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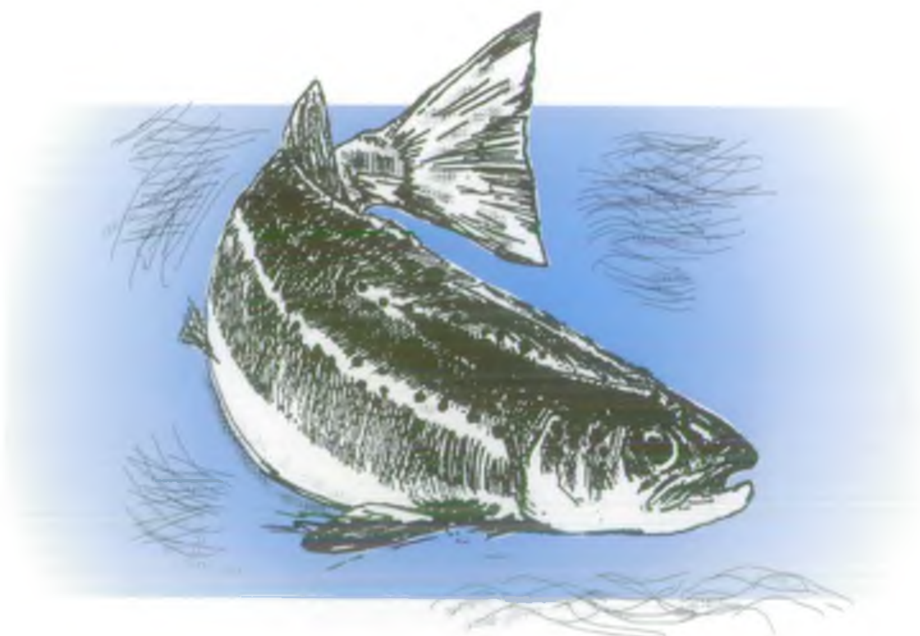
SEA TROUT
LITERATURE REVIEW



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Tele: 0454 624400
Fax: 0454 624409

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FISHERIES TECHNICAL REPORT NO.3

SEA TROUT LITERATURE REVIEW AND BIBLIOGRAPHY

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J M Elliott, D T Crisp, R H K Mann,
I Pettman, A D Pickering, T G Pottinger
and I J Winfield
Institute of Freshwater Ecology
Windermere Laboratory

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SUMMARY

The chief objective was to provide a bibliography and review of the literature on sea-trout, *Salmo trutta* L. The review covers the literature originating from England, Wales, Scotland, Ireland, France and Scandinavia (including Denmark).

There are four expert reviews: the early life stages (spawning, eggs, emerging fry), ecology of the juveniles in fresh water (growth, feeding, population dynamics, smoltification), ecology of the adults (marine/coastal stages, anadromous migration), and physiology (including smoltification) and diseases. The last review also includes a brief account of genetics and taxonomy. All four expert reviews are based on key papers, rather than all publications in the bibliography.

The comprehensive bibliography includes references from 1866 to March 1991. Titles of papers, where possible, have been given in English, but the principal language of the paper is also given where it differs from English. All journal titles have been abbreviated in compliance with the World List of Scientific Periodicals. The major sources for the bibliography were Aquatic Sciences and Fisheries Abstracts, British Books in Print, Biological Abstracts, Zoological Record and the extensive library of the Freshwater Biological Association.

The report includes a general overview that highlights the main points from each of the four expert reviews, identifies areas in which information is scarce and summarises priorities for future research. It is emphasized that long-term studies of sea-trout populations provide essential background data for the interpretation of short-term fluctuations and trends. Suggestions for further work are presented as twelve projects arranged in an approximate order of priority that is chiefly determined by need and cost. Although this order will change according to future developments and personal preferences, the twelve topics will probably remain as succinct summaries of research requirements in the immediate future.

KEY WORDS

Salmo trutta, sea-trout, salmonid life-history, salmonid physiology, research requirements, bibliography.

1. GENERAL INTRODUCTION

1.1 Objectives

The purpose of this report is to provide a bibliography and review of the literature on sea-trout. The review covers the literature originating from England, Wales, Scotland, Ireland, France and Scandinavia (including Denmark). There are four expert reviews:- the early life stages (spawning, eggs, emerging fry), ecology of the juveniles in fresh water (growth, feeding, population dynamics, smoltification), ecology of the adults (marine/coastal stages, anadromous migration), and physiology (including smoltification) and diseases. The last review also includes a brief account of genetics and taxonomy. These expert reviews are based on key papers, rather than all publications listed in the bibliography. Finally, a general overview highlights the main points from each review, identifies areas in which information is scarce and summarises priorities for future research.

1.2 Polymorphism in Brown Trout

The brown trout is a polymorphic species that has been classified in the past under several different Latin names because of its morphological, physiological and ecological variation. Some workers still recognize two sub-species to separate trout that migrate to sea (*Salmo trutta trutta*) from those that do not (*S. trutta fario*). Such a distinction is of doubtful value because, in some populations, eggs of female sea-trout are fertilized by sperm from smaller male resident trout that have never left their native stream. It is therefore more logical to assume that there is only one species of brown trout, namely *Salmo trutta* L.

For this reason, the bibliography includes references to work on brown trout, rather than exclusively sea-trout, because it was often impossible to separate the latter from migratory trout, lake trout or resident trout. Similarly, the expert reviews frequently refer to work on brown trout, rather than sea-trout, but a distinction has been made whenever possible.

Until relatively recently, the prevalent view was that sea-trout and resident trout were freely interbreeding fractions of a single spawning stock (e.g. Frost and Brown, 1967; Mills, 1971; Solomon, 1982a). Evidence is now accumulating that there are sympatric, reproductively-isolated, populations which qualify at least as races or perhaps sub-species. Support for this conclusion is provided by biochemical genetic information from several regions, e.g. France (Krieg and Guyomard, 1983), Russia (Osinov, 1984), Scandinavia (Allendorf et al., 1976; Allendorf et al., 1977; Ryman et al., 1979; Ryman and Stahl, 1981; Jonsson, 1982; Skaala and Naevdal, 1989), Ireland (Taggart et al., 1981; Ferguson and Mason, 1981; Crozier and Ferguson, 1986; Cawdery and Ferguson, 1988; Cross, 1988; Ferguson, 1989).

Ecological differences between brown trout populations, often within the same catchment, also provide strong support for genotypic differences between stocks (numerous examples are provided in the expert reviews). It has even been suggested that there are distinct races of sea-trout. For example, there appears to be at least two races in the British Isles, one corresponding with rivers flowing into the Irish Sea and the other with rivers entering the Atlantic Ocean (Fahy, 1978a; Fahy and Warren, 1984).

1.3 Sea-Trout Fisheries in England and Wales

Sea-trout must rank second to Atlantic salmon (*Salmo salar* L.) in a list of economically-important freshwater fish species in the British Isles. A summation of commercial and rod catches of sea-trout in England and Wales provided a mean annual catch of 110,547 fish, and the minimum saleable value of these fisheries is £55 million (Elliott, 1989d). The estimated value of the fisheries is over £6 million in each of five NRA regions (North West, Welsh, South West, Yorkshire, Northumbria).

A recent analysis of sea-trout catches from 67 rivers in England and Wales has shown clear patterns of spatial and temporal variability in both rod and commercial catches (Elliott, 1991). The analyses of spatial variability (variation in catches from different rivers for each year) demonstrate that catches from different rivers within an NRA region vary synchronously with time. A mean catch for all rivers in a region and the corresponding coefficient of variation therefore provide succinct summaries of changes in catches with time and the relative variability between catches from different rivers.

The analyses of temporal variability (variation in catches between years for each river) demonstrate that rivers can be arranged along a gradient with relative temporal variability decreasing as the mean annual catch for individual rivers increases. At one end of this gradient, there are the poor rivers with a low mean annual catch and high variability between catches. At the opposite end, there are the good rivers with a high mean annual catch and relatively low variability between catches. Ecological theory suggests that in the poor rivers, population density will be affected largely by density-independent factors, especially those associated with fluctuations in climate. In the good rivers, density-dependent factors will predominate over density-independent factors in the regulation of population size, and this "self-regulation" leads to greater stability between years. Clearly, most sea-trout rivers lie between these two extremes, but these analyses of sea-trout catches provide a basis for classifying the major sea-trout rivers in England and Wales.

Differences in the relative roles of density-dependent and density-independent factors account for some of the apparent contradictions in the literature. This is a common theme in the expert reviews. Such differences also have implications for the management of the different sea-trout populations. For example, in a population regulated chiefly by density-dependent factors, stocking in a year with good recruitment of young trout would actually reduce the number of survivors and decrease variation in their size (see also discussion in Elliott, 1987a, 1988, 1989e). It is therefore important for the management of sea-trout fisheries in England and Wales to establish a classification scheme for the major rivers.

2. EARLY LIFE STAGES: SPAWNING, EGG SURVIVAL AND DEVELOPMENT HATCHING AND EMERGENCE.

2.1 Introduction

Published information on the spawning and intragravel stages of *Salmo trutta* is patchy. However, most of the general principles are common to most salmonid species during this particular part of the life cycle and it is, therefore, necessary to refer rather freely to information from other species. This has been done in the following account but every effort has been made to indicate which statements refer specifically to studies on *Salmo trutta* and which are based on other species but are assumed applicable to *Salmo trutta*.

2.2 Spawning

Spawning behaviour, redd formation and structure have been described for *Salmo trutta* by Greeley (1932); Hobbs (1937); Stuart (1953b, 1954); Jones and Ball (1954); Ottaway et al. (1981); Crisp and Carling (1989) and some general discussion is given by Milner et al. (1981). The cues which stimulate spawning at a particular site are not fully understood. Various mechanisms have been proposed including groundwater seepage (Hansen, 1975) and downward movement of stream water into the gravel (Stuart, 1953b, 1954), and oxygen concentration (Hansen, 1975). The behaviour of the spawners usually results in redd placement in areas of low silt content and high intragravel flows (Stuart, 1953b, 1954) although the site selected is not always suitable (Hobbs, 1937). A minimum water velocity is probably required to initiate motion of bed material and to enable the fish to cut efficiently (McCart, 1969).

The spawning behaviour of British salmonids has been described in detail by Jones and Ball (1954) and the following quotation gives the essential details of the process:

"1. The female explores the gravel and carries out exploratory cutting.
2. Some of the males fight. One male assumes dominance and quivers against the female.
3. The female concentrates on cutting in one place. The dominant male continues to quiver against her and repels any other males, or females, which try to intrude. The female tests her bed by means of her anal fin and, sometimes, her pelvic fins.
4. When the female trout has made a bed about three inches deep she crouches into it (six or more inches in salmon). The male darts forward alongside her and quivers: eggs and sperm are extruded almost simultaneously as the fish lie in the bed with their mouths open.
5. Immediately afterwards, the female moves upstream and by rapid cutting sends down gravel to cover up her eggs; subsequently she starts preparing her next bed.
6. The whole process may be repeated several times."

Crisp and Carling (1989) studied the sizes of female spawners and the dimensions and physical characteristics of redds of UK salmonids, chiefly *Salmo trutta*. The following main points arise:-

(a) The percentage of fine sediments (<1 mm diameter) in the spawning beds was rarely >20% and usually <15%. Porosity was in the range 0.16 to 0.35.

(b) Water velocity at 0.6 of depth usually exceeded 15 cm s^{-1} and was always less than two female body lengths s^{-1}.
(c) There was preference for water deeper than the body depth of the spawners (c. 0.2 body lengths).
(d) The area of a typical redd is 3.5 times the body length of the female fish on the axis parallel to the streamflow and 0.3 to 0.6 body lengths on the short axis.
(e) Most eggs in most redds were found to be closely aggregated in discrete egg pockets but a small proportion of eggs were widely scattered about these positions.

The maximum size of gravel in which a salmonid can spawn also appears to be related to her size and Kondolf (in press) suggests the equation $P = 0.5L + 4.6$ where P is median grain size (mm) and L is fish length (cm).

As in *Salmo salar*, precocious sexual maturation of male *Salmo trutta* parr has been observed in some rivers (L'Abée-Lund et al., 1989). The proportion of such fish varied from 0.06 to 0.6 in various rivers in Norway and was positively correlated with mean total length of 0- and 1- year old parr. These precocious males participate in spawning activity and may be attacked and injured by larger males (Bohlin, 1975).

A significant proportion of sea-trout may spawn several times and live for many years (Le Cren, 1984). In a sample of 29 Norwegian rivers the incidence of repeat spawners varied from almost none to over 70%. The percentage showed significant positive correlations with river length ($r^2 = 0.166$) and mean discharge ($r^2 = 0.254$) but not with latitude (L' Abée-Lund et al., 1989).

Some degree of spawning segregation of *Salmo trutta* and *S. salar* is apparent in most river systems insofar as sea-trout show a greater willingness than salmon to spawn in small tributaries and salmon, on average, tend to spawn rather later than trout in any given water. However, different authors vary in the amount of stress they lay upon spatial segregation (Le Cren, 1984) and temporal segregation (Heggberget, 1988). Nevertheless, the two species do overlap both spatially and temporally during spawning and some hybridization is known to occur. Payne et al. (1972) used serological techniques to examine 4431 fish which appear to be *S. salar* and which were all taken in or near the estuaries of eleven rivers in Ireland and the U.K. Hybrids were found in the samples from five rivers (Teigh, Lune, Amble, N.Esk and Erne) and formed 0.3 to 0.9% of the samples from those rivers. Additional samples brought the total of "salmon" examined to 9166 of which 0.3% were hybrids (Solomon and Child, 1978). No similar analyses have been made amongst supposed "sea-trout" in the U.K., despite the fact that amongst hatchery-produced hybrids, the F_1 forms closely resemble *S. trutta* (Alabaster and Durbin, 1965).

Two hybrid smolts and one parr were caught in the R. Piddle, Dorset (Solomon and Child, 1978) and spawning by a male salmon and a female sea trout was observed in the same river (Crisp and Carling, 1989). A hybrid was found in Nova Scotia (Beland et al., 1981) and widespread hybridization at a mean frequency of 0.9% was observed in eastern Newfoundland (Verspoor, 1988). Verspoor commented that the higher frequency in N.America than in Britain (0.3%) or Sweden (0.07%) is in accord with the prediction that hybridization will be more frequent where one species (*S. trutta* in Newfoundland) is introduced than in areas where both are native.

Within any given population of *Salmo trutta*, the egg number can generally be related to female length by a power law model. Under carefully controlled conditions in screened reaches, better-fed trout became sexually mature earlier and produced more and smaller eggs than did less well-fed trout (Bagenal, 1969). In natural populations the mean size (weight) of ripe eggs can be positively correlated with female size (Elliott, 1984; Crisp et al., 1990). In general, larger eggs give rise to larger fry. Initial size influences the length of time for which fry can tolerate starvation after emerge from the gravel (Elliott, 1984) and this may have some practical consequences downstream of large impoundments (Crisp, 1989b).

2.3 Intragravel Stages & Emergence

2.3.1 Egg Burial Depth

Early work suggested that the depth of salmonid egg burial increased with fish size (Greeley, 1932; White, 1942) and probably depended more on female fish size than on species. Hardy (1962) reported trout eggs at depths of 8 - 22 cm. Ottaway et al. (1981) obtained a small number of data points which suggested that the burial depths of trout eggs in upper Teesdale and Weardale were correlated with female fish length. Elliott (1984) compared burial depths of sea-trout eggs (25-45 cm length) in Black Brows Beck and brown trout (17 - 27 cm) in Wilfin Beck. The eggs were buried deeper (c. 17.5 cm) in the former than in the latter (c. 4 cm) but there were no correlations between burial depth and fish size within streams. The work of Ottaway et al. (1981) was expanded by Crisp and Carling (1989) to include more data points from NE England and additional sites in SW Wales and from chalk streams in S England. They found that in NE England and SW Wales there was a significant correlation between fish length (x) and egg burial depth (y) of the form $y = bx + a$ (where a ± 95% C.L. and b ± 95% C.L. were 2.4 ± 7.53 and 0.262 ± 0.098 respectively). This regression accounted for over 60% of the variance of burial depth and covered fish of 24 to 74 cm length. No correlation could be shown in the chalk streams and this may reflect the occurrence of a "cemented layer" in the beds of many chalk streams. It should also be noted that the data from chalk streams covered a relatively narrow range of fish lengths (47 to 85 cm), as did the data from each of Elliott's two streams. Information on egg burial depth is relevant to the problems of egg washout, incubation rate and sedimentation.

