

ICES SGBICEPS REPORT 2009

ICES DIADROMOUS FISH COMMITTEE

ICES CM 2009/DFC:02

REF. WGNAS
ACOM
TGRECORDS
SCICOM

Report of the Study Group on Biological Characteristics as Predictors of Salmon Abundance (SGBICEPS)

3–5 March 2009

Lowestoft, UK



ICES
CIEM

International Council for
the Exploration of the Sea

Conseil International pour
l'Exploration de la Mer

International Council for the Exploration of the Sea Conseil International pour l'Exploration de la Mer

H. C. Andersens Boulevard 44–46
DK-1553 Copenhagen V
Denmark
Telephone (+45) 33 38 67 00
Telefax (+45) 33 93 42 15
www.ices.dk
info@ices.dk

Recommended format for purposes of citation:

ICES. 2009. Report of the Study Group on Biological Characteristics as Predictors of Salmon Abundance (SGBICEPS), 3–5 March 2009, Lowestoft, UK. ICES CM 2009/DFC:02. 119 pp. <https://doi.org/10.17895/ices.pub.8773>

For permission to reproduce material from this publication, please apply to the General Secretary.

The document is a report of an Expert Group under the auspices of the International Council for the Exploration of the Sea and does not necessarily represent the views of the Council.

© 2009 International Council for the Exploration of the Sea

Contents

Executive summary	3
1 Introduction	4
1.1 Main tasks	4
1.2 Background.....	4
2 Summary of literature.....	6
2.1 Salmon life history strategies	6
2.2 Salmon in the Sea.....	7
2.3 Climatic/oceanic factors	17
2.4 Salmon in Freshwater.....	21
3 Data sets.....	31
3.1 Data sources and requirements	31
3.2 Data on biological characteristics	31
3.3 Data quality issues – caveats and limitations	33
3.4 Salmon abundance	35
3.5 Environmental data sets	37
4 Case Studies.....	41
4.1 Biological characteristics of the River Bush salmon stock – UK (N. Ireland).....	41
4.2 Biological characteristics of salmon from the River Dee, North Wales and other monitored rivers in UK (England & Wales)	44
4.3 Biological characteristics of salmon from the River Frome – UK (England & Wales).....	48
4.4 Biological characteristics of salmon from the River Test – UK (England & Wales).....	51
4.5 Evidence for later age at maturity in Norwegian salmon stocks in recent years.....	54
4.6 Baltic Sea – changes in post-smolt survival and the factors affecting it.....	55
4.7 Baltic Sea – review of Swedish tagging experiments and implications for estimating post-smolt survival.....	59
4.8 Fecundity of Penobscot River broodstock.....	64
5 Exploratory analyses	66
5.1 Condition Factors – considerations in their application and use.....	66
5.2 Assessment of Fulton’s K versus Relative Mass Index, W_R	70
5.3 Biological characteristics data sets – temporal trends	72
5.4 Biological characteristics data sets – spatial patterns.....	75
5.5 Overview of preliminary analyses of temporal and spatial trends	83

5.6	Exploration of two-way relationships	87
5.7	Effect of smolt size and sex on sea-age of returning adult salmon.....	95
6	Overview and recommendations	96
	Annex 1: List of participants.....	99
	Annex 2: List of working documents and data sets.....	101
	Annex 3: References	103
	Annex 4: Draft ToRs for proposed follow-up meeting	118

Executive summary

A Study Group on the identification of biological characteristics for use as predictors of salmon abundance [SGBICEPS] was agreed by ICES at the 2008 Science Conference (C. Res. 2008/2/DFC02) and met in Lowestoft, England, from 3 to 5 March, 2009.

The meeting was chaired by Ian Russell, UK and attended by 14 people from five European countries; data were made available for analysis for stocks throughout the geographic range of Atlantic salmon - Canada, USA, Iceland, Russia, Finland, Norway, Sweden, UK (Scotland), UK (England & Wales), UK (N. Ireland) and France.

The main objectives of the meeting were to identify and compile time series of data on biological characteristics of Atlantic salmon and conduct preliminary analyses on these data as a basis for developing, and where possible testing, hypotheses relating any observed changes in these data to marine mortality and/or abundance trends for Atlantic salmon stocks and/or environmental changes.

The meeting reviewed the literature and a number of case studies, and critically analysed available data sets in addressing the ToRs. The report structure reflects these activities and provides: (1) a summary of the available literature; (2) a description of the data sets compiled; (3) an overview of a number of case studies; (4) details of provisional exploratory analyses completed and hypotheses tested; and (5) recommendations for the future.

In brief:

- Literature - the review summarises the life history strategies of salmon and changes in biological characteristics of different life stages across the geographic range of the species in relation to key environmental variables. A number of existing hypotheses concerning the factors regulating the mortality of salmon are considered.
- Data sets - building on work started by WGNAS, time series of various biological characteristics were compiled using a standardised data entry spreadsheet for 24 separate salmon stocks. In taking forward preliminary analyses of these data sets, a number of constraints and caveats were noted, mostly relating to sampling programmes and methodological differences. Data providing abundance metrics and survival/mortality information for different indicator stocks were also assembled, and potential data sources on N. Atlantic environmental variables explored.
- Case studies - information from a number of river or area-specific investigations were presented and reviewed.
- Exploratory analyses - the various stock-specific biological characteristics were examined for possible time trends and different approaches were used to examine changes in biological characteristics over broader spatial scales. Significant trends were apparent for many of the variables explored, as well as a number of significant inter-relationships between selected stock characteristics. Some preliminary hypotheses were investigated.
- Recommendations – the Study Group recommends that work should continue to explore trends, investigate possible common patterns and regional groupings, and develop and test hypotheses. This should be accompanied by efforts to extend the available data and further rigorous quality assurance of the data sets used.

1 Introduction

1.1 Main tasks

In June 2008, NASCO asked ICES to 'continue the work already initiated to investigate associations between changes in biological characteristics of all life stages of Atlantic salmon, environmental changes and variations in marine survival with a view to identifying predictors of abundance'. WGNAS had begun work on this question but had been unable to make significant progress due to other work pressures. A need was therefore identified for a separate expert group to take on this task if significant progress was to be made with addressing NASCO's request for this advice.

At the 2008 Science Conference, ICES made a resolution (C. Res. 2008/2/DFC02) that a Study Group on the identification of biological characteristics for use as predictors of salmon abundance [SGBICEPS] (Chair: Ian Russell, UK) will meet in Lowestoft, England, from 3 to 5 March, 2009. By addressing this topic within a Study Group, ICES hoped it would be possible to provide the opportunity for scientists working on both Baltic and Atlantic salmon to contribute to the work. The terms of reference given by ICES were as follows:

- a) identify data sources and compile time series of data on marine mortality of salmon, salmon abundance, biological characteristics of salmon and related environmental information;
- b) consider hypotheses relating marine mortality and/or abundance trends for Atlantic salmon stocks with changes in biological characteristics of all life stages and environmental changes;
- c) conduct preliminary analyses to explore the available datasets and test the hypotheses.

The Study Group was attended by 14 people; the full address list of the participants is provided at Annex 1. The Study Group considered 12 working documents; the working documents are listed at Annex 2. In addition, the Study Group examined data relating to biological characteristics of salmon from a wide range of stocks around the North Atlantic. Many of these data were collated prior to the last NASWG meeting (April 2008) using a spreadsheet designed by Tim Sheehan (USA & NASWG Chair at that time), although additional data sets were also provided in the run up to the Study Group meeting. Data were available for analysis from salmon stocks in Canada, USA, Iceland, Russia, Finland, Norway, Sweden, UK (Scotland), UK (England & Wales), UK (N. Ireland) and France. A full list of the data sources and the contributors is also provided in Annex 2.

1.2 Background

Over the past 20–30 years there has been a marked decline in the abundance of Atlantic salmon across the species' distributional range (Figure 1.2.1). Wild Atlantic salmon populations are declining across most of their home range and, in some cases, disappearing (ICES, 2008). Generally, populations on the southern edge of the distribution seem to have suffered the greatest decline (Parrish *et al.*, 1998). This may be linked to climatic factors. The decline in salmon abundance has coincided with a variety of environmental changes linked to an increase in greenhouse gases and a corresponding increase in temperatures (IPCC, 2001), which is most likely to have manifest effects at the edge of the species range. However, these areas are often also the ones with higher human population density and therefore, typically, where potential impacts on the freshwater environment may also be greater. This has potential implications

for the survival of juvenile salmon and their resulting fitness when they migrate to sea as smolts (e.g. Fairchild *et al.*, 2002). In addition to changes in climate and potential freshwater issues, various other factors have been postulated as possibly contributing to the decline in stock abundance, including predation, aquaculture impacts and the effects of fisheries.

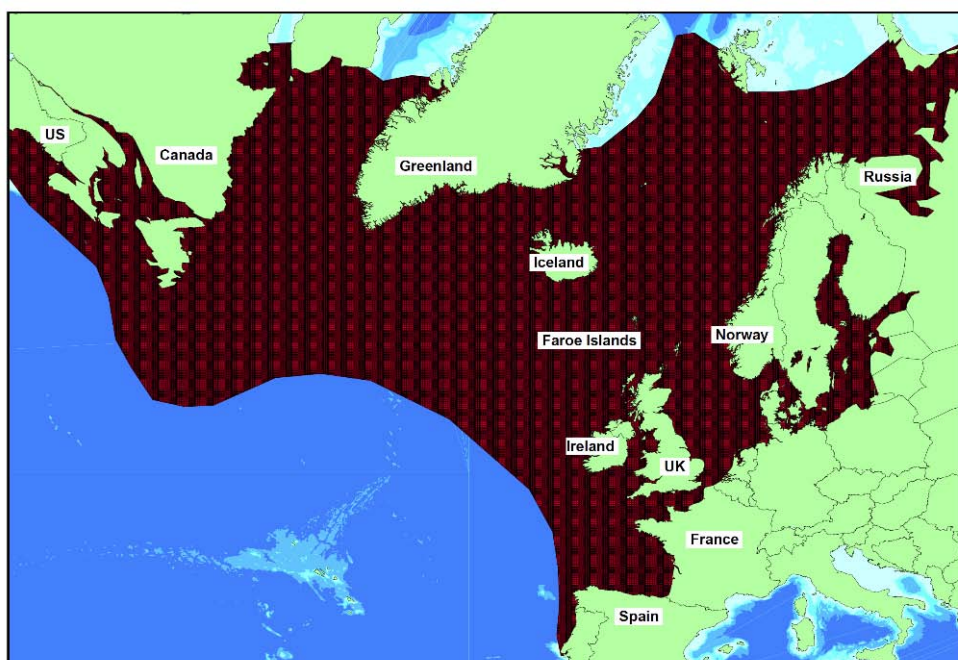


Figure 1.2.1. Approximate oceanic distribution area of Atlantic salmon.

Atlantic salmon occupy three aquatic habitats during their life-cycle: freshwater, estuarine and marine. Similar factors contribute to mortality in each of these habitats – competition, predation and environmental factors – but despite occurring in different habitats these are not independent. Conditions experienced within the freshwater environment can affect the survival of emigrating smolts and marine conditions may subsequently modify the spawning success of fish in freshwater.

It should be noted that the decline in salmon populations has occurred despite significant reductions in exploitation, although this does not preclude possible fishery effects. An underlying cause has been a marked increase in the natural mortality of salmon at sea – the proportion of fish surviving between the smolts' seaward migration and their return to freshwater as adult fish (e.g. Peyronnet *et al.*, 2008). The processes controlling marine survival are relatively poorly understood (Friedland, 1998), although there is growing support for the hypotheses that survival and recruitment is mediated by growth during the post-smolt year, for European stocks at least (Friedland *et al.*, 2009).

In addition to the declines in abundance, changes in salmon life histories are also widely reported throughout their geographic range, affecting factors such as sea-age composition, size at age, age at maturity, condition, sex ratio and growth rates (e.g. Nicieza & Braña, 1993; Hutchings & Jones, 1998; Niemelä *et al.*, 2006; Peyronnet *et al.*, 2007; Aprahamian *et al.*, 2008; Todd *et al.*, 2008). Changes are also manifest in freshwater stages, affecting factors such as the size and growth of parr and the age of smolting (e.g. Davidson & Hazelwood, 2005; Jutila *et al.*, 2006).

In addressing the terms of reference posed by NASCO, the Study Group have been asked to consider hypotheses relating marine mortality and/or abundance trends for Atlantic salmon stocks with changes in biological characteristics of all life stages and environmental changes. The purpose is to determine whether declines in marine survival and abundance coincide with changes in the biological characteristics of juveniles in fresh water or are modifying characteristics of adult fish (e.g. size at age, age at maturity, condition, sex ratio, growth rates, etc.), and whether these changes are linked with environmental change. As a foundation for addressing these questions, the following sections attempt to summarise available information on the life history strategies of salmon and changes in their biological characteristics in relation to some of the key environmental variables as a basis for developing hypotheses as to what the possible underlying mechanisms might be.

