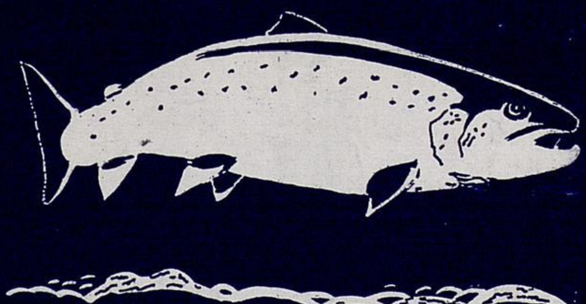
ATLANTIC SALMON TRUST

ATLANTIC SALMON FEDERATION

SPRING SALMON

1994 Bensinger-Liddell Memorial Fellowship

ALAN YOUNGSON



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Foreword

The present demise of spring salmon stocks in some Scottish rivers began in the late 1960s. I say present demise because there is evidence that spring salmon numbers were also at low levels during the latter half of the last century. For that reason some will state that spring salmon abundance is cyclical and that this may well be linked to climatic and marine conditions. There was a time, not so long ago and during the good spring salmon years, when there was concern over the low numbers of grilse. This, too, may have been related to conditions prevailing at sea. There are others who firmly believe that spring fish have declined due to either man-made factors such as land use and hydro power development or natural causes such as the UDN disease. Another school considers that heavy exploitation on one part of the population has caused one component to decrease and another to increase. Calderwood, one-time Inspector of Salmon Fisheries for Scotland, argued that the heavy netting of salmon in the summer and autumn on many parts of the Scottish coast caused the late-running grilse to decline and the spring salmon to increase, and that large catches of salmon in the summer and autumn in the Tweed district resulted in the Tweed changing in 25 years from a late river into an early one. It would be interesting to have Calderwood's views now.

However, before we can determine the reasons for the reduced numbers of spring salmon returning to our rivers we must know more about them. For example, what is a "spring" salmon? So-called spring salmon can start entering our rivers as early as October and November in the year before that in which they will spawn, while others will be ascending our rivers in December and January - hardly "spring". Our early eminent salmon biologists such as Calderwood, Menzies, Went and Jones referred to these early-running fish as "winter" fish. They based their interpretation as to when they entered the rivers on the degree of erosion on their scales, the presence of winter rings on the edge of these scales and whether or not there was any evidence of current year's summer growth on the scale. The debate continues!

The rapid advance in genetic studies has been invaluable in identifying different salmon stocks and this is now being applied to research on spring salmon and complements our marine studies. In the marine field, present work is centred on habitat studies based on sea surface temperature data collected by satellite.

In the following chapters Alan Youngson has produced an excellent and intelligible up-to-date account of this genetic and marine work in relation to spring fish studies and presents a number of interesting hypotheses. It is a thought-provoking treatise which will generate a great deal of discussion and help stimulate sensible measures to conserve and restore this valuable animal to its previous abundance.

Derek Mills
Chairman, Honorary Scientific Advisory Panel
Atlantic Salmon Trust

Spring Salmon

Contents

1. Introduction

This Blue Book has resulted from my tenure of the Bensinger-Liddell Memorial Fellowship for 1994. The project proposal that I submitted to the AST in late 1993 stemmed directly from a study that I had recently completed, in collaboration with Professor A D Hawkins of the SOAFD Marine Laboratory, on the condition of the salmon fishery of the River Dee in Aberdeenshire. This study was part of a wider study commissioned from Coopers & Lybrand by Grampian Enterprise Ltd in 1992. At the time, Grampian Enterprise was responding to disquiet among proprietors and business interests in the Dee valley regarding the particular downturn in the river's fortunes that - in retrospect - can be seen to have started in the late 1980s.

As we shall see, the fortunes of the various rod fisheries have differed since official records began to be kept. In many rivers, catches of some classes of fish have increased. In contrast, the spring component of fisheries has been reduced everywhere that spring fish occur - without notable exception. The Aberdeenshire Dee is probably the purest spring fishing river of all and, as a consequence, the rod fishery on the Dee has been particularly exposed to reductions in the abundance of spring fish.

As part of the Coopers & Lybrand study, it was necessary to attempt forecasts of the Dee fishery's performance in the years beyond 1992. It proved possible to provide quite accurate predictions for the spring component of the Dee angling catch for 1993 and 1994, on the basis of predictions of abundance made by North American researchers studying the salmon fisheries of the western North Atlantic coasts and rivers. It was quite possible (and it remains so) that the accuracy of the Dee predictions was entirely fortuitous in being based on relationships that will eventually prove to have been spurious. But, in the short term, at least, the relationships have appeared to be informative.

Putting Dee springers - and perhaps other classes of European salmon - in a North American context is not so bizarre as it might seem. Salmon travel widely in the north Atlantic Ocean. In particular, some European fish share the feeding areas off the West Greenland coast with fish from New England and eastern Canada. Tagging studies have shown that potential Dee springers, for example, occurred relatively frequently at West Greenland when the drift-net fishery operated there while they were almost absent from the fishery that, until recently, was pursued north of the Faroe Islands in the north-east Atlantic. One of the purposes of the 1994 Bensinger-Liddell Memorial Fellowship was to examine the fortunes of the European spring fisheries in the context of the north-west Atlantic Ocean and the changing North American salmon fisheries.

The decline of the spring fisheries is a matter for profound regret for anglers, river managers and others whose livelihoods depend on springers being in the rivers. Spring salmon bring variety to the range of fishing experiences that can be had world-wide and catching them ranks among the most sought after angling experiences. From a more general point of view, spring fish comprise an important part of the diversity that makes the lives of salmon so interesting and study of the species so rewarding.

As we shall see, the numbers of springers being caught have been declining for many years. Recent declines, however, have been notable for being especially marked and this has sparked a flurry of discussion. A number of recent contributions to the scientific literature have dealt specifically with the nature of the problems and their likely causes and possible remedies, too (see for example, Gough *et al.*, 1992; Rogan *et al.*, 1993; Anon, 1994).

The extent of the concern in the angling community has been reflected in the pages of the specialist angling and the national presses. Many remedies have been proposed for what seems to have gone wrong. Although it is heartening that all these views are being so freely expressed it is also unfortunate that some of the most strongly held of them are mistaken. Yet, only when all the arguments have been presented and weighed will it be possible to decide what may be done to counteract - or more probably to absorb - the changes that are taking place in the spring fisheries. The second purpose of the Fellowship was to contribute to these discussions.

It might be thought that little remains to be said on the spring fisheries - most of the issues have been widely aired recently. But many of the issues are complex and, unfortunately, the key pieces of information often cannot be obtained. In these circumstances, and because the issues are so important, the few facts we possess must be weighed in a wider context in trying to decide what might be done. Everyone has a personal context that differs from every other one. The context in which this Blue Book is written will therefore differ to some extent from the contexts in which the subject of spring fish has been treated before.

In particular, many previous considerations of run timing in salmon have made the implicit assumption that, as each fish leaves fresh water, the form that its adult life will take is indeterminate. This is probably not so. Further, previous accounts have not acknowledged that salmon populations are highly structured geographically (and genetically) among and within rivers. The existence of population structuring means that almost all fisheries (including rod fisheries) are mixed stock fisheries. Caution must be exercised therefore, regarding combined catch figures from different rivers or different parts of rivers - they may not tell the whole truth. Finally, if structuring is a marked feature of fresh water life, it does not seem unreasonable to consider that ocean life may also take different courses in the case of different populations. Certainly, as we shall see, the migratory journeys of different populations of other migrant species differ markedly and in a highly structured way.

Direct estimates of the numbers of fish entering rivers are not widely available. In taking a general, historical approach to trying to assess changes in the abundance of salmon, the only possible sources of information are from catch records. For a number of reasons, the abundance of salmon is not always reflected accurately in catches, although a general correspondence would be expected to exist. By good fortune, the catch records are particularly useful in the present context. Among all the classes of salmon, the rod catch figures for the spring fisheries are likely to be the most informative - for reasons that are discussed later.

The present study is concerned principally with changes in the runs of springers and especially changes within the last decade when the numbers being caught has diminished so markedly. As we shall see, the chance that any potential springer will survive to contribute to the fisheries (or to spawn) has been reduced, probably because of recent increases in marine mortality rates peculiar to that class of fish. The most important questions of all are whether these changes are temporary and, if they are not, whether and by what means the natural trends can be reversed.

2. What are Springers?

The earliest stage at which fish can break off ocean-life to enter the rivers is in May or June, almost exactly one year after they go to sea as smolts. Fish like these are the first of the grilse. Grilse continue to enter rivers over the next six months or so, up to and beyond the end of the angling season. All salmon spawn in late autumn or in winter and the latest running among the grilse spawn almost immediately after river entry. Since grilse bear one winter band on the marine zone of their scales they are classed formally as 1SW fish.

By the time they spawn, all the classes of fish that are older than the grilse have lived for at least two winters and two springs since going to sea. These fish are classed collectively as multi-sea-winter (MSW) fish and the MSW class is made up of two-sea-winter (2SW) and three-sea-winter (3SW) classes. Fish older than this are uncommon.

The fish that the rods catch in spring (the springers of angling terminology) enter the rivers over the winter months from about October onwards, as well as during the spring season itself. The earliest springers are more properly termed winter-running fish. In the interests of simplicity however, and because much of this study is based on rod catch figures, the angling term "springer" will be used (as it has been already) to denote fish that are available for capture by the rods in the spring months.

In autumn, early-running springers may enter rivers in the company of late-running grilse. The late grilse and the early springers are not fellow-travellers, however, and their subsequent lives take quite different courses. The earliest springers, returning in October, have spent about 17 months at sea including only *one* winter. This winter is marked on the sea-zone of their scales. Scales from the late running grilse that also enter rivers in October show them to be of the exactly the same sea-age. What distinguishes the last of the grilse from the first of the springers is the state of their reproductive organs and the age at which the two groups are committed to spawn. In late-running grilse, the gonads are in a highly advanced state of development as they enter rivers and the fish will spawn soon thereafter. In contrast, the springers are not in a sexually advanced condition and they will not spawn until a year or so later. Before they eventually spawn, and before the angling season opens, the springers will show an additional sea-winter on their scales. Thus although springers are described as being of the so-called 2SW or older *sea*-age classes, the terminology is slightly defective and in the earliest running of the springers the final sea-winter is passed in *fresh* water.

Towards the end of the spring run, there is no well-defined biological measure that distinguishes late spring fish from summer MSW fish. Scale patterns are sometimes used as a defining criterion. By this measure, summer fish are distinguished from spring fish when they show evidence of resumed, new-season growth on the edge of the scales. However, most sets of fisheries figures are not backed up by parallel data sets based on scale reading. As an expedient therefore, we must take the calendar as a guide. Thus, we may regard the entry of spring fish as terminating towards the end of April. Correspondingly, we may regard the capture of fresh spring fish by rod-and-line as terminating towards the end of May - although, of course, stale springers may be caught at any date thereafter.

The annual catch figures suggest that this operational classification is appropriate from a biological point of view. Springers appear to comprise a separate class within the MSW group of salmon that is quite well-defined. Figure 1 shows the average monthly rod catches in Scottish rivers of fish declared as MSW salmon for the spring period and over the transition to summer. The season commences in January only in some of the Scottish rivers but by February all are open. The average catch rises through the spring months to peak

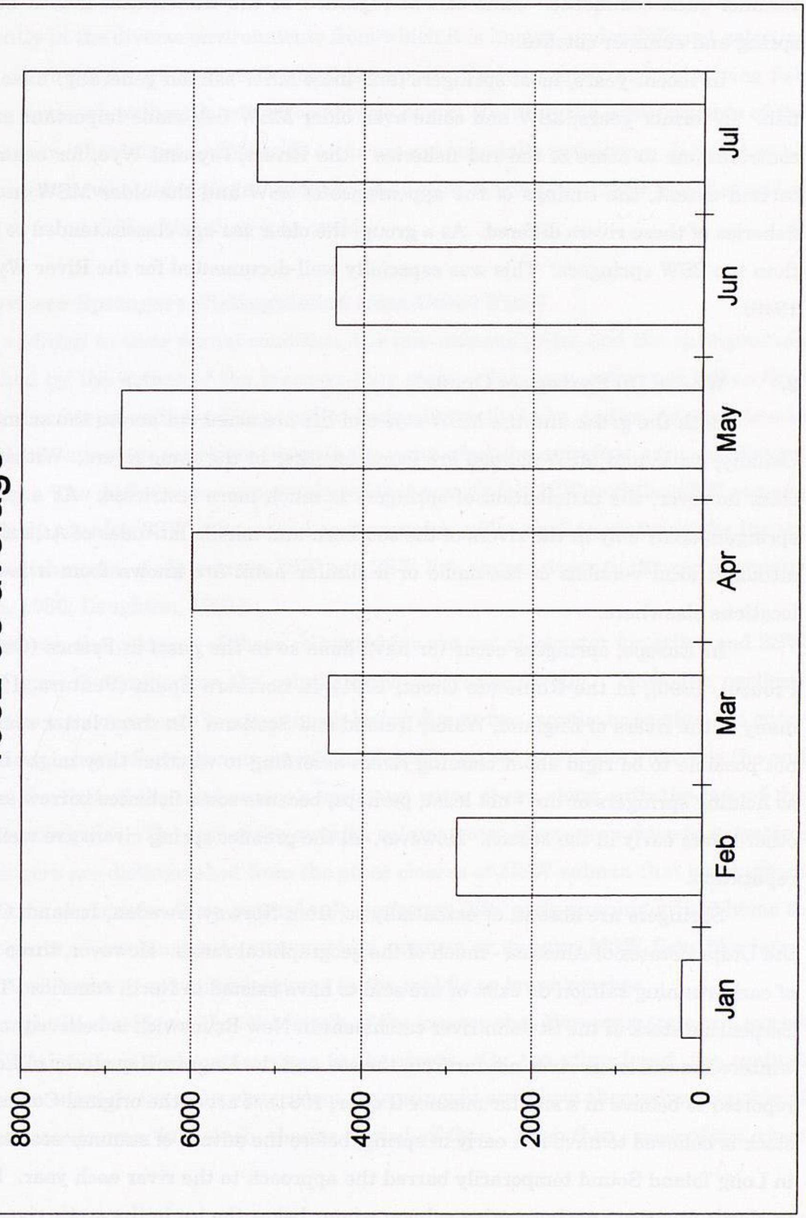


Fig. 1 Scottish rod catch of salmon 1952-93 average

in May. Catches are briefly lower in June, as the spring catch draws to a close and the summer runs commence. June can be regarded as the transitional month between the spring and summer catches.