2.3.2 Rate of Embryonic Development

Data published by Gray (1928) and Embody (1934) suggest that temperature is the most useful, single, predictor of the rate of development of salmonid eggs. Crisp (1981) brought together published data for five salmonid species (including *Salmo trutta*), compared the fit to the data of six different mathematical models and concluded that, on balance, a power law curve, with temperature correction, of the linear form $\log D_2 = b \log (T\alpha) + \log a$ was the most useful. D_2 is the time in days to median hatch and T is temperature in °C. For *Salmo trutta* the values of b, log a and α are: -13.93, 28.839 and -80, respectively. Subsequently, Jungwirth and Winkler (1984) and Humpesch (1985) generated new data sets and developed mathematical models for several species, including *Salmo trutta*. These models gave similar predictions to those given by the model of Crisp (1981). The Humpesch data were reexamined by Elliott et al. (1987) in a comparative study of eight mathematical models. All of the models had high coefficients of determination (r_2 = 0.937 to 0.999) and were, therefore, useful for practical prediction. Extension of models of this type to predict time to median eyeing (D_1) and median "swim-up" (D_3) are possible and very simple models of the type $D_1 = 0.5D_2$ and $D_3 = 1.7D_2$ are applicable to *Salmo trutta* and several other species (Crisp, 1988).

It is important to note that although temperature is the best single predictor of embryonic development rate, a number of complicating effects may occur which cause some degree of deviation from the predicted values. Various writers have suggested effects upon salmonid egg development of the level of incident light (Bieniarz, 1973 - rainbow trout; Hamor and Garside, 1975 - Atlantic salmon) and dissolved oxygen concentration (Hamor and Garside, 1976 - Atlantic salmon). Modification of hatching time in *Salmo trutta* has been associated with application of sub-lethal mechanical shock (Crisp, 1990a) and with low temperature at the time of predicted hatch (Crisp, 1988). The latter observation supports the suggestion of Gray (1928) that embryonic development and hatching may be a complex of processes, each with its own temperature relationship and that hatching may have a higher temperature threshold than embryonic development.

Some care must be exercised in predicting embryonic development within stream gravels because temperature within the gravel may differ from that in the free stream water both in North America (Ringler and Hall, 1975; Shepherd et al., 1986) and in the U.K. (Crisp, 1990b). Jungwirth and Winkler (1984) suggest that the upper and lower thermal death points of *Salmo trutta* eggs are c. 16°C and <4°C, respectively, and that mortality rate rises sharply above about 9°C; whilst Humpesch (1985) suggests upper and lower limits of c. 15°C and <1.4°C, respectively. General hatchery experience suggests that the lower limit is at or below 0°C (Crisp, 1989b). Gray (1928) noted that the temperature of embryonic development influenced the relative amounts of energy required for growth and for metabolism. Development at low temperatures led to a larger proportion of the yolk being used for growth and, hence, gave rise to larger fry.

2.3.3 Oxygen Requirements

The oxygen requirements of salmonid eggs depend upon water temperature and stage of development (Hayes et al., 1951) and both total consumption per egg and critical concentration (the ambient level below which there is a reduction in demand by the embryo) increase during development and then decrease sharply after hatching. Oxygen consumption data for Atlantic salmon eggs have been summarized by Hamor and Garside (1975) and similar values are likely to hold for *S. trutta*. Sublethal effects of oxygen deficit include reduced growth, reduced efficiency of yolk conversion, premature hatching, reduced size at hatching and morphological changes (Garside, 1959; Garside, 1966; Hamor and Garside, 1977). Delayed effects of hypoxia have been noted (Mason, 1969).

Marckmann (1958) examined the effects of thermal shock administered at various stages of embryonic development upon the number of vertebrae in *Salmo trutta*. The results from his control experiments are valuable data on the oxygen consumption of the embryos (as ml 0_2 $hour^{-1}$ $individual^{-1}$) from fertilization up to and beyond hatching at temperatures from 3 to 12°C. The supply of oxygen to intragravel stages depends upon the concentration of dissolved oxygen in the intragravel water, the seepage velocity of the intragravel water and the spatial arrangement of the intragravel stages. Literature on these topics is summarized by Milner et al. (1981) and the interrelations are summarized by Crisp (1989b - Fig. 2). The removal of toxic metabolic products, chiefly ammonia, is also dependant upon the flow of intergravel water.

2.3.4 Mechanical Shock

Detailed studies have been made on the effects of mechanical shock (impact or vibration) upon survival of salmonid eggs at various stages of development, mainly upon Pacific salmon of the genus *Oncorhynchus* (e.g. Jensen and Alderdice, 1989). Simpler and cruder experts on *Salmo trutta* (Crisp, 1990b) showed a similar pattern, in that sensitivity to impact shock increased after fertilization and then decreased after eyeing.

2.3.5 Washout and Drift

The destruction of eggs and alevins by spate washout has been considered to be a major cause of mortality in some populations of Pacific salmon (Wickett, 1952; Gangmark and Bakkale, 1960; Lister and Walker, 1966). Studies on *Salmo trutta* have been more limited. Egg burial in U.K. streams is usually to a depth of 5-25 cm (Crisp and Carling, 1989) and studies with artificial eggs in Pennine streams have shown that spates of fairly frequent occurrence can wash out most eggs (>90%) at 5 cm depth, variable numbers at 10 cm and few at 15 cm. However, a spate of c. 10 - 20 years' return period washed out nearly all eggs at 5 and 10 cm and some (43%) at 15 cm (Crisp, 1989a). In natural stream channels the displaced eggs travel several tens of metres (Crisp, 1989a) and the effect of simply drifting c. 10m is sufficient to cause about 50% mortality amongst trout eggs prior to eyeing (Crisp, 1990b). Harris (unpublished thesis, Liverpool University, 1970) estimated that 27% (range 0-58%) of *Salmo trutta* redds were washed away in tributaries of the Afon Dyfi (Wales). Elliott (1976) studied the drift of trout eggs relative to water velocity in two small streams. The temporal occurrence of eggs in the drift appeared to be related to the presence of eggs in the gravel. In any given season, in each stream, the number and the concentration of drifting eggs could be related to water velocity. The fact that these relationships held over a period of 3-4 months implies that, although large numbers of eggs drifted, little depletion of eggs occurred and, therefore, the numbers washed out were negligible compared with the numbers present in these two streams.

2.3.6 Gravel Composition, Sediment Deposition and Alevin/Fry Emergence

The composition of the gravel at the redd site and the deposition of sediment in the gravel will influence intragravel flow and, hence, oxygen supply to the embryos and the removal of waste products from the embryos. The same factors also influence the ease, or otherwise, with which alevins can emerge from the gravel at the time of "swim-up". Studies on Pacific salmon have shown that this can be a significant cause of mortality and that rate of entrapment increases with the proportion of fine particles (Shelton, 1955; Philips, 1964; Cooper, 1965; Hall and Lantz, 1969; Philips and Koski, 1969; Hausle and Coble, 1976 Platts et al., 1979).

Generalised statements (as above) are widespread in the literature and are probably true for most salmonid species in some habitats. There are a number of papers which describe experiments in which the survival of eggs/alevins have been examined relative to various compositions of gravel and mixtures of gravel with sand and peat. Only two of these refer to *Salmo trutta* and, in both instances, the experimental design did not permit separation of the effects of gravel composition upon egg survival and upon alevin entrapment. Witzel and MacCrimmon (1983) examined survival from fertilization to "swim-up" relative to gravel composition and concluded that:

(a) Alevins emerged earlier (prematurely) from finer gravels and gravels with higher sand loads.

(b) Coarser gravels gave longer total periods of emergence (from first to median and median to last emergence).

(c) Size and development at emergence were positively related to gravel size and negatively related to sand content.

(d) Survival increased fourfold with an increase in mean gravel particle diameter from 5 to 9 mm.

Olsson and Persson (1986a) studied the effects upon survival to emergence of the admixture of various percentages of sand (0.75 mm diameter) to a standard gravel mix (75% at 18 m diameter, 25% at 4.8 mm diameter). Survival to emergence was high (83 to 96%) when the percentage, by volume, of sand was up to 10%. At higher percentages of sand, survival decreased and was only 4% at a sand content of 40%.

Olsson and Persson (1986b) found that survival increased from 33% at mean gravel size 1.5 mm to 80-90% at gravel sizes of 9.6 and 32 mm. Emergence was premature at gravel sizes of 1.5 and 4.8 mm but not at 9.6 mm and larger. Peat had little effect on survival to emergence except at very high concentrations (40% or more by volume).
Hershberger and Porter (1982) compared survival from eyeing to swim-up between eggs planted in Whitlock-Vibert boxes and eggs directly planted. Sediments probably accounted for the fact that direct planting gave rise to 3.5 times as many swim-up fry as did box planting.

Although it is clear that intergravel development and survival are influenced by gravel composition and sediment deposition, no detailed field studies have been made on *Salmo trutta* eggs relative to these factors. Studies on other species have been beset by various problems on methodology and comparability and it is doubtful whether or not any of the findings are widely applicable in a quantitative sense (see also Milner et al., 1981). In at least some salmonid species, feeding may occur before or during emergence from the gravel but there is rapid mortality after the yolk reserves have been exhausted, if emergence is delayed (Dill, 1967; Hurley and Brannon, 1969).

2.3.7 Effects of Acid Water, Calcium Ions and Iron

Carrick (1979) showed that acid water at pH 3.5 was lethal to trout eggs within 10 days but no effect of acidity alone could be shown at pH 4.5 or above, though it is likely that pHs around 4.5 will be lethal in the presence of some toxic metals. Tests at pH 4.5 (Brown and Lynam, 1981) showed that a calcium concentration of 10ppm was required for survival of freshly fertilized eggs but that eyed ova could tolerate deionized water acidified with sulphuric acid with no other ions added. Concentrations of 1ppm each of sodium and calcium were sufficient to ensure hatching from the eyed ova stage and also alevin survival.

Geertz-Hansen and Mortensen (1983) showed that naturally-occurring concentrations of iron in some Danish streams (pH 6.55 - 7.05) caused increased mortality of eggs and alevins of *Salmo trutta*.

3. ECOLOGY OF THE JUVENILES IN FRESH WATER

3.1 Introduction

The trout *Salmo trutta* L. is a polymorphic species, which exhibits a range of migratory characteristics in different rivers. Some populations contain juveniles that eventually migrate to the sea as smolts, in others this downstream movement is less pronounced and individuals remain in fresh water throughout their life. Anadromous populations may contain non-migratory adults, mostly males; these spawn with returning adult female sea-trout (Campbell, 1977). The progeny of anadromous parents, resident (non-migratory) parents or mixed parents cannot be distinguished by their external appearance during the parr stage, although biochemical genetic differences have been found (Jonsson, 1982; Ferguson, 1989, Skaala et al. 1989).

In this review, some papers on juvenile resident trout have been included where the results are of relevance to the ecology of sea-trout parr. Unfortunately, many authors do not state if their populations contain resident and/or anadromous fish, although the presence of sympatric Atlantic salmon *Salmo salar* L. in some rivers suggests that at least some of them also contain sea-trout.

3.2. Parr

3.2.1 Numbers and Mortality Rates

3.2.1.1 Methods of population estimation

Electrofishing is the principal method of capture of juvenile trout in streams, and estimates are derived from two or more successive removals (Zippin, 1956, 1958; Seber and Le Cren, 1967; Seber and Whale, 1970; Carle and Strub, 1978). The practical and statistical problems that can arise in these types of population estimates have been reviewed by Bohlin et al. (1982). He concluded that 2-catch methods are adequate if the efficiency of capture and the number of fish in the study area are both high. In other cases, a minimum of three successive catches is required. Mann (1971) combined 2-catch estimates with occasional multiple catch estimates, and Crisp et al. (1984) combined 2-catch estimates with single catches, estimates being made for the latter using mean catch efficiencies derived from the former.

3.2.1.2 Intraspecific competition

Strong evidence exists that the major processes regulating trout populations occur during the juvenile, post-emergent stage (up to c. 3 -4 months old). During this period of their life-cycle juvenile trout exhibit strong territorial behaviour and regulation operates through density-dependent factors that are principally related to the establishment of feeding territories (Elliott, 1984a, 1985a, b,c 1989, a,b, 1990 a,b). Alm (1950) showed that the production of trout in streams is limited by their strong territorial behaviour. This limitation was demonstrated by comparing stocked and unstocked sections of a trout nursery stream in Ireland (Kelly-Quinn and Bracken, 1989a). The final autumn densities of 0+ trout were the same in all cases, regardless of the initial densities in April. Complications to this territoriality and hence to the level of production can be created by the presence of other salmonid species. Variations in environmental conditions between or within streams can give one or other species a local advantage.

The size of individual territories influences the population density of the juvenile trout, and the number of territories and their size is strongly influenced by river flows and substratum topography. Le Cren (1973) recorded a mean territory size of 0.05 m^2 in an experimental stream in northern England. In another study, Elliott (1984a) recorded maximum densities of 0+ sea-trout during the end May/early June of 7.2 ind. m^2 (= mean territory size of 0.14 m^{-2}, which fell to 2.0 ind. m^2 (= mean 0.5 m^{-2} territory) by end August/early September. However, visual isolation through the presence of stones or aquatic plants can decrease aggressive interactions between fish in adjacent territories (Kalleberg, 1958), and Le Cren (1973) suggested that this mechanism could explain the higher population densities of juvenile trout in some streams. Conversely, Mortensen (1977c) found lower numbers in a stream following weed-cutting and cleaning of the stream bed.

In a small Danish stream, density-dependent regulation only operated at densities greater than 3.1 ind. m^{-2} (Mortensen 1977c). At low densities abiotic factors are more important; Crisp et al., (1974, 1984) described a population of non-migratory trout in north Pennine streams in which the densities of 0+ trout were never sufficiently high for density-dependent regulation to operate. In this catchment, severe spates often caused extremely high mortality rates among eggs or alevins and there were very wide year to year fluctuations in recruitment success.

Populations of sea-trout with similar densities have not been reported and, in view of the higher fecundity of female sea-trout (because they are larger than most female resident trout - Elliott, 1984a), they may be rare. However, Alm (1950) described a population of sea-trout in a small Swedish stream in which limited areas of suitable spawning gravel restricted the number of recruits to the population. When the number of spawning fish was high, many eggs were lost through over-cutting of the redds.

The regulation of the numbers of older trout fry (over 3-4 months) is usually via density-independent factors (Elliott, 1985b; Mortensen 1977a,b,c, 1978). Rasmussen (1986) found that the numbers of 0+ trout clearly influenced the numbers of older trout up to age 17 months. He concluded that density-dependent processes were the cause, but his results support the concept of density-independent regulation. They are similar to the results of Solomon and Paterson (1980) who found that, in a particular year-class, the density of 1+ trout was related to their previous October 0+ densities. Le Cren (1973) suggested that downstream dispersal of trout fry could offset the effects of density-dependent mortality, but Heland (1980) and Elliott (1987a) found that fry dispersed downstream had a slower growth rate, smaller size and lower survival rate compared with those that established territories.

Although many trout populations contain anadromous and non-migratory individuals, some streams in France have been described (Bagliniere et al., 1989a; Maisse et al., 1987) in which the resident fish spawn in the upper reaches and the sea-trout spawn in the lower reaches, the latter sites being less subject to sudden changes in flow and temperature.

3.2.1.3 Effects of stream discharge

In a small chalk stream, Solomon and Paterson (1980) found a strong correlation between the October densities of 0+ parr and river discharge in April. They concluded that higher April discharges increased the number of refugia (= territories) suitable for trout fry at a time when density-dependent regulation was taking place. Similarly, Cowx and Gould (1989) recorded a decrease in the population density of juvenile trout in tributaries of the Upper Severn following a reduction in river discharge after impoundment. In a neighbouring stream, also regulated, flows were augmented by inputs from other sources and no decrease in trout densities occurred. In an extreme case in Norway, Hvidsten (1985) reported high mortalities of trout in a stream subjected to severe fluctuations in discharge associated with hydropower development (e.g 30 to 150 m^{-3} s^{-1} increase in 10 min.); often sudden reductions in flow caused trout to become stranded.

3.2.1.4 Interspecific competition

The presence of salmon parr can add to the complexity of density-dependent relationships. Egglishaw and Shackley (1982) found that the numbers of 1+ trout were correlated with the numbers of 0+ salmon in a small Scottish stream, and Kennedy and Strange (1980) found that the survival (hence numbers) of 0+ trout was influenced by the numbers of salmon parr.