2 Summary of literature

2.1 Salmon life history strategies

Atlantic salmon have highly diverse and plastic life-history traits and occupy a diverse array of environments (Elliott *et al.*, 1998). This diversity has been suggested as the mechanism that enables small populations to persist (Saunders & Schom, 1985). Atlantic salmon populations vary from fully freshwater resident to anadromous forms. Freshwater resident populations occur throughout the range of the species in North America, but are relatively uncommon in Europe (MacCrimmon & Gots, 1979). Non anadromous populations exist in water courses that are isolated from the sea but also in sympatry with anadromous populations. In contrast to Arctic charr, there is no correlation between the prevalence of anadromous forms and latitude (Klemetsen *et al.*, 2003). Atlantic salmon also exhibit variability, both within and among populations, in factors such as freshwater habitat use, length of freshwater residence and age at maturity (Klemetsen *et al.*, 2003).

Most Atlantic salmon populations are anadromous, with smolts migrating to sea to exploit the more abundant marine food resources and attain a large size at maturity before returning to freshwater to breed. The majority of these fish undergo extensive oceanic migrations (Hansen & Quinn, 1998). However, stocks in the Baltic Sea (Karls-son & Karlström, 1994) and Inner Bay of Fundy (Amiro, 1998) tend to stay within the confines of these respective areas, although there is evidence that the latter may not be a successful strategy and may be changing (Hubley *et al.*, 2008). Some stocks at the northern extremity of the North American distribution remain close to the river, mature after just a few months at sea and are known as 'estuarine' salmon. There is some evidence that the incidence of these fish has become more prevalent in recent years in certain rivers (Downton *et al.*, 2001).

Fish typically return to their natal rivers to spawn, resulting in a certain degree of reproductive isolation between different populations, although some straying into other rivers does usually occur (Marshall *et al.*, 1998). Salmon normally spawn in the same season that they return to freshwater, but this does not always apply (Webb & Campbell, 2000).

Unlike most Pacific salmon, Atlantic salmon can spawn repeatedly (i.e. they are iteroparous), although there is wide variability between populations. Salmon mature at various sea-ages, typically maturing for the first time as 1 to 3 sea-winter (SW) fish, but also sometimes at older sea-ages. The biological characteristics (e.g. size at age, sex ratio, smolt age, fecundity, etc.) of these sea-age groups vary widely among stocks and with geographic location. For example, maiden 5SW salmon occur in the

River Tana (Teno) in northern Europe (Erkinaro *et al.*, 1997), while stocks in Newfoundland consist almost entirely of salmon which mature as 1SW fish (Dempson *et al.*, 1986).

Life-history characteristics are further complicated by the fact that parr can also become sexually mature. This is typically restricted to males, although there are isolated reports of mature female parr (e.g. Power, 1969; Moore & Riley, 1992). Sexually mature male parr successfully mate with mature adult females both in the presence and absence of adult males (Myers & Hutchings, 1987) and are thought to play an important role in maintaining small populations (L'Abée-Lund, 1989). Reduction of the effective population size (N_e) can radically alter the rate of loss of genetic heterozygosity in any population and this may be especially pertinent to small river stocks. Martinez *et al.* (2000), for example, assessed the frequency of successful fertilizations by precocious male parr in three threatened river stocks at the southern distributional limit of salmon in Europe. They found frequent multiple paternity of eggs within redds, and that precocious parr were sufficiently successful to have significant effects in increasing N_e .

Life-history strategies are a means to successful reproduction and flexibility of these strategies is a characteristic of salmonid species (Thorpe, 1990). Stocks of salmonids are often defined by a propensity to migrate and mature at particular ages, but if transplanted to a non-native environment they perform differently (Thorpe, 1990). Hence, the environment influences their genetic predisposition to follow a particular life-history strategy. However, the direction of those decisions may depend on the current metabolic performance of the individual. Therefore, such developmental decisions may be viewed within an abiotic-biotic regulatory continuum, depending on the abiotic environment for their initiation and the biotic environment for their completion (Thorpe, 1990).

The high degree of variability in life-history characteristics and phenotypic plasticity needs to be borne in mind and provides a necessary backdrop for reviewing and assessing recent changes in biological characteristics of the fish. It is also important to bear in mind that many of these biological characteristics are inextricably linked – e.g. growth, maturation and run timing – and thus impossible to consider in isolation.

2.2 Salmon in the Sea

Marine survival

Marine survival of salmon is typically expressed as the proportion of emigrating smolts that return to homewaters (to the coast) or to their river of origin as 1SW or 2SW adults. In reality, these ratios are return rates rather than survival rates (SALMODEL, 2003) since they reflect the effects of both mortality and maturation. Changes in the age at maturation may affect the relative proportions of a smolt cohort that return as 1SW or 2SW fish, but this can also result from changes in natural mortality in different areas of the ocean. Nevertheless, these return rates can be considered as convenient indicators of survival (SALMODEL, 2003).

Numerous factors are thought to affect the survival of salmon in the sea, both biotic and abiotic, although their relative impact and the interaction between them are poorly understood. Marine mortality of salmon is considered to be density-independent since salmon abundance is not constrained by the carrying capacity of the NE Atlantic (Jonsson & Jonsson, 2004). Instead, density-independent processes are believed to regulate marine mortality either directly (physiologically) or indi-

rectly by controlling a fish's ability to feed (find high densities of prey), migrate or escape predators.

Sources of marine mortality, in general, are poorly understood due to a lack of basic knowledge about post-smolt distributions and habits (Friedland, 1998), although information on post-smolt distribution is improving (e.g. Holm *et al.*, 2000). However, it is generally accepted that the main marine mortality events take place during the first year of sea life when survival, maturation, and migration trajectories are being defined (Hansen & Quinn, 1998; Potter & Crozier, 2000; Friedland *et al.*, 2005, 2009). The key factors influencing the mortality of salmon in the sea are believed to be:

- Environment – climatic variations play a key role in shaping the marine environment, affecting currents, gyres and sea surface temperatures (SST). Such factors can impact upon salmon directly (e.g. migration routes) or indirectly (e.g. effects on the abundance and distribution of prey species or predators). The broad scale declines in salmon abundance and the more pronounced declines for MSW salmon point to changes in the marine environment affecting the survival of salmon at sea. Friedland & Reddin (1993) demonstrated correlations between the area of potential post-smolt habitat in the sea, defined as the area combining their optimal temperature and full salinity, and catches of salmon from that area. More recent studies have confirmed such links for European stocks occupying the eastern North Atlantic, though the pattern for North American stocks and the western North Atlantic (e.g. Gulf of St Lawrence) are rather more complex (Friedland *et al.*, 2003a, b, 2009).
- Food – growth and survival are likely to be affected by the abundance and distribution of suitable prey, particularly during the period of initial marine residence. When smolts enter saltwater their energy expenditure increases and scarce food resources at this time may result in increased mortality. A lack of food would also reduce growth and increase the likelihood of predation. The diet of salmon has been shown to change over time (Andreassen *et al.*, 2001; Haugland *et al.*, 2006) and with sea-age (Jacobsen & Hansen, 2001), but is still poorly understood. For example, although stomach contents analysis permits an appraisal and comparison of prey items taken in differing locations and for salmon of differing size and sea-age, no detailed assessment of active prey choice is yet possible because of a lack of comprehensive data on prey availability.
- Growth - salmon exhibit higher rates of growth and mortality than other pelagic species (Cairns, 2003). This strategy is speculated to represent a trade-off between the two and highlights the possible importance of marine growth in controlling marine survival and recruitment. It is generally accepted that mortality at sea is growth mediated (Friedland *et al.*, 1996,) and significant relationships have been demonstrated between SST, survival and growth in the first sea year (Friedland *et al.*, 2000), and particularly in the first summer (Friedland *et al.*, 2009). Distinguishing between environmental and genetic influences on growth is difficult. Differences in growth may reflect variable food supply or more general changes in oceanographic processes, which could affect some populations more than others depending on their marine distribution. Differences in growth rates may also be influenced by natural selection processes in individual rivers.

- Predation – this may be the most important source of salmon mortality, although quantitative information on predation in the sea is scarce. Predation is believed to be most severe on smolts and post-smolts - small fish are vulnerable to a larger range of predators than large fish and more predators occur on the continental shelf than in oceanic areas. Mortality is generally lower for larger smolts (Lundqvist *et al.*, 1994). Size clearly is an important factor determining the survival of hatchery-reared smolts (e.g. Kallio-Nyberg *et al.*, 2004; Lacroix & Knox, 2005) and the typically larger size of hatchery-reared smolts may, to some extent, compensate for their origin in comparison to wild smolts (Jutila *et al.*, 2006; Kallio-Nyberg *et al.*, 2004, 2006). But the role of smolt size in influencing the performance of wild stocks has been poorly studied and remains unclear. For example, for wild fish from the River North Esk (Scotland), smolt size clearly had no influence on resultant survival rate to adulthood, whereas for the River Figgjo (Norway), adult survival rate was correlated with size at sea entry (Friedland *et al.*, 2009).
- Competition – while intra-specific competition may be unlikely in the North Atlantic, there is some evidence to suggest that inter-specific competition could occur. For example, negative relationships have been observed between herring abundance in the Norwegian Sea and salmon catch and between herring abundance and marine survival of smolts from the River Figgjo (SALMODEL, 2003). For salmon in the Baltic Sea, survival indices have been correlated with both the total production of wild and hatchery-reared smolts in the Baltic and herring recruitment (ICES, 2008b).

A number of these possible regulatory factors are considered in greater detail below in relation to different salmon stock characteristics.

Age at Maturation

Age at maturation is believed to be a key life-history trait, as fitness is reported to be more sensitive to changes in this trait than to changes in many other life-history traits (Stearns, 1992). Early maturation reduces the generation time and increases the chance of surviving to breed, but early maturing individuals are smaller and produce fewer or smaller progeny. Hence, an optimal trade-off will depend on age-specific growth and mortality rates (Stearns, 1992). In salmon, any such trade-offs are also likely to be influenced by the levels of repeat spawning. Life-history theory suggests that a trait will change in relation to changes in age-specific mortality, growth and fecundity to ensure fitness is maximized (Roff, 1992).

Thorpe (2007) cautions that age at first maturity or size at first maturity in salmon can be misleading measures, since they appear to suggest that steps toward reproductive ripeness have not taken place until a specific age or size is reached at which spawning can occur. In Atlantic salmon, maturation begins in the egg soon after fertilization and continues intermittently until the individual is capable of spawning. Thorpe (2007) suggests that the fish's developmental decisions are likely to be based on proximate cues, both internal and external, largely independent of size and age.

In Atlantic salmon, fish mature at various ages and this affects the patterns of return - run timing - of adult fish to freshwater.

Run Timing and Sea-age

Run timing in adult Atlantic salmon is highly variable. Different sea-age classes of salmon have different patterns of run timing and these vary on a geographic scale,

but also between stocks in a region and within stocks over time. A change in the pattern of run timing could therefore result from a change in the balance between the various sea-age classes, a change in run timing within sea-age classes or both. There is widespread evidence of change in the sea-age composition of salmon throughout their geographic range (e.g. Gough *et al.*, 1992; Anon., 1994; Summers, 1995; Gudjonsson *et al.*, 1995; Welton *et al.*, 1999; Juanes *et al.*, 2005; Quinn *et al.*, 2006; Aprahamian *et al.*, 2008).

In the UK, 1SW salmon mainly enter rivers from June to August, though some rivers have strong autumn runs, 2SW fish enter throughout the year, but sometimes with spring, summer or later peaks, while 3SW fish generally enter rivers early in the year, with few entering after about May. Fish spawning for a second time tend to adopt similar run timing to that of their first migration. In Norway, most salmon enter rivers from May to October, with MSW salmon tending to enter earlier than 1SW fish (Jonsson *et al.*, 1990a,b). Broadly similar patterns apply in eastern Canada, although some stocks are characterized as 'early' or 'late' running stocks (Klemetsen *et al.*, 2003). In Scotland, some fish have been reported to enter rivers over a year before they will spawn (Webb & Campbell, 2000).

An analysis of long-term data sets for 12 salmon stocks in the UK (Anon., 1994), indicated similar changes in the monthly pattern of catches and in the contribution of different sea-age classes. The spring component of the catches increased both numerically and as a proportion of total catch from 1910 to about 1930, remained generally stable until the early 1950s, but subsequently showed a steady decline to the current low levels. It was concluded that the dominant process in these shifts in timing of runs and catches was a change in sea-age composition. While there was some evidence of a shift in run timing within sea-age classes, this was evidently not the main mechanism of change.

Extensive variability in the sea-age composition of stocks over the past 100 years or more has been demonstrated in other studies (George, 1984, 1991; Martin & Mitchell, 1985; Summers, 1995; Heddell-Cowie, 2005), with evidence of 1SW salmon being predominant for some periods and MSW salmon at others. These changes have occurred at broadly similar times among rivers, suggesting that common factors operating in the marine environment have been the main cause of change in age at maturity (Aprahamian *et al.*, 2008). Over recent decades, many stocks around the North Atlantic have experienced long-term declines in the MSW 'spring' component, which appears to be driven primarily by an increase in marine mortality (ICES, 2008).