In recent years, most springers (and most MSW salmon generally) have been 2SW fish. In former years, 3SW and some even older MSW fish made important and distinct contributions to some of the rod fisheries - the Rivers Tay and Wye, for example. To a certain extent, the timings of the appearance of 2SW and the older MSW in the spring fisheries of these rivers differed. As a group, the older sea-age classes tended to run earlier than the 2SW springers. This was especially well-documented for the River Wye (Hutton, 1949).

3. Where Do Springers Occur?

Both the grilse and the MSW styles of life are acted out across the salmon's range. Usually, grilse and MSW salmon are found together in the same rivers. Within the MSW class however, the distribution of springers is much more restricted. As a general rule, springers occur only in the rivers of the southern and middle latitudes of Atlantic Europe - although local versions of the same or a similar habit are known from a few scattered locations elsewhere.

In Europe, springers occur (or have done so in the past) in France (Cuinat, 1988; Prouzet, 1990), in the Rhine (de Groot, 1991), in northern Spain (Ventura, 1988) and in many of the rivers of England, Wales, Ireland and Scotland. In these latter countries, it is not possible to be rigid about classing rivers according to whether they might be regarded as holding springers or not - not least, perhaps, because some fisheries borrow salmon from other rivers early in the season. However, all the premier spring rivers are well-known by reputation.

Springers are absent, or essentially so, from Norway, Sweden, Iceland, Canada and the United States of America - much of the geographical range. However, three local forms of early-running salmon do exist or are said to have existed in North America. The original Serpentine stock of the St John river catchment in New Brunswick is believed to have over-wintered in the lower river not far from the sea and the Ungava Bay stocks of Labrador are reported to behave in a similar manner (Power, 1981). Part of the original Connecticut river stock is believed to have run early in spring, before the advent of summer sea temperatures in Long Island Sound temporarily barred the approach to the river each year. Finally - as in North America - early-running salmon winter below the ice in the arctic rivers of Russia (Dahl quoted by Stabell, 1984).

The general similarities that each of these over-wintering stocks shows or showed to the European springers may be illusory. The early-running habit may have developed independently in the diverse environments from which it is known, under different selective pressures. Two points are noteworthy in this respect. Early-running, over-wintering fish are not the norm where hostile winter conditions occur. Further, the environments of the European rivers where most springers do occur are not especially restricting. It is not at all obvious therefore, what advantages springers may gain by running rivers so far ahead of spawning, or what difficulties they may avoid.

4. How are Springers Distinguished from Other Fish?

In addition to their sexual condition, the late-running grilse and the springers are distinguished by the extent of the journeys they make after river entry and before they spawn. A number of radiotracking studies have shown that the earliest river entrants among each sea-age class penetrate towards the parts of catchments that are most distant from the sea. The patterns are separately evident among the 1SW and the 2SW sea-age classes. Early running 2SW salmon and early running grilse tend to spawn in the higher reaches of catchments. Late entrant 1SW and 2SW fish spawn closer to the sea (Hawkins and Smith, 1986; Laughton, 1991).

However, the patterns of these relationships are out of register for grilse and 2SW salmon. Figure 2 summarises the relationships diagrammatically. Thus, the earliest-running grilse are not present in rivers much before June - two months or so after the entry of the previous cohort of springers is complete. Equally - as we saw above - towards the end of the year the first of the next season's springers enter rivers along with the last of the current season's grilse. The last of the autumn salmon enter rivers very close to spawning time. Springers are distinguished from the other classes of MSW salmon that enter rivers in the summer or autumn. As a general rule, springers (like early-running grilse) home to the upper parts of catchments to spawn while summer or autumn MSW fish (like later-running grilse) home to spawn in locations in the middle or lower reaches.

It might be considered that the length of the journey that European springers expect to make explains their early appearance in the rivers. On the other hand, the earliest running grilse enter rivers rather later than the springers and show themselves capable of making the same journey in a much shorter period of time. Even then, none of the river

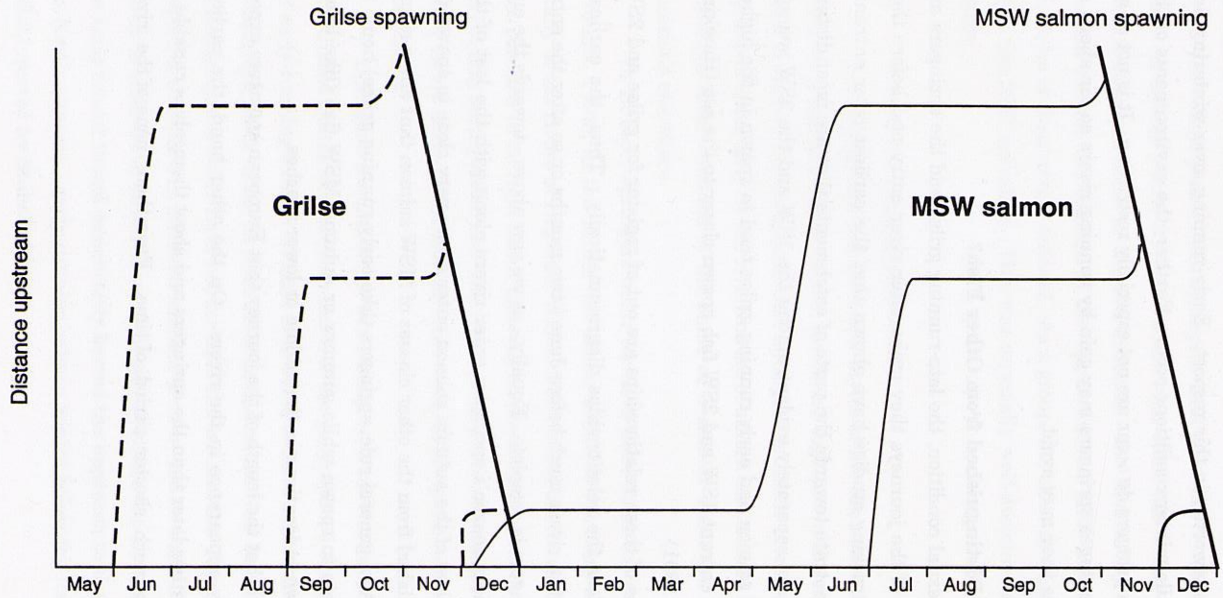


Figure 2 Patterns of migration to final locations in grilse (......) and in MSW salmon (___) entering rivers at different times of year. For illustration, the migration patterns of grilse running in June, September and December of the first year are shown. The migrations of springers entering in December of that same year and of summer salmon and autumn salmon entering in June or December of the next year are also shown. In the early months of the year, the migration of springers is often impeded by low water temperatures

journeys that Atlantic salmon make are especially long. Indeed, all salmon spend only a short part of the time they spend in rivers actually engaged in travelling. Salmon are physically capable of making the journeys that take springers 12 months and grilse six months to complete, in only two or three weeks. It seems unlikely therefore that springers (or early-running grilse) enter rivers so long before spawning time, in anticipation of a particularly arduous journey to the head-waters. Yet springers are not frequent in the minor rivers of the regions where they occur.

5. Population Structuring

5.1 Homing

Tagging studies have shown that the homing of salmon is rather accurate even within rivers (Saunders, 1967). At the Girnock Burn and the Baddoch Burn fish-traps on the River Dee, about one half of all the adult fish that are caught ascending the stream each year have been tagged there previously as smolts (Youngson *et al.*, 1994). This figure probably under-estimates the true extent of homing to the streams because some tagged fish spawn close to but below the trap. Although these fish are not accounted for at the fish-trap, they should probably still be regarded as having homed accurately. Equally, the untagged fish caught at the fish-trap may have originated as smolts nearby but further downstream. If this is the case, fish like these should probably also be regarded as having homed. In any case, about half of all the adults entering the stream have proved themselves capable of homing with a precision that is at least as fine as the length of the stream above the fish-trap (several kilometres). For some of these fish, homing must be presumed to be even more precise.

5.2 Reproductive isolation

Over the last decade, incontrovertible genetic evidence has been obtained that salmon form distinct, geographical breeding populations (Stahl, 1987; Verspoor, 1988; Jordan *et al.*, 1992). Population structure is especially evident as homing adult fish re-assemble for spawning and before their progeny disperse in their own turn, from their native streams or rivers. Usually, genetic studies are performed by examining young fish because they are much easier to sample in the necessary numbers and because sampling at this young stage causes minimal harm to the populations being studied. The forms of the genes the sampled fish contain are analysed and tallied in the way that Cross (1989) described in a previous Blue Book. Typically, although the same types of genes occur in most populations, the frequency of their occurrence varies markedly from place to place. Using these genetic techniques, discrete salmon populations can be shown to exist, sometimes on quite a local scale.

After the young fish disperse and before they come together again as adults to breed, population structure is harder to discern. Nevertheless, population structure can be seen in comparisons of the West Greenland and Faroese fisheries, where salmon originating from North American or European river populations were not equally represented - European and North American populations were unevenly mixed (Shearer, 1992). Population structuring may exist elsewhere at other stages of life, although direct genetic evidence has not been obtained. As we shall see later, speculation based on what is known of other migratory species must suffice instead.

Where geographically separate populations of salmon occur, isolated from one another by precise homing, reproductive mixing is limited. As a result, genetic strategies that have developed and been tested over time in particular places are not shared freely with other populations living elsewhere and in different environments. Equally, because of homing, the genetic development of particular local populations is not hampered by the continual admixture of large quantities of genetic material more suited - perhaps - to life elsewhere.

Most of the genes that scientists have been able to examine in past studies are assumed to be neutral in their effect on the lives of the animals that carry them. That is to say, it is considered that having one form or another of these particular genes probably has no special effect on fishes' lives. However, the assumption of neutrality may not be fully justified. One of the small, standard group of genes that scientists routinely examine (the so-called MEP-2 gene) appears not to be neutral in its effects. Two forms of the MEP-2 gene occur. The frequency of young salmon carrying the different genes tends to vary among stream populations of salmon that live at relatively warm or cool temperatures (Verspoor and Jordan, 1989). Salmon that carry different forms of the gene differ also with respect to growth and age at maturity (Jordan *et al.*, 1990; Jordan and Youngson, 1991). All these differences may reflect a local adaptation that makes certain types of salmon more fitted for life in particular places.

5.3 Local adaptation

The genetic make-up of locally adapted individuals confers advantage over other individuals that do not share the same adaptation, in the particular local environment in which the two types compete. The advantages conferred will usually be subtle and difficult to pin down. For example, experiments designed to demonstrate the basis of the MEP-2 gene's possibly adaptive nature, suggest a picture of considerable complexity that has not yet been resolved. If the spring running habit is a local adaptation, as might be supposed, it is rather unlikely that the habit will be shown to confer outright advantage over other styles of life. On the other hand, springers differ from other fish in ways that can be rationalised as being adaptive.

Thus, it is possible that the spring running habit is part of a local adaptation and that springers are particularly adapted to propagate life in upland streams, especially in Great Britain and Ireland. All adult salmon enter rivers to spawn, although for many fish (and especially springers) river entry and spawning are separated by many months. In particular places, spawning takes place over a short period, extending at most to a few weeks and sometimes only to days. Spawning is seasonal and, in particular places, it takes place each year at about the same time of year. At the Girnock Burn, for example, spawning starts in late October or early November and is essentially complete before mid-November. However, differences in the timing of spawning occur among rivers and within rivers too (Menzies, 1931). Within the River Dee for example, spawning starts first of all in the upper catchment streams, extending downstream over a period of six weeks or so. Most spawning is complete in the highest streams of the upper catchment before spawning has even started in the lowland streams nearest to the sea (Webb and McLay, in preparation).

Salmon home before spawning. Indeed, homing itself may be an adaptation in ensuring that returning adults spawn in patterns that match the likely capacity of particular places to support their progeny. In addition, the precise timing of spawning may be a local adaption matching the duration of egg incubation and the hatching and emergence of young fish with the advent of appropriate conditions for first-feeding in spring or early summer (Brannon, 1987). Over-winter temperatures control the rate at which incubating eggs develop. Incubation times are shortened at high temperatures and extended where temperatures are lower (in upper catchments). Seasonal variation in the timing of the adults' spawning may match the timing of emergence of the young fish from the redds to the onset of suitable feeding conditions in different local climates. Perhaps homing ensures that adult fish that are capable of spawning at the appropriate time are matched to the range of local environments that distinguishes different rivers and different streams within the same rivers. Perhaps early spawning in cold locations, where emergence is delayed until early summer is part of a complex of adaptations that characterises springers.

5.4 The concept of fitness

As every fish leaves the ocean feeding grounds, three factors will determine its chances of going on to complete its life-cycle successfully. Firstly, it must complete the journey from its final feeding location in the oceans to its own home river. Secondly, it must arrive in its home stream to spawn there at the appropriate time. Thirdly, it must find the energy required for the return journey, for the formation of the reproductive organs and for spawning itself from the reserves it has accumulated at sea. Any shortfall will lead to total or partial failure. For each fish, the degree of success or failure is measured in terms of being able to spawn, in terms of the number of progeny produced and in terms of the survival of those progeny. At some point before they leave the ocean, different classes of fish deal with these complex considerations at critical times that differ among the different classes of fish. Springers, for example, make the crucial decisions a year or more before spawning will take place and grilse do so later on - in patterns that broadly parallel those already considered in Figure 2.

No entirely convincing explanation has been proposed for why springers choose to exercise their unusual style of life. By migrating to the oceans, all salmon increase their growth rates and their size at sexual maturity. In the oceans, annual weight gain is measured in kilograms: in streams it is measured only in grams. For each female, greater weight leads directly to the production of greater numbers of eggs at spawning. For each male spawner, large size is one of the factors that increases the chances of sexual success. Early running 2SW salmon are the smallest class among MSW salmon and, presumably, their size and fecundity might be increased to near average MSW levels if they were to extend their ocean stay. It might be wondered why if springers take steps to go to the ocean feeding grounds to grow large, they cut short this phase of their lives by leaving the ocean at what appears to be an unnecessarily early stage.

Fitness is a general concept that describes the statistical chances that individuals will survive an entire life-cycle to breed and to replace themselves with progeny of their own. It encompasses many separate, contributory factors. Fitness is determined by the intrinsic characteristics of individuals and by the ways in which these properties interact with the environments in which each individual lives at the various stages of life. Age at maturity, size and fecundity are single elements of a wider array of characteristics that go together to determine overall fitness.

In the case of springers, the timing of river entry may be a single adaptation to some constraint on their lives that has not yet been recognised. It is probably more likely however, that entry timing is the indirect consequence of a more complex interaction of factors in which the timing of river entry is without special significance of its own. From a practical point of view, the most important points are that the spring-running habit is associated with particular regions, with particular rivers and with particular parts of catchments and that, in the past, it has shown itself to be thoroughly viable way of life. Indeed, on some rivers, springers once formed the principal part of the catch.

