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THE BIOLOGY OF THE SEA TROUT

Summary of a Symposium held at Plas Menai
24-26 October 1984

Edited by E. D. Le Cren

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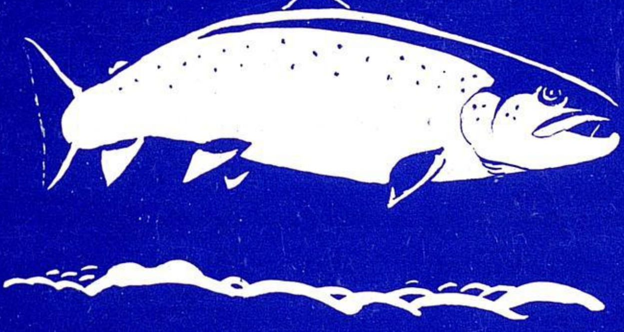
and the
Atlantic Salmon Trust Ltd.



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EDITOR'S PREFACE

This workshop on sea trout biology was organised by Dr. Graeme Harris of the Welsh Water Authority for the Atlantic Salmon Trust and held at Plas Menai, North Wales from 24-26 October 1984. An introduction and eighteen papers were contributed by the thirty-six participants most of whom participated in discussions held after the presentation of each group of papers. Nearly all the papers were made available to me in full written versions after the meeting. I have used these and notes I took at the time to write this report of the proceedings. The latter is much shorter than would have been a full compendium of the written papers and recorded discussion, but several of the papers have been published in scientific journals, or will be in the course of time. I have also thought it appropriate to include information from some recent published literature on the sea trout in British and Irish waters, but only where this seemed to be particularly relevant; no attempt has been made to review the literature generally. A list of the papers presented to the meeting is given on page 39 and references to other papers cited on page 40. (In the text, the name of an author followed by 'P' refers to his paper to the workshop; 'D' indicates a point made in discussion. Other citations use the conventional author plus year).

In the 'Discussion and Conclusion' section I have biased my account towards some personal opinions and speculations derived from my own impressions of the workshop and reflections made after reading the full papers.

I am grateful for the help I received from authors, especially those who provided figures to illustrate this account and those who have commented on the draft manuscript. I apologise to any who feel that my précis does not do full justice to their contributions.

E. D. Le Cren

June 1985

1. INTRODUCTION

The sea trout has tended to be neglected, both by biologists and those concerned with the management and development of fisheries. Yet there is a good deal of evidence to show that it is an undervalued and underexploited fish. There are also features of its biology that are difficult to elucidate and yet fascinating in their complexity and in their relevance to wider problems in ecology, genetics and evolution.

In the earlier decades of the twentieth century, a small number of amateur and professional fishery biologists in Scotland and Scandinavia carried out a series of studies on the sea trout. Many of these were based on the newly developed art of scale-reading and a considerable amount of information about the life histories and differences between stocks in different river systems was deduced (e.g. Nall 1930). With hindsight, some of these studies now seem to lack that rigour and statistical analysis really necessary for sound scientific observation and interpretation. Indeed, some of the recent investigations presented at this workshop have cast doubts on the reliability of such features of scales as spawning marks.

In more recent decades, research on sea trout has tended to take second place to work on salmon, though some long-term trapping studies on salmon populations and fisheries have provided valuable incidental information on sea trout, and reports on these were included in the workshop. As well as the papers presented at the workshop and the discussions that they provoked, reference is made to some of the more recent published information.

An introductory paper by Harris (Pa) listed features of sea trout that make it a particularly valuable fish especially when compared with salmon.
Among these are:

1) sea trout will migrate up rivers under a wide range of flow conditions and especially at relatively low flows.

2) they can be angled for day and night, and caught under a wide range of river conditions,

3) Their life history allows a quicker return from the smolts produced, many of which migrate back after only two or three months at sea. Moreover, the survival rates from smolt to returning fish appear to be higher than those for salmon, and many sea trout return to spawn several times,

4) sea trout have a varied and flexible life history which may render them less vulnerable to environmental perturbation,

5) sea trout penetrate small tributaries and thus make good use of spawning and rearing ground,

6) sea trout are not vulnerable to high-seas commercial fisheries,

7) when angled they fight hard and

8) they are excellent to eat; (in the editor's opinion, better than any other salmonid fish!)

One of the first questions asked, and one that recurred throughout the workshop was; what are sea trout? It is now agreed by icthyologists that there is one species of trout native to north-western Europe - Salmo trutta. At the end of the last ice age, as the ice retreated, the freshwaters of northern Europe were colonised via the sea by two successive forms of trout. Both of these forms gave rise to 'brown trout' that no longer migrated to sea. Evidence was presented to the workshop to show that there could be genetic differences between the trout in different river systems and in parts of the same river system. While many stocks of sea trout showed clear distinctions in migratory habits from brown trout in the same river; in other rivers the differences were less clearly distinct.

It has been known for a long time that, in some rivers at least, only female sea trout migrate, the males remaining in freshwater. In other rivers, both sexes may migrate but, among the migrants, females predominate. Yet, in papers presented to the workshop and in other published studies, the data on sex-ratio are variable, confusing and sometimes contradictary. I suspect that many researchers have not paid due attention to the great difficulty in obtaining a true measure of the sex ratio in a population from samples taken when sex may be influencing behaviour. For example, if males spend longer in a spawning area than do females they will have a greater chance of capture there and so appear relatively more abundant than they really are.

The typical sea trout spends two or three years as a parr in the river, often in relatively small streams. When between 14 and 20 cm in length it turns into a smolt and migrates to sea, usually in April, May or June. A proportion of the fish then return to freshwater in the first summer or autumn of their sea life (something that very seldom happens with salmon). These fish are known in most of Scotland as "finnock" (but elsewhere by many other local names, especially "whitling" in parts of England). Some of these finnock may mature and spawn; others do not, although in some rivers they may spend the whole of the winter in freshwater or an estuary. Other sea trout do not spawn until they have spent one or more winters in the sea. Sea trout spawn in the autumn, i.e. late October, November or December and may spend most of the following winter in freshwater as kelts and not return to the sea until the following spring, although many return to sea immediately after spawning.

The survival of kelts in sea trout appears to be greater than that of salmon and a significant proportion of sea trout may spawn several times and live for many years. Marking experiments have shown that some sea trout, especially those from rivers from the Tweed south to Yorkshire, migrate long distances in the sea while other fish, e.g. in western Scottish and Irish waters may not stray far from the coast but stay in sea lochs. Though tag recaptures show that straying can occur, much of the evidence from marking experiments and genetic differences suggests that most sea trout home to their natal stream with great accuracy. A considerable amount of information on detailed migratory behaviour was presented at the workshop. Recent information on the food of sea trout in the sea was also given.

Original and quantitative information on the population dynamics in relation to the life history in two or three river systems where traps for migrants have been operated were also presented and discussed. These, like the migration studies, emphasised the differences between river systems and the flexibility of life-history strategies within the species. One recently published long-term study has described the role of density-dependent mortality in the early parr stage in the population control of the sea trout.

Finally, the workshop identified some of the problems in developing the better utilization and management of sea trout stocks and also some of the aspects of sea trout biology where further research would be especially rewarding.

The following account will thus deal with five main aspects of sea trout biology in this order:

1. Genetics, and the different forms of sea trout
2. Migratory behaviour
3. Sex ratio in relation to migration
4. Feeding in the sea
5. Population dynamics, exploitation and enhancement

A final section will attempt to discuss the workshop as a whole in relation to future research and management needs.

2. TAXONOMY and GENETICS

It has been recognised by nearly all fish taxonomists that the trout native to northern and western Europe belongs to one species, the correct scientific name of which is Salmo trutta L. Apart from the effects of migration itself on the growth-rate, size and scales, no consistent morphological criteria have been found to distinguish sea trout from non-migratory brown trout.

Recent developments in taxonomy using the electrophoresis of proteins, have enabled genetic differences between populations of fish to be discovered. The techniques allow alleles (alternative forms) of a hundred or more genes (loci) to be identified and thus the degree of differentiation assessed. (It is not possible however to prove that two populations are genetically identical, only that they may differ). In the trout, it has been shown that there are two main races; the 'ancestral' (designated "Ldh-5 105") and the 'modern' (designated Ldh-5 100). During the re-colonisation of freshwaters in the 10,000 years since the end of the last ice age, the ancestral type arrived first followed by the, now commoner, modern type; some rivers now contain a heterogeneous mixture of the two types. In both types, colonisation will have been by migratory sea trout. Where geomorphological events led to the formation of barriers to migration such as waterfalls, populations of trout upstream of such barriers will have lost the migratory habit and this has occurred with both types. In such situations there will be strong selective pressures against migration; any fish emigrating over the falls being unable to return to perpetuate their genes in the upstream population. In many river systems without barriers to migration, populations that do not migrate to the sea may also occur.

Sets of data from two groups of rivers in Ireland were presented by Ferguson (P) and Cross (P) respectively. The river Glynn in Co. Antrim has impassable falls and there are considerable genetic differences between the trout above and below the falls with good evidence that those resident above the falls do not migrate down over the falls. The barrier has thus led to genetic differentiation between the populations each side of it. There appears to be no genetic difference between the resident and migratory populations below the falls, but there is a sex difference; very few males migrate and very few females do not migrate. (See Section 5.2 below). In the Glenariff River, Co.Antrim, two tributaries above falls contained resident trout. Below the falls resident and migratory populations were found that were genetically distinct from one another indicating that, in this small river, there was some genetic control over migration. The Spencer River in Co. Down held a sea trout population that had a unique allele that could not be found in sea trout populations in adjacent rivers only 2 km away. For such a distinction to persist, straying from the home river to spawn must have been a very rare occurence; (or perhaps, the unique allele confered a powerful disadvantage in any 'foreign' stream to which fish may have strayed).