The sea-age composition of stocks and adult run timing are influenced by various factors. Maturation rate is a function of both stock genetics (e.g. Stewart *et al.*, 2002) and environment, although the relative influence of these factors is not clear (Thorpe, 1994, 2007; Friedland & Haas, 1996; Friedland, 1998). There is evidence for an inherited link with maturation (Hansen & Jonsson, 1991) – typically, rapidly developing parents tend to produce early maturing offspring. Environment also plays a role in determining the sea-age, maturation and run timing of salmon, operating in both the marine environment and freshwater (Scarnecchia *et al.*, 1989, 1991; Jonsson *et al.*, 1991a; Nicieza & Braña, 1993; Anon., 1994; Gudjonsson *et al.*, 1995; Friedland & Haas, 1996; Friedland, 1998; Friedland *et al.*, 2003a,b; L'Abée-Lund *et al.*, 2004; Juanes *et al.*, 2005; Peyronnet *et al.*, 2008). There is, however, no mechanistic framework to explain how seasonal growth and ocean environment combine to produce annual variability in maturation. Stocks have very different maturity schedules, often associated with latitude, and age at maturity can change over time (Anon., 1994; Summers, 1995).

An examination of the variation in sea-age at maturity in 158 Norwegian rivers over large spatial and temporal scales (L'Abée-Lund *et al.*, 2004) found no general temporal trend in the proportion of 1SW salmon in the catches: the proportion decreased significantly in 10 stocks and increased significantly in 11 stocks. There was some evidence of coherence in temporal patterns at a regional level, and river-specific factors (river discharge, topographic gradient and the presence of lakes) explained a large percentage of the spatial variation in the proportions of 1SW fish. This proportion increased with decreasing river size (measured as water discharge), where most of the discharge occurred during the summer period (the main migration period), and for rivers located closer to the open ocean, probably reflecting the effect of early feeding on growth and maturation.

There were large regional differences in the 1SW proportion, not obviously associated with latitude. However, 1SW proportions were generally higher in the northern part of Norway than in the south, possibly reflecting large-scale differences such as oceanic migration routes, although there was no evidence of a general effect of the North Atlantic Oscillation Index (NAOI) on temporal trends in 1SW fish proportions. However, Jonsson & Jonsson (2004) indicated the existence of a correlation between NAOI and age at maturation for one Norwegian river, with a positive winter NAOI (indicative of a mild and stormy winter) correlated with a decreased age at maturity. It was suggested that salmon grow quicker and therefore mature earlier in mild winters, and that climatic conditions at the time of sea entry may be important for the later performance (growth) of the spawners.

Selective exploitation of older sea-age classes can also affect the sea-age composition of stocks (Gee & Milner, 1980; Moore *et al.*, 1995). Rod fisheries can be responsible for much higher levels of exploitation on MSW spring fish than of 1SW fish from the same stock. The high seas fisheries at West Greenland and Faroes have also mainly exploited potential 2SW and older returnees.

A correlation between run timing of salmon and water temperature has been demonstrated in the Baltic region (Dahl *et al.*, 2004), with a strong correlation between the migration peak and mean monthly sea and river temperatures in spring: fish ran earlier in years when the water temperature was higher. It was speculated that this may reflect earlier gonad maturation at higher temperatures; a condition-dependent initiation of migration; or a means to reduce total migration energy costs since the cost of migration increases with temperature. Further, river conditions can also directly affect run timing to a river, with low flows potentially causing considerable delays.

It is not entirely clear what role the freshwater environment plays in determining the sea-age of salmon through its influence on the growth rate of parr, and the evidence is inconclusive and sometimes contradictory (Anon., 1994). For some stocks, an inverse ratio hypothesis was proposed that suggested slow-growing parr which become smolts at older river age tended to return as younger sea-age fish. However, in other stocks it is evident that fish which develop quickly in freshwater continue to do so once they migrate (Anon., 1994). It has been concluded that there is no fundamental causal mechanism linking freshwater growth and sea-age (Gardner, 1976; Bielak & Power, 1986; Anon., 1994).

Evidence from long-term monitoring of marine processes indicates the existence of major fluctuations in parameters such as temperature, salinity and plankton productivity, occurring over a similar timescale to that in the observed shifts in salmon run timing and in the declines in many stocks (Dickson and Turrell, 1999; Beaugrand & Reid, 2003). Direct causal links have not been identified and Beaugrand & Reid (2003)

conclude that results are not necessarily indicative of a trophic cascade or bottom-up control of salmon abundance. However, it seems clear that fluctuations of such fundamental biological significance in the marine environment are likely to be key processes in regulating the sea-age composition and run timing of salmon, as well as the overall abundance of stocks.

While the mechanisms by which changing marine conditions may influence the sea-age composition of stocks are not clear, there are a number of possibilities. These include: direct physiological effects on the growth and maturation processes of individual fish; an increase in total natural mortality throughout the period of marine residence, thus reducing the proportion of older sea-age fish as well as the overall numbers; differential mortality leading to a shift in genetic tendency to a particular sea-age; and differential mortality within each smolt year class of fish destined to return as 1SW or MSW salmon, since sea-age groups are known to inhabit different areas at different times during their marine migrations.

Friedland (1998) reported that the abundance of 2SW spawners in North America is directly scaled to the size of over-wintering thermal habitat in the NW Atlantic, suggesting a link between maturation and environment. This is consistent with the migration-maturation hypothesis described by Friedland *et al.* (1998b). This hypothesis is specified for southern N. American stocks, but is intended as a general hypothesis applicable to all stocks and speculates that post-smolts that migrate to more northerly areas are affected differently by over-wintering conditions and, at the end of the winter, find themselves in areas where they fail to receive cues related to sensing their home rivers. As a result, the fish feed and grow, join feeding migrations and their maturation state regresses. Those fish that have a more southerly post-smolt migration experience different over-winter conditions and are closer to their home rivers after winter. Thus, they are more likely to sense cues, develop sexually and invoke behaviours to navigate home.

Growth and Age at Maturity

Growth in salmonids is regulated by temperature and typically increases linearly with water temperature up to an optimum rate given an adequate food supply (Brett, 1979). However, it has been reported that growth in Atlantic salmon post-smolts has a non-linear response to temperature, with optimum growth occurring at 13°C (Handeland *et al.*, 2003). Temperature can act on growth directly by affecting physiological processes or indirectly by modifying ecosystems (e.g. food availability or changes in other aspects of the rearing environment). Higher temperatures may increase metabolic demand beyond available food resources and inhibit growth. Some fish on low food rations have been shown to have a lower temperature preference than fish on high rations (Despatie *et al.*, 2001), suggesting that when food is limiting growth will be optimised at lower temperatures. However, other factors also influence fish growth and the size that fish attain at maturity.

Large body size confers certain advantages for spawning fish, but can be balanced by the greater probability of mortality associated with spending more time at sea and by potential difficulties in accessing spawning habitats, particularly in smaller rivers. Such factors are thought to drive the adaptation of locally adapted age and size distributions for fish (e.g. Jónasson *et al.*, 1997).

Mean body size has been shown to vary consistently among populations with some rivers supporting large MSW fish, while others support smaller 1SW salmon (Schaffer & Elson, 1975). River discharge volume may be the main factor determining

the among-population variation in fish size for rivers where mean annual water discharge is <40 cumecs (Schaffer & Elson, 1975; Scarnecchia, 1983; Jonsson *et al.*, 1991a). Mean size and age at maturity increase with river discharge for these smaller rivers, although there is no such relationship for larger rivers (Jonsson *et al.*, 1991a). Within populations, temperature may be a key factor influencing temporal differences in growth rate at sea through its influence on food resources and the growth potential of the fish (Friedland *et al.*, 1998a; Friedland *et al.*, 2000; Jonsson *et al.*, 2001).

There is conflicting evidence as to whether Atlantic salmon smolt size influences subsequent post-smolt growth. Both negative relationships (Skilbrei, 1989; Nicieza & Braña, 1993; Jonsson & Jonsson, 2007) and positive relationships (Lundquist *et al.*, 1988; Salminen, 1997) have been reported, and Friedland *et al.* (2006) indicated that marine growth of post-smolts in the Gulf of St. Lawrence from August to October was independent of freshwater growth history. Various hypotheses have been proposed to explain the slower growth at sea of larger smolts (Jonsson & Jonsson, 2007). This has been attributed to growth of the gill surface area, with oxygen consumption becoming gradually more limiting for growth as the fish get larger (Pauly, 1981). Wootton (1998) suggested that the surface area for absorbing food may limit growth in larger fish, and Einum *et al.* (2002) proposed that fish growing more slowly in freshwater, and which are small as smolts, may be better adapted to the marine environment.

It has also been demonstrated that the age at sexual maturity decreases with decreasing first year growth at sea (Jonsson *et al.*, 1991a; Jonsson & Jonsson, 2007). Evidence of a linkage between higher growth rates during the first winter at sea and higher age at maturity has also been demonstrated for populations in northern Spain (Nicieza & Braña, 1993). This contrasts evidence from the Baltic (Salminen, 1997) where sea-age at first spawning was inversely related to the marine growth of sea-ranched salmon. Jonsson & Jonsson (2007) suggest this discrepancy may be related to the expected fitness gain of fish exhibiting different growth trajectories resulting in different reaction norms for growth (Stearns, 1992). Fish that grow fast initially may either attain sexual maturity relatively early, when later growth is environmentally constrained, or later when the high growth rate is maintained (Jonsson & Jonsson, 1993, 2004). Thus salmon and a number of other fishes appear to delay maturity when the growth rate is consistently high throughout life, but mature early if growth rate starts to level off (Jonsson & Jonsson, 1993).

Exploitation has also been shown to affect the size and age of returning fish. For example, the cessation of drift net fishing in Norway has been shown to affect the structure of the spawning run in a number of Norwegian and Russian salmon populations (Jensen *et al.*, 1999). In the Miramichi River, Canada - increases in mean length at age and the abundance of repeat spawners have been attributed to reductions in exploitation (Moore *et al.*, 1995). Long-term declines in the size of 2SW salmon and a reduced proportion of previous spawners were also attributed to the selective effects of fishing for a stock in Quebec (Bielak & Power, 1986).

Sex Ratio

There is a tendency for male fish to mature and return to freshwater at a younger age than females. In many stocks the 1SW component of the run is predominantly male while 2SW fish are predominantly female (Anon., 1994). Female fish have predominated in the catch at West Greenland, where most fish are approaching their second sea winter when caught and where fish from a wide range of stocks are exploited.

Some studies suggest that the sex ratio in 3SW salmon is more even, while others indicate a bias towards females in some stocks and males in others (Anon., 1994).

Since many stocks have experienced a decline in the proportion of older MSW salmon and a relative increase in the predominance of 1SW fish this could have a marked effect on the sex ratio of the spawning stock and the overall level of egg deposition.

Previous/Repeat Spawners

The proportion of salmon surviving to spawn varies markedly among and within Atlantic salmon populations. In some stocks very few fish survive after spawning, while in other populations fish may return repeatedly and fish with a wide range of life histories can contribute to egg deposition in any year, even within populations with an apparently simple sea-age structure. For example, although most stocks in Newfoundland consist almost entirely of salmon which mature as 1SW fish, significant numbers of these fish can migrate back to sea after spawning to return and spawn repeatedly (Dempson *et al.*, 1986). Some fish return to spawn in a number of consecutive years (consecutive spawners) while others return every other year (alternate spawners), although fish have also been known to switch between these two strategies (Klemetsen *et al.*, 2003).

Levels of repeat spawning are clearly influenced by the overall level of exploitation and also the possible size selectivity of fishing gears. Repeat spawning is affected by the size of the fish, with the proportion of repeat spawners decreasing with size. This is possibly related to energy expenditure during spawning: 1SW salmon may allocate 50% of their energy for spawning (Jonsson *et al.*, 1991b) compared with 70% in older fish (Jonsson *et al.*, 1997). A study based on stocks in 18 Norwegian rivers (Jonsson *et al.*, 1991a) indicated that in small rivers ($<40 \text{ m}^3 \text{ sec}^{-1}$) salmon tended to mature at smaller size and age, but post-spawning survival was high with fish tending to spawn annually (consecutively). Large rivers were characterized by larger maturing salmon, with low post-spawning survival and the repeat-spawning fish mainly returning to spawn in alternate years. Within populations the proportion of alternate spawners increased with the size at first maturity.

A study conducted in a sub-arctic region at the border between Finland and Norway showed that the proportion of repeat spawners has increased in the last 10 years (Niemi *et al.*, 2006), more so in female than males. For the Miramichi stock, there has been a significant recent increase in the rate of salmon returning to spawn for a second time as consecutive spawners, but not for the alternate spawning life history strategy, for both 1SW and 2SW maiden salmon (ICES, 2008). This has been associated with years of a high biomass index of small fish in the southern Gulf of St. Lawrence, a change attributed to reduced predation pressure resulting from the collapse of the previously dominant groundfish stocks in this area (cod, skate, flatfish species) (Benoit and Swain, 2008). It has been suggested that this may reflect bottom-up effects of prey availability on adult fish abundance as prey abundance is an important factor in post-spawner survival in Atlantic salmon.

Changes in Size at Maturity

Previous investigations have demonstrated that the marine growth of salmon has decreased over the last 20 years (Crozier & Kennedy, 1999; Jonsson *et al.*, 2003). There have also been recent widespread reports of unusually small 1SW fish returning to rivers in many parts of Europe with the mean weight of fish in a number of stocks

being the lowest in the time series (ICES, 2007, 2008; Todd *et al.*, 2008). However, these changes are not manifest in all populations (Davidson & Hazelwood, 2005; ICES, 2008). The decrease in growth in recent years has been linked to warming in areas where salmon are located at sea (Todd *et al.*, 2008). The mean standardised weights of 1SW fish from 20 Norwegian rivers have also correlated positively with the estimated pre fishery abundance (PFA) of the corresponding sea year class, and the annual mean weight of small salmon (< 3 kg) from the River Drammen has correlated positively with the estimated survival of hatchery reared smolts released in the same river (ICES, 2008).

