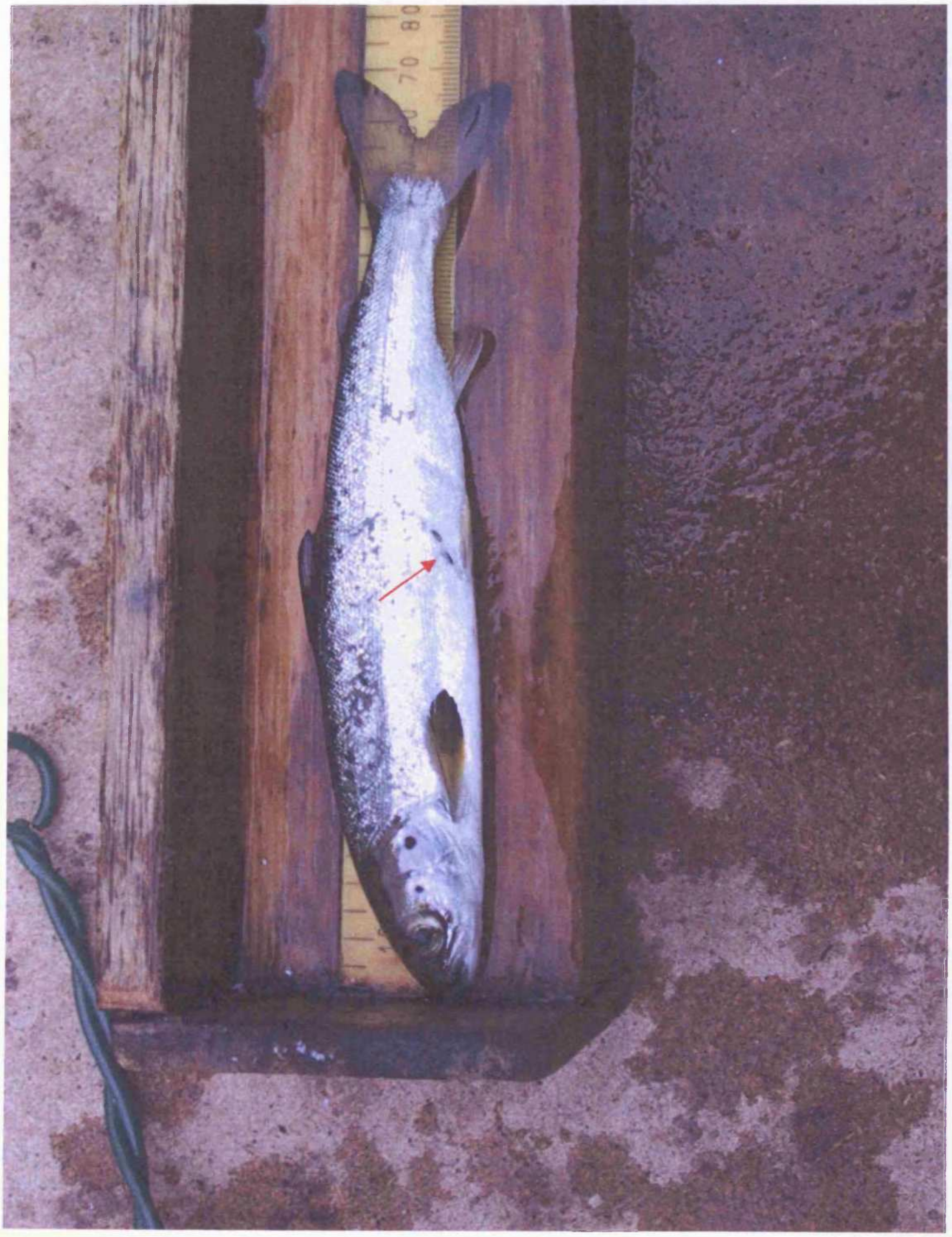
Category IV

This smolt had a single large puncture wound above the anal fin.