6. Where Have the Springers Gone?

There are two possible explanations for the decline in the spring fisheries. On the one hand, the fitness of springers may have been reduced because of some mismatch with their environment. As a result, lower survival rates may mean that potential springers are being lost to the fisheries. Alternatively, potential springers may have altered their styles of life, running the usual rivers, unrecognised, as summer or autumn MSW salmon or as grilse. In this second case, potential springers lost from the spring run would be expected to be turn up in the fisheries later in the season but in the previous year.

Figure 3 shows the Scottish rod catch of all fish in the spring (January to May) each year between 1952 and 1993. Until the late 1960s, the annual catch was running at about 25,000 fish. The catch declined thereafter before staging a brief, partial recovery in the late 1970s. Since the early 1980s, the catch has been almost uniformly low at just over 10,000 fish - a loss of about 15,000 fish from the proven capacity of the Scottish fisheries to yield springers. Figure 4 shows the catch of MSW salmon and grilse in summer and autumn (June to December) each year over the same period. Catches have increased steadily from just over 20,000 fish in the early 1950s to about 60,000 fish in the late 1980s and the 1990s - a gain of some 40,000 fish. Many factors may have contributed to this increase and, at first sight, it appears possible that the appearance of potential springers in the summer and autumn fisheries is one of them.

6.1 Reciprocation between grilse and MSW salmon

Many studies have examined long data sets that show how the relative representation of grilse and MSW salmon (the salmon: grilse ratio) in annual catches has varied over the years. Recently, for example, Turrell and Shelton (1993) presented data for the Thurso, Spey, Dee, Tay and Exe fisheries. In all these rivers, the salmon: grilse ratio has declined since about 1930 and grilse now comprise a greater portion of all the catches than they did formerly.

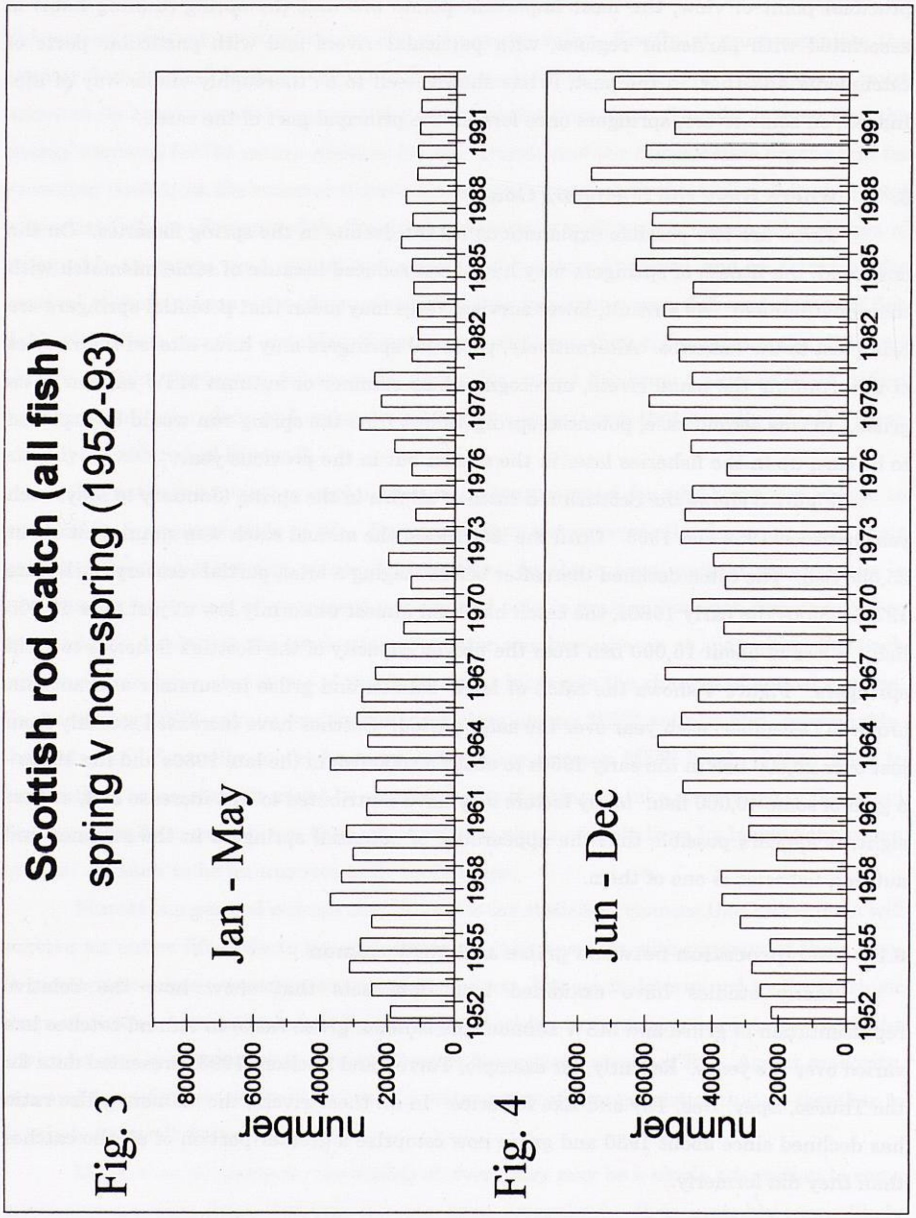


Fig. 3
Fig. 4
Scottish rod catch (all fish)
spring v non-spring (1952-93)
Jan - May
Jun - Dec
number
80000
60000
40000
20000
0
1952
1955
1958
1961
1964
1967
1970
1973
1976
1979
1982
1985
1988
1991

These changes might be explained in several different ways. Salmon numbers may have declined while grilse numbers remained the same, grilse may have increased while salmon remained the same or salmon may have declined while grilse increased. All these types of effect may have played some role in the complex explanations that are required to account for all the variety of changes that have taken place in the catches of each of the various fisheries. However, the latter explanation is often favoured (Martin and Mitchell, 1985) the implication being (although it is nowhere stated explicitly) that the same smolts that might formerly have become MSW salmon are now tending to mature as grilse instead. As we saw above, MSW springers that might convert somehow to grilse could first appear in the fisheries only in early summer. Inevitably, any move by potential MSW salmon towards grilsing would show as a decline in the spring fisheries.

6.2 Reciprocation between springers and later-running fish

Another favoured explanation for the decline of spring catches is that potential springers are returning to rivers later in the season to contribute instead to the summer and autumn catches of MSW salmon. On the basis of observations on the river- and sea-age composition of adult fish returning to the North Esk, Shearer (1984, 1990) has suggested that changes like these may occur.

In general, within any particular sea-age class, North Esk fish that have been the older smolts return in the earlier part of the year. Fish that have been younger smolts tend to return later. Shearer suggested therefore that any factor that speeded development in fresh water to produce younger smolts would also tend to delay adult returns until later in the season. Shearer also suggested that a sequence of linked events - intensified land-use, nutrient run-off, increased growth and younger smolting - might have caused adult runs on the North Esk to occur later in the year than they did before.

This view may well be mistaken. Radiotracking studies show that the earlier entrants in any sea-age class travel further (and therefore higher) into catchments to spawn. Both the earlier and the later entrants are homing to the places where they lived as juveniles. The higher catchments from which the earlier entrants derive are colder and therefore produce older smolts. Older smolts return earlier as adults to make their way to the head-waters. Thus, it is unnecessary to invoke Shearer's explanation for what he observed and there is no reason to suppose that his proposed causative link may exist.

Indeed, Struthers' (1984) study of the Tummel and Almond tributaries of the River Tay might well have been designed as a test of Shearer's hypothesis. The Tummel is further distant from the sea than the Almond. Two-year-old smolts returning to the Tummel as adults enter the Tay earlier than three-years-old smolts returning as adults to the Almond. As Struthers points out, this relationship violates the predictions of Shearer's hypothesis. Struthers findings are consistent instead with the prediction from radio-tracking studies that fish homing to the upper catchment (the Tummel) should enter the River Tay earlier than fish returning to the lower catchment (the Almond).

6.3 Evidence from the Aberdeenshire Dee

The Dee fishery is extreme among rivers, given the unique extent of its dependence on springers. It is here that any move away from springers towards later running salmon or towards grilse ought to be most evident. Yet, if we compare the changing catches of springers and other fish in the Dee fishery there is no evidence that might suggest a compensatory move away from springers to summer fish of any class. Figure 5 shows that the Dee has regularly proved capable of producing more than 5,000 fish in spring. In recent years, spring catches have been 2,500 or more below this figure. However, equivalent numbers of fish have not appeared instead in catches made in the summer and autumn.

Further, in addition to being a premier spring river, the Dee is also unusual in being equipped with fish traps on two of its upland tributaries. The Girnock and, more recently, the Baddoch Burn fish-traps provide the opportunity to confirm that spring fish have not been supplanted by later runs. Both streams support populations of salmon that have tended to return from the oceans as spring fish, ever since the traps were installed. This can be judged from the banding patterns on scales obtained from spawners captured in the fish-traps that bar entry to both streams. Those fish that are not springers are grilse. Figure 6 shows that, even in recent years, when the spring catch has been reduced, springers (represented by open bars in the figure) continue to dominate the adults that return to spawn in the Girnock Burn. As expected, grilse numbers (filled bars) were raised briefly around the time (1986) that the nets on the Dee estuary were removed. However, this increase has not been sustained more recently. There is no evidence that the Girnock Burn is producing and receiving more grilse now than it did previously. Only a shorter time series is available for the Baddoch Burn but it demonstrates the same point.

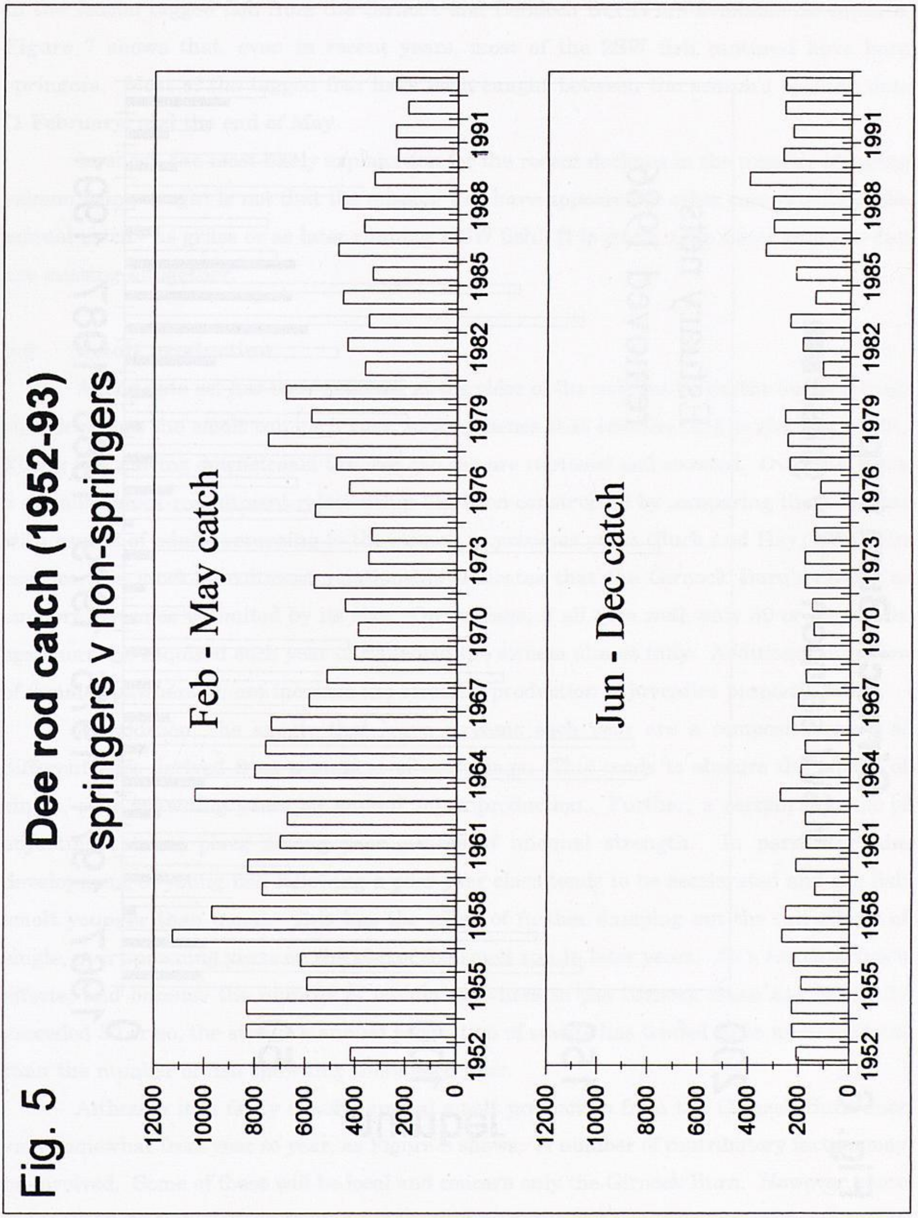
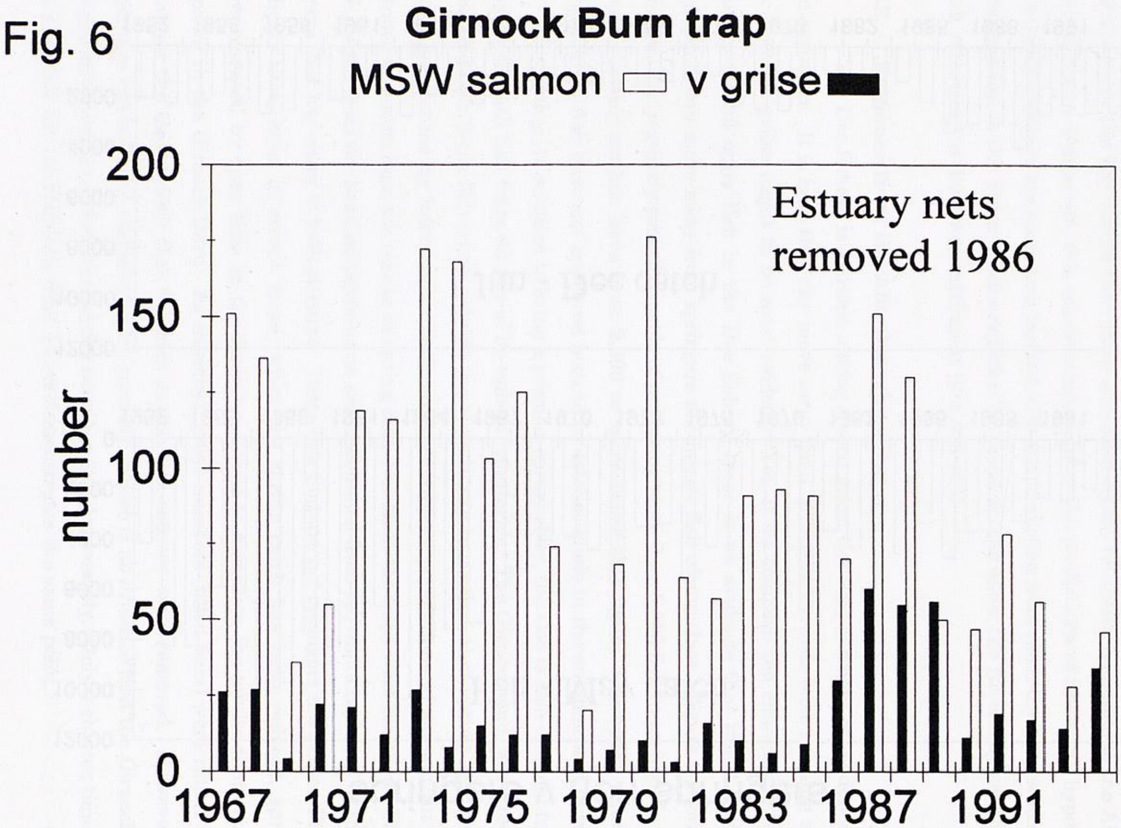


Fig. 5
Dee rod catch (1952-93)
springers v non-springers
Feb - May catch
Jun - Dec catch
12000
10000
8000
6000
4000
2000
0
1952
1955
1958
1961
1964
1967
1970
1973
1976
1979
1982
1985
1988
1991

Fig. 6


Girnock Burn trap
MSW salmon v grilse
number
200
150
100
50
0
1967
1971
1975
1979
1983
1987
1991
Estuary nets
removed 1986

Finally, tag returns from the rod fisheries on the Dee demonstrate explicitly when in the season tagged fish from the Girnock and Baddoch Burns are available for capture. Figure 7 shows that, even in recent years, most of the 2SW fish captured have been springers. Most of the tagged fish have been caught between the season's opening date (1 February) and the end of May.