Todd *et al.* (2008) have indicated almost identical temporal patterns in growth condition variation for two Scottish data sets – a single river stock and a mixed stock fishery, with an overall decrease of 11-14% over the past decade. Growth condition has fallen as SST has risen, and for each year class, a negative correlation was identified between the midwinter (January) SST anomalies in the Norwegian Sea and the final condition of the fish on return during the subsequent summer. The study explicitly drew no connection with stock abundances, but did also demonstrate that underweight individuals had disproportionately low reserves of stored lipids, which are crucial for successful spawning of individuals. It was felt that the investigation was consistent with other analyses in providing evidence of major, recent climate-driven changes in northeast Atlantic pelagic ecosystems, and the likely importance of bottom-up control mechanisms.

ICES (2008) cautioned that the growth of salmon during the first year at sea, as assessed from returning 1SW salmon, provides an indirect measure of growth rate. If the conditions that smolts experience during the first weeks or months at sea and growth during this period are crucial for size selective mortality, measurements of circuli on scales during this period (Beamish *et al.*, 2004; McCarthy *et al.*, 2008) may be better correlated with survival than growth over the whole period. Furthermore, if mortality is size selective, in years with harsh conditions, only the largest fish are likely to survive, which is likely to compromise potential correlations between survival and the size of returning fish.

Peyronnet *et al.* (2007) noted that the length of 1SW fish returning to the River Burrishoole had varied little over a 40 year period and that there was no significant correlation between average length and marine recruitment. It was suggested that length at return was unlikely to be a good indicator of the limiting effects of the environment on survival, since such effects would probably manifest mainly when fish are small and most vulnerable. At larger size, salmon would have potential to feed and grow intensively at different times. Thus, growth in the first months at sea may have a strong influence on recruitment, but may have a relatively small effect on length at return compared with growth experienced after the first winter.

The study looked at various growth measurements based on inter-circuli distances and found that the number of scale circuli deposited during the marine phase was highly correlated to both rates of Burrishoole marine survival and to the time series of PFA. However, the only significant relationship was found with the distances over the first ten scale circuli. This was a negative relationship, suggesting that high growth during early marine residency results in lower overall marine survival.

Davidson & Hazelwood (2005) found only weak correlations between weight-at-return and post-smolt growth (first-year marine) increments, indicating that the former is not heavily influenced by initial growth at sea. Cairns (2003) suggests that salmon aim to achieve a target weight prior to return and one of the consequences of

this is that fish must compensate for poor initial growth by increased foraging activity but at the cost of greater susceptibility to predation. Relatively stable return weights for 1SW salmon for stocks in the UK (Rivers Wye and Dee) over the last 40 years are consistent with this target weight hypothesis. Conversely, however, the weight of 2SW salmon appears to have been increasing in recent years (Rivers Severn, Wye and Dee). Annual variations in adult weight-at-return data for these rivers were also highly synchronous, especially within sea-age groups, but showed no strong associations with SST variables or the NAO index.

Long-term changes have been observed in the mean size of salmon caught in the fishery at West Greenland, with the mean size of European origin fish declining more markedly than that of American fish (ICES, 2008). This may suggest that ocean habitat has been more limiting for European fish, although appears to be at odds with the apparent increase in size of 2SW salmon noted for rivers in England and Wales.

Growth and Marine Survival

A number of authors have provided evidence that growth during the first year at sea has a critical influence over marine survival and that recruitment is strongly linked to growth (Friedland & Haas, 1996; Friedland *et al.*, 1998a; Friedland *et al.*, 2000; Jonsson *et al.*, 2003; Friedland *et al.*, 2005; McCarthy *et al.*, 2008; Peyronnet *et al.*, 2007; Peyronnet *et al.*, 2008). Beamish & Mahnken (2001) have proposed a 'critical size and period hypothesis' to explain the recruitment of coho salmon. This proposes that the fish must reach a threshold size (possibly varying with year) by the end of the first summer and autumn at sea to be able to cope with the metabolic demands of winter. However, while Friedland *et al.* (2009) identified a critical period of post-smolt growth and survival, their results did not suggest that a critical size mechanism was controlling recruitment.

However, Crozier & Kennedy (1999) reported that survival of cohorts to both the coast (pre fishery) and freshwater for salmon from the River Bush were unrelated to variation in growth from smolt migration to the end of the first winter in the sea. Further, variability in marine growth was much less than the variation in natural survival at sea, suggesting that factors instead of, or in addition to, growth influence natural marine survival. Davidson & Hazelwood (2005) identified common patterns of post-smolt (first-year marine) growth among salmon stocks around the UK and Ireland, suggesting these were likely to be influenced by a mixture of environmental processes operating throughout the post-smolt period and possibly indicative of shared trends in sea survival. However, no data were available in this study to explore links between smolt survival and post-smolt growth rate.

Observations that marine survival trends are correlated among some geographically separated rivers in both the NE Atlantic (Crozier & Kennedy, 1993; Friedland *et al.*, 1998a) and NW Atlantic (Friedland *et al.*, 1993) imply that major regulating factors operate when stocks mix and utilise a common shared habitat in the first autumn at sea. However, this does not necessarily support the hypothesis that growth influences natural survival (Crozier and Kennedy, 1999). Further, while there appear to be critical periods for marine mortality, differences have been indicated between European and North American stocks of Atlantic salmon.

The survival rates of 1SW and 2SW salmon from two European stocks – the Figgjo (Norway) and N. Esk (Scotland), which discharge into the North sea – were found to be correlated both within and between stocks (Friedland *et al.*, 1998a). This coherence in recruitment pattern from non-neighbouring stocks suggests that survival effects

act on the broad spatial scale or when stocks are mixed. Further, survival was found to be positively correlated with the area of 8–10°C water in May. An analysis of SST distributions indicated that when cool surface waters dominate the Norwegian coast and North Sea at this time salmon survival was poor, but when the 8°C isotherm extended along the Norwegian coast during May, survival was good. Post-smolt growth increments for returning 1SW fish also showed that enhanced growth was associated with years when temperatures were favourable, in turn resulting in higher survival rates (Friedland *et al.*, 2000). The evident link between growth and survival suggests that growth-mediated survival mechanisms (e.g. predation) are the dominant source of recruitment variability and recent work has reinforced this view (Friedland *et al.*, 2009). Further, similar fluctuations in survival for both 1SW and 2SW salmon suggest that the possible contribution of variable maturation can be discounted.

For North American stocks, correlations have also been demonstrated between survival and thermal conditions, with similar trends in return rates observed for N. American rivers over a broad geographical range, consistent with factors acting on fish when they are mixed and utilising a shared habitat. Associations have also been demonstrated between the increased summer growth of 2SW fish and increased returns of 1SW fish and a higher 1SW fraction (Friedland & Haas, 1996). Friedland *et al.* (1993) showed that the distribution of the winter habitat in the Labrador Sea and Denmark Strait was critical for post-smolt survival. However, it was recognised that the mechanisms for this correlation were somewhat obscure since the observations conflicted with conventional thinking that the spring period is more important – i.e. when the smolts first migrate to sea. Subsequent investigations (Friedland *et al.*, 2003b) compared thermal conditions in potential post-smolt nursery areas with the pre-fishery abundance of North American stocks and found that stock size was negatively correlated with mean SST during June. The results suggest that post-smolt survival is negatively affected by the early arrival of warm ocean conditions in the smolt nursery area and indicates that June conditions (the first month at sea for most stocks in the region) are pivotal to survival.

Hatchery-reared salmon

Many salmon stocks are supplemented by salmon released from hatcheries. In general, wild fish are reported to survive significantly better than hatchery-reared fish (e.g. Jonsson *et al.*, 2003). Recent studies have also indicated that hatchery fish seem to be subject to other mortality events, above those experienced by wild fish (Peyronnet *et al.*, 2007). Modelling studies (Peyronnet *et al.*, 2008) indicated that survival of hatchery fish was primarily explained by coastal SSTs one year before the migration of smolts suggesting that warmer conditions during freshwater rearing appear to affect fitness at migration.

2.3 Climatic/oceanic factors

The following section reviews certain environmental factors that have been linked with salmon recruitment; additional information in relation to environmental data sets is provided in Section 3.5.

North Atlantic Oscillation (NAO)

The NAO is the dominant atmospheric process in the North Atlantic throughout the year. It accounts for more than one third of the total variance in sea-level pressure

and represents the large-scale shift in atmospheric mass between a 'high-index' pattern, characterised by an intense Iceland Low with a strong Azores ridge to its south, and a 'low-index' pattern in which the pattern is reversed. The pressure difference between these two areas is the conventional index of NAO activity (Dickson & Turrell, 1999).

The NAO has exhibited considerable long-term variability, which appears to be amplifying with time, although the index has been weak and variable over the past decade. The 1960s exhibited the most protracted and extreme negative phase of the Index; the late 1980s–early 1990s experienced the most prolonged and extreme positive phase. Changes in the NAO Index produce a wide range of physical and biological responses in the North Atlantic, including effects on wind speed, evaporation and precipitation, SST, ocean circulation, storminess, and the production of zooplankton and fish recruitment (Dickson & Turrell, 1999).

There is thought to be a link between salmon marine survival and the NAO. There are various mechanisms by which this might occur through: (a) a positive NAO is linked to lower transport through the Faroes-Shetland Channel with important effects on mixing processes (Parsons & Lear, 2001) and recruitment of other fish species such as cod; (b) a positive NAO is correlated with high SST and reduced mixing and zooplankton abundance in the NE Atlantic (Beaugrand & Reid, 2003) and salmon growth has been negatively correlated with SST (Friedland *et al.*, 2005); (c) a positive phase of the NAO has also been reported to have had a negative effect on catches from the River Foyle (Boylan & Adams, 2006). Peyronnet *et al.* (2008) directly link the NAO signal to salmon survival (rather than catches).

Davidson & Hazlewood (2005) have demonstrated a strong correlation between the NAO index and patterns of post-smolt growth for various 1SW salmon stocks in the UK. Peyronnet *et al.* (2008) have also explored the influence of climate and oceanic conditions on the marine survival of 1SW Irish salmon using Generalised Additive Models and have demonstrated a link between a positive phase of the NAO, along with low plankton abundance and high SST in the NE Atlantic with a decrease in salmon survival.

The NAO is also known to affect freshwater ecosystems via effects on temperature, rainfall and wind speed, highlighting the over-riding influence of the NAO as the dominant atmospheric process in the North Atlantic and one which appears to serve as a general surrogate for a number of climatic effects operating over land and sea (Dickson and Turrell, 1999). For example, Jonsson *et al.* (2005) reported a positive correlation between NAOI and water temperature & discharge in the River Imsa in Norway during winter 1976–2002, indicating a significant oceanic influence on winter river conditions. Thus, while the global decline in abundance of Atlantic salmon is usually assumed to stem mainly from changes in the marine environment (Friedland, 1998), the potential for large scale processes, such as the NAO, to affect both freshwater and marine environments together may mean that the influence of freshwater factors in this decline have been understated (Crozier & Kennedy, 2003).

Davidson & Hazlewood (2005) have demonstrated that year-to-year variations in both river and sea surface temperatures around England and Wales, and the NAO index were highly synchronous. Further, Peyronnet *et al.* (2008) have shown that the NAO in the winter, prior to smolt migration, explained 70% of the deviance in marine survival of wild 1SW salmon from Ireland. This suggests that the NAO may be affecting pre-smolts in freshwater with knock-on effects for the fitness of fish during their early marine migration, although various mechanisms might apply. Warmer condi-

tions during the juvenile rearing period may be detrimental to the future survival at sea by affecting overall fitness, or the match between the migration time and the optimum migration period.

Long-term variation in catches for two rivers within the northernmost distribution area of the species has been related to mean SSTs in the Kola section of the Barents Sea in July (Niemelä *et al.*, 2004). However, no link was identified for these stocks between NAO and catches. In contrast to most of the North Atlantic area, catches in these rivers demonstrate no consistent recent trend of declining abundance.

The Atlantic Multidecadal Oscillation (AMO) provides an alternative measure of Atlantic climate variability to the NAO. Information is provided in Section 3.5.

Gulf Stream North Wall (GSNW)

The latitudinal position of the Gulf Stream is generally defined as the landward edge of the Gulf Stream (east coast of USA), and is referred to as the North Wall. The position is indicated by isotherm gradient data and is derived from satellite, aircraft and surface observations. This has also been used as an exploratory variable in relation to the changing abundance of Atlantic salmon (SALMODEL, 2003). However, while a variety of relationships between marine conditions (GSNW, NAO & SST) and survival and abundance of stocks were indicated, both at single river and wider levels, these were not always consistent or intuitively correct, and the number of significant relationships was little greater than expected by chance.