Cross (P) described the situation in the Burrishoole system and adjacent Newport River (Fig.1). Five sets of samples of trout were collected:

The Fairy Glen - above impassable falls

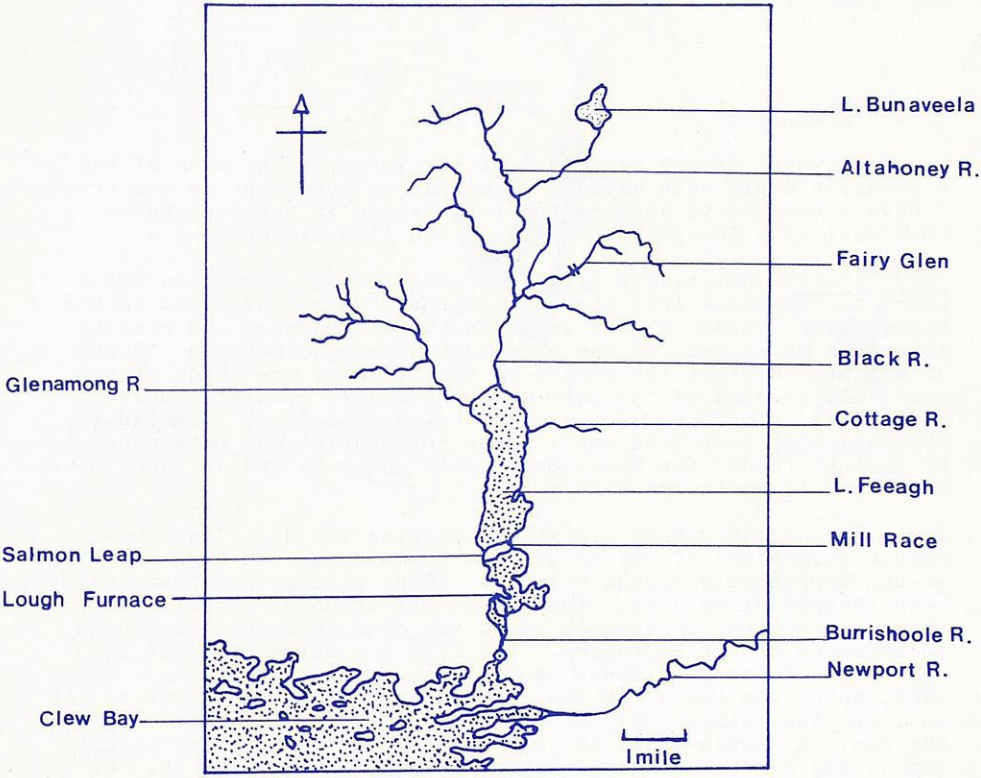
The Cottage River - above impassable falls

Resident (post smolt aged) trout from Lough Feeagh

Sea trout smolts migrating out of Lough Feeagh at the Salmon Leap

Sea trout angled from the Newport River

More than thirty loci were screened electrophoretically of which thirteen were variable. Statistical tests showed that the Fairy Glen and Cottage River fish were highly significantly different from one another and all other samples. A smaller, but significant difference ocurred at two loci between the sea trout smolts from the Burrishoole System and the sea trout from Newport River. In contrast, no differences were found between the resident trout in Lough Feeagh and the sea trout smolts migrating from it, indicating interbreeding between migrants and non-migrants. Relatively small populations isolated above falls might become distinct by both selection and genetic drift.



Burrishoole River System

In discussion, the broad differences between sea trout from West coast and East coast rivers in Scotland were noted. West coast fish tended to be longer lived and grow more slowly; while those from the East coast were larger, faster-growing and shorter lived. Sea trout from the Tweed, Northumbria and Yorkshire were believed to be particularly different. Ferguson (D) said that neither he nor his students had yet carried out any electrophoretic studies on trout from the East of Britain. Fahy (D, 1978) pointed out that similar differences existed between East coast and West coast Irish sea trout. He recognised four main types of fish on the basis of growth rate and length-weight relationship;sea trout from Welsh rivers differed from those from West coast Scottish and Irish rivers.

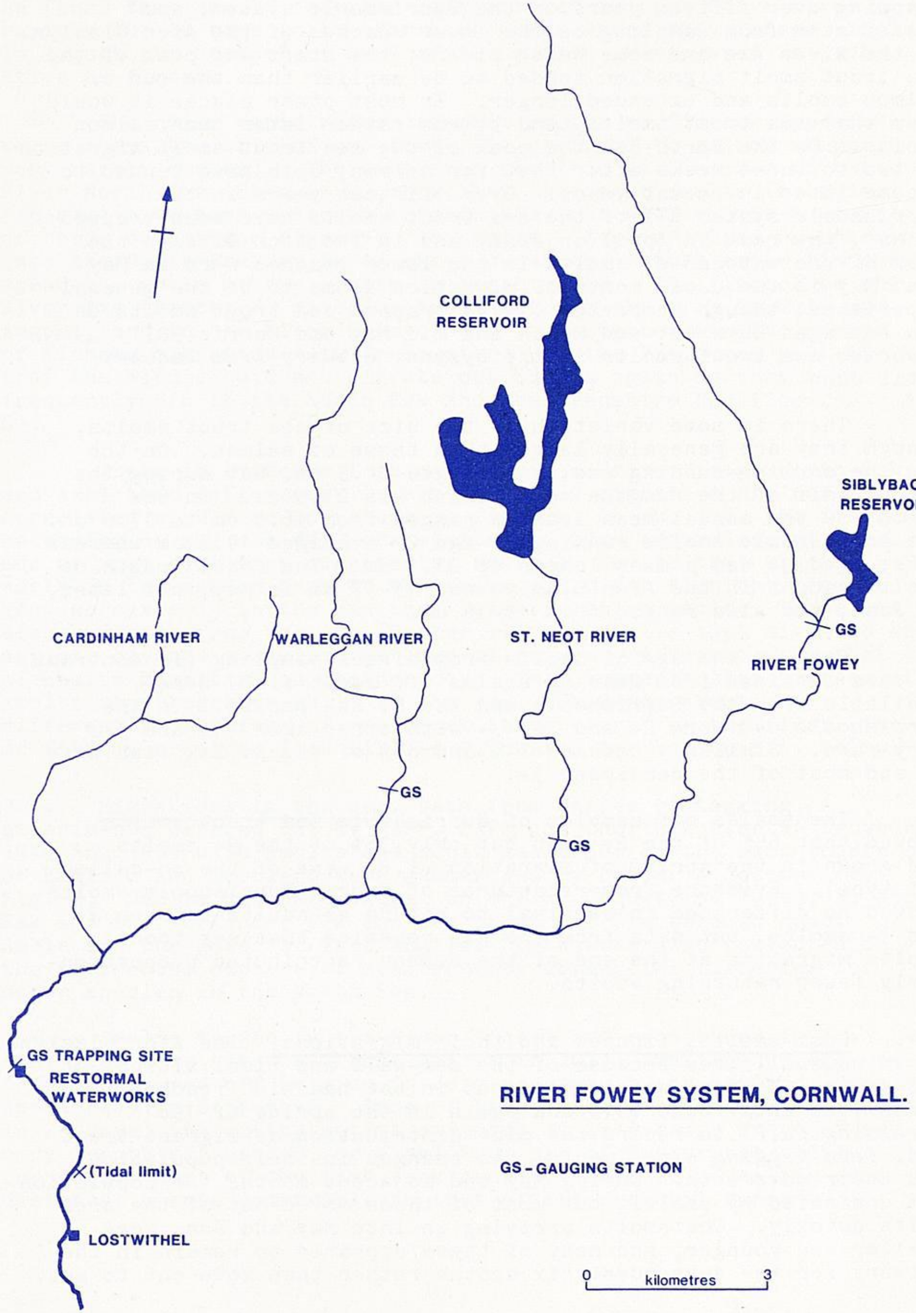
3. MIGRATIONS

Several papers presented at the Workshop and much of the discussion dealt with aspects of migratory behaviour in sea trout. I have attempted to arrange the information in sections below that deal with successive stages in the life history.

3.1. Parr. Relatively little information was presented about parr, but Sambrook (Pa) stated that the area at Colliford on the Fowey river system (Fig.2) was a sea trout spawning and rearing area from which many of the parr left when aged between 10 and 16 months. Most of the smolts in the R. Fowey are three or two years old so some of the parr must presumably complete their river life in reaches of the river below Colliford. Similar emigration of parr from small upper tributaries has been noted by Elliott (1985) for Black Brows Beck where 0+ and 1+ parr left the stream in the winter.

3.2. Pre-smolt autumn migration Piggins (P) described the autumn emigration of sea trout from Lough Feeagh to Lough Furnace in the Burrishoole system (Fig.1). Trout moving downstream have been trapped since 1969. The autumn migration of juveniles starts at the end of August, is at its peak in October and ends in December or early January. The fish are quite distinct in appearance from the silvery smolts that run in the spring. Up to 1980, about two thirds of the fish were 1+ in age and most of the rest 2+, but, since 1981, 0+ fish have comprised more than 50% of the run. A sample taken in 1980 showed mean lengths and weights for 1+ and 2+ fish respectively of 14.9cm & 36.6 g and 18.3 cm & 69.4 g. The numbers migrating have ranged from 1574 to 4171 and averaged 2672 over the fifteen year period. This average number is about 60% of the average number of smolts that ran in the spring over the same period, but evidence from mark-recaptures shows that the autumn migrants contribute a much smaller, though variable, proportion to the returning adults, on average about 10%.

Though the meeting produced no other data on autumn migrants it was generally agreed in discussion that autumn migration was a widespread phenomenon among sea trout. Migration into Loch Etive of trout 10-17 cm in length between September and November has been reported by Pemberton (1976)


COLLIFORD RESERVOIR
SIBLYBACK RESERVOIR
CARDINHAM RIVER
WARLEGGAN RIVER
ST. NEOT RIVER
GS
RIVER FOWEY
GS
GS
GS TRAPPING SITE
RESTORMAL WATERWORKS
RIVER FOWEY SYSTEM, CORNWALL.
(Tidal limit)
GS - GAUGING STATION
LOSTWITHEL
0 kilometres 3

3.3. Smolt migration. Information on smolt migration was provided from papers by Potter on the River Axe trap, Shearer on trapping and sampling on the River North Esk, Piggins from trapping over fifteen years on the Burrishoole system, and Brassington from sampling on the lower reaches of the Afon Glaslyn. On the River Axe and some Welsh rivers, the start and peak of the sea trout smolt migration tended to be earlier than the run of salmon smolts and extended longer. In most other places it would seem that sea trout smolts tend to run rather later than salmon smolts. On the North Esk the peak of the sea trout smolt migration is two to three weeks after that for salmon; both have tended to become later in recent years. Over fifteen years in the Burrishoole system 67% of the sea trout smolts have been trapped in May, the rest in April or June, and in the Afon Glaslyn the peak of the catches of smolts in the lower reaches were in May. That May is the usual month of migration seems to be the general experience, though Pemberton (1976) trapped sea trout smolts on the Lusragan Burn between March and mid-May and Harris (D) reported sea trout smolts in the Dysynni estuary from January until June.

There is some variation in the size of sea trout smolts, though they are generally larger than those of salmon. On the Axe the earlier-running smolts averaged 24.5 cm, but during the second half of the run the mean length was 21.5 cm. On the North Esk the annual mean lengths ranged from 16.6 cm to 17.5 cm. The Burrishoole smolts running at age 2+ averaged 19.3 cm whereas those aged 3+ had a mean length of 21.1 cm. The model length of smolts caught in the Afon Glaslyn was 15-17 cm in May, but later, in June, the size ranged from 10-16 cm.

Data on the age of smolts from direct sampling (in contrast to data obtained from reading scales off adult fish) were available from the Burrishoole and the N. Esk smolts. In the Burrishoole 64% were 2+ and 36% 3+ with other ages (1+ and 4+) very rare. Similarly between 71% and 85% of the N. Esk fish were 2+ and most of the remainder 3+.

The scales off samples of Burrishoole sea trout smolts showed that 65% of the 2+ fish but only 36% of the 3+ smolts had grown in the spring of migration (i.e. were of the so-called 'B' type). Evidence from recaptures of tagged Burrishoole smolts showed no difference in survival to return as adults between 2+ and 3+ smolts, but data from the Axe revealed that sea trout smolts migrating at the end of the season contributed proportionately fewer returning adults.