3.2.2 Growth

3.2.2.1 Temperature

In a 17 year study of Black Brows Beck, Elliott (1984a, 1985b,c) found that 0+ trout growth was determined by density-independent factors, chiefly water temperature and egg/alevin weight. His results showed that the population biomass (standing crop) of 0+ trout varied from year to year through changes in growth rate and not through changes in population density. Exceptions were two drought years (1976 and 1983) in which the populations densities were greatly reduced and the growth of the survivors was retarded. However, the variation in weight of alevins (determined as the coefficient of variation) was inversely related to the initial density of eggs. For a particular year-class, the coefficient of variation remained the same throughout the life-cycle. Other workers have noted the influence of egg/alevin size on the size and survival of 0+ (e.g Bagenal, 1969; Trzebratowski and Domagala, 1988).

Morrison (1989) recorded an increased growth rate of trout and salmon in a tributary of the River Spey, Scotland resulting from a warm water effluent from a distillery. This caused salmon to smolt at an earlier age than in upstream sites, but the results for sea-trout smolts were less convincing because of small sample sizes. However, Mann et al. (1989) recorded the growth of 0+ trout immediately below a chalkstream spring from which water issued at a constant temperature of 10°C throughout the year. The trout continued to grow at a reduced rate during the winter months, whereas no increase in length was observed in trout in neighbouring streams.

Elliott (1975) developed a model to describe trout growth in relation to water temperature and Edwards et al. (1979), from a survey of 36 river sites in the U.K., demonstrated that water temperature was the dominant factor determining the growth of juvenile trout. Further confirmation for this comes from growth data for trout in streams in the U.S. (Preall and Ringler, 1989). The growth in natural populations is generally in agreement with the predictions of Elliott's model during the spring/summer growth period, but not during the winter months, which is less than the model's prediction. As Elliott's model is derived from the growth of trout fed on maximum rations, it can be assumed that food becomes a limiting factor during the winter.

3.2.2.2 Population density

Although most authors have not found evidence of density-dependent regulation of trout growth, fast rates of growth have been recorded in streams in which spawning limitation resulted in low parr production despite the existence of large feeding areas (Horton et al., 1968; Fahy, 1985d). Also, Angelier (1976) found that the growth rate and condition of trout in a Pyrennean stream were correlated to density.

3.2.2.3 Interspecific competition

Egglishaw and Shackley (1977) found that the growth rate of sea-trout parr in the Shelligan Burn, Scotland was related to the number of salmon parr present and to water temperature (degree days >0°C from 1st December). A similar correlation between salmon parr numbers and mean length of 0+ trout in October has been observed in a southern chalk stream (R.H.K. Mann unpublished data). In neither case did the number of trout parr have any influence on trout growth.

3.2.2.4 Latitude

In an examination of trout in 34 Norwegian rivers, L'Abée-Lund et al. (1989) observed that the second year growth increment was negatively correlated with latitude and positively correlated with the number of degree days >4°C, the temperature component accounting for 70% of the year to year variation in growth rate. The latitude effect appears to operate partly through the decrease in temperature with increase in latitude and partly through the change in photoperiod (= time available for feeding).

3.2.2.5 Spring ('B' type) growth

Most trout growth occurs between April and October, but Berg and Berg (1987c) and Fahy (1990) have observed year to year variations in the growth of pre-smolts during the spring, just prior to migration. The extent of the spring growth determines whether or not a particular individual will achieve the size needed for smoltification. In general, the faster-growing fish of a particular year-class become smolts at an earlier age than slower-growing individuals (see section 3.3.2). In a very cold river in Norway, growth rates in the first year were so slow that some individuals did not form scales. However, growth compensation occurred in later years and fish that grew slowly in their first year of life grew faster in subsequent years (Jensen and Johnsen, 1984).

3.2.3 Habitat Preferences

3.2.3.1 Comparison with salmon parr

Several studies have identified the habitat preferences of juvenile trout, often in comparison with those of juvenile salmon. In general, juvenile sea-trout occur in more upstream reaches of a catchment, salmon often being located in higher order streams (Jones, 1970; Power, 1973; Gibson, 1988). Where the two species co-exist, juvenile salmon are primarily riffle dwellers and juvenile trout are located in slower-flowing water (Maitland, 1965; Jones, 1975; Kennedy and Strange, 1982a; Baglinière and Arribe-Moutounet, 1985; Gibson, 1988). However, this description is an over-simplification and habitat requirements can change through the year in relation to changes in feeding habitats, tolerances to water velocities, and the search for winter shelter (Bohlin, 1977). Solomon and Templeton (1975) showed that, after hatching, some juvenile trout in a small chalk stream dispersed downstream during their first 15 months of life, whereas others remained in the nursery areas. In a review, Fausch (1984) summarized these variations in habitat selection in his conclusion that all juvenile salmonids choose focal points on the basis of water velocity characteristics and food supply in order to maximize their net energy gain. Details of how juvenile trout carry out this selection have been identified in a range of field and channel studies.

3.2.3.2 Water velocity: experimental studies

The results of channel experiments (Ottaway and Clarke, 1981; Ottaway and Forrest, 1983) showed that trout fry of 25-30 mm length were washed downstream when velocities exceeded 0.73 m s^{-1}. However, the results of individual experiments were variable and later studies in the same channels (Crisp and Hurley 1991a,b,c in press) showed that downstream dispersal was lowest at 25 cm s^{-1}, slightly higher at 7.5 cm s^{-1} and increasingly higher at >25 cm s^{-1}. Dispersal was also greater at night and when water velocities were variable rather than constant. Despite these differences, the final trout numbers m^{-2} were the same in all experiments because the low dispersal rate at the lower water velocities continued for a longer period than the higher dispersal rate at higher velocities.

Shchurov and Shustov (1989) measured the physical strength and stamina of juvenile trout and salmon with a specially designed apparatus. At equal sizes, trout were stronger than salmon, which explained why they could remain in the water column at their selected water velocity for longer periods than salmon. However, trout were less well adapted to fast water velocities in which the larger pectoral fins of the salmon acted as efficient hydrofoils to deflect the water current and so enable the fish to retain station there.

3.2.3.3 Water velocity: field studies

In general, 0+ trout prefer habitats where the water velocity is less than 30 cm s^{-1} (Lambert and Hanson, 1989; Belaud et al., 1989). Depth preferences appear to be variable, but few 0+ trout are found in depths more than 40 cm. In upland streams, Kennedy and Strange (1982a) found that 72.2% of trout fry occurred in riffles compared with only 7.4% of older trout. Older but juvenile trout have less preference for water velocity and stream depth, although they were usually found in deeper waters. Mann (1971) found that in three continuous reaches of a chalk stream 0+ trout were more abundant in a shallow (<50 cm) section with considerable cover from emergent aquatic plants than in a section with the same depth but little aquatic vegetation because of extensive tree shading. Trout aged 1+ and older were more common in a deeper (75-150 cm) section of stream. Jones (1975) observed that 0+ trout and 1+ salmon predominated in riffles and runs, 0+ salmon preferred riffles and 1+ trout predominated in pools and runs. Heggenes and Traaen (1988b) observed that downstream movement of post-alevin trout could occur at water velocities <25 cm s^{-1} (even as low as 1 cm s^{-1}). Also, an increase in water temperature of 7°C resulted in a 5 cm s^{-1} increase in critical velocity. However, 0+ trout actively searched for low water velocities, although their avoidance of faster water decreased as they grew larger. At 40-50 mm length, they could tolerate velocities higher than 50 cm s^{-1}.

Changes to stream topography can have a major impact on the populations of trout through loss of, or increase to, habitat diversity and cover. Kennedy et al. (1983) recorded a decrease in trout numbers in the River Camowen, Co. Tyrone, following dredging operations. As the numbers increased again, 0+ fish were found chiefly on shallow riffles whereas older trout re-established themselves in deeper water. Kennedy and Strange (1982a) recorded that 72.2% of 0+ trout were caught in areas with a mean depth less than 20 cm, whereas only 7.4% of 1+ trout were caught in these areas. This spatial separation of 0+ and older trout is not universal; Bohlin (1977) recorded higher densities of 0+ and 1+ fish in riffle areas than in deeper, slower-flowing sections, although older fish preferred pools or areas with a rocky substratum. Also, 0+ and 1+ trout densities were directly correlated with area of water deeper than 10 cm (Egglishaw and Shackley, 1982a).

Studies by Lindroth (1955) in River Indalsalven, Sweden showed that trout fry occupied shallow margins to a depth of 20-30cm, whereas juvenile salmon were found in deeper water to a depth of 90 cm. The importance of cover has been mentioned earlier (Kalleberg, 1958) but Heggenes and Traaen (1988a) observed that trout were less responsive to plant cover during the swim-up phase than were salmon at the same stage. However, fry of both species tended to seek more cover at low temperatures (6.0 - 8.3°C).

3.2.4 Precocious Male Parr

Many studies have described the preponderance of females among sea-trout smolts, which may result from the early sexual maturation of males at the parr stage, but Svardson and Anheden, 1963) were the first to relate the predominance of females (usually 3:1) over males among smolts to the skewed sex ratio of adult sea-trout.

Studies of the early sexual maturation of male salmon parr are common, but there are few comparable studies for sea-trout. Dellefors and Faremo (1988), in a study of sea-trout in two small Swedish streams, reported a range in percentage maturity of 17.9 to 57.0, with the variation being greater between years than between streams. The within-stream differences were related to differences in growth rate between years; as precocious males are, on average, longer than immature siblings, a higher percentage maturity was observed in years when parr growth rates were high. The between-stream differences were not explained. From captures of sea-trout smolts in a trap, they observed from that only 1.3% of marked precocious males migrated to the sea as smolts, whereas 16.1% of marked immature males were recaught as smolts. Further, after the completion of the smolt run, 21.6% of precocious males were recaptured in the stream compared with only 2.8% of immature males. Their studies of osmoregulation in parr and smolts showed that the precocious males had lost their osmoregulatory capacity and were unable to tolerate the change from fresh to sea water. A seasonal pattern of osmoregulatory ability was observed in all categories of parr, with a peak during the smolt run.

Bohlin (1975) recorded that 39 of 220 (17.5%) juvenile sea-trout electro-fished from a small stream in Sweden were precocious males. Of the 39, 15 had wounds that, from observations of spawning activity, appeared to be caused by the aggression of adult male sea trout. However, he concluded that the wounds were not sufficiently severe to cause the death of the parr. L'Abee-Lund et al. (1990) recorded a percentage range of 6 to 60 for precocious male parr in nine Norwegian rivers, the percentage being strongly correlated with the mean lengths of 0+ and 1+ parr. They noted that the percentage decreased with increase in age of the parr. Thus, in poor growth rivers in which the mean smolt age was high, few precocious males occurred and the spawning males were almost entirely sea-run fish. In contrast, in fast growth rivers the level of male precocity was high. They concluded that individual males had the capacity to contribute twice to the genetic make-up of their offspring, because they could fertilise eggs as precocious males and as returning sea-trout adults - hence increasing the effective population size of male fish. However, in view of the studies by Dellefors and Faremo (1988) that few precocious males become smolts, this seems unlikely.

3.3 Smolts

3.3.1 Growth and Mean Smolt Age (MSA)

In general, sea-trout parr become smolts at an older age than salmon parr in the same stream, but not all individuals of particular year-class smoltify at the same age. Six year-classes of sea-trout smolts have been recorded from the British Isles (Fahy, 1978a; Randall et al., 1987), with mean lengths ranging from 140 to 250 mm. Fahy (1978a) found that MSA is higher in Scotland (range 2.4 - 3.4 years) than in Irish and Welsh rivers (range 2.1 - 2.8 years).

Variations in MSA have been related to parr growth rates, and faster-growing parr usually become smolt at an earlier age than slower-growing siblings. Jonsson (1985) found this to be true for smolts aged 2 years, but 4 year old smolts were slower-growing than 4 year old resident parr. The latitude of the stream can influence MSA (Fahy, 1978a); L'Abée-Lund et al., 1989) and the mechanism whereby this occurs can be seen from the experimental studies by Elliott (1975). He showed that the weight gained by trout fed on maximum rations was related to water temperature and the length of the growing season. From field observations, Egglishaw and Shackley (1977) found that trout growth was related to the number of degree days over 0°C and the length of the growing season. Thus, the variations in mean smolt age (MSA) that have been related to the latitude of the particular stream can be explained by temperature effects. Mean water temperatures are generally lower at more northerly latitudes, hence the juvenile trout grow more slowly and have higher MSA's than in streams further south.

3.3.1.1 Spring ('B' type) growth

The earlier smoltification as a result of faster growth rates of parr (Mortensen, 1977b, Fahy 1980a) is determined in some streams by the extent of 'B' type growth in the spring just before smoltification (Fahy, 1978a, 1990; Berg and Berg, 1987c). This additional growth may enable some parr to achieve the critical size necessary for them to become smolts. Fahy (1990) recorded a 19% increase in the length of 72% of 2+ parr during the spring (=mean increase in length of 36mm), and Went (1962) reported a 56% length increase through spring growth in the Argideen, Ireland. However, from studies in the River Orkla, Sweden, Hesthagen and Garnas (1984) concluded that growth rate was more important than the attainment of a critical size to initiate smolt descent, because significantly different mean lengths of smolts between years were not reflected in different MSA's. Support for their conclusion comes from data collected by Borgstrom and Heggenes (1988) in a stream in SE Norway subject to extreme flow conditions. Here one year old parr become smolts and migrate in April/May if they are longer than 80 mm; smaller fish migrate one year later. However, many immature smolts return to the river in the autumn with the run of adult sea-trout. This small smolt size appears to be an adaptation to the extreme conditions which, in some years, results in a lack of summer flow.

3.3.2 Migration

3.3.2.1 Time of migration

Sea-trout smolt migration takes place in spring, usually April or May, although downstream movement of pre-smolts can occur earlier (Le Cren, 1985). Median times for migration are usually the same for salmon and sea-trout smolts in the same river, though sea-trout smolts start earlier and finish later e.g. River Axe, Devon (Potter, 1985b). Rasmussen (1986) found that smolt migration extended from early March into June in a Danish sea-trout stream. Analyses of smolt sizes and ages through the duration of migration have shown that older (larger smolts migrate first (Potter, 1985b; Rasmussen, 1986) and, in some rivers, the later movement of younger smolts enables the effect of 'B' type spring growth to have its maximum effect.

Gloyne (1973) and King (1973) have shown that the growing season has increased during this century, mostly by extension of the spring growing period. King (1973) related this to certain solar phenomena, but changes could also occur through global warming. More information on this aspect of smolt migration is required.

3.3.2.2 Migration stimuli

Various stimuli inducing smoltification and migration in salmonids have been identified, and Solomon (1978) noted that potential migrants had to be in physiological readiness to migrate before they responded to environmental stimuli. Pemberton (1976a) recorded a migration period from March to mid-May in Scottish sea lochs and noted that heavy rains could stimulate early runs. Solomon (1978) correlated the migration of salmon and sea-trout smolts to increase in water temperature, and Rasmussen (1986) found the highest catches in his smolt trap between sunset and midnight, small numbers from midnight to sunrise and none during daylight hours.

3.3.3 Smolt Production

There have been a few estimates of the smolt production of streams or rivers. Rasmussen (1986) related data on the smolt run to catchment area and parr production estimates. Over three years, production ranged from 12.0 to 16.6 g m^{-2} a^{-1} wet weight and this yielded from 14.6 to 19.8 smolts 100 m^{-2}. Mortensen (1977a) recorded a smolt yield of 4 ind. 100 m^{-2}, which was derived from a mean annual production of lake and sea-trout of 18.8 g m^{-2}. Potter (1985b) reported smolt catches over 6 years by the River Axe trap in Devon that ranged from 2081 to 6062, and Piggins (1976) found a range from 6000 to 9000 over 6 years in the Burrishoole river system, Ireland.

Most stocking of trout is made in order to increase the numbers of resident trout. However, in a re-stocking programme in the Vantaanjoki River, Finland, a stocking rate of 300 - 700 sea-trout alevins 100m^{-2} yielded 30 1+ parr 100 m^{-2} (Saura et al., 1990). It was further estimated that the river would produce 45000 smolts (most aged 2+) from 0.5 - 1.1 million stocked alevins.

4. ECOLOGY OF THE ADULTS

4.1 Marine/Coastal Stages

4.1.1 Introduction

Sea-trout usually spend two or three years within streams before migrating to the marine environment, typically in April, May or June, as smolts. Some of these fish, known as whitling or finnock, return to fresh water after only one summer at sea, while others stay in the marine environment for at least one winter. The return or spawning migration typically takes place in the late summer or autumn and is reviewed in detail later.