Mixed Layer Depth (MLD)

The MLD describes a thin homogeneous surface layer mixed by the wind which has consistent temperature & salinity. The thickness of the MLD varies and reflects the level of oceanic stratification. Warmer spring temperatures result in a shallower MLD and promote production since nutrients become trapped and phytoplankton can develop. This link between MLD and plankton productivity has also been related to the marine survival of coho salmon (Hobday & Boehlert, 2001).

Peyronnet *et al.* (2008) found that the depth of the MLD in June had a significant contribution to models of marine survival for Irish salmon, with June MLD < 25m being generally positively associated with survival. Peyronnet *et al.* (2008) further noted that the timing of the formation of the MLD varied between years and suggested that delays in the formation of a shallow mixed layer could affect salmon survival. This might occur through reduced primary productivity, or a mismatch between the timing of plankton abundance and the presence of post-smolts. It was also suggested that since post-smolts are distributed close to the surface, a shallow mixed layer might contribute to better survival through keeping their prey close to the surface.

Temperature

Temperature has been identified as an important factor influencing growth and maturation of Atlantic salmon (Scarnecchia, 1983; Scarnecchia *et al.*, 1991). However, it has also been suggested that thermal conditions can influence maturation independently of growth by influencing migration patterns (Friedland *et al.*, 1998b). For example, temperature may directly affect the physiology of post-smolts through increased swimming requirements as a response to migration cues or to avoid unfavourable thermal conditions (Salminen, 1994). This assumes post-smolts have very specific thermal preferences and would seek to locate optimum temperatures during the first months at sea.

A number of authors have noted a negative correlation between the growth of salmon and SST, affecting fish in both the NE and NW Atlantic (Peyronnet *et al.*, 2007; Friedland *et al.*, 2003b) and the Pacific (Wells *et al.*, 2008). Since growth in salmonids typically increases linearly with water temperature up to an optimum rate given an adequate food supply (Brett, 1979), and there is an evident link between size and survival, this presents something of a dilemma in making sense of the observation that warmer conditions are associated with poorer survival, at least for fish which are experiencing temperatures which are at or below the optimum for growth. This possibly suggests a shortage of food - under warmer conditions this could result in higher mortality rates, possibly due to an increasingly fragmented distribution of prey exacerbated by the effects of higher temperatures on fish's metabolism. Friedland *et al.* (2003b) explored four hypotheses: how ocean conditions may affect growth of post-smolts, whether variations in climate have altered predation pressure or prey abundance, and how migration might be affected by variations in climate. Having reviewed the evidence, and given that post-smolts represent a relatively minor component of the food web, they suggested that post-smolts may not be affected by fluctuations in predator and prey levels as much as they are controlled by the individual demands of swimming and migration. Strong migrational behaviours that select for particular preferred temperature ranges could impose significant energetic costs on fish as they seek optimal temperatures.

Davidson & Hazlewood (2005) have reported increasing trends in temperature for rivers and coastal waters in England over the last 20–40 years. These are consistent with warming trends across the north Atlantic (Hughes and Turrell, 2003) and globally (IPCC, 2001). Temperature fluctuations among river and sea sites were highly synchronous, suggesting large-scale climatic processes are influencing both freshwater and marine environments simultaneously. However, for both rivers and coastal waters there were geographical differences in warming rates with southerly sites warming faster than northerly sites. Rises in temperature have been linked to marked declines in the status of salmon stocks in parts of southern England (Solomon & Lightfoot, 2007). For example, in some instances - during very warm summers - high estuarial temperatures appear to deter adult salmon from entering freshwater, or may even prove lethal (Solomon & Lightfoot, 2007).

Given these common patterns in freshwater and marine temperature change, and the importance of temperature to the biology of fishes, Davidson & Hazlewood (2005) suggested that coherent trends in the age and growth of pre- and post-smolt salmon might be expected. However, SST data were generally poorly associated with post-smolt growth patterns. Similarly, more direct measures of sea survival and adult abundance have shown a poor association with SSTs (SALMODEL, 2003). This does not mean that environmental temperature is unimportant for salmon in the sea, rather that other (perhaps more complex) factors have been the main cause of change and/or the temperature variables examined have poorly represented the true influence of temperature on salmonid biology/ecology

A correlation between SST and survival has been observed for salmon stocks in the NE Atlantic suggesting temperature either directly affects growth or modifies post-smolt behaviour (Friedland *et al.*, 2000). Beaugrand & Reid (2003) demonstrated highly significant relationships between SST in the NE Atlantic, Northern Hemisphere temperatures, the NAO and long-term changes in 3 trophic levels (phytoplankton, zooplankton and salmon). A stepwise shift was identified that started after a pronounced increase in Northern Hemisphere temperature anomalies at the end of the 1970s. The biological variables showed a pronounced shift after ~1982 for

euphausiids (decline), 1984 for total abundance of small copepods (increase), 1986 for phytoplankton biomass (increase) and the copepod *Calanus finmarchius* (decrease) and 1988 for salmon (decrease).

Beaugrand & Reid (2003) concluded that regional temperature increases were an important parameter currently governing the dynamic equilibrium of NE Atlantic pelagic ecosystems with possible consequences for fisheries. However, the results did not necessarily indicate a trophic cascade or bottom-up control of salmon abundance. Nonetheless, it was suggested that the findings possibly open the way to the development of predictive tools, based on physical and plankton indicators, which might be used to assess future changes in the abundance and distribution of salmon.

Scenarios for future climate change (UKCIP, 2002) suggest that warming trends are likely to be far more severe in the coming decades than those experienced in the past – even under the best case ‘low emissions’ scenario.

Davidson & Hazlewood (2005) used temperature profiles forecast to the end of this century (UKCIP, 2002) to predict the growth rates of salmon in freshwater based on the model of Elliott & Hurley (1997). This indicated that for rivers in the south-west and north of England, freshwater growth rates could generally improve under the ‘low emissions’ scenario but may fall below current levels under the ‘high-emissions’ scenario as temperatures exceed optimum levels in the latter half of the century. On rivers in the south-east of England (represented by the Thames) – where warming is expected to be greatest – declining growth rates may result, with adverse consequences for abundance and survival.

Warming is only one aspect of climate change that might prove detrimental at extreme levels; expected increases in the frequency of summer droughts and winter floods could also adversely affect survival and abundance (UKCIP, 2002).

The effects of global warming on salmon in the sea are more speculative given our poorer knowledge of ocean processes and of the marine life of Atlantic salmon (Hughes & Turrell, 2003). However, given that temperature increases over land are expected to exceed those over the surface of the oceans, the changing state of conditions in freshwater may be the more important factor controlling future distribution and viability of the species, while change in the marine environment may be the main factor regulating stock productivity (Friedland *et al.*, 2009).

2.4 Salmon in Freshwater

Both density-dependent and density-independent factors regulate the abundance of Atlantic salmon in freshwater (Elliott, 2001). The carrying capacity for salmon juveniles is limited and the response of juvenile abundance to intra-specific competition is strongly compensatory (Elliott, 2001). Aside from the effects that density may have on freshwater survival, other factors such as disease, predation and displacement by adverse environmental conditions may vary with the abundance of juveniles.

There are many estimates of mortality rates for the juvenile stages of salmon because the freshwater life stages are readily accessible and are not subject to fisheries (SALMODEL, 2003). Thus, freshwater mortality is relatively well characterised and tends to be less variable than marine mortality (Friedland, 1998).

Estimating mortality during the marine phase is more difficult because the returning adults have commonly been exposed to both natural and fishing mortality at sea. Factors which act in freshwater, but may be manifest as variations in sea survival (e.g. Peyronnet *et al.*, 2008) also need to be borne in mind in the context of marine survival.

In addition, conditions experienced within the marine environment (e.g. prey availability, growth rate, climatic conditions), clearly have an impact on the subsequent freshwater stages of the salmon through modifications to run timing and spawning

High densities of juveniles, among other factors, can affect juvenile growth and ultimately the size of migrating smolts (Jutila *et al.*, 2006). As there is evidence of size-dependent survival at sea, the conditions experienced in freshwater are likely to directly affect survival in the ocean. Environmental conditions in freshwater, independent of abundance, can also affect the physiology and energy reserves of salmon as they migrate to sea.

Recent research has demonstrated very clearly that the conditions experienced within the freshwater environment are critical to the survival of salmon in the marine environment. For instance exposure of juvenile salmon to diffuse pollution in freshwater (e.g. pesticides) modifies run timing, development of the parr-smolt transformation and the subsequent survival and behaviour of post-smolts during the freshwater/marine transition and once they enter the marine environment (Fairchild *et al.*, 2002; Moore *et al.*, 2003, 2007, 2008; Lower & Moore, 2007). However, poor water quality is simply one factor within the freshwater environment that may regulate and modify juvenile salmonid production. Habitat availability, feeding opportunities, and modifications to the thermal and flow regimes of rivers and streams may all interact to influence the “quality” of the smolt, which may compromise its ability to survive in the marine environment and successfully complete its extensive marine migrations.

Spawning

Salmon spawn in river systems in the autumn and winter wherever suitable spawning and nursery habitat areas exist; spawning habitat requirements are described by Armstrong *et al.* (2003). Female fish exhibit a degree of parental care burying their eggs in redds (Marshall *et al.*, 1998). Fish typically spawn earlier in more northerly areas and in the upper reaches of rivers where water temperatures are lower and later in more southerly areas and in the warmer, lower reaches of rivers. Although the spawning season may last only a few weeks, fish may enter the river at any time and some fish can spend over a year in freshwater prior to spawning (Webb & Campbell, 2000). It is presumed that entering the river well in advance of spawning confers some benefit in terms of reproductive success. This might be due to: better survival in freshwater; easier upstream migration past falls and rapids prior to full gonad development; optimising opportunities for encountering specific, favourable river conditions for upstream migration; and avoiding migration through estuaries and the lower reaches of rivers during warmer periods when flows, temperature and water quality may be less suitable for migration (Anon., 1994).

In many river systems, the earliest running fish in each sea-age class tend to penetrate furthest into the river system. It is not clear whether this is because the fish happened to enter first or whether they specifically did so because they had farthest to go within the system. A genetic component to run timing has also been indicated (e.g. Stewart *et al.*, 2002).

Large body size enables female fish to produce more and larger eggs, compete more effectively for spawning sites and dig deeper redds. Large males are better able to compete for access to females and are preferred by females as mates (Quinn, 2005). However, the benefits of large size are likely to be balanced by the greater probability of mortality associated with spending more time at sea and possibly by difficulties in

accessing spawning sites in smaller streams. In each river, these factors are expected to drive local adaptations in age and size distribution (e.g. Jónasson *et al.*, 1997)

There is also evidence that females arrive on the spawning ground earlier than males (Dahl *et al.*, 2004). This could be due to the fact that females are commonly older, and older individuals often migrate earlier. Another possibility is that females try to monopolize preferred spawning sites, while males normally compete only for access to a specific female. It is also known, however, that pheromones released by female salmon attract male fish and help to synchronise spawning events (Moore & Waring, 1996).

Spawning date seems to have evolved to allow progeny to emerge at a locally appropriate time in the spring relative to the average temperature regime that occurs during incubation (Quinn, 2005). However, there can be significant variation in the time of spawning among salmon within a river system (Webb & McLay, 1996), and there is some evidence to suggest a recent shift in the timing of spawning, in some rivers at least (W. Riley, pers comm).

The temperatures experienced by female salmon in the months before spawning can have a major effect on egg quality and subsequent survival. Elevated temperatures and temperature 'spikes' can have a negative effect on egg size and fertility rates (King *et al.*, 2003, 2007), affect physiological pathways (Watts *et al.*, 2004) and ovulation (Taranger & Hansen, 1993).

Fecundity

Fecundity is another trait that is highly variable both within and among stocks. Larger fish typically produce more and larger eggs (Thorpe *et al.*, 1984; Jonsson *et al.*, 1996). Thus, absolute fecundity varies greatly among individual fish relative to their size at maturity. Relative fecundity (eggs per kg total egg mass) varies much less, typically by a factor of 1.5 to 2.0 within a population (Klemetsen *et al.*, 2003).

Eggs are large and incubation relatively long, with embryos relying on endogenous food reserves for a lengthy period before first feeding (Marshall *et al.*, 1998). There is a reported trade-off between egg size and fecundity (Jonsson *et al.*, 1996) – fish may either spawn large and few eggs or small and many eggs. The faster that fish grow in freshwater before smolting, the smaller their relative egg size on reaching maturity. This has been explained as a phenotypic response to the potential growth opportunities in the natal river and assumes that the freshwater feeding conditions experienced by the parents as juveniles is a good predictor of what their offspring would experience.

Sexual maturity in parr

The sexual maturity of salmon parr is common for males. Development is thought to have both heritable and environmental components. Therefore, the proportion of mature male parr can vary considerably between rivers, between river stretches and between years depending on stock-specific characteristics and growing conditions (Dalley *et al.*, 1983; Bagliniere & Maisse, 1985; Hutchings & Jones, 1998), but usually increases with parr age (Dalley *et al.*, 1983). O'Connell & Ash (1993) also reported a higher incidence of precocious parr in lacustrine habitats compared with fluvial habitats in the same river catchment.