3.4. Post-smolts, finnock and their migrations. The Afon Glaslyn is an unusual river because of the sea-wall and tidal sluices at its mouth. Netting was carried out in the brackish reaches from March 1978 until June 1979 and again in the spring of 1981 (Brassington,P) to record the size distribution of migrant trout and, from tagging experiments, the changes in their populations and their movements. During May and adjacent months the population was dominated by smolts, but most of these moved out of the area quite quickly. The smolts arriving in late May and June were smaller and younger, and many of these appeared to remain in the estuary for the subsequent six months rather than move out to sea.

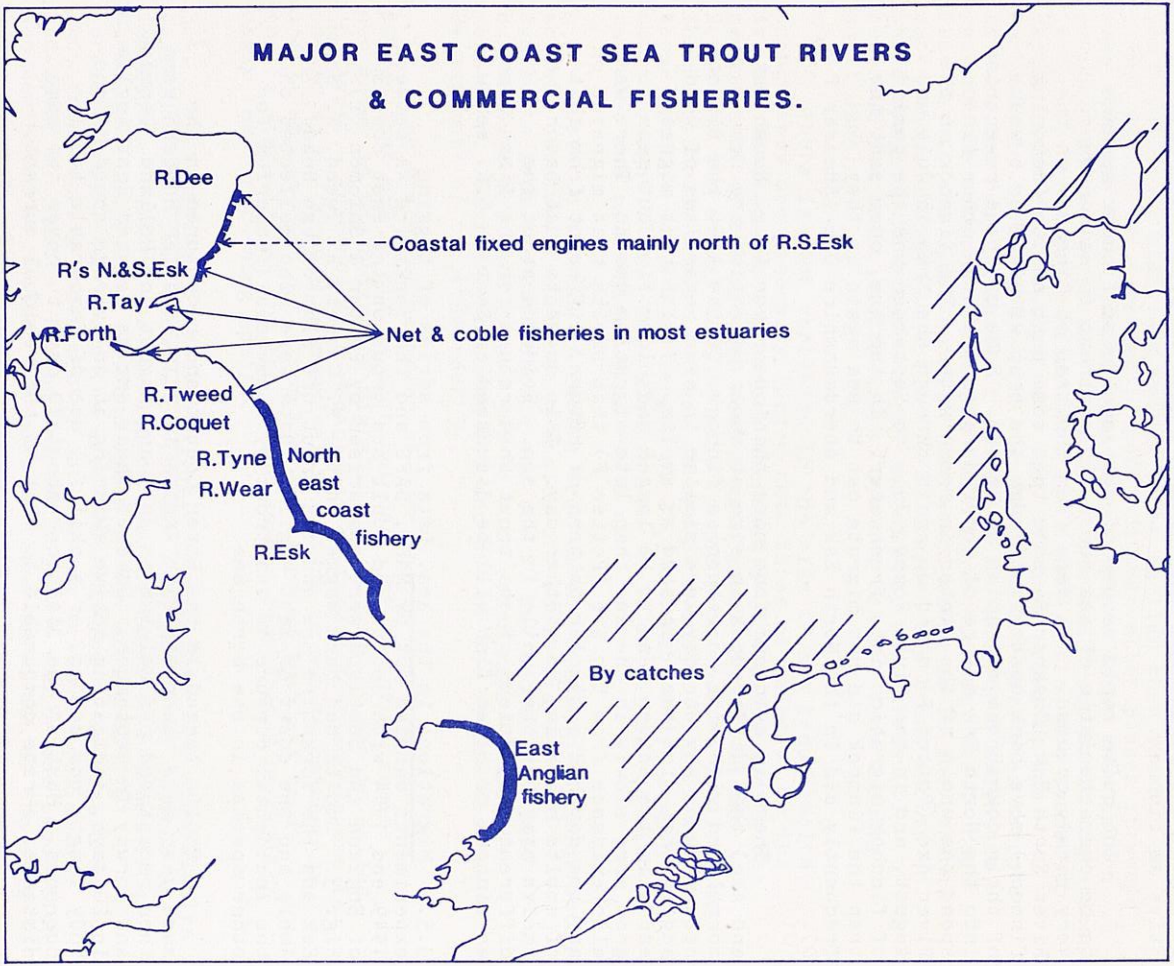
This rapid migration of smolts away from fresh and brackish water is paralleled by the studies of Henderson (1976) on sea trout in Loch Etive and neighbouring sea lochs in Argyll. He found that smolts that had just arrived in Loch Etive moved rapidly out to bays in the Firth of Lorne where they formed shoals. In August and September, many of these fish re-appeared in Loch Etive as finnock.

The quite rapid return of post smolts as finnock appears to be characteristic of sea trout (in contrast to salmon where it very rarely occurs). The data from the trap at Kinnabar on the River North Esk (Shearer P) show that some post smolts (becoming finnock) move back upstream through the trap within 5 or 6 weeks of their downstream migration as smolts. Some of these re-entries into the North Esk may be of short duration, though other finnock spend the whole of the winter in fresh water. The finnock on the River Axe (Potter P) moved up again through the trap in July and August, and in the River Fowey, July to September was the period of finnock migration into freshwater. In the Axe, once past the trap the finnock did not migrate out to sea again as they frequently did in the North Esk and Aberdeenshire Dee (Shearer P & D).

There is evidence from more than one river (e.g. North Esk and Axe) that differences in size at smolt migration are not correlated with size on return as finnock. On the Axe, the finnock returning on any one day were similar in size regardless of when and at what size they migrated as smolts. Smolts that migrate early in the season tend to be larger and older fish but seem to grow more slowly in the sea than late-migration smolts. There was also evidence from the Axe (Potter P) that smolts that migrated on any one day had a similar pattern of return, different from that of smolts migrating on another day. This suggests that batches of smolts stay together while in the sea. Evidence about the different proportions of sea trout that return for the first time as finnock or older fish will be discussed in Section 5.6. below.

3.5. Migrations in the sea. Data from series of tagging experiments carried out by MAFF, DAFS and the Yorkshire WA between 1949 and 1984 with smolts and adult sea trout on the east coasts of England and Scotland were summarised by Potter & Solomon (P) Fig. 3. Smolts had been tagged on the R. Coquet, R. Tweed, R. North Esk and the Yorkshire Esk and sea trout off Flamborough Head, Amble and the coast of East Anglia. Data were also collected on the incidental capture of sea trout by commercial fisheries for other species in the North Sea.

Smolts tagged in the River Coquet and recaptured in the same year were taken off East Anglia in July; smaller numbers were then recaptured off Belgium in July and August and Holland, Denmark and Norway in September. Some of these smolts reached East Anglia in 20 days, indicating active swimming at an average speed of one body length per second, or a skillful use of favourable tidal currents. Most of the fish took about 70 days to cover the same distance; a rate comparable to that of the residual current.



MAJOR EAST COAST SEA TROUT RIVERS & COMMERCIAL FISHERIES.

The smolts tagged in the R. Tweed showed a similar pattern of recaptures, while those tagged in the Yorkshire Esk were recaptured nearby in the Esk itself or off East Anglia. A year or more after tagging most of the recaptures were made in or near the river where the smolts had been tagged. Apart from two fish caught in the R. Tweed, none of the Coquet smolts were recaptured in any other river.

Of the sea trout kelts tagged in the Couquet most were recaptured in the same river but some off East Anglia or in the North Sea and a few in other nearby rivers such as the Tyne and Tweed. The sea trout tagged off East Anglia were recaptured locally soon afterwards, or in the following year off the north-east coast or in rivers between the Yorkshire Esk and the Tweed. Most of the fish tagged off Flamborough Head were recaptured further north, and, of those tagged at Amble, nearly half were recaptured nearby or in the Coquet and another large proportion in the R. Tweed. The captures of sea trout in marine fisheries may well be biased by mesh sizes towards larger fish but quite a few have been reported from various parts of the North Sea.

The general picture derived from all these different experiments, carried out over a period of thirty-five years, is of a movement of smolts from rivers between the Tweed and Yorkshire Esk south towards East Anglia and then in an anti-clockwise direction round the southern North Sea. On arriving back at the English east coast, the fish then move northwards up the coast towards their home river. A similar movement seems to be carried out by kelts, but with more variation and slightly less consistency of homing. It should also be noted that although the Tweed does have a small run of finnock, they are rare in Northumbrian rivers (Champion 'D'); very few sea trout tagged in north-east England were recaptured north of the Tweed.

Smolts and kelts tagged on the North Esk showed less distant movements. Many were recaptured in the North or South Esk rivers or on the coast nearby, some as finnock soon after tagging, but a few had travelled as far south as the Tweed or north as the Spey and three were recaptured in Scandinavia.

Recaptures of smolts and kelts tagged on the River Axe (Potter 'P') showed movement to both the east as far as the Hampshire Avon or west to the River Otter. Kelts were recaptured in and around several rivers in South Devon and Cornwall. Again, comparisons between the movements of fish of different ages and size-groups are complicated by mesh selection in the gears available for their recapture.

No other comparable sets of tag-recapture data were presented for other areas but it was reported that most of the recaptures of fish tagged in the Burrishoole were made in the same river system itself, or in inshore nets to the north or south. One fish was recaptured in Killary, another at Stranraer and a few in freshwater in other rivers. Of the 780 fish tagged on the Afon Glaslyn, only eight were recaptured after a period of sea-absence. Four of these in the Afon Glaslyn, the other four in rivers not far away. A few examples of recapture a long way from the place of tagging were cited; e.g.Burrishoole River to Stranraer, R. Axe to the Tweed, Dufi (Wales) to Fenit (western

Ireland) and North Esk to Lewis. As well as these there was apparently normal migration of Coquet fish round the North Sea to the Norwegian coast. Data on the food of sea trout in the sea and their parasite burdens can also provide indirect information on their movements (Fahy P). Stomach contents from sea trout caught in shallow inshore waters confirmed that most of them had been feeding in such waters.

3.6 Seasonal timing of migration into freshwater. Data were presented for migration past traps or counters near the foot of several rivers, though in not every case were these data quantitative or complete. Finnock, both maturing and immature, generally ran into freshwater later in the season than older sea trout, usually between July and September. The timing of the main runs of sea trout that had spent at least one winter in the sea varied from river to river. In the south-west of England it was early, starting in March with a peak in May in the R. Fowey (Solomon P) and in June in the R. Axe (Potter P), though in the latter river some fish ran in the autumn. In the Burrishoole River 60% of the entire run was in June and July (Piggins P). In Cumbrian rivers (Cragg-Hine P) the peak of the sea trout run was in July, that in the R. Kent beginning in May and continuing until September. The run in the R. North Esk similarly stretched from May to October (Shearer P). The considerable series of data from the trap on the R. Coquet (Champion P) showed small numbers in April and May, increasing through the summer to a marked peak in October followed by a decline to December , though there was considerable variation from year to year. If an arbitrary, but reasonable, adjustment were made for the effect of the fishery up to the end of September, the relative importance of the migration in July, August and September would be increased but October would still remain the peak month of migration in the Coquet.