In addition, sea-trout of many populations return to the marine environment after spawning, when they are known as kelts, and continue to spawn for several more years until their deaths. Many of the papers cited in the following sections thus refer to both young post-smolts, and larger and older kelts. These two marine stages of sea-trout are quite distinct in many aspects of their biology.

Research on the marine stages of the sea-trout has been relatively restricted, as the following sections show. However, the recent collapses of sea-trout populations in parts of Ireland have resulted in a major marine research programme being initiated which should make a significant contribution to research in this area. While some initial results have been disclosed already (Anon., 1990), and are cited where relevant below, it is likely to be some time before the full results of this work are published.

4.1.2 Arrival and Residence in the Marine Environment

Berg and Berg (1989) described in some detail the marine arrival and residence of sea-trout from the Vardnes River in northern Norway, largely by inspection of catches from downstream and upstream traps. The following conclusions were the result of tagging 15,788 sea-trout over a period of 11 years. Females tended to enter the marine environment slightly earlier than males, and ascended the river slightly later. Mean duration of stay in the sea for females was as a result slightly longer than that for males (69 and 66 days respectively). This duration was found to be lengthened by a fall in the river water level in August, due to a subsequent delay in the return migration.

The sea-trout of a more southerly Norwegian river, the River Istra in western Norway, were studied by Jensen (1968) in the early 1950s, again using downstream and upstream traps. Smolts arrived in the sea from this river in the spring, as did kelts from the previous spawning season which had overwintered in freshwater. Only a small fraction of the smolt population attained maturity after their first or second summer at sea, instead most spawners spent three summers at sea although the durations of each stay were as short as 45 days.

Within the coastal waters of the British Isles, detailed studies of arrival and residence are presented by Pemberton (1976a) and Pratten and Shearer (1983a) in Scotland, and Piggins (1964) in Ireland. By fortnightly seine netting, Pemberton (1976a) was able to produce a detailed picture of the arrival and departure of sea-trout in five sea lochs on the west coast of Scotland. The arrival of post-smolts in mid May was remarkably consistent between years, after which they aggregated in tight shoals in localised areas before leaving for the open sea in July. Whitling first returned to the sea lochs in August, where they remained a major feature of catches through to the late spring. In October there was sudden appearance of small recruits from the rivers, a feature which will be returned to below. Small numbers of kelts featured in the catches from December onwards. On the east coast of Scotland, Pratten and Shearer (1983a) noted that most smolts arrived in the marine environment from the River North Esk in May or June, before leaving it as finnock from July onwards with a peak in autumn.

Upstream and downstream traps on the Burrishoole system of the Atlantic coast of Ireland were used by Piggins (1964) to study temporal aspects of the marine phase of kelts. The marine residence time was found to be very variable between 43 and 362 days, with a mean time of 105 days over the period 1953-1961. The first kelts appeared in November, with a descending trickle through the winter, but the major kelt descent was between mid March and the end of April. Typically, an early outgoing run of kelts resulted in most of them returning in July in good condition, while if the run was late the sea residence was shortened and the fish returned at the same time but in poorer condition.

Le Cren (1985) reviewed several relevant studies carried out in the British Isles. Smolt arrival in the brackish reaches of the Afon Glaslyn in Wales peaked in May before they quickly moved out to sea. Sea-trout in the River North Esk in Scotland were found to move back upstream within five to six weeks of their previous arrival as smolts, while in the River Axe and River Fowey in England, the fish ascended between July and September. Potter (1985b) noted that the major smolt run in the River Axe is in April, with the start of the return by whitling in July such that by the end of August 87% of them have returned.

As noted above, the October catches of Pemberton (1976a) in the Scottish sea lochs showed a sudden appearance of small sea-trout which were interpreted as being autumn recruits from the rivers. These fish were only slightly silvered and thus distinct from the spring smolts, but Pemberton considered that they were intentional migrants rather than fish accidentally washed downstream by spates. Le Cren (1985) noted that a similar pre-smolt autumn migration, peaking in October, had been observed in the Burrishoole system in Ireland where up to 1981 it was dominated by 1+ and 2+ fish, but since this time 0+ have made up most of the catches. The size of this run on the Burrishoole was approximately 60% of the spring smolt run and so involved significant numbers of fish. In contrast, Sambrook (1983) reported that only five such 'autumn smolts' were found over two years in the River Fowey in Cornwall.

4.1.3 Migrations in the Marine Environment

Studies of the migrations of sea-trout within the marine environment are very rare, no doubt due in large part to the considerable practical difficulties involved in such work. Mills and Piggins (1988) noted that it is ironic that so little is known about the sea movements of Irish sea-trout. Nevertheless, some information is available for Norwegian, Irish and British stocks, although it must be remembered that the locations of recaptures depends on the distribution of sampling (fishing) effort rather than just the distributions of the fish themselves.

The extensive sea-trout trapping and stocking programme on the Vardnes River in northern Norway cited earlier has also produced information on marine migrations through the recapture of several thousand fish (Berg and Berg, 1987b). Of 2,122 recaptures made in the sea, 52.8% were made within 3 km of the mouth of the Vardnes River while only 0.7% were made more than 80 km away. The four highest values recorded for mean distances of daily travel away from the river were 20,8,8 and 6 km day^{-1} by smolts and 6,6,5 and 5 km day^{-1} by larger fish. No significant correlations could be found between the distance migrated and any environmental factors. Berg and Berg (1987b) noted that similar movements were shown by sea-trout in other parts of Norway and Sweden.

Jensen (1968) also presented some information on the sea movements of kelts originating from the River Istra in western Norway. These migrations were again relatively short with all recaptures being made within 70 km of the river, most of them being within 15km. Limited information on movements within British coastal waters was given by Pemberton (1976a) for the populations passing through sea lochs on the west coast of Scotland. Migrations of smolt out of the lochs into the open sea were largely complete by late spring or early summer, while movement back as whitling occurred in the late summer and early autumn. The distribution of tagging returns was additional evidence for these movements. Pratten and Shearer (1983b) tagged all life stages of sea-trout taken in traps on the River North Esk on the east coast of Scotland. Significant numbers of finnock were found to move along the coast to adjacent estuaries, although most of these marine migrations were again relatively short. Limited tagging of Irish sea-trout reported by Went (1962) also showed generally short marine migrations.

Further British studies were reviewed by Le Cren (1985), particularly the results of smolt and kelt tagging carried out by MAFF, DAFS and Yorkshire WA between 1949 and 1984. Smolts were tagged on the River Coquet, River Tweed, River North Esk and the Yorkshire Esk, while adults were tagged off Flamborough Head, Amble and East Anglia. The general picture which resulted form this work was 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. Smolts arriving back at the English coast then moved northways to their home rivers. Similar movements were carried out by kelts, although with more variation. Work by other researchers in southern England showed that smolts and kelts tagged in the River Axe undertook marine movement as far east as the Hampshire Avon and as far west as the River Otter, while limited recaptures of fish tagged in the Afon Glaslyn in Wales showed very limited movements in the sea. Potter (1985) reported a similar marine movement of smolts from the River Axe, noting that the patterns of tag returns suggested that post-smolts stayed together throughout their stay in the sea and that during this period their movements were active and not simply controlled by residual water movement. Le Cren (1985) also noted that marine recaptures of sea-trout tagged in the Burrishoole system in Ireland were made in nearby nets north and south of the river.

4.1.4 Feeding in the Marine Environment

While some very old accounts of marine feeding by sea-trout exist from the early part of this century, these studies give few details. Works published in recent years have been by Pemberton (1976b) for a Scottish stock, and Fahy (1983c, 1985b) for two Irish stocks. A general account of the diet of sea-trout is also given by Fahy (1985a). Such feeding in the marine environment may be particularly important in iteroparous populations where it enables kelts to replace the considerable amounts of energy lost during spawning, in preparation for the next upstream migration and egg production. Given the rarity of such diet studies, each will be reviewed here in some detail.

The study by Pemberton (1976b) relied mainly on the seine net catches described previously for Pemberton (1976a), although additional samples were obtained from anglers and netsmen. In his analysis, Pemberton divided the fish into two groups of fish of less than and greater than 21 cm in length, which effectively covered the post-smolt and whitling stages respectively. In all, approximately 50 prey types were recognised from 1,277 stomachs examined over one year. In terms of frequency of occurrence, the main prey were crustaceans (found in 43.0% of stomachs examined), insects (31.1%) and fish (30.6%, mainly herring *Clupea harengus*, and sand eel *Ammodytes* spp.). Annelids (5%) and molluscs (very occasional finds) were considerably less important. In terms of dry weights, fish were the greatest contributors to the diet (69.2%), followed by crustaceans (17.5%), insects (8.9%) and annelids (4.4%). Post-smolts tended to feed more on crustaceans and insects than did whitling, which consumed relatively more fish. Newly-arrived smolts also concentrated on crustaceans, particularly amphipods. On a seasonal basis, feeding was most intense in the early summer with the peak incidence of empty stomachs occurring in November and December. Feeding in the winter and spring tended to be benthic, as evidenced by the diet composition, while in summer and autumn the food was more likely to be taken in mid-water or at the surface. On a diel basis, feeding increased at sunset and sunrise while mid-water and surface feeding was more common at night.

The study of sea-trout diet by Fahy (1983c) was less extensive and restricted to fish greater than 23 cm in length taken in the Irish Sea between April and July. Nevertheless, it did include post-smolts and both pre- and post-spawning adults. The most important food types were 0+ and 1+ sand eel (*Ammodytes marinus*), although some greater sand eel (*Hyperoplus lanceolatus*) were also taken. The younger sand eels were taken by post-smolt sea-trout, while the older sand eels were taken by older sea-trout (Fahy, 1985a). The polychaete *Eunereis longissima* was particularly important in May and was the second most important food. Sprats (*Sprattus sprattus*) constituted the third most important prey, with greatest abundance in the diet after May, while a very few individuals of other fish species were also taken. Known distributions of these prey are strong evidence that sea-trout in the Irish Sea forage mainly in inshore regions. Like the Scottish fish, feeding intensity in the sea-trout in the Irish Sea was highest in early summer, peaking in May.

A subsequent study by Fahy (1985b) of the diet of sea-trout from Mulroy Bay, a long marine lough on the Atlantic coast of Ireland, revealed important differences when compared with the diet of the Irish Sea stock described above. The diets of the Mulro Bay fish were examined over a year and showed significant feeding levels in all seasons, although the amounts of food in their guts were consistently less than those of the Irish Sea fish. The diversity of the diet in Mulroy Bay was relatively higher, with fish including sand smelts (*Atherina*), sticklebacks (*Gasterosteus*), sprats (*Sprattus*) and sand eels (*Ammodytes*) dominating the diets of larger trout, while crustaceans and insects were more important in smaller individuals. Polychaete worms were consumed by all size classes of sea trout.

Finally, Went (1962) also referred to reports of the diet of sea-trout captured 10 miles offshore in the Atlantic. The diet of these fish, which were all greater than 24 cm in length, was dominated by sand eels and sprats, although some unidentifiable gadoids were also consumed.

Recent investigations of the declining sea-trout populations off the coast of Ireland have shown that many fish are thin and show classic starvation symptoms, although this is unlikely to have been the result of the non-availability of food (Anon., 1990). Further studies are currently underway.

4.1.5 Parasites in the Marine Environment

Little work has been published on the parasites of sea-trout in the marine environment. Fahy (1983c) examined the guts of sea-trout from the Irish Sea and recorded the cestode *Eubothrium crassum*, the nematode *Thynnascaris adunca*, and the trematodes *Hemiurus communis, Lecithaster gibbosus* and *Derogenes varicus*. Fahy concluded that only *E. crassum* had a permanent presence in the gut, with the other parasites probably reinfesting on an annual basis. In sea-trout from Mulroy Bay, Fahy (1985b) recorded the digeneans *Crepidosteum metoecus, Derogenes varicus, Hemiurus communis, Lecithochirium musculus* and *Prodocotyle reflexa*, the nematode *Thynnascaris adunca*, and the cestode *Eubothrium crassum* which was the most common gut parasite being found in 82% of the sea-trout examined.

In a detailed study of *E. crassum* in 125 sea-trout caught between April and July off the Irish coast of the Irish Sea, Fahy (1980b) found that post-smolts contained only immature parasites while gravid specimens were found in both unspawned and previously spawned adult fish. Fahy concluded that large numbers of *E. crassum* are accumulated by sea-trout within weeks of their arrival in the marine environment. In contrast to the typical pattern shown by brown trout, larger sea-trout did not always carry the largest burdens, possibly because the tapeworms were stressed by the repeated migrations of older sea-trout between the sea and fresh water.

Pemberton (1976a) found the ectoparasitic copepod *Lepeotheirus salmonis*, known commonly as sea lice, on Scottish sea-trout, with higher levels of incidence on larger individuals. Sea lice (species unspecified) infestations have also been found in the declining sea-trout stocks off Ireland and their presence in large numbers has been identified as one of the most obvious features of the decline (Anon., 1990). A major research programme has consequently been started to determine the cause of the apparent sea lice population explosion.

4.1.6 Growth in the Marine Environment

Studies of growth in the marine environment are more common than investigations of the above topics, although in practice they have been essentially freshwater sampling operations at the beginning and end of the marine phase.

The marine growth of the sea-trout from the Vardnes River in Norway was studied in detail by Berg and Berg (1987c). It is difficult to draw general conclusions because of the complexity of this population, with several descending classes present each year, although the patterns observed for smolts and kelts are worth noting. Following their first descent to the sea, smolts grew at a rate of just over 1 mm day $^{-1}$ with a peak towards the end of June, with the result that those fish which had entered the marine environment in May showed an increase in length of 8.5 cm before their return to freshwater in the following autumn. Larger trout showed growth peaks in later June and early August, with kelts on their second and third descents showing increases in length of 6.4 and 3.9 cm respectively. In a subsequent analysis of this population, Berg and Jonsson (1990) found that the growth was positively correlated with the length of the summer sojourn.

Studies of sea growth in waters around the British Isles are less detailed. Went (1962) noted that Irish smolt populations typically increased in length from between 17 and 24 cm on entering the marine environment to around 30 cm by the end of their first sea year. Piggins (1964) presented some information on the growth of kelts in the Atlantic and noted that there was little difference in the growth rates of males and females, and that small fish of both sexes grew better than larger individuals. Increases in length of kelts over the summer in the early 1960s were in the region of 4 to 5 cm. The study by Pemberton (1976a) of sea-trout in Scottish sea lochs produced some information on the growth of post-smolts. Following their arrival from fresh water in April-July as 13-20 cm long individuals, by the time that they had returned from their open sea migration in October-November they were 17 to 25 cm in length, with a peak around 20-21 cm. More detailed information on growth rates was not given. Pratten and Shearer (1983a) recorded that the marine growth of finnock from the River North Esk on the east coast of Scotland tended to eliminate any marked differences which may have existed at the time of smoltification. In contrast, Elliott (1985c) found that mean sizes of returning adults were related directly to mean sizes of juveniles at the start of their migration to the sea/estuary. Potter (1985b) provided some information on the marine growth of sea-trout from the River Axe in Devon. The mean lengths of smolts were found to be very similar between years at between 21 and 22 cm, while the typical size of a returning whitling was 32 cm, showing growth rates of 1.0 and 0.4 mm day^{-1} for early and late returning fish respectively. One sea winter fish returning in April were 50 cm in length, in contrast to those returning in July which were 42 cm.

In a review of sea-trout studies in the British Isles, Fahy (1978a) reached several general conclusions concerning marine growth. Most notably, while different stocks were often very different in length at the time of their seaward migration, these differences were greatly reduced by the following winter due to differential growth at sea. Around the British Isles, the lengths of two and three year old smolt fish at the end of their first post-migration winter were very similar for Irish and Scottish stocks at around 31 cm, while Welsh populations were slightly larger at around 34 cm. More detailed comparisons, including the investigation of condition factors, were precluded by complications arising from many factors including differences in time of sampling and the state of the fish. If any trend was apparent, it was that the Scottish and Irish populations were more similar than the Welsh. In this study, and subsequently (Fahy, 1985a), Fahy commented at length on fast-growing, good condition 'Irish sea' populations and slow-growing, poor condition 'Atlantic' stocks of sea-trout.

Finally, Le Cren (1985) briefly reviewed more recent data on the growth of sea-trout from the Burrishoole system in Ireland. Mean sizes on return to freshwater of 0+, 1+ and 2+ sea year fish were 28.0, 36.2 and 41.5 cm respectively. While there was some evidence that kelts began to feed and grow while still in the freshwater environment, most of the growth of repeat spawners was likely to have been made in the three months or so that the fish were at sea.