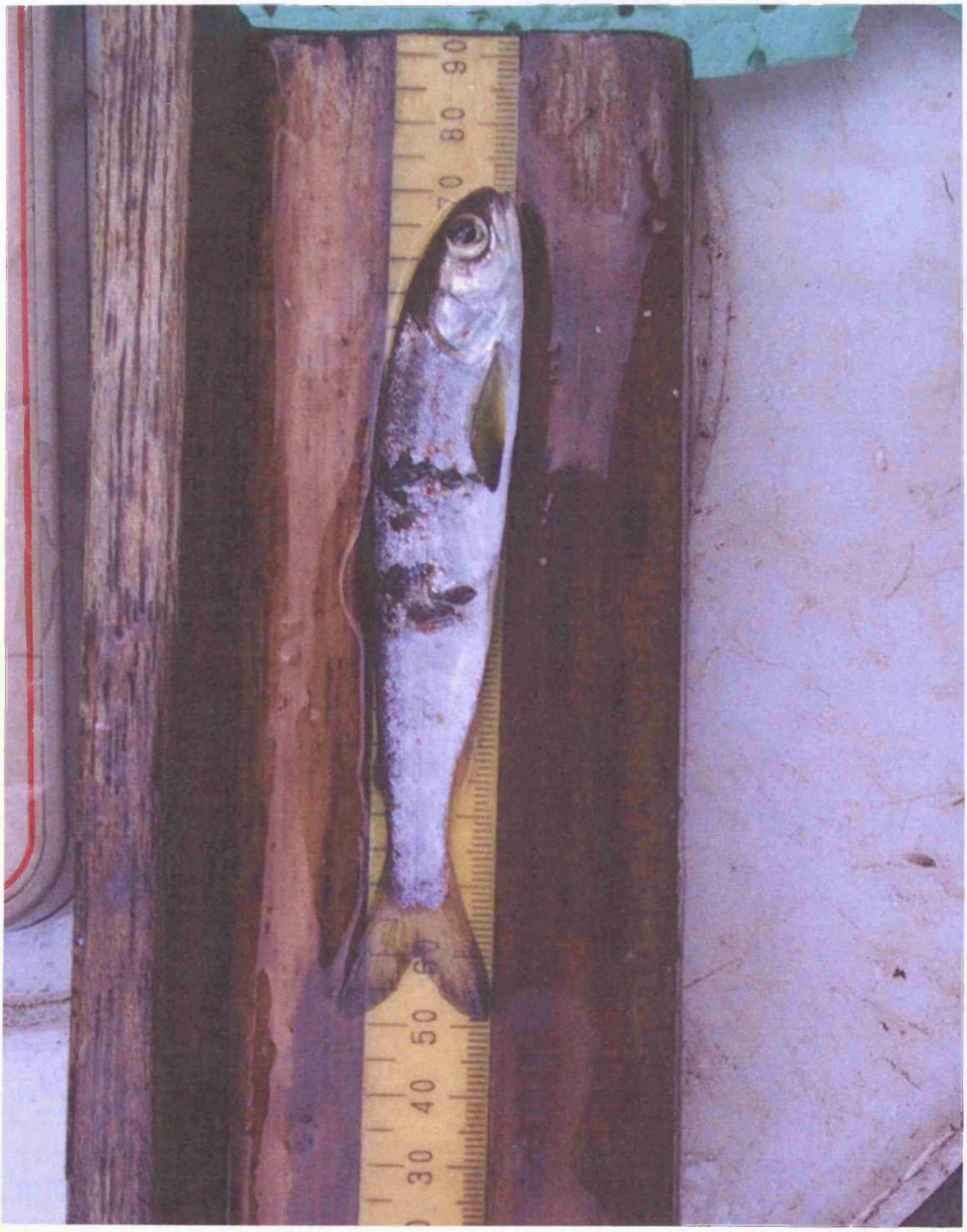
Category V

The red arrow points to two small puncture wounds above the pelvic fin



Category VI

This smolt has numerous large puncture wounds between the dorsal and pectoral fins.



Category VII

This smolt has been almost totally descaled posterior to the pectoral fin.