3.7 Detailed upstream migratory behaviour. Milner (P) and Solomon (P) presented information from the analysis of data obtained from individual sea trout tagged, respectively, with acoustic tags (on the Afon Glaslyn) and radio tags (on the R. Fowey). The Afon Glaslyn estuary is unusual in having an outer shallow estuary, an inner deeper harbour area and, upstream of these, tidal doors. Tagged fish spent some time in the sea or outer estuary where they tended to move up and down with the tidal currents but then moved into the deeper saline layers of the inner estuary where they tended to hold their position. When they eventually moved out of the estuary and up into the river, they appeared to be responding to changes in salinity or temperature in the deeper water where they were resting caused by the increase in discharge of freshwater 1.5 - 3.5 hrs. after the opening of the tidal doors. There was some vacillation of the fish below a road bridge or the doors themselves; a similar hesitation was noticed at a road bridge over the Fowey (Solomon D). Once they had passed into the river, the sea trout moved upstream for distances of 4 - 8km within 1 - 10 days without any pause in the lower 4km of the semi-tidal zone. After this initial migration, however, the fish held-up for long periods (3-79 days, mean 47 days) near the confluences of tributaries.

While in the estuary, fish spent long periods holding their position or swimming very slowly. When they did move, their speed over the ground was 20-30 cm s^{-1} (approximately 0.3 - 0.5 body lengths per second; There were only short bursts of fast swimming (1 m s^{-1}).

In the experiments in the R. Fowey (Solomon 'P'), fish were tagged after being trapped at Restormel and then followed while they moved up river. At low and medium discharges, the fish moved at night, making about 3km each night. During or after a freshet they would move during daylight hours, but otherwise they spent the day lying-up under cover. In the Fowey, sea trout came into freshwater in early summer, and the tagged fish completed most of their upstream movement within two or three weeks; they then lay-up for the rest of the summer. While they were migrating the fish moved over the ground at speeds of up to 2km $hr.^{-1}$. Much of the movement was at a speed above that of the current of 0.5 body lengths per second; this is known to be an efficient rate of swimming in terms of energy use.

Information on up-stream migration was also available from resistivity counters on rivers in Cumbria: the Lune, Kent and Derwent (Cragg-Hine 'P'). These counters could record only larger sea trout and an arbitrary distinction,of approximately 4 lb (1.8kg) in weight, had to be made between sea trout and salmon. There was also the problem, when interpreting movement through a counter in relation to the stimulus for migration, of knowing the numbers of fish below the counter that are available to move; ideally, there should be pairs of counters one above the other on each river. Nevertheless, the data from these three counters showed that sea trout will move upstream under a wide range of flow conditions. On the R. Kent, 80% of the fish moved during discharges of 20-30% of the average daily flow (ADF) and similar results were obtained on the other rivers. Some response was shown to increases in flow, especially in the latter part of the season. While most movement took place at night, fish did move during the day when there was a freshet or the water was coloured.

These findings seemed to reflect those observed elsewhere and there was a general conclusion that while sea trout do respond to the stimulus of a freshet, they will move without such a stimulus and require much smaller discharges for up-stream migration than do salmon.

Data from the Findhu Burn in the upper reaches of the River Earn (Walker 'P'), show that spates are required for sea trout to reach this burn past falls and that during the dry summers of 1983 and 1984 their migration into the burn was delayed. The final migration of sea trout onto the spawning grounds appears typically to take place just before spawning, especially among the female fish, and to be in response to a freshet (General Discussion).

3.8. Homing The evidence for the homing of sea trout to spawn in the same river where they had been hatched is conflicting, and more data were presented by various contributors to this symposium. In the discussions it became clearer what kinds of data did provide unequivocal evidence for either homing or straying. The following points were noted:

a) Only fish tagged as parr or smolts in a river can be reliably identified as having been hatched in that river.

b) Only fish recaptured while actual spawning in a certain river can be reliably designated as having homed or strayed to that river; fish may move into a river and then out again. (Though capture in a ripe or freshly spent condition on or near spawning grounds is strong circumstantial evidence that the fish was about to spawn or had spawned in that river)

c) The proportion of marked fish recaptured in a certain place will depend not only on the presence of fish at that site but also on the intensity of fishing there. Fishing effort will vary from site to site, especially where there is a trap at one of the sites.

d) Captures of sea trout on the coast or in an estuary is not evidence that these fish were about to run up the nearest river.

Two papers that were contributed to the workshop provided evidence about marked fish recaptured on or near their spawning grounds. Sambrook (P) gave details of sea trout tagged as parr, smolts or adults in the St. Neot River. This river is a principal tributary of the River Fowey and its headwaters, at Colliford, were the site of a reservoir under construction (Fig.2). Juvenile trout, hatched and reared above Colliford, were batch marked as they moved downstream before becoming smolts, 0.3 - 3.5% of these were recaptured as ripening adults in the same stream. Smolts marked at Colliford were recaptured as adults at Colliford, with returns of 5.8 - 15.1%, and kelts tagged at Colliford have been recaptured at the same place in successive years. In 1981 and 1982 (while the reservoir was being built), all sea trout trapped at Colliford were moved to the headwaters of the main R. Fowey; several of these fish were recaptured at Colliford in subsequent years. Radio tags were also used to follow the behaviour of individual fish; some St. Neot River fish did swim past the junction at Two Water Foot, but later returned to go up the St. Neot. Only one fish was 'confused' enough to take the 'wrong' river and that was after it had been moved twice. Six of the sea trout that had been marked on the Fowey system were recaptured outside the river; five in coastal nets, only one in another, nearby, river.

Walker (P) tagged pre-smolts and adult sea trout in the Findhu Glen Burn (a tributary of the River Earn), but the results from adult fish were much more satisfactory than those from pre-smolts. Out of 759 adults tagged, to date there have been 110 recaptures. All but two of these have been in the R. Earn system or its common estuary with the R. Tay; the two exceptions were taken in coastal nets at Montrose and Amble respectively. Although there was no complete sampling of spawning fish, 68% of the recaptures were made in the Findhu Burn itself. In 1984, there were 40 recaptures in the burn from the 210 fish released in 1983 (19%), and these recaptures comprised 42% of the 92 previous spawners sampled. These data indicate a high accuracy of homing.

The returns from the smolts **tagged** in the R. Coquet and R. Tweed, which were described in section 3.5. above, showed a high accuracy of homing after extensive migrations round the North Sea. Kelts tagged in the Coquet and Tweed exhibited rather more straying, though recaptures in the 'wrong' rivers were made only in their lower reaches.

All these experiments, then, showed a high degree of accuracy in homing, not only to the correct river system, but to the correct tributary and even to a particular pool in that tributary.

In contrast, the extensive data from the tagging of smolts, finnock, adults and kelts in the River North Esk (Shearer P and Pratten & Shearer, 1983) show recaptures in the sea, estuaries and lower reaches of rivers along a considerable length of coast to the north and south.The data from smolts that were recaptured as finnock (very few of which were maturing) and recaptures of fish that were tagged as finnock show that it must be characteristic of finnock in the Scottish east coast to move in and out of estuaries and even up and down the lower parts of rivers during their first autumn and winter. It is also significant that some of the marked adults were recaptured in the same year in a river different from that in which they had been tagged; This shows that in some areas at least, adult sea trout can move up one river and then back to sea before they migrate up a river to spawn. A high proportion of the fish marked in the North Esk were recaptured in the South Esk; this suggests either that the sea trout in the two rivers form one inter-mixing stock or that the large estuary of the South Esk (the Montrose Basin) has particular attractions for 'visiting' sea trout from neighbouring rivers.

Quite a large proportion of the recaptures of sea trout tagged on the River Axe (Potter P) were made in other rivers - mostly those nearby on the Devon and Cornwall coast. Moreover, there was no evidence that sea trout that had moved up through the trap on the Axe ever moved downstream again before they had spawned.

Sea trout tagged as smolts on the Burrishoole system (Piggins P, Mills P) were mostly recaptured in the traps in the Burrishoole (Fig.1), but a few were caught in sea nets and a small number in rivers some distance away. The small, but significant, genetic distinction between sea trout in the Burrishoole and Newport Rivers (Cross P & D) suggests that straying must be rare, although at least one such instance has been recorded. The quite strong genetic distinctions found between the fish in some neighbouring Antrim and Down rivers (Ferguson P) would not have come about or persisted if there had not been very accurate homing among fish that actually spawned.

The general picture that emerges remains equivocal. There is no doubt that sea trout can return with remarkable accuracy to spawn in its home river and with remarkable precision to a particular reach within that river. In some rivers, at least, this appears to be the consistent behaviour. Nevertheless many marked fish have been recaptured in the lower reaches of the 'wrong' river, albeit usually one not far from their home river. Some of these fish, if not caught, might have gone to sea again and eventually have spawned in their home stream; the evidence is inconclusive. In too few cases have tagged fish been released again and rather rarely has effort been made to catch tagged fish on their spawning grounds. It does seem to be the normal behaviour for finnock, and perhaps some adults, to spend the winter moving into and out of the lower reaches and estuaries of rivers. Perhaps, if their home river does not have a suitable estuary in which to spend the winter they will move into another river (Walker, D)? The Coquet and Tweed sea trout seem to be able to find their home river after extensive migrations in the sea, but those few tagged sea trout which have been recaptured a long way from their home river may have lost their way in the sea. Perhaps we should regard homing as involving two processes(Mills, D): a) finding the correct home river after marine migration, and b) finding the correct spawning area once in the home river. The first may frequently involve some trial-and-error sampling of rivers while the fish moves along a coast, but the second seems to be carried out with great accuracy.

4. FOOD AND PARASITES OF THE SEA TROUT IN THE SEA

Relatively few studies have been made of the feeding of sea trout while they are in the sea, but Fahy (P and 1983 & 1985) presented a comparative study of the diet of two groups of sea trout.

The fish caught in the Irish Sea off the east coast of Ireland had fed principally on sand eels (mostly *Ammodytes marinus*), the worm *Euneries longissima*, and sprat (*Sprattus sprattus*) and a few other small species of fish. There was a correlation between the size of the fish and the size of the prey and changes in the intensity of feeding with the season; the older fish fed most heavily in May, the post-smolts later in the summer.

A contrasting sample of sea trout were netted in Mulroy Bay, a long narrow marine lough on the north coast of Ireland, connected to the Atlantic. The fish here did not have as full stomachs as the Irish Sea fish but neither did they have one period of intensive feeding. Their diet was more varied and, while small fish such as sand smelts, sand eels, sticklebacks, sprats and other species made up the heaviest portion of the food, invertebrates were also important. These included various crustaceans, polychaetes, molluscs and insects (including some blown off the land).

One of the few other recent studies of sea trout food is that of Pemberton (1976). He found that the food in the sea lochs in Argyll consisted mostly of small fish such as sand eels and crustacea.

Fahy also studied the parasites of the sea trout. The species found in the Irish Sea fish were *Eubothrium crassum*, *Thymnascaris adunca*, *Hemiurus communis*, *Lecithaster gibbosus* and *Derogenes varicus*. The fish in Mulroy Bay had a rather lighter load of parasites, including, as well as *Eubothrium*, *Lecithaster* and *Derogenes*; *Crespidostomum*, *Lecithochirium*, *hemiurus* and *Podocotyle*.

5. POPULATION DYNAMICS AND LIFE HISTORY

5.1. Sources, methods and problems in interpretation. A quantitative analysis of the population dynamics of a fish such as the sea trout requires data about the basic variables that are involved. These latter include: population numbers, survival (or loss) rates at the various life-history stages, growth rates, the proportions adopting each life-history option, sex ratios, fecundity, and, where there is a fishery, rates of exploitation, fishing effort and fishing mortality. In a species that has a complex life-history with many behavioural options which may be linked to sex, size, age etc. it is particularly difficult to obtain unbiased estimates of these important variables. This section discusses these problems, and new information or suggestions about them that were presented to the workshop. The data of later sections must be interpreted with these problems in mind.