In short, the most likely explanation for the recent declines in the number of spring salmon being caught is not that the missing fish have appeared in other components of the annual catch - as grilse or as later running MSW fish. It is much more likely that the fish are missing altogether.

6.4 Smolt production

A long data set has been gathered at the older of the two Dee traps (the Girnock trap) that describes the smolt run each year, in a sequence that extends back to the late 1960s. Young fish moving downstream towards the sea are captured and counted. Over the years a so-called stock-recruitment relationship has been constructed by comparing these figures with counts of adults returning to the stream in previous years (Buck and Hay, 1984). In essence, the stock-recruitment relationship indicates that the Girnock Burn's ability to support juveniles is limited by its size. On average, if all goes well, only 30 or 40 female spawners are required each year to replenish the stream almost fully. Additional numbers of female spawners do not increase the stream's production of juveniles proportionately.

In addition, the smolts that leave streams each year are a composite group of different ages derived from a number of spawnings. This tends to obscure the effects of single, poor spawning years on annual smolt production. Further, a certain amount of adjustment takes place among year classes of unequal strength. In particular, the development of young fish following a poor year class tends to be accelerated and the fish smolt younger than usual. This has the effect of further damping out the full effects of single, poor spawning years on the size of the smolt run in later years. As a result of these effects, and because the number of female spawners in the Girnock Burn has generally exceeded 30 or so, the stream's annual production of smolts has tended to be more uniform than the number of fish spawning there each year.

Although it is fairly steady, annual smolt production from the Girnock Burn does vary somewhat from year to year, as Figure 8 shows. A number of contributory factors may be involved. Some of these will be local and concern only the Girnock Burn. However, more general effects also seem to be at play. For example, the number of smolts produced by the

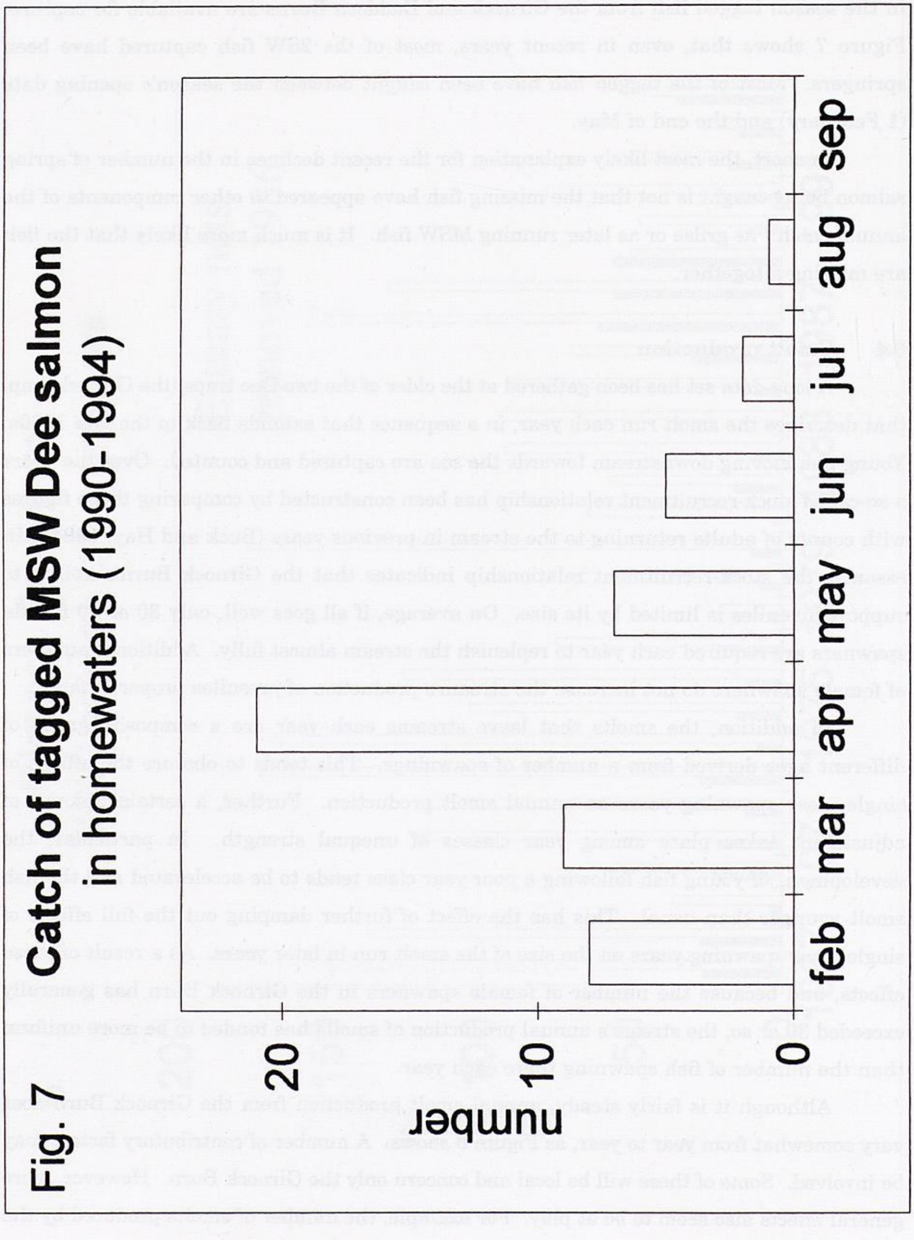


Fig. 7 Catch of tagged MSW Dee salmon in homewaters (1990-1994)

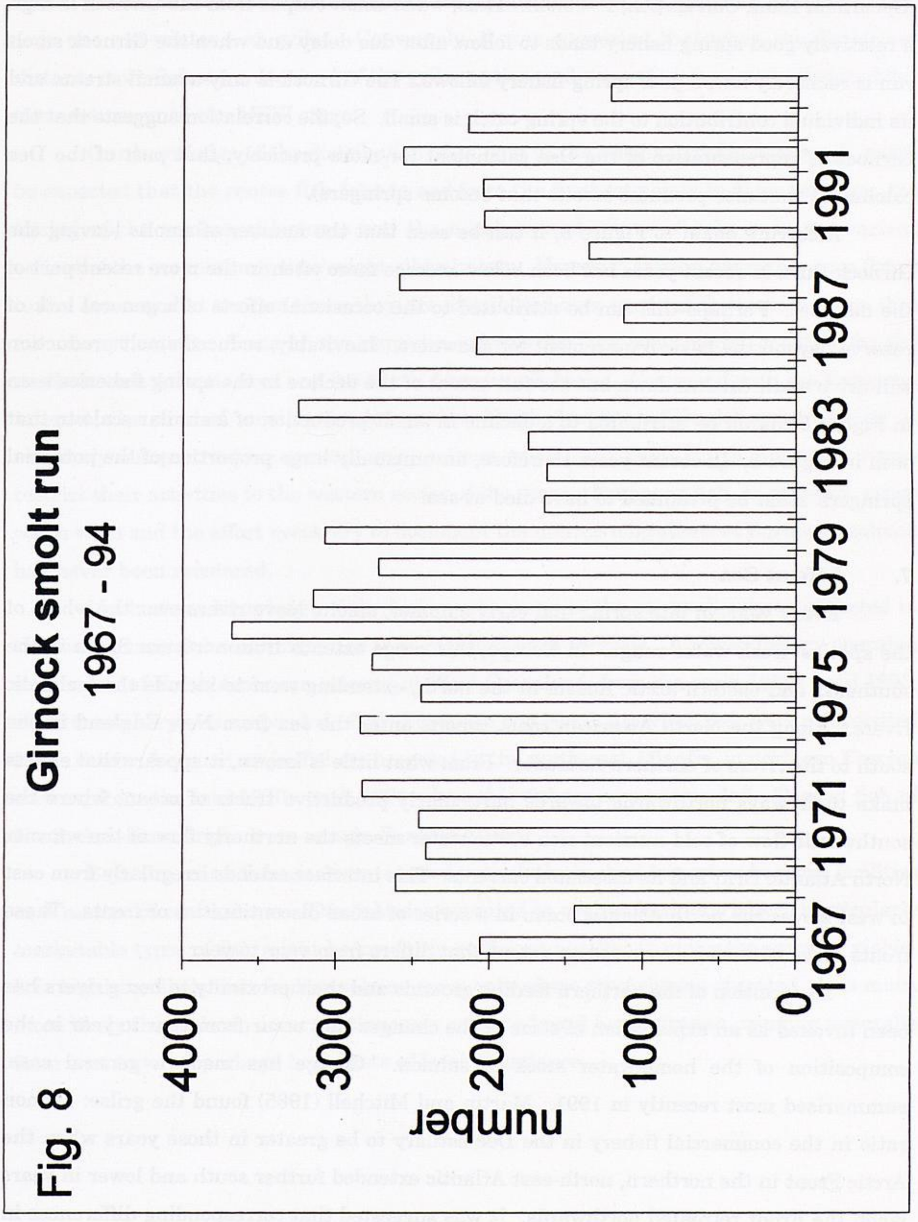


Fig. 8 Girnock smolt run 1967 - 94

Girnock each year and the Dee's spring catch two years later are weakly correlated (Spearman Rank Correlation; $P < 0.02$). Thus, when smolt output from the Girnock is high a relatively good spring fishery tends to follow after due delay and when the Girnock smolt run is relatively low, a poor spring fishery follows. The Girnock is only a small stream and its individual contribution to the spring catch is small. So, the correlation suggests that the Girnock is representative of the Dee catchment (or more precisely, that part of the Dee catchment that also produces smolts that become springers).

Referring again to Figure 8, it can be seen that the number of smolts leaving the Girnock Burn in recent years has been below average more often in the more recent part of the data set. Perhaps this can be attributed to the occasional effects of a general lack of reserve beyond the basic requirement for spawners. Inevitably, reduced smolt production will drive adult catches down but the full extent of the decline in the spring fisheries seen in Figure 5 cannot be attributed to a decline in smolt production of a similar scale to that seen in Figure 8. In recent years therefore, an unusually large proportion of the potential springers' must be presumed to have died at sea.

7. Life at Sea

Every year, in late spring and early summer, smolts leave rivers over the whole of the species' fresh water range. In Europe, this range extends from northern Spain in the southeast and eastern arctic Russia in the north, extending west to include the Icelandic rivers. Along the North American coast, smolts enter the sea from New England in the south to the rivers of northern Labrador. From what little is known, it appears that smolts make their ways northwards towards particularly productive tracts of ocean, where the southwards flow of cold nutrient-rich arctic water meets the northerly flow of the warmer North Atlantic Drift and its associated currents. This interface extends irregularly from east to west across the north Atlantic ocean in a series of broad discontinuities or fronts. These fronts move with the seasons to an extent that differs from year to year.

The position of the northern feeding grounds and their proximity to home rivers has been invoked as an explanation of some of the changes that occur from year to year in the composition of the home-water stock of salmon. George has made a general case, summarised most recently in 1991. Martin and Mitchell (1985) found the grilse: salmon ratio in the commercial fishery in the Dee estuary to be greater in those years when the Arctic Front in the northern, north-east Atlantic extended further south and lower in years when the Front retreated northwards. It was suggested that corresponding differences in the length of the outward migration towards the Arctic Front acted to limit the fishes' options for when they might return. Specifically, it was suggested that in years when the Front was relatively close at hand, more fish might exercise the option of returning after only one sea-winter - as grilse. Conversely, it was suggested that when the Front was distant, more fish were deprived of the grilse option and were therefore compelled to delay their return until the MSW stage.

Our knowledge of the distribution of salmon in the oceans is rudimentary. It might be expected that the routes fish take to and from the furthest points in their journeys, the timing of the various milestones and the numbers and source of salmon in the various sectors of the ocean at any time might all be known. However, salmon are rather rare fishes in the ocean and at various times they are distributed over tracts of the remote ocean that are of vast extent. Some of the requisite information has been pieced together for the northwestern Atlantic area and the North American fisheries. Compared with the European interest, the area of most interest from the North American fisheries point of view is relatively compact. As a general rule, salmon originating from North American rivers restrict their activities to the western sector of the ocean. European fish, in contrast, range ocean-wide and the effort necessary to document the marine migrations of European salmon has never been mustered.

Much of our knowledge of the biology of salmon in the oceans has been gathered in the two commercial ocean fisheries that operated until recently. A major fishery operated in the area of North American interest at West Greenland, from the early 1960s until 1993, when the fishery was suspended. Both European and North American fish were represented in the catch. A second major fishery operated in the north-east Atlantic, in northern Faroese waters, from the late 1970s until 1991 when this fishery was suspended. Tagged fish of North American origin were rare in Faroese waters.