Possible environmental triggers for precocious male parr are fast early growth in favourable conditions (e.g. Thorpe, 1990), with high seasonal fat content possibly the most important precondition for maturation (Rowe & Thorpe, 1990; Rowe *et al.*, 1991;

Simpson, 1992). Prevost *et al.* (1992) found that large size after the first year and short winters favoured maturation of 1+ male parr; and that the incidence of maturing 1+ males was greater where high densities of parr were recorded in the second season of growth.

In northern (sub-arctic) Atlantic salmon rivers the reported maturation rates of male parr are low (0-25%, typically ~10%) (Elo *et al.*, 1995; Heinimaa & Erkinaro, 2004; Hutchings & Jones, 1998) compared with mean reported proportions among 1+ parr elsewhere – 57% in Newfoundland, 53% in Maritimes and 22% in Quebec (Hutchings & Jones, 1998); 28-52% in east coast rivers in the U.S.A. (Whalen & Parrish, 1999); 0-100% in France (Bagliniere & Maisse, 1985). The short growing season, poor seasonal growth and long winters consuming body lipid reserves may explain this finding (Heinimaa & Erkinaro, 2004).

In New England, U.S.A, where maturation of male 0+ parr is rare (~5%) Letcher & Terrick (1998) reported a high incidence of 0+ parr maturation (74%) following a massive, localised flood that appeared to be the result of increased growth of parr following the flood. They suggested that such strong environmental disturbances can alter the direction and timing of salmon life-histories by influencing community structure and growth opportunity.

It has also been suggested that maturity in male parr will be evolutionary stable only if adult mortality is high (Myers, 1984), and that over-fishing could eventually eliminate anadromy in male members of a population (Myers & Hutchings, 1987). If true, male precocity should be expected to be less common in lightly exploited stocks. Riley & Power (1987) carried out a study to test this hypothesis using data from landlocked and anadromous stocks in Canada. They concluded that high post-smolt mortality in anadromous stocks is conducive to male parr maturity at an early age, and suggested the lower proportion of maturing male parr in landlocked stocks was related to competition among males for mates and the smaller size of the spawning adult landlocked salmon.

The incidence of mature female parr is rare (Fleming, 1996), with only a few recorded incidences in anadromous Atlantic salmon (e.g. Moore & Riley, 1992). There is no evidence to suggest any change.

Egg and alevin development

Salmon spawning substrates vary in composition (Armstrong *et al.*, 2003). Spawning redds generally cover areas of 1–11 m² (Bardonnnet & Bagliniere, 2000) and consist of a 'pot' or 'pit' and a 'tail' (Crisp & Carling, 1989). The pot is the deepest excavated part at the upstream end of the redd, where most eggs are deposited. The depth to which eggs are buried in spawning gravels is related to female fish length (e.g. Crisp & Carling, 1989) and typically in the range 15–25 cm. The eggs are buried to protect them from light, predators and high water flow, which can result in mortality due to mechanical shock (Bardonnnet & Bagliniere, 2000). Egg burial depth also has some influence on rate of development (temperature) and on the likelihood of washout, asphyxiation or exposure during low flows (Crisp, 1996).

Egg development is influenced strongly by temperature and this provides the best predictor of hatching time (Crisp, 1996). However, a number of other factors can influence hatching time, including incident light, dissolved oxygen concentration, sub-lethal mechanical shock and low temperatures at the time of hatching (Crisp, 1996).

A number of factors also affect the survival of the intragravel stages (eggs and alevins) of salmon (e.g. Crisp, 1996; Youngson *et al.*, 2004; Lapointe *et al.*, 2004). Temperature has a direct effect on the survival of eggs and can also influence the size of alevins at hatching through regulating the relative proportions of the yolk sac used for metabolism and tissue growth. Oxygen supply rate is also critical. Oxygen requirements vary at different stages of development and are further influenced by factors such as egg size, temperature, the spatial arrangement of eggs within the redd and the velocity of intragravel water flow (Crisp, 1996; Youngson *et al.*, 2004). Other factors affecting egg and alevin survival include the gravel composition, stream bed conformation and hydraulics, patterns of discharge and mechanical shock (Crisp, 1996). A range of factors thus influence the survival of salmonid eggs and alevins, and these can interact in a complex manner (Crisp, 1996).

Fry emergence and dispersal

The period of emergence and establishment of feeding territories is a time when mortality can be very high, and during which the strength of a cohort may be established, and can be regarded as a critical period (Armstrong *et al.*, 2003). The timing of fry emergence in salmon is influenced by environmental conditions during egg development, most notably water temperature (e.g. Elliott & Hurley, 1998; Garcia de Leaniz *et al.*, 2000). Thus the combination of spawning date and the temperature-dependent rate of egg and alevin development effectively determine when this will occur (e.g. Jensen *et al.*, 1989). It is generally accepted that spawning dates are adapted to current thermal and flow conditions such that juvenile emergence timing is optimized as a result of selection pressures (e.g. Heggberget 1988; Jensen *et al.*, 1991). Marked changes in temperature or flow during early development may therefore create a mismatch between emergence and environmental conditions, resulting in increased levels of early juvenile mortality (Jensen *et al.*, 1991).

Emergence from the redd is generally associated with the initiation of exogenous feeding (Dill, 1977), although fry may also disperse with varying amounts of unabsorbed yolk sac, particularly during the early part of the dispersal period (Garcia de Leaniz *et al.*, 2000). Emergence is typically clumped, with the majority of fry from a redd emerging over a short period (e.g. 80% over a 2–3 day period reported by Gustafson-Marjanen & Dowse, 1983), and occurs at night (e.g. Gustafson-Marjanen & Dowse, 1983). Clumped emergence at night is considered to be a predator avoidance tactic through avoidance of visual detection by predators and reducing the individual risk of predation through being in a large group (Gustafson-Marjanen & Dowse, 1983). In Chinook salmon (*Oncorhynchus tshawytscha*), Field-Dodgson (1988) noted that flow rate had a strong effect on emergence timing, while the effects of temperature and light level were less.

After emergence from the gravel, some 0+ young-of-the-year fry drift, while others, so called resident fry, remain close to the redd area and seek to establish and defend territories (Bujold *et al.*, 2004). It has been suggested that those fry that fail to gain territories close to the redd will be displaced downstream and die (Elliott, 1984), but others suggest dispersal of viable fry may be an important means of maximizing use of available habitat, particularly where redds are widely spaced (Crisp, 1995), or of avoiding densely-populated areas and obtaining individual territories elsewhere (Mikheev *et al.*, 1994).

As with emergence, dispersal occurs mostly at night (Kennedy & Strange, 1986), and is typically downstream of the redd, although upstream dispersal can also occur (Egglishaw & Shackley, 1973; Crisp, 1995). The most intensive dispersal of 0+ fry oc-

curs during the two months after emergence (Beall *et al.*, 1994), and Marty & Beall (1989) reported two distinct waves of dispersal, one soon after emergence and another 10 to 20 days later. The majority of fry typically remain close to the redd site – less than 1 km downstream, with a high proportion within 50 m (e.g. Egglshaw & Shackley, 1973; Kennedy & Strange, 1986; Marty & Beall, 1989; Crisp, 1995; Webb *et al.*, 2001). Dispersal distances also appear to be affected by rainfall and thus flow rates (Crisp, 1995). Once settled, salmon appear to die in situ rather than move during the summer (Egglshaw & Shackley, 1980; Armstrong *et al.*, 1994), although a further dispersal may occur in autumn (Rimmer *et al.*, 1983; Rimmer *et al.*, 1984).

Garcia de Leaniz *et al.* (2000) report marked variability in the developmental stage of fry at dispersal - early in the dispersal period all fry had remnants of a yolk sac, but fry dispersing later in the season had no yolk sack left. Bujold *et al.* (2004) report that larger (but not older) fry tended to stay near the redd while smaller fry tended to drift/disperse downstream, probably as a result of intraspecific competition for food and space. Differences in the dispersal behaviour of emerged fry may also be related to gender; in masu salmon (Nagata & Irvine, 1997) found that male fry were more likely to remain near the redd and female fry to move downstream.

After dispersal, Garcia de Leaniz *et al.*, (2000) report that individual growth of fry is highly variable. Crisp (1995) found that the weight of 0+ fry in the autumn following dispersal was directly related to the distance dispersed and inversely related to population density. Two hypotheses were proposed to explain this observation: (a) that the fry that dispersed the longest distances tended to be of above average size at the time of dispersal, and (b) that the fish which dispersed farthest were of average or below average size at the time of dispersal, but, once dispersed, encountered less competition and were able to grow more rapidly. It was noted that hypothesis (a) was contrary to the view that displaced fish are typically smaller than the population average.

Metcalf & Thorpe (1992) demonstrated that earlier-feeding fry were dominant over their later-feeding siblings, despite not being any larger, but soon established and maintained a size advantage. This led to an increased probability of early-feeding fish migrating to sea as one-year-old smolts (rather than 2 or more) (Metcalf & Thorpe, 1992), indicating the link between growth rates and future life-history traits (Thorpe, 1989). It was subsequently demonstrated (Metcalf *et al.*, 1995) that the correlation between date of first feeding and dominance was a consequence of early-feeding fry having relatively higher metabolic rates (Metcalf *et al.*, 1995). However, environmental factors such as temperature or flow can also have an important influence on fry survival. Good *et al.*, (2001) reported that size-selective mortality of salmon fry was relative weak and directed towards the smaller fry in the population during a drought year (1995), but that during a subsequent wet year (1996), selective mortality was relatively strong and directed towards the larger fry from the same population. They concluded that hydrolimatic events can select against either small or large fish and is a key determinant in the mean size of juvenile salmon fry at the end of their first summer.

Growth in freshwater

Aprahamian *et al.* (2008) reported relatively stable freshwater growth of salmon parr on the River Dee, Wales between the late 1930s and mid-1980s (using mean lengths back calculated from adult scales). However, by the end of the 1990s they reported that juvenile salmon were, by the end of their first and second year, respectively, ~60% and ~ 19% larger, on average, than between the late 1930s and mid-1980s. Pos-

sible explanations proposed included: a reduction in density dependent processes; an increase in river temperature affecting both parr growth rate and timing and size of alevins at emergence; and changes in agricultural practices in the late 1970s resulting in enhanced invertebrate production so that food was no longer limiting growth.

Rivot *et al.* (unpublished data) reported a significant increase in the length of one-year old juveniles between 1973 and 2002 in Brittany and Lower Normandy. Stable isotope analysis on archived scales of juveniles showed that the C¹³ ratio in scales also increased. They suggested that the changes in juvenile growth were in response to warming (climate change) and/ or a change in primary production.

Jonsson *et al.* (2005) reported a positive correlation between growth rate of parr in their first year and river temperature, flow and NAOI during the winter of egg incubation, but only NAOI was significant when cross-correlating the two series using a time difference of 1 year.

Jensen (2003) analysed the effects of altered water temperature on parr growth, due to hydropower regulation of the River Alta, N. Norway. After hydropower development, water temperature decreased 1–2°C during June, July and the first half of August and parr growth rates decreased; later in the season when water temperature increased by up to 3°C parr growth increased. However, only minor overall changes in annual growth rates were observed.

In contrast, mean annual size-at-age of juvenile salmon decreased in the Northwest Miramichi and Southwest Miramichi Rivers in the Maritime Provinces of eastern Canada between 1971 and 1999 (Swansburg *et al.*, 2002). Fork lengths of parr were significantly and negatively associated with spring air and water temperatures. Therefore, increases in air and water temperatures as predicted from climate change models may adversely affect growth of juvenile salmon parr, reducing overall productivity.

Davidson & Hazelwood (2005) used the model of Elliott and Hurley (1997) to predict pre-smolt (freshwater) growth rates for the Rivers Wye and Dee, Wales. These suggested that growth rates had improved on these rivers in response to increasing temperatures, but not significantly so. These relatively stable growth predictions contrast a marked decline in mean smolt age observed on some rivers (Severn, Wye and Dee), which began around the early 1980s but has proceeded at different rates thereafter. It was suggested, therefore, that factors other than, or in addition to, temperature were promoting faster growth in pre-smolt salmon on these rivers and, as a result, a decline in the mean smolt age. Gurney *et al.* (2008) also reported changes in age at smolting (and growth) consistent with changes in temperature regime, but indicated that changes in early density-dependent mortality, rather than the physiological effects of temperature, explained the large attenuation between a dramatic fall in spawner numbers and a relatively minor diminution in total smolt production in the Girnock Burn, Scotland.

In general, it is anticipated that parr would be expected to grow faster (and hence probably smolt at a younger age) with increased temperature, up to the optimal temperature for growth (16–19°C) (numerous authors). With further increases in temperature, growth would be reduced (resulting in probable increased age at smoltification). However, at temperatures ranging from 22–24°C juveniles seek refuge from thermal stress (Cunjak *et al.*, 1993), at 28°C they die in 7 days and at 33°C they die in 10 minutes (Elliot, 1991).

Parr movement / migration

Downstream movement of salmon parr during the autumn has been recorded in populations in both North America and Europe (Youngson *et al.*, 1983; Cunjak & Chadwick, 1989; Riley *et al.*, 2002). Studies of the migration patterns of Atlantic salmon parr tagged with passive integrated transponder (PIT) tags on the River Frome, a chalk stream in southern England, have demonstrated that a substantial proportion (25% of the spring smolt run in absolute terms) of the population can migrate downstream during the autumn with the peak movement occurring during October and November (Pinder *et al.*, 2007).