4.1.7 Survival in the Marine Environment

Studies of survival in the marine environment have again in practice been essentially freshwater sampling operations at the beginning and end of the marine phase.

The marine survival of the sea-trout from the Vardnes River in Norway was studied in detail by Berg and Jonsson (1990) through an analysis of 15,788 sea-trout which were tagged and recaptured. Smolt survival over the summer was estimated at 37% while it varied between 56 and 68% for older fish. The annual minimum survivals were 25% for smolts, 37% for second time migrants and 50% for older fish. Prolongation of the sea residence, due to low water levels in the river at the normal time of ascent, resulted in a further decrease in survival rate in addition to that caused by the increase in marine residence time *per se*.

The study by Jensen (1968) of the sea-trout of the River Istra in Norway cited above also contained some information on survival rates, although as the author admitted, these estimates were likely to have been biased by the short duration of the study (two years) and the restriction of sampling to the mature part of the population. From a knowledge of the age distributions, and after making a number of assumptions, Jensen arrived at annual survival rates after the fourth sea year of between 0.30 and 0.31. An equivalent estimate using tagging data produced a value of 0.44 for survival from autumn to autumn, while for spring to autumn the value was higher at 0.56.

The survival of kelts originating from the Burrishoole system in Ireland was analysed by Piggins (1964) on the basis of tag returns. Minimum survival rates of small males and females were 23% and 29% respectively, while for larger males and females equivalent values were 15% and 31%. Further figures from the Burrishoole system were reviewed by Le Cren (1985) and are considered below.

Mills and Piggins (1988) stated that in general terms, the survival from juvenile to finnock in Irish populations varies between 20 and 30%, while the overwinter survival of kelts is higher at between 60 and 65%. Kelts tagged at sea typically show survival levels of 29 to 41%.

In England, a long-term study of sea-trout in Cumbria by Elliott (1985c) produced detailed information on survival rates of the young freshwater stages, and of the final life stage (k5 in Elliott's analysis) which included the marine phase. Survival during this latter period was density-independent with respect to the initial number of eggs in the cohort. While proportionate survival thus occurred during the marine stage, the effects of earlier density dependent regulation persisted throughout the life cycle and accounted for 40% of the variance in total egg production. Potter (1985b) recorded that the total minimum survival rates of smolts from the River Axe in Devon returning as whitling or older fish varied from 7.6 to 14.7%, and suggested that relatively higher mortality rates occurred amongst the smaller individuals. The minimum survival of kelts in the River Fowey in Cornwall was found to be 33% (Sambrook, 1983).

In the review already cited above, Fahy (1978a) remarked upon the scarcity of studies of sea-trout survival during the marine phase, but he did conclude that the rate of survival is constant for all year classes in a stock and found that coefficients of instantaneous mortality varied between 0.35 and 2.30.

Le Cren (1985) also commented on the difficulties of studies of survival during the marine stage, although he too was able to review at least some data on post-smolt survival. Trapping studies on the Burrishoole system in Ireland showed that survival from the smolt to finnock or older stages varied between 9.1 to 43.4% over a 15 year period, while a figure of 12% was suggested by the examination of age structure of fish from the Erriff River. Equivalent minimum survival values from marked smolts to adults at Colliford on the St.Neot River in England were between 5.8 and 15.1%, while equivalent values for the river North Esk in Scotland were between 1.3 and 6.2%. Elliott (1985c) found that the average survival of fish in a Cumbrian stream for the period between 1+ parr and female spawners two years later was 24% with some variation between year classes, with two years in particular showing much reduced survival down to about 5%, possibly due to the smaller sizes of the fish following poor growth in drought summers.

For kelts, Le Cren (1985) noted that an average of 40.5% of Burrishoole fish in Ireland were subsequently recaptured, while this value was 25.7% on the St.Neot River in England and between 16 and 21% on the River North Esk in Scotland.

4.2. Return Migration

4.2.1 Introduction

As the above sections have shown, an individual sea-trout may make several return migrations to the freshwater environment over the course of its life time, and these movements may themselves include several spawning migrations. Much of the following review is relevant to both such types of return migrations, although particular emphasis is given to accounts of the latter.

4.2.2 Timing

The timing of the departure of sea-trout from the marine environment as whitling or older fish has already been noted in the proceeding sections. Data from most of these previously cited populations were succinctly summarised by Le Cren (1985) who noted that finnock, both maturing and immature, usually run into the freshwater environment later in the year than older sea-trout, generally between July and September. The timing of the run of the older fish varies considerably, from a peak in May in the south-west of England, to June and July in Cumbrian rivers and in the Burrishoole system in Ireland, although it is sometimes as late as October on the River Coquet in northern England.

4.2.3 Homing

Evidence concerning the homing of sea-trout to the river from which they originated has been conflicting, and Banks (1969) considered that they do not show the same degree of homing as does the salmon. However, after considering the complicated picture that has emerged from the tagging studies that have been carried out in the British Isles in recent years, Le Cren (1985) concluded that sea-trout can home with considerable precision to their natal river, and even to particular stretches within that river. A good example of this ability was found in the sea-trout population of the River Fowey in Cornwall by Sambrook (1983) who used both conventional tags and radio-tracking. Nordeng (1977) suggested that the entire return migration of sea-trout and other salmonids is navigated by response to pheromones originating from the mucus of descending smolts, while Fahy (1985a) referred to experimental studies which have shown that such olfaction is important for juveniles but adult fish use visual cues when in their home river.

Many sea-trout, however, have been recaptured in the lower reaches of non-natal rivers, although such fish were of course not necessarily about to spawn in those rivers. Finnock, and perhaps some adults, appear to spend the winter moving into and out of the lower reaches of non-natal rivers, as seen for example in a study by Shearer and Pratten (1981b) on the sea trout of the River North Esk which showed considerable movements along the west coast of Scotland.

The strongest evidence for the homing ability of sea-trout on their spawning migrations, as opposed to overwintering migrations, is the marked differences which exist between the genetic compositions of populations from different rivers, even when they are only a few kilometres apart. Obviously, such differences could not persist with anything more than very limited straying. Examples of such evidence were given earlier in this review.

4.2.4 Movement in the River System

In an extensive review of upstream migration in salmonids, Banks (1969) commented that few data existed at that time for sea-trout, although he was able to note that in the River Axe in England they move up at lower flows more readily than salmon, and that such movement was more likely to occur at night, particularly during periods of low flows.

Over the subsequent years, studies of fish movements have been carried out using acoustic or radio-tags. The sea-trout populations returning to the Afon Glaslyn in Wales and the River Fowey in England have been particularly well studied in this way and were reviewed by Le Cren (1985). In the Afon Glaslyn, the sea-trout moved up the river for distances of between 4 and 8 km over 1 to 10 days without any pause in the lower 4 km of the semi-tidal zone. After this initial progress up the river, the fish held up for long periods of between 3 and 79 days near the confluences of tributaries. While in the estuary, the fish spent long periods with little movement, although when they did move their speed over the ground was usually 20 to 30 cm s^{-1}, with only short bursts of fast swimming at 100 cm s^{-1}.

Le Cren (1985) also provided details of findings on the upstream migration of River Fowey sea-trout. The fish moved at night at low and medium discharges, covering about 3 km each night at speeds up to 2 km $hour^{-1}$ (55 cm s^{-1}). During or after a period of increased flow they also moved during daylight, but otherwise they spent such time lying-up under cover. Thus, after arriving in fresh water in the early summer, the tagged fish completed most of their upstream migration within 2 or 3 weeks and then spent the rest of the summer laid-up.

Upstream movements of sea-trout in Cumbria rivers as revealed by resistivity counters were also reviewed by Le Cren (1985). On the River Kent, 80% of the fish moved upstream during discharges of 0.2-0.3 ADF (average daily flow), and similar results were obtained on the other rivers. As in the River Fowey, most movement took place at night although fish did move during daylight when there was a freshet or the water was coloured.

4.2.5 Feeding in the River System

Only two accounts have been published of the feeding of adult sea-trout in fresh water. In the early part of the century, Nall (1926a) examined the diet of 150 sea-trout form Loch Maree in Scotland and found that they had consumed a range of macroinvertebrates, including water and terrestrial beetles, other insects and crustaceans, but no fish. There was no indication, however, that the amounts of food consumed were sufficient to allow the fish to grow while in the freshwater environment.

More recently, Harris (1972) studied the diet of 150 sea-trout from the Afon Dyfi in Wales. These fish, which were taken between May and December by electrofishing, angling and from poachers, were between 24 and 71 cm in length and had been in fresh water for at least several weeks. However, only 2% of the fish contained appreciable amounts of food, which included salmonid eggs, trout parr, salmon parr, and a range of macroinvertebrates.

4.3 Fecundity and Egg Size

4.3.1 Introduction

Few studies have been published on sea-trout fecundity and egg size. The review of Le Cren (1985) considered several works on populations in the British Isles and forms the basis of the present review.

4.3.2 Fecundity

Le Cren (1985) presented information on the egg production of Irish, Scottish and English populations, the latter being the work of Elliott reviewed in more detail below. In all of these examples, larger fish produced significantly more egg than smaller fish such as finnock. This relationship has subsequently been shown in more detail in a study of sea-trout from the River

Erriff in Ireland by O'Farrell et al. (1989), where the length-fecundity relationship was also found to depend on the age at which the individual had migrated to sea. Average fecundities ranged from 481 eggs for finnocks up to 2,405 eggs for larger fish of four sea years of age. For comparative purposes, a 35 cm fish from the Erriff typically contained around 750 eggs. Fahy (1985a) stated that a 50 cm sea-trout from an 'Irish Sea' population could contain around 2,700 eggs, while a fish of similar length from 'Atlantic' population is likely to contain around 2,000 eggs per female.

The investigation by Elliott (1984b) did not measure fecundity as such, but rather the number of eggs actually laid by individual females as revealed by the excavation of redds. Again, larger females laid significantly more eggs than smaller individuals. As an example of the absolute values shown, a typical female 35 cm in length laid around 1,000 eggs.

4.3.3 Egg Size

The studies reviewed by Le Cren (1985) also showed that larger sea-trout produced larger eggs. Thus, eggs of Burrishoole finnock had an average wet weight of 110 mg while those from older fish were around 170 mg, values which are similar to those obtained by Elliott (1984b) for the English population in Cumbria. A similar trend of increasing egg size was also found for fish from the River Erriff in Ireland, and the Findhu Burn in Scotland.

The more recent study by L'Abee-Lund and Hindar (1990) of 9 Norwegian sea-trout populations also found positive correlations between fish length and egg size in all but two populations, where the relationship was still positive but not significant.

5. PHYSIOLOGY, GENETICS AND DISEASES

5.1 Physiology

5.1.1 Introduction

As few publications on the physiology and genetics of brown trout, *Salmo trutta*, explicitly refer to sea-trout (i.e the migratory brown trout), the scope of this review has been broadened to encompass work carried out on all brown trout, irrespective of whether reference to the migratory potential of the fish is made. It is now generally accepted that the two forms of brown trout, migratory and non-migratory, are representatives of the same species. However, the debate has continued, and many authors have felt it necessary to justify their position with regard to the 'single species' concept. Gordon (1959a), in his paper on ionic regulation in the brown trout, outlines the debate on the status of resident and migratory brown trout, citing Trewavas (1953) who favoured the view that the two forms are ecotypes of a single species. Similarly, Skaala and Naevdal (1989) conclude that the previously described 'separate species' (Gunther, 1868), are in fact one polytypic species. Furthermore, Elliott (1989d) has recently pointed out that any distinction between migratory and non-migratory brown trout is probably meaningless since extensive interbreeding between the two forms is common. On the basis of this evidence it is assumed in this review that in physiological terms, excluding the process of smoltification, brown and sea-trout are indivisible.

Most physiological studies on salmonids have employed either rainbow trout, *Oncorhynchus mykiss*, or Pacific salmon, *Oncorhynchus* spp., because of the economic importance of these species as both farmed and sport fish, particularly in North America. Although the brown trout is the most abundant, native European, freshwater salmonid, literature on the physiology of this species is fragmentary and, in many cases, the choice of brown trout as an experimental subject appears arbitary. The range of physiological topics within which the brown trout has been studied is fairly limited, and this scarcity of information in many areas underlines the need for substantial expansion in our knowledge base, particularly now that it is clear that the brown trout and rainbow trout are not as closely related taxonomically, as was once believed.

5.1.2 Reproduction

5.1.2.1 Gonadotropin

The hormonal control of reproduction has received a great deal of attention in salmonid fish, though to a lesser extent in brown trout. An early event, in endocrine terms, in the reproductive cycle is the release of gonadotropin (or gonadotropic hormone, GTH) from the pituitary. Gonadotropin release is believed to be influenced by a hypothalamic releasing-hormone and Crim and Cluett (1974) demonstrated that a single injection of the mammalian releasing-hormone, LHRH, resulted in a dose-dependent increase in plasma GTH levels in male brown trout. Plasma GTH levels have been measured in brown trout during the reproductive cycle by Crim and Idler (1978) who noted no increase in GTH levels until the start of oocyte maturation, and Breton et al. (1983) who observed a correlation between GTH levels, estradiol levels, and oocyte diameter during exogenous vitellogenesis.

5.1.2.2 Sex steroids

A major function of GTH is to stimulate production of the reproductive steroid hormones by the gonads. The levels of the major androgens, and their glucuronide conjugates, in the plasma of maturing male brown trout has been reported by Kime and Manning (1982) who observed a pattern similar to that occurring in other salmonids studied, a result confirmed by subsequent work (Pottinger and Pickering, 1985; Pottinger and Pickering, 1987). Plasma testosterone levels have also been examined in female brown trout (Pottinger and Pickering, 1987; Soivio et al., 1982) and, in the former case at least, found to be higher than androgen levels in the male fish. Plasma levels of estradiol in mature female brown trout have been reported (Breton et al., 1983; Crim and Idler, 1978; Pottinger and Pickering, 1987; Soivio et al., 1982) and appear to be lower than the levels measured in some other salmonid species while showing a similar time-course of variation during the reproductive cycle.

The action of androgens at their respective target tissues is mediated by reversible binding of the steroid with a specific receptor protein. The androgen receptor in the skin (a secondary sexual tissue) of male brown trout has been identified and characterised (Pottinger, 1987). The number of testosterone-binding sites within the nucleii of cells within the skin shows a marked increase during the period in which maximum changes in skin structure occur (Pottinger, 1988).

The plasma of most vertebrates so far studied contains a protein to which sex steroids bind with moderate affinity and specificity; the protein is believed to be involved in the regulation of steroid activity. The sex hormone binding globulin in the plasma of brown trout has been characterised (Pottinger, 1987) and shown to vary inversely with plasma steroid levels (Pottinger, 1988).

5.1.2.3 Vitellogenesis

A major role of estradiol in fish is to stimulate yolk protein precursor (vitellogenin, Vg) production by the liver. An early report describes the development of a serological technique for the detection of Vg in both brown and sea-trout (Le Bail et al., 1981) and its application for the identification of vitellogenic females among captured wild stock (Bagliniere et al., 1981). Using more sensitive methods, the plasma profile of Vg in female brown trout during the reproductive cycle has been studied (Crim and Idler, 1978) and Vg levels were found to parallel estradiol levels, both showing marked increases during this period. More recently, a highly specific radioimmunoassay has been developed to measure Vg in brown trout (Norberg and Haux, 1988) overcoming problems of assay heterology experienced by previous authors.

Estradiol stimulates the hepatic vitellogenic process by interaction with a specific receptor protein. The brown trout estradiol receptor has been characterised (Pottinger, 1986) and shown to be twice as abundant in the female as in the male.

5.1.2.4 Cortisol and thyroxine

Pickering and Christie (1981) measured cortisol and thyroxine in the plasma of both male and female brown trout during the later stages of the reproductive cycle and found elevation of both hormones, although changes were more pronounced in the female. The physiological significance of these observations awaits clarification.

5.1.2.5 Haematology

Changes in the number of circulating blood cells during the reproductive cycle were reported by Pickering (1986) who noted a marked lymphocytopenia (reduction in the number of circulating lymphocytes) in mature male and female brown trout during this period, concomitant with an increase in the number of erythrocytes in male fish only. These changes were subsequently suggested to be due to the maturity-related increase in plasma cortisol observed in both sexes (Pickering and Pottinger, 1987a) and elevated androgen levels in the male (Pottinger and Pickering, 1987). The functional significance of maturity-related lymphocytopenia is not clear, the changes are believed to contribute to the increased incidence of disease observed in mature brown trout during the spawning period. An increased oxygen-carrying capacity due to erythropoiesis may be of advantage during the physical rigours of spawning, but erythropoiesis occurs only in the male. However, Beamish (1964) reported that the oxygen consumption of male brown trout rose during the spawning period while that of females did not, suggesting a possible respiratory significance to the elevation in erythrocyte numbers.