5.1.1 Sampling. Where a trap has been operated in a river efficiently enough to catch the whole of a migrating population it is possible to obtain unbiased information about the population. (It is not necessary to sample the whole of the trap's catch if the sub-sampling is properly stratified with reference to time, size, age or sex groups). In practice it can be very difficult to operate traps in such a way; Piggins (P) described how the Burrishoole traps failed to retain the smaller finnock that were migrating upstream. However, the data from efficient traps can often highlight the biases that may occur in other forms of sampling. Potter (P) described the analysis of the returns from smolts tagged when leaving the Axe and returning as finnock or maiden fish. On the whole there was not much general trend in age at return or survival between smolts migrating at different times of the run, except that smolts migrating in the last week survived less well, as too did the smallest smolts among the early migrants. There was, however, some variation in the time and age of return between batches of smolts migrating on successive days. Among the data from the Burrishoole traps (Piggins P) the scale sample from the 1983 smolts showed a biased age distribution, probably due to chance sampling error. In all other years there did not seem to be differences between the survival rates or migratory behaviour of different samples of smolts.

Relatively few large samples of sea trout have been taken for sex ratio analysis, but it is clear that it is particularly difficult to sample for the estimation of sex ratios among mature fish of any species when behaviour is so often linked to sex. To take one example, samples of charr (Salvelinus alpinus) taken on the spawning beds suggested a 1:1 sex ratio until mark-recapture experiments showed that each male spent very much longer on the spawning beds than did females, who moved onto the spawning beds, spawned and then moved away again very soon. The within-season mark-recapture results were confirmed by between-season tagging and both showed that the adult sex ratios were really between 1:2 and 1:4 (males to females) (Le Cren & Kipling 1963).

5.1.2 Tagging and recapture. The biases that may be introduced into tagging experiments by differential survival, tag loss and effects of tags on behaviour are well known, but further examples were described. The data on smolts tagged in the Burrishoole River (Piggins P) showed that their survival was only about 1/4 to 1/3 that of untagged smolts, but that tagged smolts that did survive grew as well as untagged fish.

Walker (P) tagged both parr and adult sea trout in the Findhu Burn. At first he used 28 mm x 2 mm Floy tags but later used modified Carlin tags, with much greater success, though even then some fish lost their tags. (Tagged fish were marked as well with a Panjet so as to check tag losses). Parr were much less successfully tagged than were adults.

Other papers did not provide actual data on tag losses or any extra mortality caused by tagging; but there was an implication that the rates of return given by tagged fish (especially those tagged as parr or smolts) will be lower than the true rates. There was also a suggestion from Burrishoole data that tagged adults that were removed from the trap to be weighed and examined were less likely to be caught by anglers for about two months afterwards than the tagged fish that were passed through the trap without being handled.

5.1.3 Scale interpretation and identification as sea trout. Many of the classic investigations of sea trout biology (e.g.Nall 1930) were based largely on the examination of samples of scales obtained from commercial and sport fisheries. Quite apart from biases that may be introduced by selection by the method of capture (netting will not take a representative proportion of the smaller and younger fish (Shearer P) and angling may not catch a proper proportion of the larger fish (Piggins P)) the interpretation of the scales themselves may not always be accurate, especially in relation to spawning marks. Two contributions to the workshop dealt with this latter problem. Sambrook (Pb) had data on several individual sea trout that had been tagged and then recaptured just before or after spawning in more than one year; each time a sample of scales had been removed. These series of sclaes showed that it was easy to misinterpret spawning marks even when considerable experience had been gained from reading the scales off fish whose past spawning history was known.

O'Farrell (P) obtained samples of sea trout from the Erriff River system in 1983 and 1984 and compared the proportion of finnock maturing in 1983 obtained from an examination of their gonad/somatic indices in late summer with a) the proportion of 1+ sea winter fish caught in 1984 that had residual eggs in their abdominal cavities, and b) the proportion of the same fish that had spawning marks on their scales. The results showed that 8.1% of the female finnock had matured in 1983 and in 1984 5.5% of the 1 sea-winter fish had residual eggs but 28% showed 'spawning marks' on their scales. Among male fish the percentage of maturation in 1983 was 13.1% but 22.7% of the scales showed spawning marks.

These results were supported by implications in other papers (e.g. Walker P) and in discussion that the interpretation of spawning marks was difficult and could lead to inaccurate conclusions.

Scales are also used to identify trout that have been to sea and so to check the accuracy of distinctions made on appearance or other features between sea trout and brown trout. Fahy (D) reported that among Waterville trout 98% of the males on the redds had 'brown trout' colouring but scales showed that they had been to sea. Walker (P) used the presence of the larvae of the nematode Anasakis as well as scale-growth pattern as criteria for the fish having migrated to the sea; colour was difficult, but not impossible to use. Williamson (D) maintained that 'slob' trout (fish that had migrated to an estuary but no further) could be identified from their scales and from the presence of parasites unique to estuaries.

The use of records of migration and spawning on the scales of older mature fish for the estimation of the proportions of fish that first migrated or spawned first at particular ages will also be biased by differential survival rates between fish of the same age that do or do not spawn or migrate. The workshop did not discuss this problem nor those that may arise from attempting to 'back-calculate' the growth history of sea trout from their scales.

5.1.4 The analysis of population dynamics and life-tables. The fascination of the different migratory and spawning behaviours in sea trout (and salmon) has led many of those studying these fish to concentrate on the proportions that adopt each life-history strategy, rather than on the population dynamics of the overall life history. The classic method of tabulating and interpreting population data is by means of the 'life-table' where each cohort (or year-class or brood) of animals is traced through successive stages or ages, and data on its survival, sex-ratio, fecundity etc are entered. Even if groups within the cohort that adopt different behaviours are seperated, they should be summed for each year of age to show the overall 'progress' of the cohort and especially the total progeny resulting from its total reproductive effort. Where this has been done, interesting and valuable interpretations have been made.

5.2. Sex Ratios The idea that in the sea trout all, or a high proportion, of the females but none, or only a small proportion, of the males migrate to sea has been suggested for a long time. Several sets of data on sex ratios were provided at the workshop but only some of them were supported by a critical analysis or details of the sampling or estimating methods. The data, together with a few from recently published literature, are shown in Table 1. In this discussion (and Table 1) all ratios are expressed as the number of females (x) to each male; i.e. ♂ : ♀ or 1 : x.

The first conclusion to be drawn from the data is that stocks of trout differ in the way their sex-ratios change in relation to age and migratory behaviour. Where populations of trout are entirely non-migratory e.g. above impassable falls on the Afon Dyfi or Glyn River, the sex ratio in the whole population is approximately 1 : 1. In some other populations where all the fish appear to migrate (at least out of the headwaters where they spend the first two years as in Dale Park Beck), the sex ratio is 1 : 1 for both 1+ parr and for fish 3+ in total age. In a third type of population where part migrates and part does not, e.g. Findhu Burn and in Afon Dyfi and Glyn River below their falls, the migrants tend to be predominantly female and the non-migrants predominantly male.

Table 1. Data on sex ratio.

GROUP OF FISH	LOCATION	AUTHOR	No. in Sample	Sex ratio ♂ : ♀
MIGRATORY SEA TROUT				
1+ parr	Dale Park Beck	Elliott (1985)	278	1 : 1.02
pre-smolts	Findhu Burn	Walker (P)	42	1 : 1.47
autumn migrants	Argyll lochs	Pemberton (1976)	178	1 : 1.17
smolts	Dyfi	Harris (P)		c1 : 2
smolts	North Esk	Shearer (P)		1 : 2.17
post-smolts	Argyll lochs (d)	Pemberton (1976)	195	1 : 3.44
smolts & adults	Glyn River	Ferguson (P)		1 : 48
mature finnock	Findhu Burn	Walker (P)		c1 : 1
spawning finnock	Dale Park Beck (e)	Elliott (1985)	165	1 : 0.02
spawning finnock	Dyfi	Harris (P)		c1 : 1
population in sea	Mulroy Bay (g)	Fahy (P)	354	1 : 2.5
mature in sea	Argyll lochs	Pemberton (1976)	117	1 : 1.17
maiden spawners	Findhu Burn	Walker (P)		1 : 1.07 - 1.76
previous spawners	Findhu Burn	Walker (P)		1 : 1.76 - 4.10
spawners - 3+ total age	Dale Park Beck (e)	Elliott (1985)	217	1 : 0.92
spawners - at least 1 sea winter	Dale Park Beck (e)	Elliott (1985)	216	1 : 1.20
total spawners	Dale Park Beck (e)	Elliott (1985)	381	1 : 0.47
spawners - at least 1 sea winter	Dyfi	Harris (P)		1 : 3.3
total spawners	Dyfi	Harris (P)		1 : 1.9
spawners	Waterville	Fahy (D)		c1 : 2-3
large adults (commercial catch)	North Esk	Shearer (P)		c1 : 2.3

Table 1. (cont'd)

GROUP OF FISH	LOCATION	AUTHOR	No. in Sample	Sex ratio ♂ : ♀
NON-MIGRATORY TROUT				
parr (after smolt migration)	Findhu Burn	Walker (P)	54	1 : 0.32
	Above falls Dyfi	Harris (P)		c1 : 1
	Below falls Dyfi	Harris (P)		c1 : 0
spawning	Findhu Burn	Walker (P)		1 : almost 0
	Above falls Glyn River	Ferguson (P)		c1 : 1
	Below falls Glyn River	Ferguson (P)	284	1 : 0.02

Notes. a) The ratios are as quoted or have been calculated from quoted numbers c.

b) Some of the ratios may be subject to sampling bias.

c) Only in some cases were the numbers on which the ratios based given.

d) The post smolts from Argyll lochs showed a declining proportion of males with increasing smolt age (pemberton 1976).

e) Dale Park Beck includes some data for its tributary Black Brows Beck (Elliott 1985).

f) Several of the ratios are based on a combination of several samples e.g. from successive years.

g) The smallest size group had a sex ratio of 1 : 1; the proportion of females increased with size till the largest fish were all female.

Three other tendencies are present in several populations; a) Male smolts tend to migrate younger than female smolts b) male migrants tend to mature and return for their first spawning at a younger age than do females, and c) the survival rate between spawnings is lower for males than females so older age-groups tend to be predominantly female. These latter tendencies should really be studied by comparing the survival curves (or mortality rates) of the two sexes rather than just sex ratios. Similarly the overall sex-ratio of spawners may not be very meaningful, and some of the cited ratios among spawning fish may be subject to sampling bias. Fahy (D), for example, quoted the example of the sea trout in some Connemara rivers where males congregate on spawning grounds that were then 'visited' by females to spawn. Walker (P) said that in the Findhu Burn spawning migratory females were accompanied by non-migratory males but that there was nearly always a migratory male in attendance as well. The interpretation of these differences in migratory behaviour between the two sexes in relation to life-history strategies will be taken up in the Discussion section below.