The ecological drivers for autumn migrations of salmon are unknown (Riley *et al.*, 2008), although a number of mechanisms have been proposed. These include displacement of subordinates by dominant fish (Bjornn, 1971; Mason, 1976), the requirement for juvenile salmon to migrate to more suitable freshwater habitats (Riddell & Leggett, 1981; Huntingford *et al.*, 1992; Riley *et al.*, 2008) or the requirement for mature male parr to locate mature female adult salmon to maximise reproductive success (W. Riley unpubl. data for the Kielder Burn, England). In some cases the autumn migrations of juvenile parr have been associated with elevated stream discharge (Youngson *et al.*, 1983; A. Pinder, personal communication, for the River Frome, England; W. Riley, unpubl. data for the River Ceiriog, Wales). Such movements have also been shown to comprise predominantly precocious male parr (Buck & Youngson, 1982; W. Riley, unpubl. data for the Kielder Burn, England), but can also comprise fish of both sexes (Riley *et al.*, 2008).

Recent studies on the River Frome have indicated that the autumn migrants, including those that subsequently move to and reside within the tidal reaches of the river during the winter months, are not physiologically adapted to permit permanent, or early, entry into the marine environment (Riley *et al.*, 2008).

Frequency histograms of seasonal downstream movements of juvenile Atlantic salmon in the UK suggest a dual peak in the autumn/winter migration, the first occurring in early autumn, the second during the spawning season for the river system in question (Pinder *et al.*, 2007; Riley *et al.*, 2002; Riley, 2007; W. Riley, unpubl. data for the River Ceiriog, Wales). Although there is often no information from these studies on the sex composition of the migrants, it is speculated that the later migration may involve mature male salmon parr and be related to reproductive activity. These fish are also older than those migrating during the autumn (Riley, 2007). The extent to which the timing and relative magnitude of these migrations might vary between rivers or over time is unclear.

Whilst adult returns have previously been reported from parr leaving highland tributary spawning streams during the autumn (Youngson *et al.*, 1994), Riley *et al.* (2009) recently reported adult returns from parr that were known to have migrated downstream to the lower river/ tidal reaches thus confirming the importance of these areas as habitat utilised by juvenile salmon (Cunjak & Chadwick, 1989; Riley *et al.*, 2008) before they undergo the parr-smolt transformation.

Smolt Age

The age of smoltification of Atlantic salmon juveniles is closely associated with growth rates: fast growing populations smoltify at younger ages (Swansburg *et al.*, 2002). Over the geographic range there is a significant negative correlation between the age of smoltification and an index of growth potential based on degree days and photoperiod length (Metcalf & Thorpe, 1990).

Aprahamian *et al.* (2008) reported that juvenile salmon on the Welsh Dee were larger at the end of the 1990s than between the late 1930s and mid-1980s. This was reflected in a change in the age composition of smolts, with the mean smolt age declining from ~ 2 years prior to the 1980s to ~1.6 years in the late 1990s. Similarly, Cragg-Hine *et al.* (2006) reported a marked increase in the proportion of 1+ smolts on the Welsh Dee (from ~5% in the period to 1949, to almost 40% in the decade to 2002). They concluded that as the Welsh Dee had become colder during the period April to October (post-1964 due to flow regulation schemes) factors other than climate change were likely to be involved.

A decline in mean smolt age has been similarly observed in other British and French populations of salmon (Bagliniere *et al.*, 2004). Rivot *et al.* (unpubl.) also reported a significant reduction in the mean age at smoltification in Brittany and Lower Normandy and suggested this reduction may be due to changes in juvenile growth in response to warming (climate change) and/ or to a change in primary production, yet acknowledged that selective fishing on late maturing fish could also be responsible for a decrease in the mean age at sexual maturity. Davidson & Hazlewood (2005) reported an overall decline in the mean smolt age of 1SW and 2SW salmon returning to the Dee and Wye (Wales) and Severn (England) since the 1960s. However, the onset of this decline did not appear until the 1980s, and was notably less marked on the Severn. On the North Esk (Scotland) there has been a slow but steady decline in mean smolt age over the period 1971–2004 (J. Maclean, unpublished data) and on the R. Frome (England) the decline in smolt age has resulted in the near elimination of 2-year old smolts from the population (Section 4.3).

Englund *et al.* (1999) reported considerable inter-annual and tributary specific differences in the age structure of smolts in the River Teno, Finland between 1989 and 1995.

Jonsson *et al.* (2005) reported a positive correlation between river temperature and the proportion of salmon cohorts smolting and migrating to sea at age-1 and suggested that long-term effects of climate (e.g. NAOI) during early development may be more important than generally recognised.

Smolt size

Smolt size can vary widely among populations. Within populations, smolt size is flexibly dependent on growth rate – smolt size typically increases with age. Klemetsen *et al.* (2003) noted that large smolts (mean lengths typically >20 cm) tend to occur in rivers that enter a cold ocean, such as rivers in parts of Quebec, while small smolts (averaging 12–13 cm) can occur in cold rivers flowing into a relatively warm ocean, such as the glacier-fed rivers along the west coast of Norway. However, individual river, or even tributary, characteristics, and year to year fluctuations, may play as large a part in determining smolt size as any such broad geographical trends.

Jutila *et al.* (2006) reported a significant negative regression between the annual mean smolt size and the density of wild >1 year parr in the previous autumn in a northern Baltic river, but not between the annual mean smolt size and age. They hypothesised that the increased density of wild >1 year parr may have contributed to the decreased smolt size since the 1990s, and that the reduced size of wild smolts could result in reduced post-smolt survival.

Smolt run timing

It is generally accepted that there are two distinct processes involved in controlling the downstream movement of salmon smolts in fresh water. First, the physiological development of migratory readiness – whereby the juvenile salmon undergo the physiological and morphological changes associated with smoltification (migration disposition), and second, the environmental signals (external releasing factors) which stimulate downstream movement once smoltification has been completed (Baggerman, 1960; Solomon, 1978).

Changing day length has been suggested as the ultimate trigger to smolt migration, with river conditions such as temperature, discharge, turbidity and nightfall serving as proximate triggers controlling the smolt run in different rivers (Juttila *et al.*, 2005; McCormick *et al.*, 1998; Riley, 2007; and many others). Thus the timing of smolt migration varies with latitude, with southern populations moving out to sea earlier than northerly ones. Migration is correlated also to body size, with larger smolts typically migrating earlier, and also appears to have a genetic component (Stewart *et al.*, 2006).

Juttila *et al.* (2005) found that the onset of the smolt run was positively correlated with river temperature during 1972–2002 in a river flowing into the northern Baltic Sea; a rise in water temperature above 10°C being the main proximate environmental trigger. In addition, they found that the duration of the main run was shorter in the years when the onset of the smolt run was delayed. However, Zydlewski *et al.* (2005) found that temperature experience over time is more relevant to initiation and termination of downstream movement than a temperature threshold.

There are concerns that variations in climate might modify the run timing of smolts. As freshwater conditions are more responsive to air temperatures than the sea, and smolt migration is cued by water temperatures, mismatches relative to marine conditions might result and affect return rates. For example, Staurnes *et al.* (2001) indicated that smolts transferred to seawater in which the temperature gradient was more than 4–6°C had poorer seawater challenge performance. Evidence from some rivers in Newfoundland (SALMODEL, 2003) indicated a relationship between run timing and subsequent survival at sea, indicating a possible optimum window of opportunity for smolts entering the marine environment. However, this relationship was not consistent among rivers in the area.

Unusually early runs of smolts were observed on the River Bush in the late 1990s and a significant linear relationship determined between smolt migration date and marine survival, suggesting that smolt cohorts which migrated earlier had poorer survival (SALMODEL, 2003). Average SST taken from a coastal station 25 km north west of the river mouth indicated a temperature difference of 2.4°C with that of the river mouth during the years of poor survival, whereas the differential was only 0.3°C during earlier years when marine survival was higher (Section 4.1).

Role of lacustrine habitat

Klemetsen *et al.* (2003) have reviewed the importance of lacustrine habitat for juvenile salmon. It has been suggested that juveniles occupying such sites are displaced from preferred stream habitats. However, it appears that growth and survival is often better in lacustrine sites and that use of such habitats is of adaptive significance. In Newfoundland, a positive relationship has been identified between mean smolt size and the proportion of lacustrine habitat, with some evidence also of better survival to adult for the larger smolts.

Overall generation times have also been shown to be lower in lacustrine than fluvial systems. Although mean smolt age was similar in the two systems, there was a preponderance of 1SW adults arising from lake origin fish, while fluvial systems produced a significant component maturing at older sea-ages. This was consistent with the view that given environmental conditions conducive to rapid growth, fish will mature as soon as developmentally possible and may explain why many Newfoundland rivers are dominated by 1SW fish. Studies in other countries have also indicated that faster-growing juveniles and larger smolts favoured earlier age at first maturity (Nicieza & Braña, 1993 – northern Spain; Erkinaro *et al.*, 1997 – Finland). Provisional results for the Frome and Dee suggest that the sex of smolts may be important to the strength of relationship between smolt size and age at maturity (Section 5.7).

3 Data sets

3.1 Data sources and requirements

The exploration of biological characteristics for indicator salmon stocks and the possible relationship of such metrics with environmental parameters and abundance/survival measures requires data from three distinct areas. First, time series of standard biological measures pertaining to particular salmon stocks are needed, ideally covering an adequate (~15 year) period to account for natural variability and to facilitate trend analysis. This process was initiated through WGNAS (ICES, 2008) and was facilitated by the production of a data entry spreadsheet for pertinent biological variables (e.g. mean annual length, weight, sea-age of returning adults) to ensure the collection of time series information in a standardised format (Section 3.2).

A second requirement is the identification and compilation of appropriate environmental datasets. SGBICEPS reviewed the types of information that might be available to the Group in taking forward exploratory analyses (Section 3.5), in particular relating to the marine environment. However, the Study Group recognised that the lack of a clear understanding of the distribution of salmon at sea remained a constraint in this regard. The Study Group also recognised that specific requirements for environmental data or efforts to link these with changes in biological characteristics would need to be refined once clear hypotheses could be developed, for example in relation to specific stocks or stock complexes.

Finally, information on the relative performance of each available indicator stock, or stock complex, is required in terms of survival, mortality and abundance. The Study Group examined the available data relating to these stock status variables and these are considered in more detail in Section 3.4.

3.2 Data on biological characteristics

There is a vast amount of biological data relating to salmon stocks that is potentially available to the Study Group in pursuit of its objectives. Previously, an Excel spreadsheet was developed by Tim Sheehan (USA and Chair of WGNAS at the time) (ICES, 2008) in an attempt to begin the collation of summary parameters that might be informative in addressing the terms of reference, and this permitted some preliminary analyses of the data by WGNAS (ICES, 2008). However, the available data had remained largely unexplored prior to the SGBICEPS meeting.

In the run up to the Study Group meeting, data already collected were checked and a number of corrections made; some of the data sets were also updated and the time series extended. In addition, requests for further information were circulated, result-

ing in the provision of a number of new data sets and extending the geographic coverage of the information available. A full list of all those who provided data for use by the Study Group is provided at Annex 2.

The data entry spreadsheet requires various background information for each stock, as well as data for a range of biological characteristics. In summary, the fields are:

<u>Field</u>	<u>Description</u>
Year	Return year
River	
Country	
Stock Complex	e.g. NAC, northern & southern NEAC
Latitude	Latitude of river mouth
Origin	Origin of majority of spawning fish – hatchery/wild
Size	Approximated categorical description of the mean annual size of the spawning population
Status	Some standard estimate of stock status (e.g. count, trap catch) or index of abundance
Status type	Description of 'status' variable
Median run date	Median date of the spawning run
Mean run date	Mean date of the spawning run
Mean river age	Mean river age of returning fish
Mean sea-age	Mean sea-age of returning fish
Mean total age	Mean total age of returning fish
Proportion of run by sea-age	Proportion of the run by size/age grouping or by sea-age
Mean fork length	Mean fork length (cm) of returning fish by size/age grouping or by sea-age
Mean whole weight	Mean whole weight (kg) of returning fish by size/age grouping or by sea-age
Proportion female	Proportion of returning fish that are female by size/age grouping or by sea-age
Proportion maiden spawners	Proportion of returning fish that are maiden spawners by size/age grouping or by sea-age

Where data were requested by size/age grouping or by sea-age, the preference was for information to be split between each sea-age class – i.e. 1SW (1 sea-winter), 2SW, 3SW, 4SW, 5SW and previous spawners (PS). Where such data were not available, information was provided for small/1SW and large/MSW(multi sea-winter) categories. Table 3.2.1 summarises the information made available to the Study Group.