Both the ocean fisheries were carried out relatively close to port or harbour facilities as a matter of convenience. The fisheries operated in precise locations where particularly marketable types of fish might be caught in sufficient number to make the exercise viable. It is highly unlikely that feeding salmon occur only where the fisheries operated. It is much more likely that salmon occur continuously across a broad band of ocean, running generally from east to west, perhaps in pockets of local abundance.

8. Changes in the Abundance of Springers

8.1 The use of rod catch records

Various sets of catch figures exist that can be used to document the fortunes of the salmon fisheries on an historical basis. Indeed, rod catch figures have been used already in the present text. From the biological rather than the fisheries point of view, the assumption is made that changes in the catch figures from year to year reflect changes in the abundance of salmon after the marine phase of their lives. It is very unlikely that the correspondence between catch and abundance is exact - as all anglers will be aware. Yet, as we shall see, when the catch figures are compared among rivers, among years or among months, the patterns of variation are sufficiently similar to suggest strongly that a large part of the variation in overall catches does reflect variation in abundance.

The other data sets that might be used to infer changes in abundance are based on commercial fisheries. These are likely to be less suitable for the present purpose for a number of reasons.

1. Over the years, commercial fishing effort has decreased everywhere, for a variety of reasons. Much of the reduction in world and national catches (including the reduced spring net-catch) can be attributed to this alone.
2. The commercial fishing season is shorter than the rod season and curtailed by dates that are not especially relevant to the biology of the exploited stocks.
3. Commercial effort varies markedly over the season - especially during the spring months when conditions are often unfavourable for the deployment of coastal nets.
4. All commercial fisheries, including those pursued in estuaries, are mixed-stock fisheries that exploit salmon attempting to return to a number of home rivers.

For the following reasons the rod catch figures - and especially those for the spring fisheries - ought to be a more powerful source of information in the present context.

1. The rod season is longer than the commercial season and it covers the greater part of the period in which salmon might return to rivers.
2. Although rod fisheries are mixed-stock fisheries that exploit fish belonging to a number of local populations, fish caught by rod in rivers are more often of local origin than those caught by net along the coasts.

3. In contrast to commercial catches, rod catches have tended to increase over the years. The Scottish rod catch, for example, has increased steadily since official records were first kept. The increase is probably due in part to increased angling effort and in part to reductions in commercial effort that have permitted more fish to enter the rivers. But crucially, in the particular case of the springers, catches have declined against all the underlying trends. The rod catch figures are therefore a conservative index of the springers' decline and they can be used with particular confidence.
4. When MSW salmon and grilse occur together, they can be distinguished reliably only by scale-reading. In the absence of this information, the catches reported by sea-age class tend to include inaccuracies. In particular, 1SW fish are often reported as 2SW fish. During the period of the spring fisheries however, 1SW fish are largely absent in rivers and therefore only slight reporting inaccuracies are possible. In the present context, catches of grilse declared before June can assumed to be catches of spring fish without risk of debasing the figures.
5. Some salmon can be found in fresh water on more than a single occasion in their adult lives. Some spawners survive their first spawning, return to sea and enter fresh water a year or more later to spawn for a second time. The particular demands associated with the early-running habit are not consistent with survival much beyond the first spawning. The catch figures for the springers are not complicated by the presence of fish returning to spawn for a second time.

8.2 Changes in catches

Figure 9a-h shows the spring catch figures (January-May) for eight rivers over the period 1952-93. Each of the rivers has proved capable of producing an annual rod catch of more than 500 springers in some years. The catch figures for each river have been made comparable by expressing each year's catch as a fraction of the average catch over all the years considered. A catch of average size therefore has a value of one. An above-average annual catch is denoted by a value that exceeds unity and a below-average catch by a value of less than unity.

Although all the catch patterns are different, some prominent features recur. Greater than average catches were general until the late 1960s on all the rivers, with the possible exception of the Wye where catches were more uniformly near to average. A decline in catches in the late 1960s was a clear feature of all the fisheries, excepting the Deveron

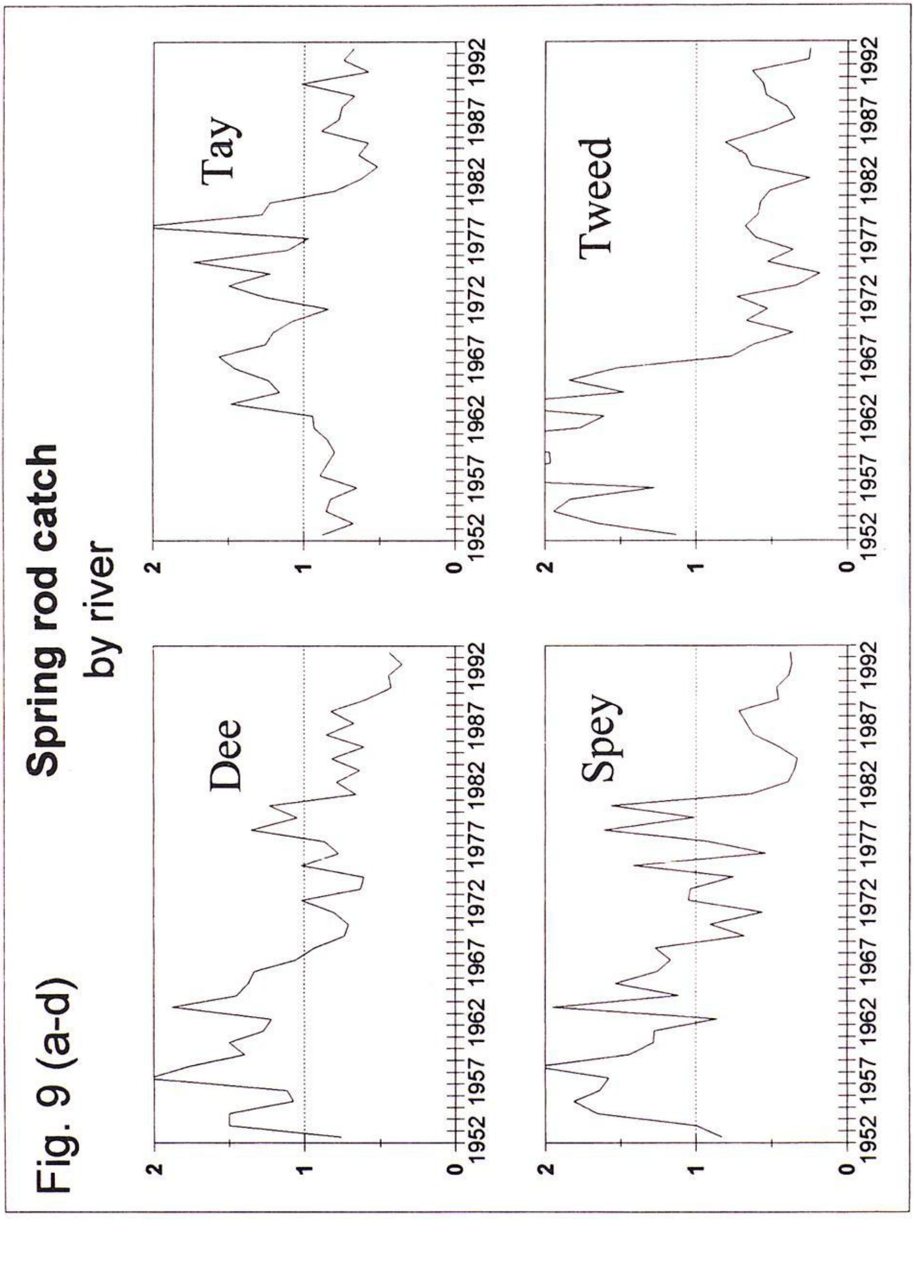
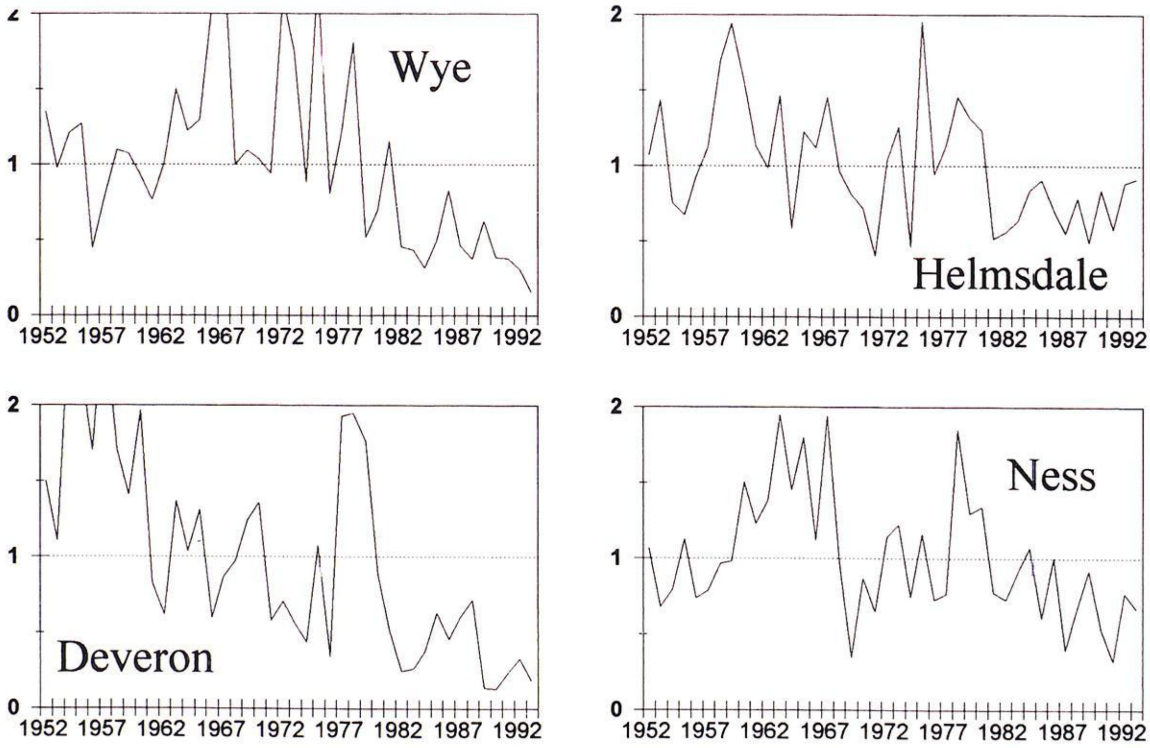

Spring rod catch
by river
Dee
Tay
Spey
Tweed
0
1
2
1952 1957 1962 1967 1972 1977 1982 1987 1992

Fig. 9 (a-d)

Fig. 9 (e-h)

Spring rod catch
by river



and the Wye. A period of irregular resurgence in the late 1970s was evident in almost every case. Catches fell thereafter and all the rivers have been below average every year in the last decade (1984-93), with the exceptions of the Tay in 1990 and the Ness in 1984 and 1986. In each of these special cases catches were only marginally better than average.

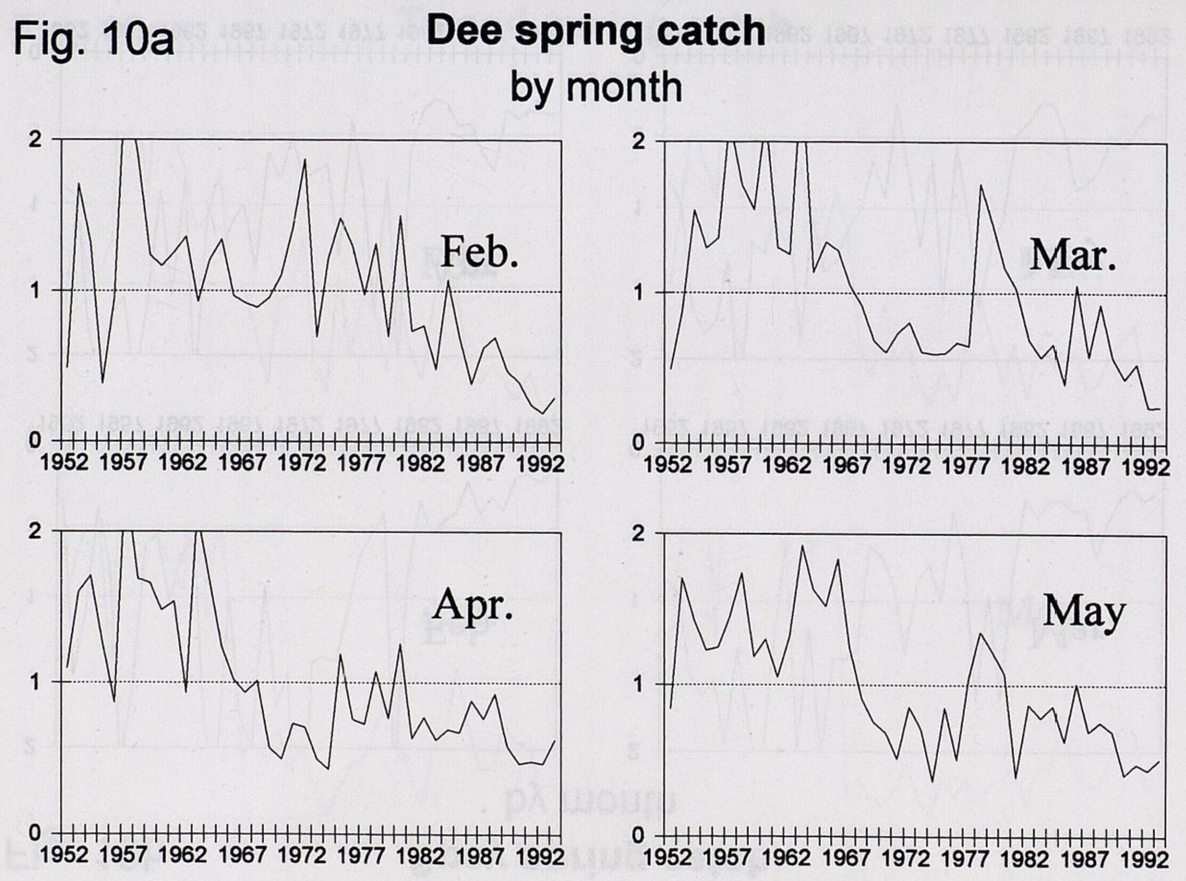
The patterns evident in the total catches obscure important differences among the spring months. Of the fisheries described in Figure 9, the Dee, Spey, Tweed and Wye are the major ones and each has proved capable of producing more than 5,000 springers annually to the rods. Figure 10 a-d show the patterns of change for each month of the spring season for the Dee, Spey, Tweed and Wye, respectively. On the whole, the general features evident in Figure 9 - including the recent run of below average catches - are evident in the monthly patterns for Dee, Spey and Tweed - although the Wye appears somewhat divergent in the early years. However, the most important feature of Figure 10 is that the extent of the catch declines can be seen to differ among months.