5.3. Fecundity Three of the papers gave information on the fecundity of sea trout; two of them in the form of the regression formula:

$\log_{10}E = a + b \log_{10}L$, where E = number of eggs and L = fork length.

The data are summarised in Table 2, where the formula published by Elliott (1984a) on the number of eggs found in redds dug by fish of known size is also included. It will be seen (Table2) that the exponent (b) in the relationships is substantially less than 3, the exponent that would be expected if the fecundity were proportional to the weight of the fish. Piggins (P) points out that the eggs of finnock from the Burrishoole River have an average wet weight of about 110mg whereas the everage wet weight of an egg from a typical older fish is 167mg. These wet weights are not greatly different from those given by Elliott (1984a) for the smallest and largest of the spawners in Black Brows Beck. He shows that the wet and dry weights of eggs are closely correlated both with the numbers of eggs laid and with the size of the parent fish.

Table 2. The fecundity of sea trout: the variables in the regression formula

$\log_{10}E = a + b \log_{10}L$ (where E = no. eggs L = length)

River	a	b	S.E.b.	n	r	Author
Erriff 1983	0.7895	2.3875	0.2242	38	0.871	Fahy (P)
Erriff 1984	0.7720	2.3858	0.1723	38	0.917	Fahy (P)
Findhu Burn	-1.127	2.639	-	44	0.921	Walker (P)
Black Brows Beck	0.72	2.04	0.20	22	0.97	Elliott (1984)
		(egg size: finnock 9000 per litre, older fish 6000 per litre)				
Burrishoole	1190 to 1690 per kg of fish.					

O'Farrell (P) estimated the mean fedundity of spawners of different ages and also their relative abundance in the catch (and thus approximate relative abundance in the spawning population).

From these estimates he calculated the percentage contribution to egg deposition of each age-group. For 771 fish in the Erriff River for each sea-age this was 0 - 26.2%, 2 - 12.5% and 3 - 5.8%. He also points out that, as the 0 sea-age fish (finnock) lay smaller eggs that may not survive as well when parr (Bagenal 1969, Elliott 1984a), the contribution that finnock make to the next generation may be relatively smaller still than 26%. Walker (P) also noted that larger sea trout laid larger eggs and spawned earlier in the season than smaller fish, as was recorded by Elliott (1984a). Walker estimated the spawning populations in the Findhu Burn as about 950 fish and the total number of aggs laid as about one million.

5.4. Growth. Although the early studies of sea trout scales (e.g. Nall 1931) provided many data on the growth of sea trout, little more information was produced at this workshop. Information on the size of smolts was, however, included in some papers; the data summarised in Table 3. The evidence in this Table that it is the faster growing parr that smolt earlier was supported in discussion. Piggins (P) also presented data on growth in the sea; the mean lengths of Burrishoole fish on return to freshwater were: 0+ sea years - 28cm, 1+ sea years - 36.2cm and 2+ sea years 41.5cm. There was some evidence that kelts began to feed and grow while still in freshwater, but most of the sea growth of repeat spawners would have been made in the three months or so that the fish were in the sea.

Table 3. The growth of sea trout in freshwater.

River	Type of smolt	Mean length (cm) at end of 1st winter	2nd winter	3rd winter	Mean Length of Smolts
Burrishoole	2A	9.1	18.6	-	18.6
(Piggins P)	2B	7.4	16.1	-	19.5
	3A	6.2	14.6	21.5	21.5
	3B	5.6	12.8	19.5	20.8
North Esk (Shearer P)					16.6 - 17.5
Axe (Potter P)					21.5 (Earlysmolts 24.5)
Mulroy	2	8.19	20.37		-
(Fahy P)	3	5.83	13.08		-

No other data on the growth of sea trout in the sea were presented, but there was some information on the size of returning sea trout. Those caught in the Northumbrian fisheries, e.g. on or near the River Coquet (Champion P) seemed to be exceptional; the average weight was 3.8 - 4.8lb (1.72 - 2.18kg). The average weights for fish taken in the Morphie Dyke fishery on the North Esk were for successive months from April until August: 1.7, 2.0, 2.1, 2.3 and 2.8lb (0.77, 0.91, 0.95 and 1.04kg) (Shearer P). Fish caught in such fisheries are likely to have been subjected to some selection for size. The sea trout spawning in the Findhu Burn ranged in length from 28cm to 65cm (Walker P); the predominant 2.1+ age group were 42 - 44cm, and the 2.1+SM group 48 - 50cm; the males were, on average, slightly longer than the females.

5.5. Length-weight relationship. Fahy's paper presented a length-weight relationship for 96 fish caught in Mulroy Harbour:

$\log_{10}W = 2.9570 \log_{10}L - 1.9201$ (where W = weight in g, and L = length in cm.)

He compared this with the length-weight relationship of 114 sea trout from the Irish Sea (Fahy 1981):

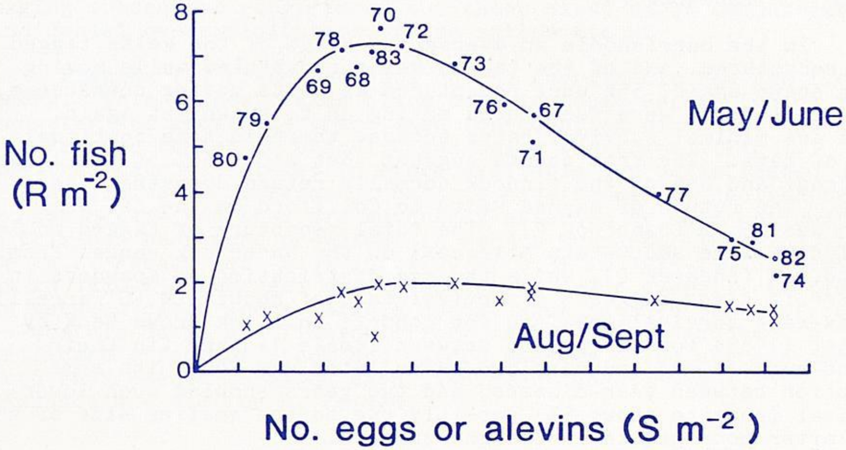
$\log_{10}W = 2.6070 \log L - 1.273$

The coefficients b were significantly different from one another and that for the Irish Sea fish was significantly different from 3. The Irish Sea fish thus weighed more at all likely lengths but were especially heavier among the shorter fish.

5.6. Survival rates. Relatively few data on survival rates were presented at the workshop, perhaps because most of the studies that were reported had not set out to answer demographic questions; or the data that had been accumulated so far had not yet been analysed for this purpose. However, Elliott (1984a,b & 1985) has recently published the results of eighteen years' observations on a population of migratory trout in Black Brows Beck in Cumbria that was aimed at determining the factors controlling population numbers. It is appropriate, then, to include here a very brief summary of his findings.

The study concentrated on quantitative estimates of the number of eggs laid and their subsequent survival through the alevin, fry and parr stages, and the eventual return to spawn of the survivors of each year-class (or 'cohort'). The numbers of eggs laid varied from year to year and survival in the egg and alevin stages was very high. (The beck has stable gravel and generally good conditions for survival in the young stages). Survival in the first spring was strongly negatively correlated with the density of eggs (and thus alevins and fry) and mortality in the first summer was also density dependent. Survival in the subsequent stages was higher and not correlated with density. The effects of several other factors, such as temperature and the presence of older trout and other species, were explored in the analysis but the only one, apart from initial population density, that showed any effect was drought; in three very dry summers survival (and growth) was reduced. The striking relationship between the numbers of eggs and the numbers of 0+ parr in May/early June is illustrated in Fig.4. Elliott also derived a simple predictive equation for total survival from eggs to 3+ female spawners that proved to work well except when parr survival was affected by severe summer drought. (Some of the implications of Elliott's findings will be discussed in a later section).

The investigation of the survival of the sea-trout in its migratory and marine stages is complicated by its flexible life-


8
6
4
2
0
No. fish
(R m-2)
70
72
78
83
69
68
73
79
76
67
80
71
77
81
75
82
74
May/June
Aug/Sept
No. eggs or alevins (S m-2)

history patterns and the problems in tagging mortality and tag loss and in sampling and trapping complete runs that were discussed in Section 5.1.2. above. However, some data on post-parr survival were presented to the workshop.

The Burrishoole River system (Fig.1), that has traps that can catch both upstream and downstream migrants, provided a series of good data on survival during some parts of the life history (Piggins P). No data were available from this or other rivers on survival from eggs to smolts (but see discussion of Elliott's papers above). The survival from smolt to return as finnock or older fish on the Burrishoole ranged, over 15 years, from 9.1 to 43.4% (when adjustments have been made for incomplete capture of finnock in the traps). Roughly comparable percentage returns from marked smolts to adults at Colliford on the St. Neot River (Sambrook P) were 5.8 - 15.1 for marked fish; these will be minimal estimates because of handling mortality and mark loss. On the River North Esk the percentage recapture as maiden fish of tagged smolts ranged from 1.3 to 6.2 (Shearer P).

In the Burrishoole an average of 40.5% of the kelts tagged were recaptured, and of the tagged kelts recaptured while moving up to spawn again, 55% were recaptured as kelts moving downstream, and 31% of these were recaptured moving up to spawn yet again. These are minimal survival rates because there is some continual loss of tags. The trap counts suggest that about 60% of the larger sea trout and 66% of the finnock normally return downstream as kelts. The return of marked kelts to Colliford on the St. Neot River was 25.7% (Sambrook P). The total recapture of tagged adults (including some short-term absences) on the North Esk ranged from 16% to 21% (Shearer P), while the age distribution of spawners in the Erriff River suggests a survival rate of about 12% (O'Farrell). The average survival obtained for cohorts in Black Brows Beck by Elliott (1985) for the period between female 1+ parr (in their second summer) and spawners two years later was 24%, with some variation between year-classes, and two years showing much lower survival (down to about 5%) possibly due to the smaller size of the fish after poor growth in drought summers.

5.7.Exploitation: Although often thought to have a role subsidiary to that of the salmon, the sea trout is subject to significant exploitation in many places. In all Welsh rivers except the Wye the sea trout fisheries are more valuable, especially for recreation, than those for the salmon, and this also applies in other parts of the British Isles. Three papers presented information about sea trout fisheries.

In Scotland, an annual catch of between 100 and 200 tons of sea trout is reported but this is certainly a gross underestimate of the real total catch. About 60% of this catch is made by net and cobble fisheries in estuaries, the rest is taken in coastal fixed engines and by rod and line. On the North Esk Shearer (P) suggested that the exploitation rate imposed by the entire net and coble fishery is about 30%.

One of the most substantial commercial sea trout fisheries is that on the Northumbrian coast, which has a reported catch ranging from 19,000 to 46,000 fish per annum; averaging over the past twenty years about 29,000. The average weight of the fish is between 3.8lb and 4.8lb (1.7 - 2.2kg); this means that the total catch will weigh about 55 tons. The main estuaries and nearby coasts contributing to this catch are those of the Coquet, Tyne, Wear and Aln but many of the fish have been reared in the Tweed (Champion P) (Fig 4). The trap on the River Coquet allows some comparison between the catch and the total upstream migration as all the migrants are normally counted. The total run averaged, over twenty-four years, 11,000 fish. Champion (P) postulated that perhaps a fifth of the total catch (i.e. an average of 4,800 fish) might have been destined for the Coquet, so the commercial fishery might be taking about 30% of the total run; but this exploitation rate is really a somewhat speculative estimate. The rod and line fishery in the river may take little more than 1% of the migration through the trap. Legal netting ends on 31st August, and a major part of the migration takes place in September, October and November. An extension of the commercial fishing season would increase the yield of the sea trout without necessarily damaging subsequent recruitment but there might be an undesireable coincidental overexploitation of the salmon stock.