5.1.2.6 Changes in skin structure

The cellular composition of the skin of brown trout has been described (Pickering, 1974) and changes in skin structure have been shown to occur with age (Blackstock and Pickering, 1982), on a seasonal basis (Stoklosowa, 1966, 1970; Pickering, 1977) and following physical trauma (Pickering et al., 1982). Most notable of these changes are the sex-related difference in structure observed during maturation, when the skin of the male thickens and almost completely demucifies (Pickering, 1977; Pottinger and Pickering, 1985a). These alterations in structure have been demonstrated to be due to androgenic stimulation (Pottinger and Pickering, 1985b) and it has further been demonstrated that the effects of androgens on the skin are likely to be mediated via a specific androgen receptor, which shows changes in abundance related to plasma androgen levels and skin structure (Pottinger, 1988).

5.1.3 Osmoregulation

Fish are under a continual osmotic stress; in fresh water they must deal with an influx of water and maintain their internal ion balance against a steep concentration gradient, whereas in sea water, they experience osmotic loss of water and an influx of ions. Since the migratory brown trout must possess mechanisms to deal with both a freshwater and seawater environment, it is an attractive experimental subject for those interested in the process of osmotic adaptation.

5.1.3.1 Seawater osmoregulation and smoltification

An early examination of ionic regulation in brown/sea-trout was carried out by Gordon (1959a) in experiments duplicating the osmotic stresses experienced by fish migrating from fresh water to sea water. He found that brown trout will survive indefinitely in sea water if acclimatized at rates inversely proportional to temperature. Within one week of transfer, blood ion levels were regulated to pre-transfer values. Both survival and regulatory ability were reduced during the summer. A second paper (Gordon, 1959b) describes experiments in which brown trout were maintained in sea water for up to 5 months. Blood samples were analyzed for osmolarity, Cl^-, Na^+ and K^+ concentrations. The pattern of regulation was found to be virtually identical before and after transfer to sea water, values in sea water being maintained to within 10% of those pre-transfer. The author presented this evidence as strongly indicative that brown trout and sea-trout are ecotypes of a single species.

Talbot et al. (1982) showed that sea-trout alevins experience a progressive decrease in resistance to seawater challenge. This they ascribed to the decrease in body surface area occupied by the relatively impermeable vitelline membrane and to the development of functional gills leading to increased salt and water permeability.

Boeuf and Harache (1984) exposed brown trout to high salinity water and noted that fish so treated displayed characteristics of smolting; increases in gill Na^+/K^+-ATPase activity, rapid control of osmotic balance after seawater transfer and good growth and survival post-transfer. The author suggested that the level of gill Na^+/K^+-ATPase activity in fresh water appears to be a good indicator of the adaptability of the organism to hyperosmotic environments.

Similarly, Hogstrand and Haux (1985), studied the change in hypoosmoregulatory ability in smolting sea-trout monitored by regular seawater challenge from February to July. Seawater tolerance was found to be fully developed by April and was maintained during the spring and summer months. The ability of the fish to regulate Mg^{+2} levels was found to correlate well with smoltification. The authors emphasized that smoltification in sea-trout had been little studied.

Madsen (1990) examined the hormonal basis of adaption to high salinity in sea-trout, and found that cortisol and the pituitary hormone, growth hormone, synergize to promote survival during transfer from fresh water to sea water. Treatment with the two hormones was found to increase gill Na^+/K^+-ATPase levels, and the size and abundance of gill choride (ion-transporting) cells, suggesting a functional basis for the effect.

Battram (1987), found no evidence for an anion-dependent ATPase responsible for Cl^- uptake in the membrane fraction of freshwater brown trout gills. He suggested instead that Cl^- uptake in fresh water may be achieved by ions binding to a mucopolysaccharide matrix at the gill cell surface, followed by a pinocytotic process.

A further contribution to the debate on migrant versus non-migrant brown trout was supplied by Belaud et al. (1984) who found no difference in the ability of fish from populations of either type to osmoregulate in sea water.

5.1.3.2 Osmoregulation under acid conditions

A major consequence of exposure to fresh water of reduced pH is ionoregulatory imbalance. Stuart and Morris (1985) monitored the ion content of body compartments in brown trout exposed to either gradual or abrupt transfer to low pH and found the majority of Na^+ loss to occur from extracellular fluid, while K^+ was lost primarily from the intracellular compartment. Fish were more susceptible to low pH during the summer months.

Ambient Ca^{2+} levels are an important factor in the survival of acid-exposed fish. Brown (1981) found that the survival of brown trout exposed to low pH (3.5, 4.0) was enhanced by addition of Ca^{2+}, and that fish from a naturally acid river survived longer than hatchery-reared individuals, suggesting an element of adaptation, or acclimation.

McWilliams (1982b) pursued this line of inquiry, comparing brown trout from a naturally acid, low Ca^{2+}, stream and from a neutral, high Ca^{2+}, stream. Sodium fluxes in fish from the acid stream were found to be less sensitive to environmental pH than in fish form the neutral stream. The acid-tolerant fish were found to have a reduced gill permeability to both Na^+ and H^+, allowing Na^+ balance to be maintained over a wider range of pH. The same author has suggested (McWilliams, 1983) that one effect of acid exposure may be to remove Ca^{2+} from the gill surface, thereby increasing the permeability of the gill to various ions. Surface-bound calcium is removed more rapidly in acid than neutral conditions, but the loss rate is reduced in acid-tolerant strains of brown trout.

The importance of Ca^{2+} to survival in acid water was also demonstrated by Brown and Lynam (1981) who determined that Ca^{2+} had a protective action on the survival of newly-fertilized brown trout eggs at low pH and was necessary to ensure the survival of alevins. However, eyed ova appeared to be tolerant of pH, independent of added ions. See also section 5.1.6 on the physiological effects of pollution.

5.1.4 Stress

The physiology of the stress response has received much attention in salmonid fish, predominantly from an aquacultural perspective. However, some of this work is of broader significance, and includes a number of papers detailing the effects of stress on brown trout.

The basic time-course and nature of the stress-response in brown trout have been established (Pickering et al., 1982) and follow the pattern common to all vertebrates so far studied. Following a single incidence of acute (handling) stress, significant perturbations occur in the levels of plasma cortisol, glucose, lactate and in the number of circulating lymphocytes. Nearly 2 weeks following stress is required for reestablishment of physiological equilibrium. Stress also disrupts the fishes ionic balance; stressed brown trout experience a net efflux of Na^+ and K^+ in fresh water (Vinogradov and Klerman, 1987), an imbalance lasting for several days. Similar results have been reported by Nikinmaa et al. (1983) who observed that transport stress caused a reduction in mean cell haemoglobin content, a reduction in plasma osmolality, a hyperglycaemia, and reduced muscle fat and liver glycogen levels, with recovery occurring within 1 week.

A consistent feature of the endocrine response to stress, activation of the pituitary-interrenal axis resulting in rapid elevation of plasma cortisol levels, was noted by Fuller et al. (1976) who used gas-liquid chromatography to identify the major corticosteroids in brown trout and observed higher levels in stressed fish. The elevation of plasma cortisol levels is now routinely used as a reliable index of stress.

In addition, cortisol has itself been shown to be pivotal in causing many of the deleterious effects of prolonged, or chronic, stress. A single pulse of exogenous cortisol, mimicking the effect of an acute stress, causes a pronounced lymphocytopenia in brown trout (Pickering, 1984) and a direct relationship between plasma cortisol elevation and a reduction in resistance to disease has been demonstrated (Pickering and Duston, 1983; Pickering and Pottinger, 1989). In addition to effects of stress on the immune system, the reproductive process has been demonstrated to be highly stress-susceptible. Plasma levels of the major androgens, testosterone and 11-ketotestosterone, are suppressed by acute and chronic stress in mature male brown trout (Pickering et al., 1987a). Artificial elevation of plasma cortisol in male and female brown trout to levels similar to those observed during chronic stress results in wide-ranging effects on the reproductive system (Carragher et al., 1989), including reduction in gonad weight and suppression of plasma and pituitary reproductive hormone levels. Brown trout appear to be more sensitive than rainbow trout to the catabolic and immunosuppressive effects of cortisol (Pickering et al., 1989). Artificial elevation of plasma cortisol levels resulted in a reduction in condition factor and a decline in the number of circulating lymphocytes in immature brown trout, but not in immature rainbow trout. Long-term elevation of plasma cortisol levels resulted in a greater incidence of mortality due to bacterial and fungal infection in brown trout, than in rainbow trout. In addition to elevation following stress, plasma cortisol levels in unstressed brown trout also display an underlying rhythmicity, characterized for most of the year by a nocturnal peak in plasma cortisol levels (Pickering and Pottinger, 1983).

Under certain conditions, brown trout exposed to a stressful stimulus, which initially evokes a classical stress response, will, with repeated exposure to the stimulus show acclimation. This is the case with brown trout under hatchery conditions, exposed to daily treatment with the anti-fungal agent malachite green. Although initially stressful, 4 weeks of exposure results in no measurable response by the fish (Pickering and Pottinger, 1985).

The stress response is a multiple component phenomenon, and in addition to post-stress cortisol levels, the effect of stress on the pituitary hormones α-melanocyte stimulating hormone (α-MSH), endorphin, and adrenocorticotropin (ACTH, the factor stimulating cortisol release) have been studied. The nature of the stress was found to be crucial in controlling the release of α-MSH and endorphin, simple physical stress was ineffective whereas a thermal stress resulted in significant elevation of the two hormones (Sumpter et al., 1985). As might be expected, ACTH secretion during stress (Pickering et al., 1986) precedes the elevation of plasma cortisol levels (Pickering et al., 1987a) and can be blocked by administration of the corticosteroid antagonist, dexamethasone, (Pickering et al., 1987b).

Water quality has also been found to be a factor modifying the stress response in brown trout. Reduced oxygen levels in combination with elevated ammonia and carbon dioxide were shown to markedly suppress the cortisol response to a confinement stress (Pickering and Pottinger, 1987b). Cortisol elevation as a consequence of stress appear to be closely related to environmental temperature in brown trout (Sumpter et al., 1985; Pickering and Pottinger, 1987b) though whether this is a rate effect or an effect on absolute levels attained post-stress is not clear.

5.1.5 Respiration

Carrick (1981) measured oxygen uptake by brown trout fry reared in either acid or neutral pH. He found no difference in uptake at either pH. Data are also presented for oxygen uptake by sea-trout fry. Priede and Tytler (1977) demonstrated that measurement of oxygen consumption and heart rate show wide variation in brown trout, indicating, according to the authors, that heart rate cannot be used as an index of metabolic rate. However, they suggest that by defining the maximum oxygen pulse, a precise relationship can be established between maximum metabolic rate and heart rate.

5.1.6 Physiological Effects of Pollution

Most interest in the effects of pollution on the physiology of the brown trout has centered on the interaction between low pH and dissolved metals, particularly aluminium, because this combination of factors may be responsible for fish kills in acid waters. The brown trout appears to have been rarely the subject of toxicological study.

Sadler and Lynam (1987) exposed yearling brown trout to a range of concentrations of inorganic aluminium at various pH levels. They found that low pH, in the absence of Al had little effect on growth or survival but that the addition of Al resulted in growth retardation. The same authors extended this work, exposing the fish to varying concentrations of Ca and Al, and observed that the high mortality and reduced growth obtained at elevated Al concentrations was abolished by elevating the ambient Ca concentration (Sadler and Lynam, 1988). Similar links between survival under acid conditions and the presence of Al and Ca were established by Brown (1983) who determined that the survival of juvenile brown trout is impaired by exposure to a combination of low pH and Al. Swim-up fry were found to be more sensitive to low pH/Al than alevins, a dramatic increase in sensitivity occurring 30-80 days post-hatch. Calcium was again found to have a protective role. Similarly, Reader et al. (1988) found that during 30 days exposure to Al and Mn in soft acid water, growth, mineral uptake and skeletal calcium deposition in brown trout alevins were not effected by low pH, low Ca^{2+} or Mn but were impaired by Al, irrespective of pH. At low pH, Ca^{2+} influx was impaired and Ca^{2+} efflux was stimulated. Cd and Mn, but not Al, at concentrations within the range observed within acid waters experiencing declines in fish populations, inhibited Ca^{2+} influx (Reader and Morris, 1988). A more complex investigation was carried out by Reader et al. (1989) who exposed brown trout fry to eight trace metals, both singly and as a mixture, at concentrations typical of soft acid water and at two pH's, acid and neutral. At low pH, in the absence of metals, mortality was low, but this trend was reversed when metals were added. Even at neutral pH, metals impaired ion uptake. The authors suggested that fishery decline in acid water may not be due entirely to aluminium toxicity at low pH. Everall et al. (1989) examined the toxicity of zinc to brown trout and concluded that toxicity was determined by a complex interaction of biological and physico-chemical factors with pH and water hardness both important.

In addition to monitoring growth in post-hatch and juvenile brown trout exposed to low pH and Al, Segner et al. (1988) studied superficial mucous cell morphometrics. They found that no changes in mucous cell morphometrics occurred in the fry but, in contrast, acid stress stimulated a rapid hyperplasia of mucous cells in the juvenile fish. Linnenbach et al. (1987) also observed a stimulation of excessive mucous production at low pH and suggested that in functional terms this might lead to impairment of gill function.

The degree of physiological stress caused by exposure to low pH has also been studied. Brown et al. (1989) found that in cannulated and non-cannulated brown trout exposed to low pH, with or without Ca, high Ca promoted survival and reduced stress, measured as plasma cortisol elevation. However, the elevation of plasma thyroxine in response to acid exposure was unaffected by the addition of Ca. A combination of low pH and low Ca was found to be the most effective stressor. A similar experiment was carried out in situ using brown trout maintained in cages in either an acidic softwater hill stream, or in an adjacent stream with a neutral pH (Whitehead and Brown, 1989). Acid conditions resulted in elevation of both plasma cortisol and plasma glucose while a combined acid/Al episode also elevated thyroxine levels.

A number of studies on various other aspects of potential pollutants have employed brown trout. Fivelstand and Lievestad (1984) examined mortality and parameters of physiological stress in brown trout exposed to varying levels of Al. Leland (1983) found that although copper was not inhibitory to the final stages of gonadal development, ultrastructural changes were observed in liver cells, including mitochondrial contraction and nuclear enlargement. Activity of the hepatic detoxification enzyme, glutathione S-transferase, directed towards chlorotharonil has been identified in brown trout (Davies, 1985) and Drewett and Abel (1983) have studied the pathology of lindane poisoning in brown trout. They found the symptoms of cellular damage to the liver, vascular congestion and gill damage, to be similar to the effects of acute hypoxia.

5.1.7 Olfaction

Although olfaction in fish has received a considerable amount of attention, little of this work has been on the brown trout. A series of papers by Bertmar (1972a,b,c,d) describe in detail the morphology of the olfactory organs in sea-trout, culminating in a more recent paper (Bertmar, 1978) which emphasizes the many unique cell types found in this tissue. The olfactory mucosa of adult and juvenile sea-trout show only minor differences (Bertmar, 1973). A recent investigation describes the degeneration of olfactory receptors in wild brown trout following transfer to an aquarium (Moran et al., 1987). However, complete regeneration occurred when the fish were returned to their home stream. The authors suggested this phenomenon may be due to the ionic profile of the two environments. Situations leading to damage of the olfactory apparatus are potentially of great significance, since the stream phase of homeward migration by anadromous trout is believed to be an olfaction-dependent process, whether by recognition of characteristic stream odours, or by the detection of chemical messengers, or pheromones, released by conspecifics within the river (Nordeng, 1977).

5.2 Genetics

Genetics, within the context of this review, refers to the assessment of the degree of genetic diversity between and within populations of fish. As Ferguson (1989) provides a thorough review of the various techniques available and their application to the study of genetic variation among brown trout, this overview will be confined to data published since 1989 or those not covered by Ferguson. His major conclusions were: that European brown trout populations possess abundant geographical variation in gene frequency of which that observed in individual populations represents only a limited proportion of the gene diversity of the species; that of the 70 gene loci examined, 38 (54%) have been found to be polymorphic with an average population showing polymorphism at 16% of its loci; that the brown trout is subdivided into a large number of reproductively isolated and genetically distinct populations within, as well as among, catchments; and that many genetically unique populations have been lost during the past century. Ferguson emphasises that there is an urgent requirement to identify and conserve the remaining genetic diversity, and that genetically unique populations are an irreplaceable resource for the management of sport and commercial fisheries.