Table 1 shows this even more clearly. For the four major spring fisheries, recent May catches have been about half of average. In every case, April, March and February catches have been progressively more severely reduced and, overall, the February catch is running at about 20% of the long-term average. The same patterns are evident in the Tay and Ness but not in the Helmsdale or Deveron. These are the lesser spring fisheries, however, and the catch numbers are lower and less amenable to analysis (the lowest catch figures of all have been omitted from Table 1).

Table 1
Monthly catch figures (1990-93) expressed as a fraction of the long-term (1952-1993) average values

	February	March	April	May
Dee	0.28	0.36	0.51	0.46
Tay	0.39	0.54	0.96	1.18
Spey	0.20	0.30	0.39	0.47
Tweed	0.27	0.47	0.44	0.50
Wye	0.11	0.16	0.32	0.41
Helmsdale	-	0.87	0.85	0.74
Deveron	-	0.16	0.18	0.25
Ness	0.43	0.49	0.60	0.74

Fig. 10a


Dee spring catch
by month
Feb.
Mar.
Apr.
May
0
1
2
1952 1957 1962 1967 1972 1977 1982 1987 1992

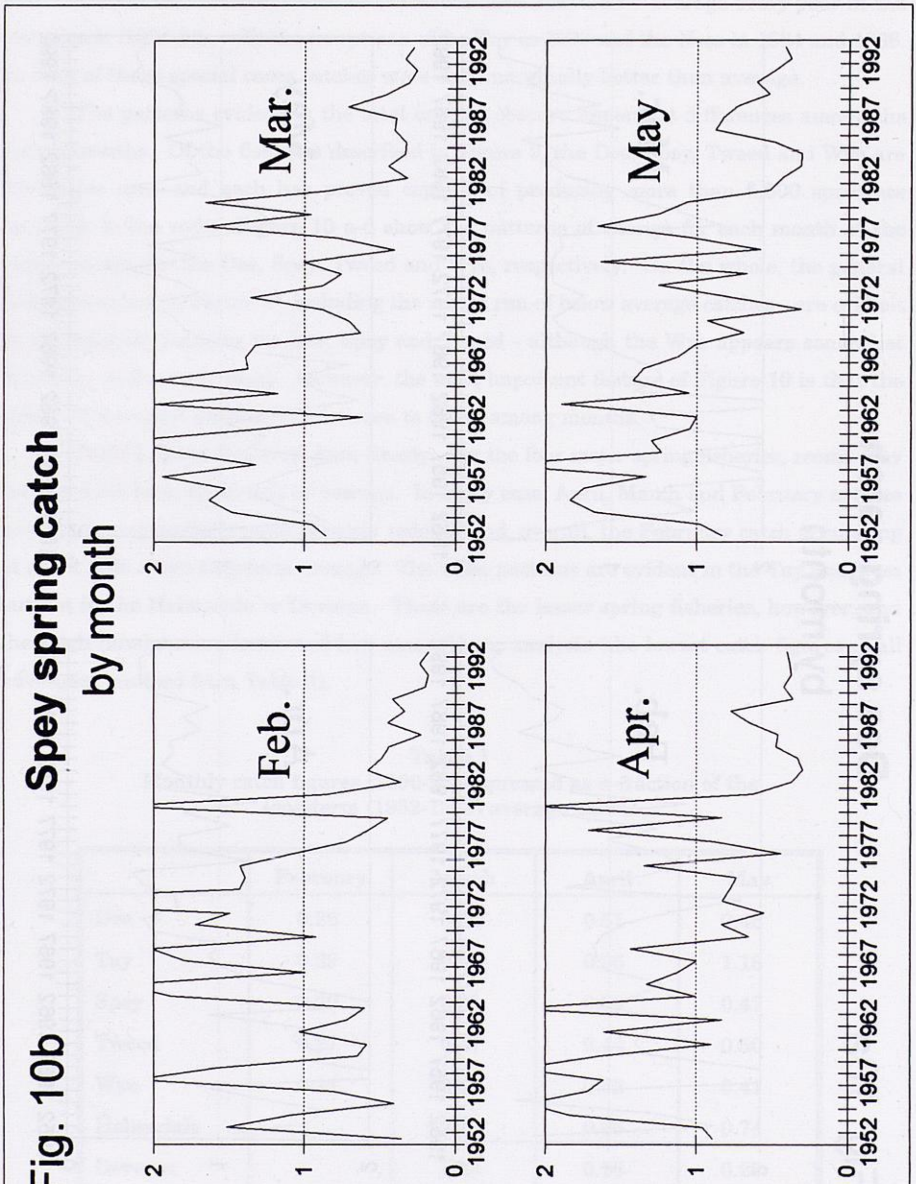


Fig. 10b Spey spring catch by month

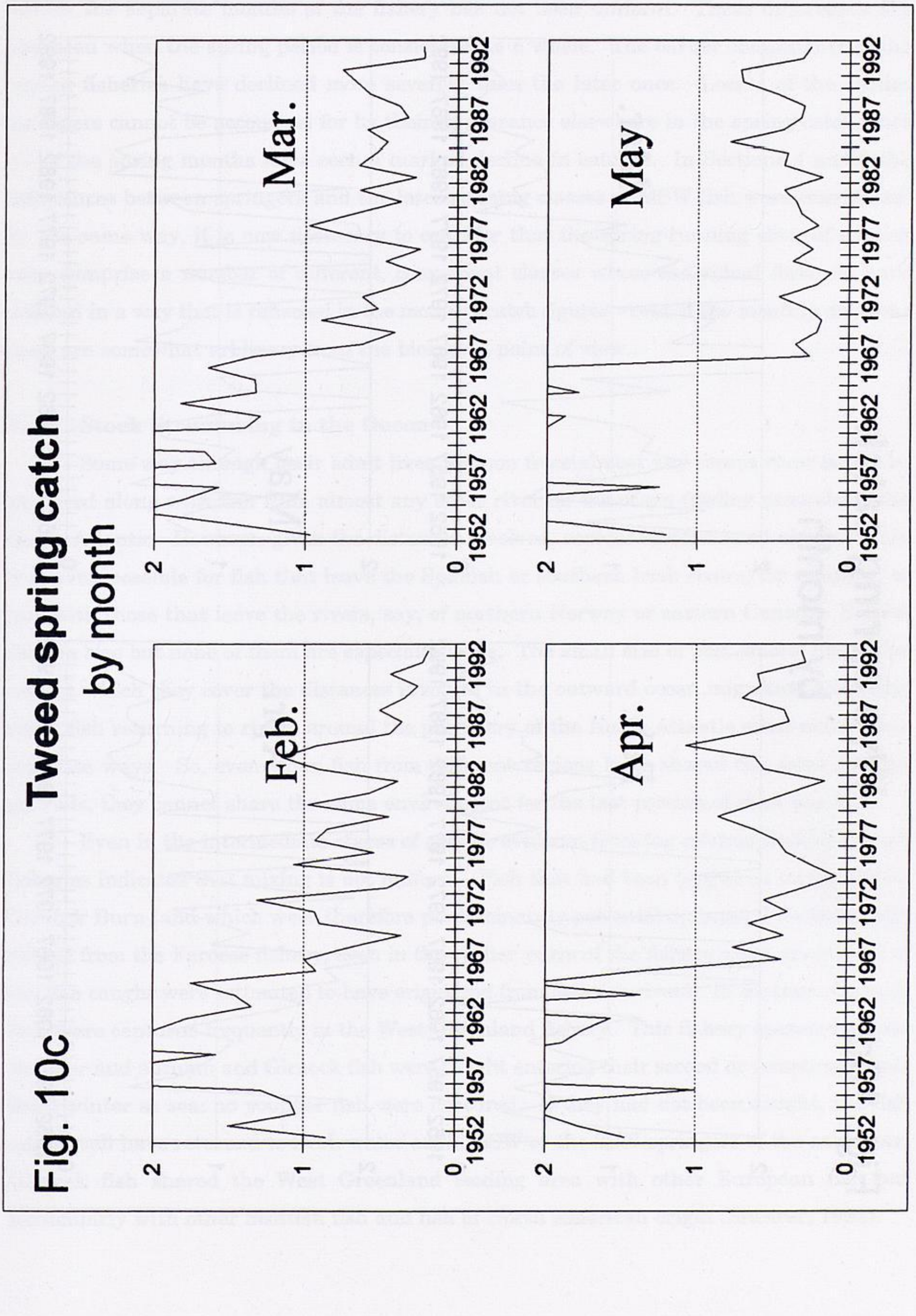
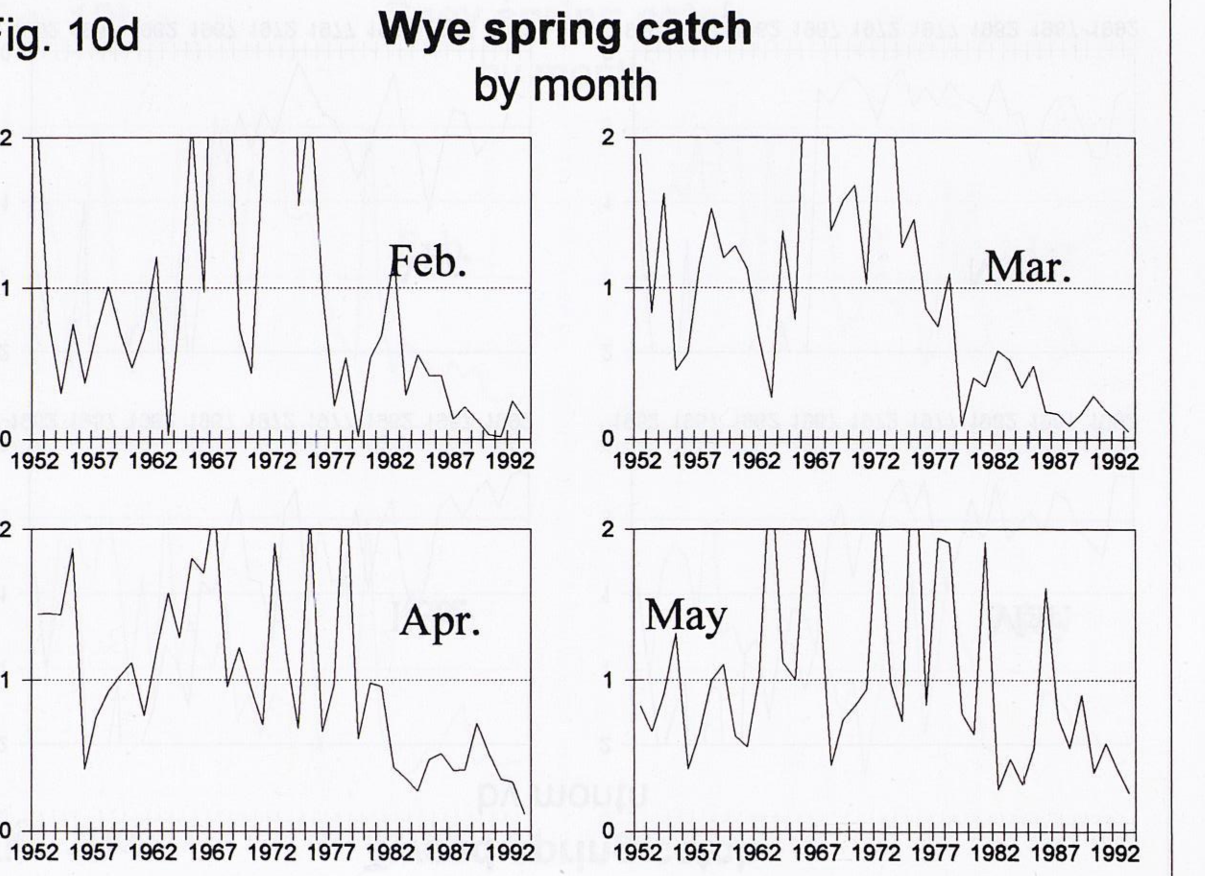


Fig. 10c Tweed spring catch by month

Fig. 10d


Wye spring catch
by month
Feb.
Mar.
Apr.
May
2
1
0
1952 1957 1962 1967 1972 1977 1982 1987 1992

In short, the spring fisheries have declined overall but the extent of the decline within the separate months of the fishery has not been uniform. These differences are obscured when the spring period is considered as a whole. The earlier components of the spring fisheries have declined more severely than the later ones. Losses of the earlier springers cannot be accounted for by their appearance elsewhere in the spring catch since all of the spring months have seen a marked decline in catches. In Sections 4 and 5 the differences between springers and the later running classes of MSW fish were considered. In the same way, it is now necessary to consider that the spring-running class of salmon may comprise a number of different, component classes whose individual fortunes have differed in a way that is reflected in the monthly catch figures - even if the monthly divisions used are somewhat arbitrary from the biological point of view.

9. Stock Structuring in the Ocean

Some way through their adult lives, salmon from almost any source river might be captured along with fish from almost any other river on the ocean feeding grounds in the North Atlantic. However, given the distances involved, several months must elapse before it is even possible for fish that leave the Spanish or southern Irish rivers, for example, to mix with those that leave the rivers, say, of northern Norway or eastern Canada. Smolts vary in size but none of them are especially large. The small size of post-smolts limits the rate at which they cover the distances involved in the outward ocean migration. Equally, adult fish returning to rivers around the periphery of the North Atlantic must make their separate ways. So, even when fish from different regions have shared the same feeding grounds, they cannot share the same environment for the last portion of their sea-lives.

Even in the intermediate stages of sea-life evidence from tag returns from the ocean fisheries indicates that mixing is not uniform. Fish that had been tagged as smolts at the Girnock Burn (and which were therefore predominantly potential springers) were signally absent from the Faroese fishery, even in the earlier years of the fishery when about 30% of the fish caught were estimated to have originated from Scottish rivers. In contrast, Girnock fish, were captured frequently in the West Greenland fishery. This fishery operated in late summer and autumn and Girnock fish were caught entering their second or sometimes their third winter at sea: no younger fish were captured. If they had not been caught, the fish might well have returned to fresh water as the 2SW or the 3SW springers of the next year. Girnock fish shared the West Greenland feeding area with other European fish but particularly with other Scottish fish and fish of North American origin (Shearer, 1992).

9.1 Ocean habitat and North American salmon

In a series of reports (Reddin and Short, 1991; Reddin and Friedland, 1993; Reddin *et al.*, 1993), North American fisheries scientists have described possible relationships between oceanographic changes in the northwestern Atlantic and the biology of salmon feeding at sea. A series of indices of the extent of potential ocean habitat available to salmon was calculated on a month-by-month basis from 1970 onwards. A knowledge of the distribution of sea surface temperatures throughout each year and of the salmon's preferred temperature range were used to construct these indices. In addition, calculations carried out using North American catch data available for the years after 1975 made it possible to re-construct the abundance of feeding salmon in the ocean the year before, prior to their return to North American rivers as MSW fish (Rago *et al.*, 1993).