Piggins (P) presented data on the Burrishoole rod and line fishery. This fishery takes place both in Lough Feeagh (which is freshwater and above the traps used for counting migrants) and also in L. Furnace (which is brackish and below the traps) (Fig 1). This means that catches related to stock available can be estimated only for the fishing in L. Feeagh. Catches have tended to decline over the past decade and they are adversely affected by calm hot weather, and this has been more prevalent in recent summers. The exploitation rate on L. Feeagh was 16.0% in 1970-74, 8.3% in 1975-79 and 6.6% in 6.6% in 1980-83. Whereas there appears to be no overall relationship between catch and available stock, when catches are analysed on a monthly basis and fishing effort is taken into account, a significant effect of stock and effort emerges. The average number of rod-days needed to catch each fish over 1980-83 was 1.3 for L. Furnace and 1.8 for L. Feeagh.

5.8 Enhancement: Mills et al (P) described experiments on the rearing of sea trout by the Salmon Research Trust of Ireland and attempts to enhance the stocks in the Burrishoole system. Sea trout were reared using techniques similar to those successfully developed for rearing salmon smolts, but survival rates for sea trout were much lower than those achieved for salmon; about 10% compared to 50% for the first year. The causes of this low survival appeared to be the quality of the available brood stock and thus eggs, problems in feeding in the early atages and susceptibility to disease.

Various batches of reared sea trout were marked or tagged and then released. There was some loss of tags but the number that were recaptured did provide information on behaviour and survival. Recapture rates tended to be lower than those of wild tagged fish and about half the reared sea trout did not seem to have migrated to sea. Total recapture rates have ranged from 0 to 7%. In spite of these problems,Mills (P & D) pointed out that very recent rearings showed improvements in survival and that, with further experience, sea trout might become a suitable fish for ranching. Though there had been a few reared fish recaptured some distance away from the Burrishoole, most had homed very accurately to the point of release. Further, the sea trout, being relatively small, was much less liable to capture by commercial nets in the sea.

Discussion on artificial rearing centred on the problems of migratory behaviour and what experiments might be appropriate to elucidate the factors controlling it, and why some fish behaved as sea trout but others as non-migratory 'brown' trout.

6. DISCUSSION AND CONCLUSIONS:

The workshop, and this Report, began with the question: 'What is a sea trout?' This question was not answered but was extensively explored and reviewed, and will be discussed here in relation to the selective advantages and disadvantages (in the evolutionary sense) of the various life-history options available to a fish like the trout. Aspects of these life-history options will be discussed in turn.

6.1. Homing: Though circumstancial evidence was presented that sea trout in some rivers or geographical areas may not always home, this evidence was not unequivocal, and the general conclusion must be that sea trout normally home with great accuracy. This is also the case with other migratory salmonids and is probably the case with many migratory species of fish. There is likely to be some advantage to a species if its adults can spawn in the place that proved suitable for their own survival when young, and this advantage may have led to the evolution of homing. Homing may be an advantageous and typical (though not absolutely essential) part of a migratory life history. It should also be noted that accurate homing will lead to the genetic isolation of stocks and thus their genetic differentiation. The mechanisms used by sea trout in homing were not discussed at the workshop, but presumably are similar to those currently postulated for salmon of various species.

6.2. Freshwater spawning and rearing: Though the freshwater reproduction of salmonids may be an inheritance from a distant evolutionary origin in freshwater, it is plausible to assume that there are advantages to the eggs and fry (and probably parr) stages in being reared in freshwater streams. While there may also be physiological gains, it is probable that small streams do provide an environment that is relatively safe from predators, and often a steady supply of drifting food. In the more favourable conditions, high rates of survival have been recorded for eggs and alevins, and most of the losses in the parr stage are due to density-dependent mortality (Elliott 1985, Le Cren 1973). Sea trout often but not always spawn in the upper reaches of river systems, where other species are relatively few in number and rates of predation can be small. The limiting factor is likely to be space, because the strong density-dependent mortality appears to act through territorial behaviour (Le Cren 1973). Physical factors such as droughts may cause parr mortality and reduce growth rate (Elliott 1985, 1984b). The population regulation that occurs in the early parr stage does so before the fish have made substantial demands upon their food supply and the evidence from Elliott (1984b) is that (except in droughts) growth in the first year is close to that shown by trout grown in the laboratory at similar temperatures that are given maximum food rations.

Several pieces of evidence show that sea trout often begin to move downstream before they smolt. There may be advantages in fish moving to rather larger streams as they increase in size (and, for example, require more space) but the discussion did not suggest any advantages in the 'pre-smolt' autumn migration to sea that occurs in some populations; this remains an enigma.

6.3. Advantages and disadvantages of migration: The workshop did not produce any detailed analyses of growth in the sea, but it is clear that trout that do migrate attain sizes much larger than those of fish that remain in headwater streams. The maximum length ('1_{00}') of the sea trout in the Burrishoole system and the Findhu Burn is about 70cm, while the (1_{00}) of non-migratory trout in the same streams must be much less that half that. There appears to be no evidence to show why sea trout grow faster in the sea, but an approximate 'Walford/Ford' plot of the data from the Burrishoole suggests that migration allows the continuation of the growth pattern begun in the parr stage rather than any acceleration in annual growth. Residence in freshwater would have restricted and slowed down early growth. (I am not aware of any study that compares the food-temperature-growth relationships of salmonids in sea water with those in fresh water).

It is clear that the great increase in the size of the mature female resulting from migration does allow a much greater fecundity, a larger egg size and an earlier spawning (Elliott 1984a). The data given in Table 2 and by Elliott (1984a) for the exponent b in the formulae relating fecundity and egg size to length suggest that about two thirds of the increase in female size results in an increase in egg numbers and about one third in an increase in egg weight. Fry derived from larger eggs have a greater chance of surviving starvation; it would be interesting to know if they have any advantage over their smaller brethren in competition for territories.

The workshop produced some data on survival in the marine phase, though the tag-recapture data need careful analysis if unbiased quantitative estimates are to be derived from them. The results from the Burrishoole River suggest that, under good conditions, there will be an annual survival rate of about 40%. The maximum may be rather less in some other rivers, but more good data are needed. The sea trout, unlike the Atlantic Salmon, has a high survival after spawning; up to 60% to the return to the sea as kelts and 40% to a further spawning. Repeat spawning has obvious advantages for stock survival where the eggs and juveniles live in habitats where events such as floods or droughts may now and then cause high mortalities to a year-class.

It might be advantageous to the management and culture of both sea trout and salmon to study the physiology of smoltification, migration, spawning and post-spawning recovery in sea trout to find out why the sea trout survives these events better than does the salmon.

Migration may, nevertheless, impose additional hazards on the trout. The workshop did not provide comparative data from similar, but resident, populations of trout, e.g. those in streams above waterfalls in the same river systems; we need data from which the whole life-tables of migratory and resident populations could be compared. Trout above impassable falls have adapted and evolved into resident populations, which while small in individual size can be considered as 'successful' in terms of population numbers. Obviously such populations must have lost virtually all the urge to migrate to have persisted and survived.

6.4. Sexual differences in migratory behaviour: It is clear that it is a feature of sea trout that, while in some stocks most or perhaps all of the males migrate, in other stocks most or all of the males stay in the river. In the latter stocks there is good evidence that small mature resident males successfully fertilize the eggs of large migratory females. (Just as precocious male salmon parr can fertilize the eggs of large female salmon (Jones and King 1952)). Thus there appears to be no essential need for male sea trout to migrate and, if the survival of residents is greater than that of migrants, there may well be an advantage in a system where the females migrate but the males do not. Hence a possible explanation of why, in some rivers, sea trout have evolved this practice.

There is also a tendency for males to return to spawn when younger than females, more finnock are males than females; this too could arise by selection. There does not appear to be any evidence on the relative chances of small or large males fertilizing eggs on the redd when in competition with one another; O'Farrell (D) said that spawning sea trout females could be seen each surrounded by several males. More research is needed that will provide good comparative data on the survivorships of migratory and non-migratory males and females under similar conditions that will determine the chances of each leaving progeny.

6.5. Life-history options: The ages of smoltification, migration and return to spawn also provide the sea trout with life-history options. In most of the rivers for which data were provided, nearly all the smolts were either two or three years old; the proportions varied from river to river and sometimes had changed over recent decades.The age at first return also varied; in some rivers many fish, especially males, returned as finnock, in others finnock were rare. Other things being equal, there is a long-term demographic advantage in a fish spawning when as young as possible, but this can be counter balanced by the ability to lay more and larger eggs with increasing age and size. Again, more unbiased data are needed that can provide comparative life-tables for fish under similar conditions but following different life-history options.

6.6. Options in migratory behaviour: Little is known about the extent and paths of migration in the sea for trout from many river systems. The sea trout of the Northumbrian Rivers and the River Tweed appear to be unusual in the extent of their migration round the southern North Sea, the virtual absence (except in the

Tweed) of finnock, and their large size. Individual tagged fish from some other rivers have been recaptured at distant sites but these may have strayed rather than been following a normal lengthy migration. In the North Esk and neighbouring rivers, a good many sea trout appear to spend much of their time moving into and out of estuaries and the lower reaches of rivers. West coast Scottish and Irish Sea trout also seem to spend time in sea lochs and may not go far into the open sea.

It must also be remembered that most brown trout also migrate to varying distances downstream or, often, into lakes before returning upstream to spawn. The so-called 'slob' trout migrate into estuaries but it is claimed, not to the sea; they can evidently occur in the same rivers as genuine sea trout. Indeed, trout that spend their whole life within a hundred metres or so of stream are probably rare.

The evidence, from the Burrishoole (and elsewhere) that some of the artificially-reared progeny of genuine sea trout do not migrate to sea but behave like brown trout, and the apparent lack of electrophoretic characters to seperate the sea and brown trout of Lough Feeagh, do suggest that, at least in some rivers, there is no genetic difference between sea-running and freshwater forms of Salmo trutta. Indeed, Harris (Pb) suggested that the trout could be regarded as a 'composite species'.

Perhaps the 'trout' possesses a genetic make up that gives it an ability to 'adopt' the life-history and behavioural options that will best be to its advantage in one of a wide range of different stream and marine environmental systems. Further research into the genetics of sea trout, and into the environmental triggers and physiological mechanisms through which they operate, may eventually lead to a better understanding of why and how a particular sea trout chooses the migratory and life-history option it does.

Meanwhile it is perhaps convenient to label trout that carry out a distinct and deliberate migration to the sea 'sea trout', and those that remain in freshwater 'brown trout'. At the same time we might recognise that these forms may interbreed and are really the two major parts of a continuous spectrum of migratory behaviour within one species with an ancestral migratory origin.