A detailed comparison of migratory and non-migratory brown trout from three rivers in Scandinavia was carried out by Skaala and Naevdal (1989). A total of 10 enzyme systems coded for by 30 loci were analyzed and significant differences were found between the two life-history forms in all three watercourses, and between all three anadromous populations. In a similar study by Semenova and Slyn'ko (1988) on salmon and sea-trout populations of the Baltic, White and Barents Seas, a comparative analysis of electrophoretic spectra in 6 enzyme systems revealed the inhomogeneity of species composition of individual river populations. Only two of the enzyme marker systems were found to be species specific. The proportion of sea-trout/salmon hybrids varied between 0 - 31%. Verspoor (1988) has also reported widespread hybridization between Atlantic salmon and brown trout and Payne et al. (1972) detected natural hybrids between Atlantic salmon and sea-trout in a large sample of salmon. Skaala et al. (1990) examined the evidence for interbreeding between wild trout and farm escapees. They found evidence for successful reproduction and genetic interaction to be rare, pointing out that stocked fish sometimes have lower reproductive success than wild populations. They also note that analysis of mitochondrial DNA provides a further means by which genetic makers may be quantified. Berg and Ferris (1984), using restriction endonuclease analysis of salmonid mitochondrial DNA demonstrated that rainbow trout and Pacific salmon are more closely related than either is to the brown trout. An evaluation of methods available to permit discrimination between natural populations of brown trout and hatchery-reared fish suggested the use of a diagnostic mitochondrial DNA restriction pattern as a marker (Hynes et al., 1989).

Cytogenetics, the study of physical aspects of the chromosomes, has received little attention in fish. Examination of the chromosomes for numerical abnormalities, general morphology and banding patterns allows the detection of changes due to exposure to pollutants and disease. Blaxhall (1983c) described methodology by which the chromosomes of brown trout can be prepared from an enriched lymphocyte fraction to allow karyotyping to be carried out (karyotyping is the characterization and analysis of the chromosome complement at metaphase, within the nucleus). Hartley and Horne (1984) described the chromosome number and polymorphism in brown trout and compared this species with rainbow trout and Atlantic salmon. The karyotypes of each species were compared with each other and with other species in the same genera. More recently, Hartley (1987) has reviewed extant data on chromosome constitution in the major salmonid species, including brown trout.

5.3 Disease

5.3.1 Bacterial Infections and Immunology

The occurrence and clinical signs of infection caused by an atypical strain of *Aeromonas salmonicida* in brown trout on Swedish fish farms is described by Wichardt (1982a), together with some biochemical characteristics of the organism. The author further described the epizootic, demonstrated the effect of water temperature and stocking density on the infection rate and discussed differences in the susceptibility of Atlantic salmon and brown trout to disease (Wichardt, 1983b). Ellis and Stapleton (1988) also examined the differing susceptibility of various species to *A. salmonicida* and found that rainbow trout, Atlantic salmon and brown trout display an increasing order of sensitivity to infection. Examination of serum from each species revealed that while rainbow trout serum inhibited *A. salmonicida* protease activity, and salmon serum had little effect, serum from brown trout actually enhanced its activity. The authors suggest this may represent an important virulence mechanism. Ilyassov (1987) reports that breeding programmes designed to increase the resistance of fish to disease have succeeded in selecting brown trout with an enhanced resistance to furunculosis, the disease for which *A. salmonicida* is responsible.

The immune response of brown trout has been studied by a number of authors. Ingram and Alexander (1981) challenged brown trout with lipopolysaccharide (LPS) and monitored antibody production and antibody-producing cells following injection. The same authors also noted that a single injection of LPS, haemocyanin, or sheep red blood cells increased the numbers of antigen-binding cells and antibody-secreting cells in the spleen and anterior kidney of brown trout. Examination of a large number of sea-trout, including both smolts and ripe fish, revealed natural antibodies with haemagglutinating and haemolytic properties (Siwicki and Studnicka, 1986). Antibody titres were lower in smolts than in ripe fish, and much higher titres were observed in fish exhibiting signs of disease. Ingram also identified natural haemagglutinins in brown trout serum following challenge with sheep and human erythrocytes (Ingram, 1985). Tatner and Horne (1985) describe the optimum conditions and difficulties encountered when vaccinating brown trout, by direct immersion, against *Yersinia ruckeri*, the causative agent of enteric red mouth disease. The cellular defence mechanisms of brown trout have been examined O'Neill (1985b) who carried out an in vitro study on the activity of polymorphonuclear phagocytes isolated from the blood, examined their ability to phagocytose yeast cells and the effects of temperature on this process. Blaxhall (1985) provides information on the methodology required to separate and cultivate brown trout lymphocytes.

5.3.2 Parasitic Infestations

Kennedy (1978) described in detail the biology of the cestode parasite *Eubothrium* sp., suggesting that there are two races, a freshwater race which may infect smolts and parr, and a marine race preferentially found in Atlantic salmon, but which also infects sea-trout. Fahy (1980b), examined the same organism in migratory trout but interpreted his data to indicate that a marine race of *Eubothrium* is largely responsible for the burdens observed in sea-trout. The occurrence of metazoan parasites on brown trout was recorded by Conneely and McCarthy (1988) for both lake and river populations. They found that the diversity of lake parasite fauna was greater than that of the river fauna.

The of severity of ectoparasite infestations in brown trout were examined by Pickering and Christie (1980). Eight genera of parasites were identified with as many as five different genera occurring on single fish. Sexually mature male fish were consistently more severely infested than either mature females, or immature fish of either sex. A previously undescribed species of *Scyphidia* was identified on the skin of brown trout, but despite being present in heavy infestations on this species, was found to be incapable of transfecting brook, *Salvelinus fontinalis* (Pickering et al., 1985). Parasite infestation was found to produce a reduction in the number of superficial mucus-secreting goblet cells, the extent of demucification being proportional to the parasite burden (Pottinger et al., 1984). Parasite infestations are also associated with variation in the abundance of two other cell types within the epidermis of the brown trout, the acidophilic granular cell (Blackstock and Pickering, 1980) and the sacciform cell (Pickering and Fletcher, 1987). A potential protective role is hypothesized for both cell types.

5.3.3 Fungal Infections

The biology of *Saprolegnia* infections of salmonid fish, including brown trout, has been summarized by Pickering and Willoughby (1982). More recently, Wood et al., (1988) have studied the uptake and interaction of spores of the *Saprolegnia diclina-parasitica* complex with the external mucous layer of brown trout. They found that the pathogen *S. parasitica* was more efficient at establishing itself on the surface of the fish than the saprophyte *S. diclina*. These authors also found evidence that brown trout mucus was capable of inhibiting the growth of the fungus (Wood et al., 1988).

5.3.4 Viral Infections

The literature review and bibliography did not produce any references specifically referring to viral infections of brown trout.

6. OVERVIEW AND RECOMMENDATIONS FOR FUTURE RESEARCH

6.1 General Aspects

This report provides a bibliography and expert review of the literature on sea-trout. The expert reviews are based on key papers, rather than all publications listed in the bibliography.

The brown trout, *Salmo trutta*, is a highly polymorphic species and therefore it has been impossible to separate literature on sea-trout from that on migratory trout, lake trout or resident trout. Until relatively recently, the prevalent view was that sea-trout and resident trout were interbreeding fractions of a single spawning stock. Recent genetic and ecological evidence now suggests that there are sympatric, reproductively isolated, populations which qualify at least as distinct races or sub-species. There also appear to be at least two races of sea-trout in the British Isles and therefore there must be also major differences between allopatric populations. It would be clearly opportune to investigate the genetic basis for these differences between sympatric and allopatric stocks for the major sea-trout rivers in England and Wales.

Sea-trout fisheries in England and Wales are a valuable resource with a minimum value of £55 million. A recent analysis of sea-trout catches from 67 rivers in England and Wales has revealed clear patterns of spatial and temporal variability. The rivers can be arranged along a gradient so that as the mean annual catch for each river increases, there is a corresponding decrease in temporal variability (variation in catches between years for each river). This means that there is high variability between annual catches for poor rivers with a low mean annual catch, and low variability between catches for good rivers with a high mean annual catch.

These differences are important for the evaluation of the relative roles of density-dependent and density-independent factors in the regulation of population size. They also have important implications for the management of the different sea-trout populations. It is therefore important to establish a classification scheme for the major sea-trout rivers in England and Wales.

6.2 Early Life Stages

There is a large amount of qualitative information and some quantitative information on spawning behaviour, redd formation and redd structure, but the cues that stimulate spawning at a particular site are not fully understood. The dimensions and physical features of the redds are correlated with female size and there is also a positive relationship between female size and the grain size of the spawning gravels. Female sea-trout sometimes spawn with precocious resident males but the latter may be attacked and injured by the larger sea-trout males. The proportion of repeat spawners varies considerably between rivers (e.g. 0 to 71% in 29 rivers in Norway) but no comparative information is available for the major sea-trout rivers in England and Wales.

Spawning segregation of sea-trout and Atlantic salmon occurs in most rivers with the sea-trout spawning in small tributaries that are usually avoided by the salmon. Hybrids between the two species have been recorded in several rivers but these usually constitute a very small proportion of the total population of either species. There is some evidence to suggest that hybridization is more frequent when one species is deliberately introduced than when both species are naturally sympatric.

Both egg number and egg size are usually related positively to female size. In general, larger female sea-trout produce larger eggs, alevins and fry than smaller females and the larger fry can survive starvation longer than smaller fry. Female size therefore positively affects the probability of survival for the progeny. There is also a positive relationship between female size and egg burial depth in a redd, but this relationship does not hold for all streams (e.g. chalk streams) and there may be large variations in burial depth for females of similar size in the same stream.

If water temperature is known, a power function provides a useful model for predicting the times for eggs to develop to eyeing, median hatching and median emergence. Upper and lower limits for egg survival in brown trout are c. 16°C and 0°C, but values vary between studies. It would be useful to discover if such differences are within experimental error, or represent real, but subtle, differences between populations in different habitats or geographical areas. Although temperature predominates, other factors can influence hatching time, e.g. dissolved oxygen concentration, level of incident light, sub-lethal mechanical shock, low temperatures at the time of predicted hatch. A good flow of water through the gravel of the redd is also essential for ensuring a constant supply of oxygen and the removal of waste products.

Although losses in the egg and alevin stages are usually low in high density, stable populations regulated largely by density-dependent factors, they can be very high in low density, unstable populations that are affected chiefly by density-independent factors. The latter populations are those mentioned earlier as providing high variability between annual catches with a low overall mean catch. They are characteristically found in naturally harsh environments or in streams that have been affected adversely by human activities. The high losses in the egg and alevin stages are due to washout and drift. More information is needed on the relationship between the frequency and magnitude of spates and both gravel composition and the extent of gravel disturbance. Such work would include experimental studies on the effects of spates on planted eggs and alevins buried at various depths, including the use of artificial eggs. As it is in these poorer streams that there is scope for improvement, such work should provide information that would lead to habitat improvements to increase survival in the early life stages of sea-trout and thus stock enhancement.

A closely related problem is the effects of gravel composition and sediment deposition on the survival of alevins and the emergence of fry. Although this problem has been addressed for several salmonid species, little information is available for brown trout. Laboratory experiments indicate that both factors are important for the survival of the early stages but no detailed field studies have been made on this relationship for brown trout. More information is therefore needed on the ideal composition of spawning gravel for sea-trout eggs, alevins and fry, and the effect of sediment deposition on all these early life stages. Such studies should include detailed work in both field and laboratory on intragravel flow, oxygen supply, egg and alevin survival, and fry emergence.

Three problems that require further work have therefore been identified:
(i) The cues that stimulate and maintain spawning behaviour of sea-trout at a particular site.
(ii) The effects of washout and drift on the eggs, alevins and fry of sea-trout.
(iii) The ideal composition of spawning gravels for sea-trout eggs, alevins and fry, and the effects of sediment deposition on all these early life-stages. Although this subject has been worked on extensively in the past, the experimental designs are often simplistic and could be improved.

6.3 Ecology of the Juveniles in Fresh Water

There is strong evidence that the major processes regulating trout population density occur during the juvenile post-emergent stage (fish age <3-4 months). There is a critical period for survival in the first few weeks after fry emergence. It is in this period that most mechanisms for density-dependent survival appear to operate. The length of the critical period is itself density-dependent, becoming shorter as initial fry density increases. Density dependence during this period is linked to the establishment of feeding territories.

Although a great deal has been discovered recently about the mechanisms responsible for population regulation in juvenile sea-trout, information is still incomplete. The ultimate resource for which the young trout compete is energy, but little is known about the energy requirements of fish and why only a few positions in the stream are favoured as territories. It is remarkable that the total territorial area occupied by the young sea-trout is less than 10% of the total available stream bed, even in highly productive nursery streams. Until more is known about the energy and habitat requirements of juvenile sea-trout, adequate advice cannot be given on their management to improve production in these streams. Such information is also important to ensure that the high production is maintained in the best sea-trout rivers in England and Wales, and that potentially harmful management practices are not introduced, e.g. overstocking, introduction of competitive species, introduction of brown trout with markedly different genotypes. The policy of stocking is questionable in many rivers. Although the stocked fish usually have lower rates of survival, they may increase density-dependent competition in the indigenous population with a subsequent decrease in the population density of juveniles and a much more uniform fish size.

It should be stressed that such density-dependent processes predominate over density-independent processes only in the relatively stable, more productive streams, i.e. those mentioned earlier as having high annual catches with relatively small variation between catches. In poorer streams, losses are high in the egg and alevin stages, as mentioned in the previous section, and population densities of juveniles rarely attain the level at which density-dependent processes operate. Population density of juvenile sea-trout in such streams is largely controlled by environmental factors, especially extreme events. This is one of the reasons why annual sea-trout catches are usually highly variable in such rivers. It is therefore essential to obtain information on the mechanisms affecting survival in these poorer streams as well as more productive streams.

As juvenile of sea-trout and Atlantic salmon are sometimes sympatric, more information is required on interaction between the two species, especially on any differences in their habitat requirements. Although a great deal of information now exists on this subject, the results are often contradictory and far from complete. Once again, some discrepancies could be due to variations in the relative roles of density-dependent and density-independent factors in the different streams. A better understanding of these interactions between the two species would facilitate the optimum management of sympatric populations, especially in relation to habitat change or restoration.

Growth of juvenile sea-trout appears to be nearly always density-independent and is chiefly influenced by water temperature and initial size of the newly emerged fry. These factors are incorporated in a model for trout growth that was developed over 15 years ago. Although the model has been used successfully by several workers and has identified periods when food is limiting for growth, a new more sophisticated model is required. A large amount of additional information now exists in FBA/IFE and could be used to develop such a model, using dedicated computer programs that did not exist when the original model was developed. Such a model would be a useful management tool to determine if juvenile sea-trout in a particular stream were realising their full growth potential. It might even explain why the present model occasionally underestimates the growth rate in a few populations!

In general, faster-growing fish become smolts at an earlier age than slower-growing individuals. Smoltification in individuals is partially dependent on their growth rate in the spring period just prior to the smolt migration. Many studies describe the preponderance of females among sea-trout smolts and this may result from the early sexual maturation of males at the parr stage. Although there are many studies on precocious male salmon parr, few similar studies exist for sea-trout. Precocious male sea-trout parr apparently lose their osmoregulatory capacity that is essential for the migration from fresh to sea water. The proportion of precocious males in a population varies considerably from river to river. It would be useful to establish the extent of such differences, as well as the sex ratio of the smolts, for the major sea-trout rivers in England and Wales.

Six age-groups of sea-trout smolts have been recorded from the British Isles and mean smolt age is generally higher in Scotland (2.4 - 3.4 years) than in Ireland and Wales (2.1 -2.8 years). Again it would be useful to know the mean smolt age in the major sea-trout rivers in England and Wales.

Sea-trout smolt migration occurs in spring, usually April/May, with the migration normally starting earlier and finishing later than that for Atlantic salmon smolts. It has been suggested that the growing season has increased during this century, chiefly by extension of the spring growth period. More information is required on this aspect of smolt migration as well as the stimuli for migration.