When both these data sets are compared they show a marked measure of correspondence (Reddin *et al.*, 1993). The habitat index for the month of March shown in Figure 11 (courtesy of Dave Reddin) is particularly closely correlated with the estimated number of North American salmon present in the northwestern Atlantic several months later, more than a year before the same fish return to North American rivers.

The attractions of predictive relationships of this type and their potential importance are self-evident. If the relationship between ocean habitat and pre-fishery salmon numbers is valid, the ocean habitat index can be used to attempt prediction of the numbers of 2SW salmon returning to the North American fisheries in the next year. In this way, the appropriate management measures can be developed to set catches and to apportion fish most effectively (or most equitably), knowing the likely strength of the stock. Because the relationships are predictive, all the necessary arrangements may be put in place before any of the competing fisheries (including the rods) commences.

9.2 European springers and the northwest Atlantic

Some components of the Scottish catch of springers are correlated with the estimated abundance of North American fish in the ocean the year before. The January, February and March catches are correlated in this way (Spearman Rank Correlation; $P<0.05$, 0.01 and 0.05, respectively) although the April and May catches are not. The question arises therefore, whether the habitat indices that appear to predict the abundance of North American fish are also predictive for parts of the European spring catch.

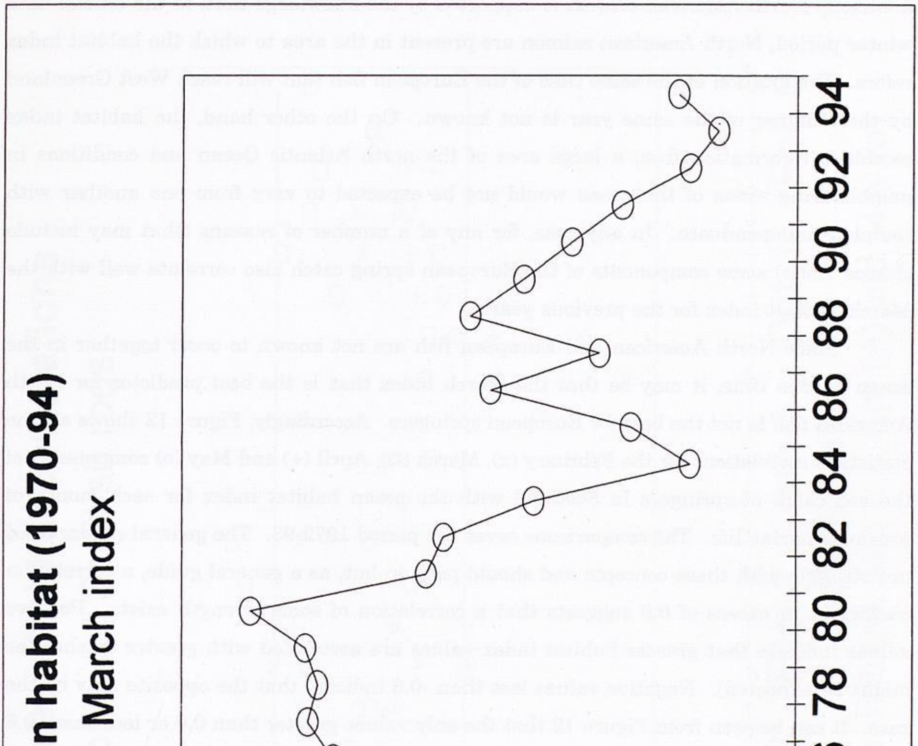


Fig. 11 Ocean habitat (1970-94) March index

The case for the likely validity of the relationship between habitat and abundance in a strictly North American context is supported by the knowledge that, in the crucial late winter period, North American salmon are present in the area to which the habitat index refers. The location at the same time of the European fish that will reach West Greenland by the summer of the same year is not known. On the other hand, the habitat index combines information from a large area of the north Atlantic Ocean and conditions in neighbouring areas of the ocean would not be expected to vary from one another with complete independence. In any case, for any of a number of reasons (that may include chance alone) some components of the European spring catch also correlate well with the March habitat index for the previous year.

Since North American and European fish are not known to occur together in the ocean at this time, it may be that the March index that is the best predictor for North American fish is not the best for European springers. Accordingly, Figure 12 shows all the statistical correlations for the February (x), March (□), April (+) and May (o) components of the rod catch of springers in Scotland with the ocean habitat index for each month of previous marine life. The comparisons cover the period 1972-93. The general reader need not struggle with these concepts and should pass on but, as a general guide, a correlation coefficient in excess of 0.6 suggests that a correlation of some strength exists. Positive values indicate that greater habitat index values are associated with greater catches (as might be expected). Negative values less than -0.6 indicate that the opposite may be the case. It can be seen from Figure 12 that the only values greater than 0.6 or less than -0.6 are positive ones and that they centre on the period around March of the year before the catches were made. It can also be seen that the more extreme values relate only to the February and March catches - and not to the catches of April or May.

Extending this approach to include the monthly catches made in the rivers included in Table 1 yields the patterns of association shown in Table 2. Each cell of the table displays a coded account of a single river and the degree of association of a single month's catch with each of the ocean habitat indices for January to May (JFMAM) in the preceding year. Strong associations are coded by capitalisation, modest associations by lower case and lack of association is denoted by a dash.

Fig. 12 **Catch v. ocean habitat correlations**
by month for Scottish rods

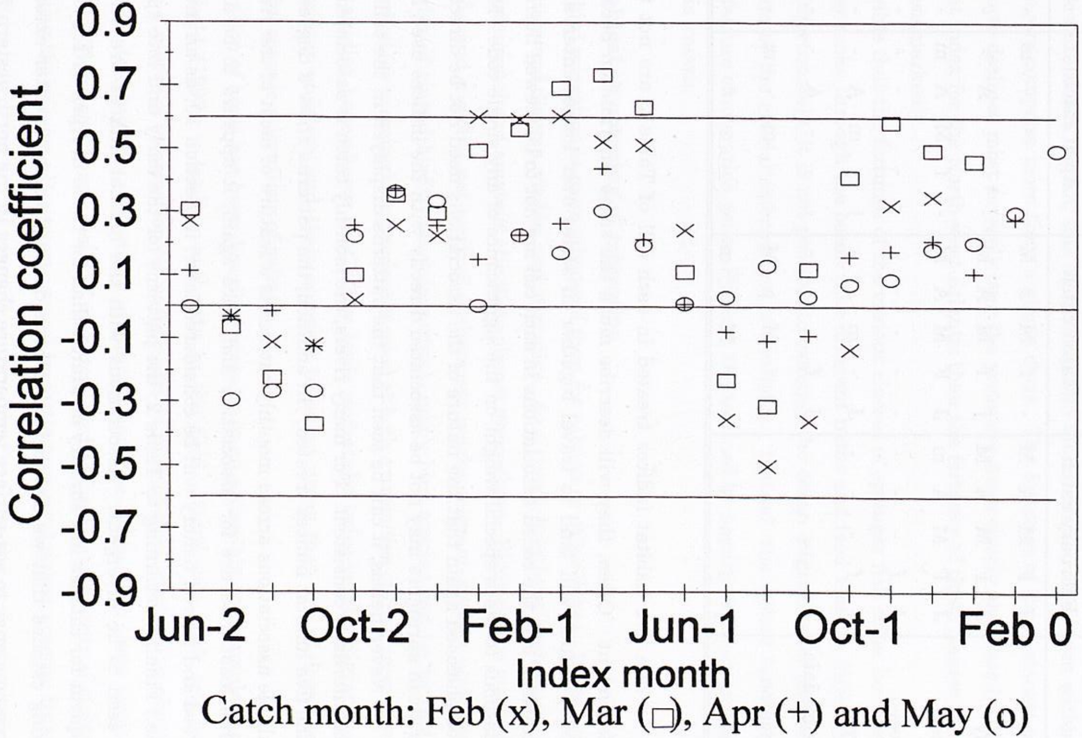


Table 2
Correlations of monthly rod catches of spring salmon with the ocean habitat indices of the preceding year

	February catch					March catch					April catch					May catch				
Dee	J	F	M	A	M	-	f	M	a	M	-	-	-	-	m	-	-	-	-	-
Tay	J	F	M	A	M	j	f	M	A	M	-	-	-	A	-	-	-	-	a	-
Spey	J	F	M	A	m	J	F	M	A	M	-	f	M	A	m	-	-	m	a	-
Tweed	J	f	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Wye	J	f	-	-	-	J	-	m	-	-	j	-	m	A	-	-	-	-	-	-
Helmsdale						J	f	-	-	-	-	-	-	A	-	-	-	-	-	-
Deveron						-	f	M	a	M	-	-	m	-	m	-	-	-	-	-
Ness	j	f	m	a	-	-	F	M	A	m	-	-	-	a	-	-	-	-	-	-

The five habitat indices treated in each cell of Table 2 are not to be considered independent. Often, they will describe much the same information because high or low habitat values will tend to travel together in series over longer intervals than months. Because of this the coded associations in each cell are not to be viewed literally and it would be fatuous to place special weight on the significance of any single code. Moreover, it must be emphasised again that the nature of the associations need not be direct: the fortunes of European springers may not be associated directly with the indices used here.

Nevertheless, it can be seen that the patterns displayed in the cells of Table 2 tend to be internally consistent. For many rivers, the monthly catch is associated with all or most of the five habitat indices treated. In addition, the patterns show a degree of cohesion and multiple associations across monthly catches is a feature of most of the rivers. The Tweed shows least evidence for association and, once again, it appears to be anomalous. (The Tweed and its rod fishery will be considered later, in Section 10, as an interesting, special case.) Finally, returning to Table 2, the patterns for the early and late spring catches can be seen to be divergent. Associations with the habitat indices are stronger and more frequent for catches in February or March than for those in April or May. Thus, the early spring catches that we saw before to have declined to the greater extent show a closer correspondence to sea-surface temperature changes in the northwestern Atlantic than the catches of the later spring months.

It is not possible to bring these studies to any other than a tentative conclusion. Further investigation using different approaches will be required before firmer conclusions may be drawn. On the other hand, the associations between catches and ocean habitat indices are quite strong and the patterns of association are quite marked. The patterns are also consistent with the differences in the fortunes of the monthly catches of springers in many of the rivers examined. Again, this lends weight to the contention that, even within rivers, the springers comprise more than a single class. The fortunes of those classes of springers that have declined most severely over the years are more closely associated with the ocean habitat index for the North-west Atlantic than the fortunes of those classes that have declined less markedly.

It is possible that the fortunes of the various classes of springer fish differ because the journeys they make through the ocean take different paths and lead them to different destinations. Unfortunately, it is not possible to examine the ocean migrations of salmon directly and none of the crucial information is available. Instead, the extent to which structuring is a feature of migration generally must be examined by turning to other species for which more is known.

9.3 Geographical structuring of migration

Study of bird migration is more advanced than for salmon or other fishes. Birds are common everywhere and diverse, visible, and attractive. As a result, they have been studied intensively by professional and amateur scientists almost everywhere. Birds can be marked readily by ringing and a global net-work of enthusiasts marks migrant species and logs reported recoveries of ringed birds. Most important, many bird species can be located, captured and marked (or examined for previous marks) at both extremities of their migration route. Ringing studies have shown that many birds undertake twice-yearly migrations between their winter quarters and their summer breeding areas that are at least as spectacular as the oceanic migrations of salmon.

The migration of birds has been described recently in an accessible and stimulating primer by Berthold (1993), a leading authority in the field. Berthold's book can be recommended as a source of information for anyone who is interested in speculating about the mechanisms underlying the migrations of salmon and the forms that their ocean journeys may take. There are many species of migratory bird and a great diversity of styles of migration among the species. However, several important, general points emerge from Berthold's review.

Like salmon populations, breeding populations of most bird species are highly structured geographically. Like salmon, many birds home precisely to the breeding places where they were raised themselves. The migrations that take populations from the breeding areas to their traditional wintering areas are also highly structured. The constituent populations of single species or of closely related groups of sub-species often migrate in families of patterns that are similar in some respects but different in others. These patterns can be considered under various headings. However, in the present context, small and broad-front migrations, divided migrations and "leap-frog" migrations are four of the most informative categories because each is known to be enacted among populations of a single species.

Broad-front migrations consist of generally parallel movements in which geographical populations travel side-by-side. In the garden warbler (*Sylvia borin*) a southwards broad-front migration takes a continuous series of European breeding populations separately into a continuum of African over-wintering areas. The situation in the lesser whitethroat (*Sylvia curruca*) and the crane (*Crus crus*) differs slightly. Parallel southwards small-front migrations collect the more eastern and the more western Eurasian breeding populations and deliver them to winter refuges that are widely separated.

The case of the white stork (*Ciconia ciconia*) is more extreme. A small-front migration delivers western European breeding populations to west Africa via the Straits of Gibraltar. Another, independent small-front migration delivers eastern European populations to southeast Africa via the Levant. The migration of white storks is also a divided migration: the eastern and western paths are separate for their entire length. Interestingly, both the eastern and the western paths have their origins in Germany. Birds that start their migrations from locations that are only several hundred kilometres apart use migratory routes that take them through different continents. These routes deliver them finally to opposing parts of yet another continent.

Finally, the various sub-species of the fox sparrow *(Pasarella iliaca)* in North America and European populations of the ringed plover (*Charadrius hiaticula*) undertake so-called leap-frog migrations. The more northerly breeding populations undertake successively longer southwards migrations to their winter quarters, leap-frogging the summer and winter ranges of the intervening populations.

Even from this brief summary, it can be seen that in birds a wide variety of migratory patterns are in place within single species that lend a distinct geographical aspect to migration and to population structure. In many species, migration keeps populations separate from one another for all of their lives - where they breed, while they migrate and while they feed on their winter grounds.

Experimental work has shown that many aspects of bird migration are genetically controlled. The directional headings that migratory juveniles adopt as they leave their breeding grounds and the changes that they make on route are passed to them by parents (Berthold *et al.*, 1992). Parents that have led their own lives successfully, pass the same specific instructions for migration to their progeny in the form of their genes (Berthold and Pulido, 1994). Once again, if genetically determined mechanisms are used to devise, develop and guide the migrations of birds, it must be considered likely that salmon are capable of doing this too.

9.4 Changes in population structure

Population structure is not fixed. Populations continually respond and adjust to changes in circumstances, as natural selection acts on their members. Spontaneous genetic changes arising in particular populations permit migrants of all species to probe for new opportunities in unused habitat. There is no single route to improvement and different populations can test different options as they arise by chance. Because of reproductive isolation, improvements are not shared and the migrations of populations tend to become more diverse as they evolve.