6.7. Sea trout fisheries: conservation and management: The sea trout has several desirable traits as a target species for both commercial and sport fisheries (Harris Pa). However, the management and development of these fisheries is often complicated by the fact that they are closely associated with more valuable fisheries for Atlantic salmon. The salmon is larger in size, has a higher market value for food, and most (but not all) anglers will pay more to fish it than they will for sea trout. The two species are unlikely to compete while in the sea, but their preferred habitats in the parr stage do overlap. Sea trout tend to spawn in smaller streams upstream of salmon and their parr tend to occur in smaller, slower flowing streams or nearer the banks of larger rivers than do salmon, but the two species frequently occur together. A given area of water will probably produce more salmon smolts in the absence of trout than in their presence, but the combined production of the two species will often be greater than that of either alone.

In some important sea trout fisheries, extension of the legal season into autumn would enhance the catch without necessarily endangering recruitment, but care would have to be taken not to increase the exploitation of salmon to a dangerous level. A more balanced exploitation of both species over the whole season might well be a desirable objective provided an adequate escapement of all sections of the stocks of both species could be assured.

The 'stock-recruitment curve' for the sea trout (Elliott 1985 andFig.4) shows that the strong density-dependent mortality in the fry and early parr stages will compensate for a considerable fishing mortality in the adult stage. In the Black Brows Beck stock the maximum number of recruits is produced from about 75% of the 'equilibrium' numbers of spawners, while the number of spawners would have to fall to below 40% of the equilibrium number before, on average, recruitment will be less (Elliott 1985). In other words the escapement could, in theory, be as low as 40% of the run, leaving 60% for the fishery. However, exploitation of sea trout should be managed to allow some repeat spawning and a multi-aged spawning stock, so that a catastrophe in a particular spawning or rearing season would not lead to more than a temporary severe reduction in the stock. Stock-recruitment curves like that for Black Brows Beck are also needed for other, different rivers.

As sea trout populations appear to be regulated in the early parr stage, conservation of the headstream environment is clearly important for the wellbeing of the stocks. Catchment land and water use that will reduce variations in stream flow - especially droughts and, in larger streams, floods - will almost certainly be beneficial. Access for adults to spawning streams under a range of discharges is also important; sea trout do not occur upstream of impassable falls.

Attempts to rear and ranch sea trout have had limited success so far, yet brown trout have been cultured for many years, so it would seem that further research on the choice of brood stock and the details of rearing practice should soon lead to sea trout being reared as successfully as salmon. Whether the reared progeny will all migrate to sea remains uncertain; success with this may have to await better understanding of the factors controlling migration in sea trout. The market value of sea trout as food is less than that of salmon, so it may not prove profitable to farm sea trout unless there are changes in the success and economics of its culture; but if smolts can be reared cheaply ranching might become profitable.

6.8. Potentials and needs for research: The fact that the workshop raised more questions than it answered is an indication not only of the need for further research on the sea trout, but also of its fascination as a subject for study. The flexibility of its life history and the various options that sea trout can exhibit, often within one river system, make it an ideal species with which to investigate various fundamental problems in genetics, behaviour, physiology, population dynamics and evolutionary mechanisms.

Much early research on sea trout was based on a skilful but somewhat subjective interpretation of scales for age, growth, migration and spawning. The advent of microtags and other (including genetic) methods of marking should enable a rigorous re-interpretation of the techniques and accuracy of scale reading. Attempts should also be made to explore the bias involved in 'back-calculating' past migratory and spawning behaviour from scales from only the older survivors of year-classes. Such checks might enable useful re-interpretation of some of the early research and also provide evidence of any long-term changes in life history patterns that may be taking place.

Modern methods of trapping, counting, quantitative sampling by electro-fishing and tagging should make it possible to obtain accurate estimates of the parameters needed to construct life-tables and models of the sea trout's population dynamics. A comparative study of the population dynamics of the principal life history varients, and those of males and females might do much to illuminate the reasons why particular life-history options dominate in different river systems and why changes in the balance between different options may be occurring with time.

Studies using electrophoresis have revealed remarkable genetic differences between the stocks of sea trout in different rivers and between resident and migratory populations in the same river system. The possibility of even more sensitive genetic typing (e.g. by using DNA 'fingerprinting') should open up even greater potential for such research. There is an immediate need to explore the genetics of further stocks, for example the rather different sea trout of the Northumbrian rivers and the generally faster-growing and longer-living sewin of Wales. The extent to which migration is genetically controlled meeds research,both for its fundamental interest and as an aid to the development of culture and ranching. The environmental stimuli and physiological mechanisms operating in such events as smoltification, migration, osmoregulation, maturation, spawning and post-spawning recovery should be explored.

The economic value of the sea trout, especially for commercial fisheries, is often less than that of the salmon, yet many of the research facilities, such as counters, traps and hatcheries, can be used for sea trout as well as salmon at very little extra cost - as the workshop demonstrated. Moreover, the comparative approach is a powerful tool in biological research, and much might be learnt by comparing the biology of these two species that are closely related, have basically similar life histories and yet differ in significant details. Advantage might also be taken to use the sea trout in studies of some of the many aspects of salmonid biology that are common to all species.

The results from research at such sites as the Burrishoole, North Esk and Black Brows Beck are excellent examples of the value, indeed the necessity, of patient long-term research coupled with the careful analysis and interpretation of good long-term data. Problems in the population ecology of fish cannot be solved by only short-term ad hoc research projects - useful though these may also be. It is clear that there is a need for more research directed primarily towards the management and development of sea trout fisheries. Moreover, the relevance of such research to the salmon and to fishery biology in general, and the unusual opportunities the species offers are good justifications for the further development of research on the sea trout.

I see particularly exciting potential in the use of new techniques and approaches in the three main fields of genetics, physiology and population dynamics in combination directed towards a better understanding of the basic factors controlling the life of the sea trout in relation to its environment and management.

6.9. Concluding remarks: The problems involved in the management and development of sea trout fisheries and the potential that this species offers for both food and sport were discussed at the workshop but the practical steps needed for such fishery development were not specifically addressed. To do so would have involved much more consideration of the interactions between sea trout and salmon fisheries (and their biologies) and would also have needed input on the economic, social and legal aspects of fishery management. The workshop was primarily aimed (and rightly so) towards an exchange of up-to-date information and ideas between those involved in research in the sea trout and to provide, for them, an informal review of the current status of knowledge on the species. The workshop was successful in this aim and there is no doubt that it stimulated its participants; I hope that this report may provide an adequate written summary of this success. Research on sea trout biology clearly could be at the brink of exciting advances that promise both to aid the development of salmonid fisheries and illuminate aspects of fundamental science.

7. CONTRIBUTED PAPERS:

Brassington, R.A.	Movement patterns of migratory trout in the lower Glaslyn estuary.
Champion, A.S.	Sea trout off the North-east coast of England.
Cragg-Hine, D.	Upstream migration of sea trout past five counters in relation to river flow and other environmental variables.
Cross, T.F.	An intensive electrophoretic survey of brown trout and sea trout in western Ireland.
Fahy, E.	Marine feeding of Irish sea trout.
Ferguson, A.	Electrophoretic studies of brown trout - sea trout inter-relationships.
Harris, G.S.	(a) Introduction
Harris, G.S.	(b) Paedogenesis in sea trout: some theories.
Mills, C.P.R., Quigley, D.T. & Cross, T.F.	Rearing and ranching of sea trout in the Burrishoole River system.
Milner, N.	Tracking adult sea trout movements in selected Welsh rivers.
O'Farrell, M.	Erriff sea trout: post smolt maturity and their contribution to egg deposition.
Piggins, D.J.	Sea trout in the Burrishoole system.
Potter, E.	Movements of sea trout from the River Axe.
Potter, E. & Solomon, D.	Movements of sea trout in the central and southern North Sea.
Sambrook, H.	(a) Homing specificity among sea trout of the River Fowey system.
Sambrook, H.	(b) Validation of scale reading using recaptured sea trout.
Shearer, W.M.	Sea trout studies in the North Esk.
Solomon, D.& Sambrook, H.	Observations on the upstream movements of sea trout by radio tracking.
Walker, A.F.	The trout of the Findhu Glen Burn (Tayside)

8. REFERENCES CITED:

Bagenal, T.B. 1969. Relationship between egg size and fry survival in brown trout Salmo trutta L. J. Fish Biol. 1, 349-353

Elliott, J.M. 1984a Numerical changes and population regulation in young migratory trout Salmo trutta in a Lake District stream, 1966-83. J. Anim. Ecol. 53, 327-350

Elliott, J.M. 1984b. Growth, size, biomass and production of young migratory trout Salmo trutta in a Lake District stream, 1966-83. J. Anim. Ecol. 53, 979-994

Elliott, J.M. 1985 Population regulation for different life stages of migratory trout Salmo trutta in a Lake District stream, 1966-83. J. Anim Ecol. 54, 617-638

Fahy, E. 1978 Variation in some biological characteristics of British sea trout, Salmo trutta L. J. Fish Biol. 13, 123-138

Fahy, E. 1983 Food and gut parasite burden of migratory trout Salmo trutta L. in the sea. Irish Nat. J. 21, 1-52

Fahy, E. 1985 Feeding, growth and parasites of trout Salmo trutta L. from Mulroy Bay, an Irish sea lough. (In press).

Jones, J.W. & King, G.M. 1952 The spawning of the male salmon parr (Salmo salar Linn. Juv.) Proc. zool. Soc. Lond. 122, 615-619.

Le Cren, E.D. 1973 The population dynamics of young trout (Salmo trutta) in relation to density and territorial behaviour. Rapp. et Proces-Verb. Cons. Verb. Cons. int. Explor. Mer. 164, 241-246.

Le Cren, E.D. & Kipling, C. 1973 Some marking experiments on spawning populations of char. Int. Comm. N.W. Atlantic Fish., Special Pub. No.4, 130-139.

Nall, G.H. 1930 The life of the sea trout especially in Scottish waters with chapters on the reading and measuring of scales. London: Seeley, Service & Co. 335pp.

Pemberton, R. 1976a Sea trout in North Argyll sea lochs, population, distribution and movements. J. Fish Biol. 9, 157-179

Pemberton, R. 1976b Sea trout in North Argyll sea lochs: II diet. J. Fish Biol. 9, 195-208

Pratten, D.J. & Shearer, W.M. 1983. Sea trout of the North Esk. Fish. Mgmt. 14, 49-65

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E. D. Le Cren -- Biographical note

E. David Le Cren took a degree in natural sciences at Cambridge and then, after a year at the University of Wisconsin, spent nearly all his career with the Freshwater Biological Association. For the first few years he studied the perch in Windermere and played the major part in the early stages of an experiment and study in fish populations that has now gone on for forty-five years. He then turned his attention to the trout populations of small streams in Cumbria and demonstrated the importance of territorial behaviour in young parr in the natural regulation of their population numbers. When he went to Dorset for ten years to set up and become the first Officer-in-Charge of the FBA's River Laboratory, he initiated the studies there on trout, salmon parr and other species in small chalk streams. In 1973 he returned to Windermere to become Director of the FBA until his retirement in 1983. The author of over thirty scientific papers on the biology of fish, Mr. Le Cren is a Fellow of the Institute of Biology and Institute of Fisheries Management, and was recently, for five years, President of the Fisheries Society of the British Isles.

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