There is clearly a shortage of information on the sex-ratio, age, size and numbers of migrating smolts in sea-trout rivers of England and Wales. Such information would be invaluable in the evaluation of possible reasons for the differences in sea-trout catches between rivers. If additional information could be obtained from the sea-trout catches, especially age and sex, then some very useful comparisons could be made between downstream-migrating smolts and returning adults. It would probably be impossible to obtain such information from all major sea-trout rivers but some rivers could be selected from the classification scheme proposed earlier.

Five problems that require further work have therefore been identified:
(i) In more productive streams, information is required on the mechanisms responsible for density-dependent regulation of the population density of juvenile sea-trout, especially their energy and habitat requirements.
(ii) In less productive streams, information is required on the environmental factors affecting the population density of juveniles, especially extreme events, and how these effects may be ameliorated for the fish.
(iii) In streams with sympatric juveniles of sea-trout and salmon, information is required on interactions between the two species and differences in their habitat requirements.
(iv) A new, more sophisticated, model should be developed for juvenile growth and thus replace an existing model that is simplistic and 15 years old.
(v) Information should be obtained on the sex-ratio, age, size and numbers of migrating smolts, as well as the proportion of precocious males, in as many populations as possible (rivers could be selected from the classification scheme proposed earlier). If age and sex of adult sea-trout could be obtained from rod and commercial catches, some valuable comparisons would be possible between smolts and returning adults in each river.

6.4 Ecology of the Adults

After migrating downstream as smolts in spring, some sea-trout (called whitling or finnock) return to fresh water after only one summer at sea. Other fish remain in the estuary or sea for at least one winter before returning to fresh water in late summer or autumn. A few fish, chiefly females, repeat the migration to the sea and return to fresh water so that they continue to spawn for two or more years.

As females often migrate to the sea/estuary slightly earlier than males and return to fresh water later, their period at sea is slightly longer than that for males of similar age. The marine residence time varies considerable between fish originating from different rivers, e.g. mean values of 69 days (female) and 66 days (males) for sea-trout from a Norwegian river, 43-362 days (mean 105 days) for kelts from an Irish river. There is clearly a need for information on arrival time and residence in the marine environment for fish from the major sea-trout rivers in England and Wales. Once again, differences are to be expected between the more productive and less productive rivers. If it is impossible to obtain such information for all rivers, then some rivers could be selected from the classification scheme proposed earlier.

There is very little information on migrations, feeding, growth and survival in the marine environment for sea-trout from the British Isles. Information from Norway indicates that few fish move more than 70-80 km away from their natal river and that the majority remain within a radius of 15 km or less. More limited work, using tagged fish, in Ireland, Scotland and England indicates a restricted movement along the coast. The pattern of tag returns in one study suggests that post-smolts from the same river stay together in the marine environment.

A few recent studies on feeding reveal a diverse diet ranging from crustaceans to fish (chiefly herring and sand eels) with the latter predominant. Newly-arrived smolts concentrate on crustaceans (chiefly amphipods). Known distributions of many prey items provide supporting evidence that Irish sea-trout feed mainly inshore. Recent investigations of declining populations of sea-trout in Ireland have shown that many fish are thin and starving, but it is unknown if this is due to lack of food. Sea-lice infestations have been found on these fish but this could be simply a reflection of their poor condition. Lists of parasites found on sea-trout in the marine environment are available but little is known about their effects on the fish.

The most detailed studies of growth in the marine environment are from Norway but the age-class structure of the sea-trout populations are so complex that definite conclusions cannot be drawn. Information from the British Isles indicates a rapid growth at sea, e.g. from a smolt length of 17-24 cm to c.30 cm at the end of the first sea-year in some Irish populations, from a smolt length of 13-20 cm to 17-25 cm after a summer at sea for Scottish finnock, from a smolt length of 21-22 cm to 32 cm for returning whitling in an English river.

Workers in Scotland and Ireland have suggested that marine growth eliminates differences in freshwater growth, but a detailed study in an English stream showed that the mean size of returning adults in each year-class was closely related to the mean size of juveniles at the start of their migration to the sea/estuary. Similar detailed comparisons are needed on other rivers.

Survival rates at sea vary considerably, e.g. 37% for smolts and 56-68% for older fish from a Norwegian river, 23% (males) and 29% (females) for small fish and 15% (males) and 31% (females) for larger fish together with a 15-year range of 9.1 - 43.4% from an Irish river, minimum values of 7.6 - 14.7% and 5.8 - 15.1% for two southern English rivers, c.24% for a northern English river. Kelt survival at sea also varies considerably, e.g. 40.5% for an Irish river, 25.7% for a southern English river, 16-21% for a Scottish river. More information is needed on survival, especially the relationships between the size or age of smolts and subsequent survival at sea, and between survival and time spent at sea.

Individual sea-trout may return to fresh water more than once in their lifetime and spawning does not occur in all these migrations. Mature and immature whitling usually return between July and September, but for older fish the timing of the return varies from a peak in May in southwest England to June/July in northwest England and Ireland, and as late as October in northeast England.

Although some workers have concluded that the homing instinct of sea-trout is not as good as that of Atlantic salmon, recent work suggests that they can home with considerable precision to their natal stream. This conclusion is supported by evidence of marked differences between the genetic composition of populations from different rivers. Whitling are known to spend the winter moving into and out of the lower reaches of non-natal rivers. It is possible that some of the older "smolts" taken in traps in the lower reaches in spring are actually whitling returning to sea.

Until recently, little was known about the movements of returning adults within the river. With the development of acoustic and radio-tags, information has been obtained on individual fish but numbers are always restricted by the availability of tags. Upstream movement occurs chiefly at night but sea-trout also move during the day during periods of increased flow. The distance travelled per day varies considerably but sea-trout usually move rapidly through the semi-tidal zone, complete most of their migration in 2-3 weeks and then remain near the confluence of a tributary until the final spawning migration. Resistivity counters provide information on greater numbers of fish than acoustic or radio-tags, and have shown that 80% of the fish move upstream during discharges equivalent to 20-30% of the average daily flow. Some response is shown to increases in flow, especially in the latter part of the season.

There is need for more information on the movements of sea-trout within the river because such information is essential when the construction of a barrage or weir is contemplated. It is possible that provisions for salmonid passage are based on salmon, rather than the smaller sea-trout, and therefore may be inadequate for the latter.

Only two studies on the feeding of adults in fresh water have been found in the literature; one is 65 years old and the other 19 years old! Both indicate a varied diet of terrestrial and freshwater invertebrates with occasionally eggs and juveniles of salmonids. More information would be useful, especially if it could be related to the energy requirements of the returning adults.

Three problems that require further work have therefore been identified:
(i) Information is required on the relationship between the age or size of the smolts and the arrival time, residence, growth and survival of sea-trout in the marine environment, using data obtained from catches of smolts and returning adults from rivers ranging from high to low productivity (rivers could be selected from the classification scheme proposed earlier).
(ii) Information is required on migration, feeding and parasites of sea-trout in the marine environment but such work would be difficult and very expensive with a high risk factor.
(iii) Information is required on the arrival time, movements, feeding and energetics of adult sea-trout in fresh water, especially in relation to fish passages. Use of acoustic or radio-tags could facilitate some of this work but has the disadvantage that it is laborious, expensive and inevitably restricted to few fish.

6.5 Physiology, Genetics and Diseases

The physiological literature rarely discriminates between sea-trout and brown trout, and therefore it is impossible to summarise work on only sea-trout.

The chief phases of the endocrinology of the reproductive cycle are known and summarised in this review (section 5.1.2), but a description of the complete reproductive cycle in both male and female brown trout has yet to be made, especially in wild populations. Changes associated with the reproductive cycle are not confined to the production of ova and sperm. There are major changes in blood cells with marked lymphocytopenia in both sexes and an increase in erythrocyte number in males only. The former change may contribute to the increased incidence of disease in both sexes during spawning, and the latter change may facilitate the increase in oxygen consumption by males.

Although skin structure changes with age, season and physical trauma, the most notable changes in males occur during maturation when the skin thickens and almost completely demucifies. Such changes are important because they could facilitate the incidence of disease.

The physiology of osmoregulation during smoltification is poorly understood. Experiments on osmoregulation in brown trout show that acclimation to increasing salinity is necessary. When brown trout are exposed to high salinity water, they shows the characteristics of smolting. However, most authors emphasize that little is known about the physiology of smoltification of sea-trout. There is clearly a need for more information on this subject.

Although a great deal is now known about the physiology of the stress response in captive salmonids, there is a paucity of information on wild fish. This is chiefly because the most frequent focus of such work has been salmonid aquaculture. Much of this work is also relevant to natural populations of salmonids, including sea-trout.

The basic time-course and nature of the stress response in brown trout are now established, and are summarised in this review (section 5.1.4). Stress has deleterious effects not only on the immune system of the fish but also on the reproductive process. A stressed fish will be therefore more susceptible to disease and stressed adults will exhibit a reduction in gonad weight. When repeatedly exposed to a stressful stimulus, brown trout show acclimation in captivity but it is not known if this also occurs in the wild. Little attention has been given to the stress response in wild populations of brown trout. Techniques developed for captive fish could be used to assess the probable consequences of environmental perturbations on the growth, reproductive potential and survival of wild brown trout, including sea-trout. For the latter, the effects of environmental stress on smoltification have not been investigated but may be of major significance.

The stress response of brown trout is closely related to the physiological effects of pollution. Lethal effects of low pH and dissolved metals, especially aluminium, are summarised briefly in this review (section 5.1.6). Some effects of low pH and aluminium may be ameliorated by increasing calcium levels in the water, but the decline of salmonid populations in acid waters may be due to the presence of other metals as well as aluminium. There is little information on the effects of prolonged sublethal levels of pollution on the growth, reproductive success and survival of brown trout in the wild. As mentioned earlier, physiological indicators of stress and pollutant exposure can now be measured and would allow the identification of populations 'at risk' from aquatic pollution.

Although there are many publications on olfaction in fish, few deal with brown trout. Recent work has revealed only minor differences in the olfactory mucosa of adult and juvenile sea-trout. The olfactory receptors in wild brown trout degenerate when the fish are captive in aquaria but regenerate after transfer to their home stream. There is little information on olfactory processes in sea-trout and their role in both homeward migration and spawning. The effects of pollutants on olfaction are also poorly understood and are of obvious importance if they negate the homing ability of the sea-trout by damaging the olfactory apparatus.

As mentioned earlier in this review (sections 1, 6.1), recent genetic and ecological evidence indicates clear genetic differences not only between brown trout populations in different rivers but also between populations in different tributaries within the same river system. These genetic differences are still poorly understood and, as proposed earlier (section 6.1), there is an urgent need to investigate the genetic basis for these differences between allopatric and sympatric stocks for the major sea-trout rivers in England and Wales.

Bacteria, fungi and protozoan parasites are known disease-causing agents in brown trout. Susceptibility to the same disease can vary considerably between salmonid species. It is therefore wrong to assume that conclusions from work on other salmonid species are also applicable to sea-trout. The immune response of brown trout has been studied by several workers, and both smolts and adult sea-trout are known to carry natural antibodies that increase in fish showing signs of disease. Although there is some information on the bacteria, fungi and protozoan parasites of brown trout, including sea-trout, there is little information on how disease interacts with stress responses, especially when the immune system of the fish is weakened.

Four problems that require further work have therefore been identified:
(i) Information is required on the endocrinology of the complete reproductive cycle in male and female sea-trout, especially in wild populations, and on the role of pheromones during spawning.
(ii) Information is required on the stress response in sea-trout in the wild, using techniques developed for captive fish. Such work would facilitate assessment of environmental perturbations, including pollutants, on the growth, reproduction potential and survival of brown trout, including sea-trout. The effects of environmental stress on smoltification should be part of this work and would require more detailed knowledge of the physiology of smoltification in sea-trout.
(iii) Information is required on olfactory processes in sea-trout and their role in both homeward migration and spawning. The effects of pollutants on olfaction should be addressed because they may negate the homing ability of sea-trout.
(iv) Information is required on diseases specific to sea-trout and how diseases interact with stress responses, especially when the immune system of the trout is weakened.

6.6 Recommendations for Future Research

Although they are not mentioned as a separate topic in this review, long-term studies at such sites as the Burrishoole, North Esk and Black Brows Beck provide essential background data for the interpretation of short-term fluctuations and trends. As Le Cren (1985) concludes, problems in the population ecology of sea-trout can rarely be solved by only short-term research projects, useful though these may also be. Every effort should therefore be made to protect any existing long-term studies on sea-trout populations because it is unlikely that such work will be initiated again in the present financial climate with its emphasis on short-term funding.

The following projects are essentially collations of the suggestion for further work at the end of each of the previous sections. They are arranged in an order of priority, determined by need and cost, but it is acknowledged that this order could easily change, depending upon future developments.

(i) It is important to establish a classification scheme for all 67, major sea-trout rivers in England and Wales, using the relationship between the overall mean catch for each river and the temporal variance (variation in catches between years for each river). Such a scheme would naturally lead to an analysis of the relationship between mean catch and several factors that may effect the size of the catch, e.g. weight of fish caught in each year and river, total discharge in each year and river, number of smolts leaving each river, fishing effort in each river.

(ii) It is important to investigate the genetic differences between sea-trout from all the major sea-trout rivers in England and Wales, and between both sea-trout and resident brown trout within selected rivers (these could be selected from the classification scheme already proposed).

(iii) In more productive streams, information is required on the mechanisms responsible for density-dependent regulation of the population density of juvenile sea-trout, especially their energy and habitat requirements.

(iv) In less productive streams, information is required on the effects of washout and drift on the eggs, alevins and fry of sea-trout, and on the environmental factors affecting the population density of juveniles, especially extreme events.

(v) Information is required on the ideal composition of spawning gravels for sea-trout eggs, alevins and fry, on the cues that stimulate and maintain spawning behaviour of sea-trout at a particular site, on the endocrinology of the complete reproductive cycle in wild male and female sea-trout, and on the role of pheromones during spawning.

(vi) Information is required on the sex-ratio, age, size and numbers of migrating smolts, on the proportion of precocious males in the population, and on the relationship between the age or size of the smolts and the arrival time, residence, growth and survival of sea-trout in the marine environment, using data obtained from catches of smolts and returning adults from rivers ranging from high to low productivity (these could be selected from the classification scheme already proposed).

(vii) A new, more sophisticated, model could be developed for juvenile growth and thus replace an existing model that is simplistic and 15 years old. As the data have already been collected, such a study would be relatively inexpensive.

(viii) Information is required on the stress response in sea-trout in the wild, using techniques already developed for captive fish. Such work would facilitate assessment of environmental perturbations, including pollutants, on the growth, reproduction potential and survival of sea-trout. The effects of environmental stress on smoltification should be part of this work and would require more detailed knowledge of the physiology of smoltification in sea-trout.

(ix) Information is required on the arrival time, movements, feeding and energetics of adult sea-trout in fresh water and on the role of olfactory processes in homeward migration and spawning. Acoustic or radio-tags could be used in some of this work but few fish can usually be tagged and the work will be laborious and expensive.

(x) In streams with sympatric juveniles of sea-trout and salmon, information is required on interactions between the two species and differences in their habitat requirements. Ideally, the work would have to be performed simultaneously in several streams with different proportions of the two species. This project would be laborious and very expensive.

(xi) Information is required on diseases specific to sea-trout and how diseases interact with stress responses, especially when the immune system is weakened. This project is related to (viii) and may be best performed after that project is well advanced.

(xii) Information is required on migration, feeding and parasites of sea-trout in the marine environment. This project would be difficult and very expensive with a high risk factor.

7. ACKNOWLEDGEMENTS

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8. BIBLIOGRAPHY

Scope

This bibliography lists documents relating to sea-trout from England, Wales, Scotland, Ireland, Scandinavia (including Denmark) and France. The earliest reference is dated 1866 and coverage extends to the March 1991 literature. All references quoted in the reviews in this report appear in the bibliography. This includes various methods papers etc. which might otherwise seem misplaced.

Arrangement and Citation Style

The references are listed in alphabetical order of the first author. In multiple authored papers, all authors are listed in full. Titles of papers, where possible, have been given in English. An indication is given at the end of the title if the main body of the text is in a different language e.g. (F.e.) indicates that the paper is in French with an English summary. A few references have been given two dates e.g. (1938)(1937). In such cases, the first date is the actual date of publication and the second is the year quoted on the document. Journals have been abbreviated in compliance with the World list of scientific periodicals. Annotations have been added by I. Pettman to some references and these annotations appear in square brackets e.g. [sea-trout p41-49].

Sources

The bibliography was compiled using a wide range of sources and methods. The major sources were:

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HEAD OFFICE
Rivers House
Waterside Drive
Aztec West
Almondsbury
Bristol
BS12 4UD
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