While opportunities may be identified in new locations and exploited, opportunities also close down in established ones. In the case of salmon, the time-frames involved vary considerably, from millennial scales down. As the last glaciation approached, for example, we must imagine that many established salmon populations were eliminated by the ice-sheets. All the recent history of most present-day populations is covered by the 12,000 years or so since the glaciers began to recede. Within this relatively short period, salmon have re-colonised most of the rivers that they occupy today, they have formed local, genetically discrete populations and they have developed the variety of life-styles that characterise particular populations.

On the other hand, all the changes that have taken place are not parts of an unremittingly successful progression. Some populations (in rivers like the Thames, Rhine and Tyne) were even eliminated as a result of man-made habitat changes. Within the last century or so, large swings in the numbers and the composition of the fisheries have been documented over the period since catch records were first compiled (eg see Shearer, 1992). As we have seen, it is very likely that these changes in the fisheries reflect underlying changes in the abundance or the relative abundance of the populations that contribute to them. On an even shorter time-scale, all the weight of the evidence suggests that the recent decline of spring fish (say, since 1980) is also a consequence of the changing fortunes of particular populations.

In Figure 13, the three general patterns of migration described above for birds have been translated into simple two-dimensional models. Three breeding populations (b1, b2 and b3) move separately into three feeding areas (f1, f2 and f3, respectively). Although the models are based on the migrations of birds, there is no reason to suppose that salmon populations are not capable of developing similar segregating migrations. In the simplest, front-migration model (A), neighbouring breeding populations migrate equal distances in the same direction to adjacent feeding areas. In the divided migration model (B), breeding populations migrate equal distances in different directions. In the "leap-frog" model (C), populations move different distances in the same direction.

It can be seen from any of the models that every successful member of each salmon population makes a circuit through a series of environments. Intermediate goals along the route are occupied only briefly by fish moving through. The goal areas at the extremities of the migratory route are probably used for relatively longer periods. Migrants depend on all the environments they stay in or pass through for support. At any stage, adversity will reduce the numbers of fish exiting to pass on to the next stage of the migration. Mortality at any stage in the migratory circuit will reduce the number of fish returning later to the spawning areas (and to the fisheries). Any changes in the extent or the quality of the habitat available to migratory species (at any stage of life) will affect their fitness and abundance. In the context of any of the models pictured in Figure 13, it is possible to understand how non-uniform changes in habitat at any stage (in fresh water, in transit or on the ocean feeding grounds) would affect some populations more than others. In particular, it can be seen how non-uniform reductions in ocean habitat might reduce some salmon populations more than others.

Interestingly, the Scottish rod catch figures suggest that summer and autumn fish have actually prospered while the spring fish have declined. As was cautioned earlier, it is not possible to discount the effects of reduced commercial and increased sporting effort in driving up the rod catches of summer and autumn fish over the years. On the other hand, there are two other, biological routes by which the fortunes of populations producing spring salmon or other fish might reciprocate. The more obvious possibility (that potential spring fish might transform themselves to become grilse or summer salmon) was discounted as a general explanation in Section 6. The other possibility is worth considering in more detail and a well-developed theoretical frame-work exists in which the idea may be considered.

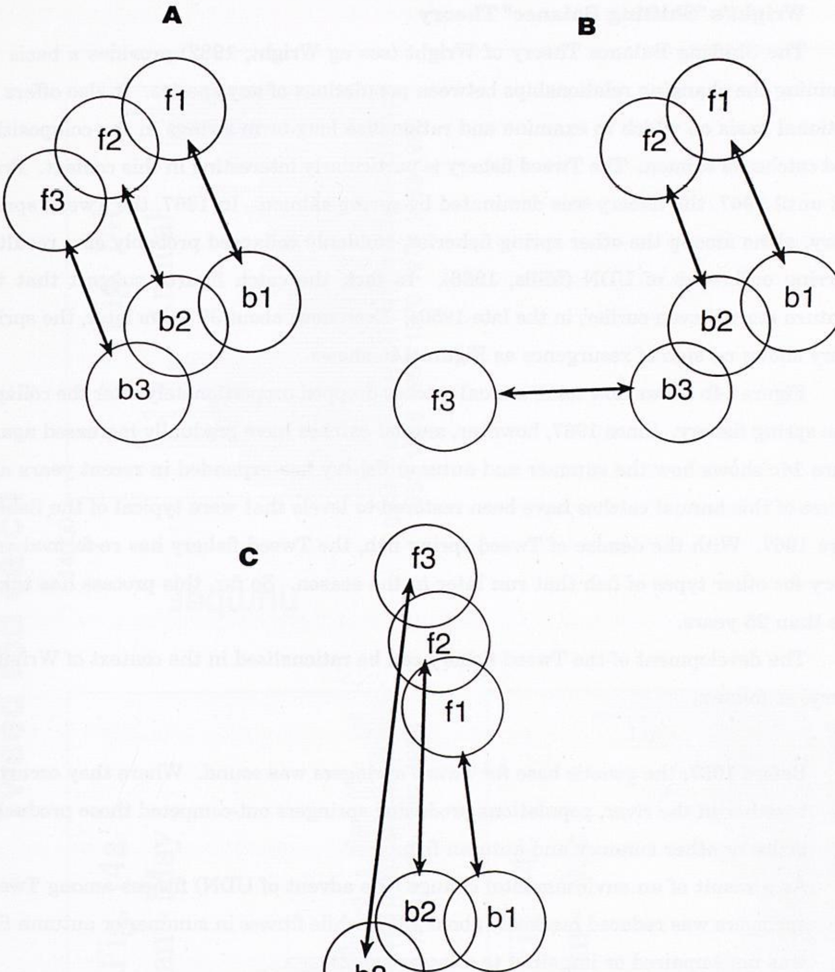


Figure 13 Simple migration models based on studies of bird species.

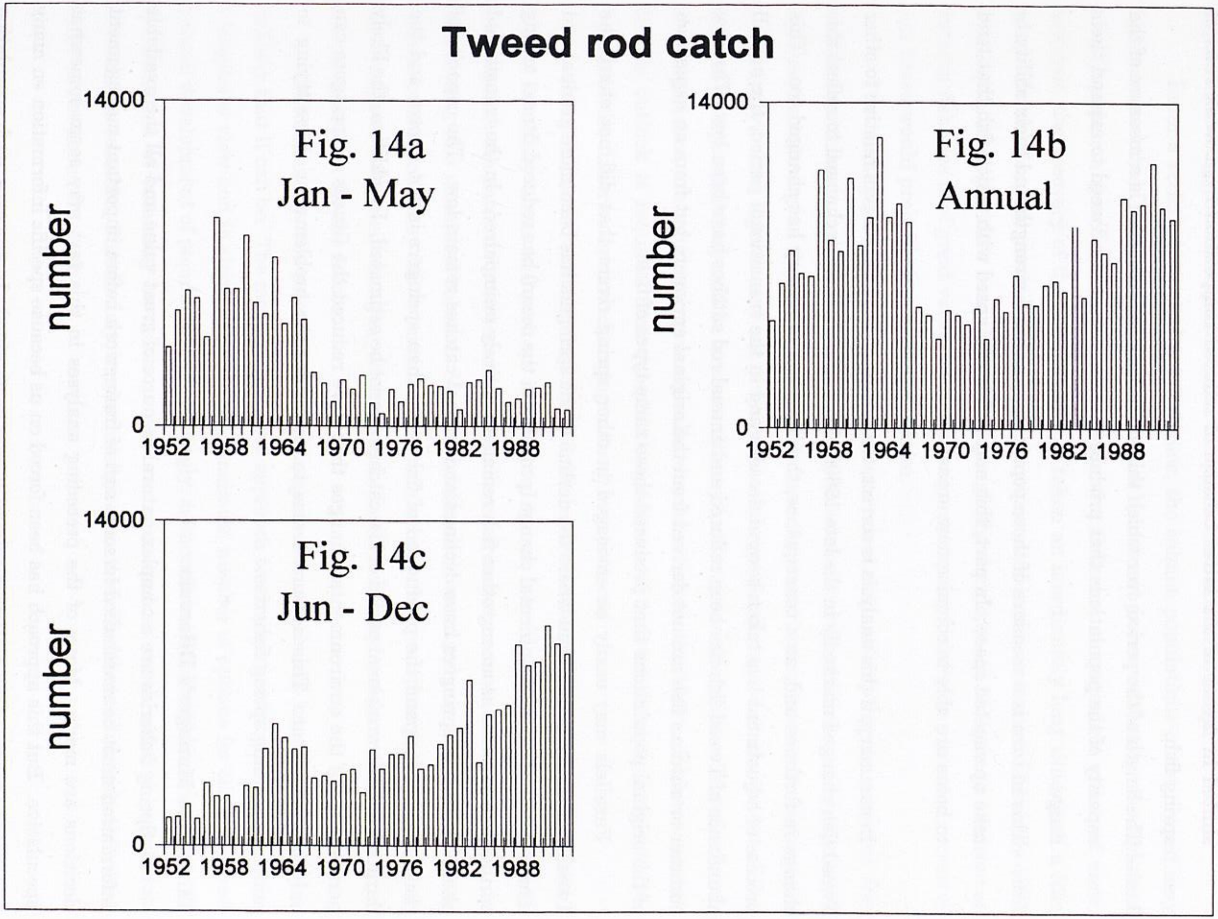
10. Wright's "Shifting Balance" Theory

The Shifting Balance Theory of Wright (see eg Wright, 1982) provides a basis for examining the changing relationships between populations of any species. It also offers an additional basis on which to examine and rationalise long-term swings in the composition of rod catches of salmon. The Tweed fishery is particularly interesting in this context. From 1952 until 1967, the fishery was dominated by spring salmon. In 1967, the Tweed spring fishery, alone among the other spring fisheries, suddenly collapsed probably as a result of recurring outbreaks of UDN (Mills, 1986). In fact, the catch figures suggest that the downturn started even earlier, in the late 1950s. Even now, about 30 years later, the spring fishery shows no sign of resurgence as Figure 14a shows.

Figure 14b shows how total, annual catches dropped proportionately after the collapse of the spring fishery. Since 1967, however, annual catches have gradually increased again. Figure 14c shows how the summer and autumn fishery has expanded in recent years and because of this annual catches have been restored to levels that were typical of the fishery before 1967. With the demise of Tweed spring fish, the Tweed fishery has re-formed as a fishery for other types of fish that run later in the season. So far, this process has taken more than 25 years.

The development of the Tweed fishery can be rationalised in the context of Wright's Theory, as follows.

1. Before 1967, the genetic base for Tweed springers was sound. Where they occurred together in the river, populations producing springers out-competed those producing grilse or other summer and autumn fish.
2. As a result of an environmental change (the advent of UDN) fitness among Tweed springers was reduced markedly about 1967, while fitness in summer or autumn fish was not impaired or impaired to a lesser extent.
3. As a result of reduced spawning, populations producing Tweed springers were weakened in the years after 1967, while those producing summer and autumn fish remained sound. Catches of springers fell.
4. The slack created by the contraction of the springers' use of river habitat was gradually absorbed over several generations by adults from different populations that had not previously been competitive in the vacated locations.



Tweed rod catch
Fig. 14a
Jan - May
Fig. 14b
Annual
Fig. 14c
Jun - Dec
number
14000
0
1952 1958 1964 1970 1976 1982 1988

5. The balance between the populations that produce springers or later-running fish had shifted in favour of the latter because of reduced competition from weak runs of spring fish.
6. The length of the period over which this adjustment has occurred is a measure of the capacity of the populations that produce summer fish in the Tweed to expand their range.
7. This in turn is a measure of these populations' original strength and their ability to take up vacated space. In part, this may reflect the speed with which fish that tend to home are able to colonise new areas.

In summary, if this analysis is correct, the fitness of Tweed springers relative to other Tweed fish changed markedly in the late 1960s. Population structure changed to reflect this change in fortunes and, as a consequence, the character of fishery has changed too. This process of adjustment has taken several decades and in the transitional period, the overall abundance of Tweed fish has been reduced and annual rod catches have been low. The new summer or autumn fish are not derived from the original springers but from an expansion of the original populations that produced these same types of fish.

Parallels may easily be envisaged in other spring rivers that did not share the Tweed's problems in 1967 and where the decline of the springers has been more gradual and more recent. Thus, environmental change (probably in the ocean) has reduced fitness among springers, while fitness among other fish remains relatively unimpaired. In the transitional phase, catches of springers have declined and annual catches remain low. The capacity of these rivers to expand the production of fish other than springers is not known and the duration of the transitional period of low catches cannot be estimated. In addition, the likely permanence of the environmental changes that have reduced the fitness of springers can only be guessed at. This account seems to crystallise the problems for those trying to manage declining spring fisheries.

11. The Manager's Dilemma

Spring fisheries are a complex natural resource of great value and all the available information must be marshalled in some sort of frame-work before important management decisions are made. Many of the preceding analyses in this text may seem somewhat speculative. But this approach has been forced on us because specific information on many important aspects of the biology of salmon cannot be obtained. In any case, each speculation is probably reasonable in that it can be backed up by theory or knowledge based on the population biology of other species and a composite case can be built up.

From a strictly biological point of view, the salmon populations of the Tweed may have resolved their recent evolutionary problems by natural processes that can be explained in a population genetics frame-work. From the fisheries management point of view, however, the recovery of the rod fishery has taken an inordinately long time (half a life-time). In addition, the process of recovery has not resulted in the restoration of the pre-1967 *status quo*, as might have been desired. Although the development of vigorous summer or autumn fisheries is of great value, an equally vigorous spring fishery or a greater spread of run times would probably be valued even more.

The manager's dilemma therefore seems clear. Is attempting to preserve the character of fisheries or to restore them quickly to some desired condition a valid objective? On a realistic biological time-scale, even a life-time of personal experience or an awareness of a century's catch figures may not prepare the manager for the speed or the extent of the natural changes that may still lie in store. It may be that present ambitions, based only on brief experience, are certain to prove unrealistic at some time in the future. Perhaps, a more flexible outlook is required that accepts the pressure of natural developments and re-organises the fisheries around changing natural run patterns.

Is it possible to resist natural change? The costs of attempting to do so will be high, both in monetary terms and perhaps in biological terms, too. Management measures that drive against the natural forces causing them will require a permanent commitment towards maintaining this unnatural balance. Moreover, intensively managed populations, freed from natural constraints, may fail to continue their natural genetic development, slipping further out of register with their changing environment. Ineffective intervention will store up even greater problems for the future.

Unfortunately, the solution to the manager's dilemma is not known and it seems unlikely that it can be. The most conservative approach to management therefore, is to take a long-term view and to strive to retain the maximum number of options for the continued natural development of populations. Accordingly, salmon fisheries should be managed with the intention of retaining as much genetic variation and as much natural population structure as possible. Fortunately, our knowledge of matters like these is already sufficient to let us set about the task.

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