Table 3.2.1. Biological characteristics data provided for each stock (Y denotes data available for some or all of the time series)

Stock complex	Country	Stock	Hatchery/Wild	Time series	Latitude	Stock status	Median run date	Mean run date	River age mean	Sea age mean	Prop. Run by sea-age	Mean fork length	Mean whole weight	Prop. female by sea-age	Prop. maiden spawners by sea-age class
NAC	Canada	Western Arm Brook	W	1971-06	51.2	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
	Canada	Middle Brook	W	1975-05	48.8	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
	Canada	Conne River	W	1986-06	47.9	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
	Canada	Miramichi	W	1971-07	47.0	Y			Y	Y	Y	Y	Y	Y	Y
	Canada	Nashwaak	W	1972-07	46.0	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
	Canada	St John (Mactaquac)	W	1978-07	45.3	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
	Canada	St John (Mactaquac)	H	1978-07	45.3	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
	Canada	La Have	W	1970-07	44.4	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
	Canada	La Have	H	1972-07	44.4	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
	USA	Penobscot	H	1978-07	44.5	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
N NEAC	Finland/Norway	Teno	W	1972-07	70.8	Y			Y	Y	Y	Y	Y	Y	
	Finland/Norway	Naatamojoki	W	1975-06	69.7	Y			Y	Y	Y	Y	Y	Y	
	Russia	Tuloma	W	1983-08	68.9	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
	Norway	Argard	W	1992-07	64.3	Y			Y	Y	Y	Y	Y		
	Norway	Gaula	W	1989-07	63.3	Y			Y	Y	Y	Y	Y		
	Iceland (N&E)	Laxa I Adaladalur	W	1974-07	65.6					Y	Y	Y	Y	Y	
	Iceland (N&E)	Hofsa	W	1971-07	65.4						Y	Y	Y	Y	
S NEAC	Iceland (S&W)	Nordura	W	1968-07	64.6						Y	Y	Y	Y	
	Iceland (S&W)	Ellidaar	W	1949-07	64.1						Y	Y	Y	Y	
	UK (Scot)	N. Esk	W	1981-07	56.7						Y	Y	Y	Y	
	UK (NI)	Bush	W	1973-07	55.1	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
	UK (E&W)	Lune	W	1987-07	54.0	Y			Y	Y	Y	Y	Y	Y	
	UK (E&W)	Dee	W	1937-07	53.4	Y			Y	Y	Y	Y	Y	Y	
	UK (E&W)	Wye	W	1910-07	51.6	Y		Y	Y	Y	Y	Y	Y	Y	
	UK (E&W)	Frome	W	1968-08	50.7	Y			Y	Y	Y	Y	Y	Y	
	France	Bresle	W	1984-08	50.1					Y	Y	Y	Y	Y	

3.3 Data quality issues – caveats and limitations

Before reaching conclusions about the relevance of any apparent links that occur between different biological variables and measures of salmon abundance/environmental variables it is important to highlight a number of data quality issues that are apparent with the information available to the Study Group:

- The “status” column permits entry of a descriptive or numerical value of abundance. However, to avoid any conflicting effects of trends in fishery catches, users would also need to know at what point of the return run to the river (i.e. before or after fishery exploitation) these abundance indicators apply.
- The data source for most, but not all, of the stock status variables available to the Study Group was evident from the “status type” field. The source is variably recorded as adult trap count, river estimate, rod catch, declared rod catch and net fishery. Information derived from traps or counters has the advantage that it can be collected throughout the entire year, whereas fishery derived information is restricted to the fishing season. However, it should be noted that even these can be affected by issues such as counter ‘downtime’ or poor trap efficiency during flood events. Accordingly, the accuracy of the estimates of median and mean spawning run dates, average weights, lengths, ages and sexes will vary depending upon the source of the data and will need to be accounted for in any analysis.
- With respect to fish weight, data derived from net fisheries are most likely to represent the mass of fresh run fish while those derived from rod fisher-

ies (and possibly in some cases trap data) will be derived from a mix of fresh run and earlier run fish which will have already lost some body weight compared to when they originally entered freshwater. Thus there are issues in comparing both weights and condition factors among stocks where the weight variable has been recorded from different sources. Further there may be problems in interpreting rod fishery derived weight trends within a stock as the proportion of fresh to non fresh run salmon in the sample may vary throughout the time series.

- Where age data are given it would be useful to have a description of how the ages were derived. Simply put, ages determined from scale readings will be more reliable than ages estimated by a size (length or weight) split. However, the Study Group recognised that scale reading can also be subject to potential differences in methodology and interpretation, which might lead to possible inconsistencies between stocks.
- It is understood that all data relating to mean river age have been derived from scale analysis of returning adults. The Study Group recognised that such data might not accurately reflect the age composition of smolt cohorts, for example if different age/size classes of smolts are subject to differential rates of mortality in the sea.
- The accuracy of the sex variable will depend on a number of factors. Data obtained from fish dissection will be the most reliable, but the Study Group understands that for the majority of the data sets sex has been determined by observation of external morphometric features. The reliability of such observations will vary at different times of the season and among different observers.
- The original request for information indicated that data should only be included where this had been derived from sample sizes of at least 10 individual fish. In practice, it is not clear that this has been applied in all cases. Provision of a "sample size" variable would allow a better appreciation of the likely error around the mean values presented for each of the variables in the spreadsheet. Some concerns were also expressed about the use of annual means and that access to raw data might be of particular added value in some instances.

In taking forward analyses, and possibly extending these to additional data sets in due course, the Study Group recognised the importance of addressing data quality issues and the need to standardise approaches, and made the following recommendations:

- i) Data for all stocks should be accompanied by a full description of data sources and of the methodology used to record each variable to aid interpretation. Further, an email address of an appropriate person who is able to provide a more detailed description of each data set should be appended to the spreadsheet.
- ii) The collection and collation of data sets should be extended to include freshwater stages (e.g. smolt age, smolt size, growth at age, etc.). The Study Group noted that the available data were restricted largely to biological data on adults. This was considered prudent given the time available at the meeting. However, the Study Group recognised that freshwater data had been largely ignored and that there was increasing

evidence that freshwater influences might be instrumental to what subsequently happens in the sea.

- iii) Data sets with less than 15 year time series should be included in the analyses where these provide greater spatial scale or allow comparison with other available datasets. The Study Group recognised that requests for additional data sets, or for the raw data behind the annual mean values, should ideally be made in response to specific lines of enquiry and where worked examples/case studies suggested useful lines to pursue.

3.4 Salmon abundance

The Study Group was tasked with compiling information on the measures used to describe stock status for different stocks and regions. In reviewing and characterising the abundance metrics, the Study Group noted potential disparities between the measures available for different rivers. For example, status on some rivers was described as returns to the river whilst in other cases status measurements also accounted for the impact of in river or coastal fisheries.

The Study Group recognised that a process of data characterisation was needed to enable future analyses to be based on standard measures of abundance, where appropriate, and/or to allow some assessment of the robustness of the various abundance estimates. Initial efforts were made to characterise the abundance measures for the different indicator rivers (provisional, incomplete information in Table 3.4.1). These were differentiated between those stocks which provided estimates of the returning stock to the river and those which also provided estimates back to the coast (prior to homewater fisheries). Where possible, the methods used to derive the abundance measures were also characterised according to the assessment methods used (e.g. trap, fish counter, mark/recapture estimate, coded wire tagging programme) and calculation methods used (e.g. run reconstruction model).

Efforts were also made to draw together the available abundance metrics and data sets on survival/mortality for the different indicator stocks, and a series of draft tables were prepared and partially populated. Information was sourced from the latest WGNAS report (ICES, 2008) and from information available to Study Group participants. However, it was not possible to complete this task in the time available during the meeting. Further targeted efforts will be necessary to collate information for a number of the stocks from people who provided the original biological characteristics data.

Table 3.4.1. Information on derivation of abundance estimates for the salmon stocks for which biological characteristics data are available (Y indicates method(s) applied). [N.B. Table currently incomplete]

Stock complex	Country	Stock	H/W	Time series	Latitude	Abundance Measure														
						Return to River								Return to Coast						
						Full Trap	Partial Trap	Fish counter	Counting fence	Rod catch	Rod Catch Extrapolation	Mark/Recapture Estimate	In River commercial fishery correction	Snorkle survey	Other	CWT run reconstruction model	External tag run reconstruction model	Coastal commercial fishery correction	Pfa Model	Other
NAC	Can	Western Arm Brook	W	1971-06	51.2				Y											
	Can	Middle Brook	W	1975-05	48.8				Y											
	Can	Conne River	W	1986-06	47.9				Y											
	Can	Miramichi	W	1971-07	47.0															
	Can	Nashwaak	W	1972-07	46.0				Y											
	Can	St John (Mactaquac)	W	1978-07	45.3				Y											
	Can	St John (Mactaquac)	H	1978-07	45.3				Y											
	Can	La Have	W	1970-07	44.4				Y											
	Can	La Have	H	1970-07	44.4				Y											
	USA	Penobscot	H	1978-07	44.5															
N NEAC	Fin/Nor	Teno	W	1972-07	70.8					Y			Y							
	Fin/Nor	Naatamojoki	W	1975-06	69.7					Y			Y							
	Russia	Tuloma	W	1983-08	68.9															
	Norway	Argard	W	1992-07	64.3					Y										
	Norway	Gaula	W	1989-07	63.3					Y										
	Iceland	Laxa I Adaldalur	W	1974-07	65.6															
	Iceland	Hofsa	W	1971-07	65.4															
	Iceland	Nordura	W	1968-07	64.6															
	Iceland	Ellidaar	W	1949-07	64.1															
S NEAC	UK (Scot)	N. Esk	W	1981-07	56.7	Y														
	UK (NI)	Bush	W	1973-07	55.1	Y										Y		Y		
	UK (E&W)	Lune	W	1987-07	54.0		Y	Y												
	UK (E&W)	Dee	W	1937-07	53.4									Y						
	UK (E&W)	Wye	W	1910-07	51.6						Y		Y							
	UK (E&W)	Frome	W	1968-08	50.7				Y					Y						
	France	Bresle	W	1984-08	50.1															

Table 3.4.2 summarises the provisional data expected to be available. This includes Pre-fishery Abundance (PFA) estimates for 1SW and MSW fish at national and regional level, individual indicator river PFA or returning stock estimates (RSE) and marine survival indices/estimates for particular stocks. However, as with Table 3.4.1, further targeted efforts will be necessary to complete Table 3.4.2 and to fully populate the underlying data tables. The latter have not been included in this report.

Table 3.4.2. Summary of information available on the abundance and marine survival of different salmon stocks and for which biological characteristics data are also available (Y denotes data available; RSE = returning stock estimate). [N.B. Table currently incomplete]

Stock complex	Country	Stock	H/W	Time series	Latitude	National PFA	Regional PFA	Stock specific PFA / RSE	Marine survival estimate
NAC	Can	Western Arm Brook	W	1971-06	51.2	Y	Y		
	Can	Middle Brook	W	1975-05	48.8	Y	Y		
	Can	Conne River	W	1986-06	47.9	Y	Y		
	Can	Miramichi	W	1971-07	47.0	Y	Y		
	Can	Nashwaak	W	1972-07	46.0	Y	Y		
	Can	St John (Mactaquac)	W	1978-07	45.3	Y	Y		
	Can	St John (Mactaquac)	H	1978-07	45.3	Y	Y		
	Can	La Have	W	1970-07	44.4	Y	Y		
	Can	La Have	H	1970-07	44.4	Y	Y		
	USA	Penobscot	H	1978-07	44.5	Y			
N NEAC	Fin/Nor	Teno	W	1972-07	70.8	Y			
	Fin/Nor	Naatamojoki	W	1975-06	69.7	Y			
	Russia	Tuloma	W	1983-08	68.9	Y			
	Norway	Argard	W	1992-07	64.3	Y			
	Norway	Gaula	W	1989-07	63.3	Y			
	Iceland	Laxa I Adaldalur	W	1974-07	65.6	Y			
	Iceland	Hofsa	W	1971-07	65.4	Y			
	Iceland	Nordura	W	1968-07	64.6	Y			
	Iceland	Ellidaar	W	1949-07	64.1	Y			Y
S NEAC	UK (Scot)	N. Esk	W	1981-07	56.7	Y		Y	Y
	UK (NI)	Bush	W	1973-07	55.1	Y		Y	Y
	UK (E&W)	Lune	W	1987-07	54.0	Y		Y	
	UK (E&W)	Dee	W	1937-07	53.4	Y		Y	Y
	UK (E&W)	Wye	W	1910-07	51.6	Y			
	UK (E&W)	Frome	W	1968-08	50.7	Y		Y	
	France	Bresle	W	1984-08	50.1	Y			

3.5 Environmental data sets

Section 2.3 summarised some of the information available in the scientific literature linking salmon abundance with key oceanic variables, specifically: the North Atlantic Oscillation (NAO), the Gulf Stream North Wall (GSNW), the Mixed Layer Depth (MLD) and sea surface temperature (SST). The Study Group further reviewed the types of environmental information that could be employed to develop exploratory analyses, with particular emphasis on marine environmental data. Brief summaries appear below.

North Atlantic Oscillation (NAO) – is the time evolution of a pattern of sea level pressure (SLP) that provides an indicator of climate conditions in the region and is indexed by a long-term instrumental record. The NAO is seen as one of the dominant processes in determining the climate in the N. Atlantic, in winter in particular. Over the last few decades the NAO pattern has described 44% of the variability in North Atlantic wintertime SLP (Hurrell, 1995, Hurrell & Dickson, 2004).

The NAO instrumental indices measure the SLP difference between two places near the centres of the dominant high and low pressure systems. Different NAO indices provide subtly different time series (e.g. the winter Hurrell NAO index (Hurrell, 1995) uses Iceland to Lisbon for the December to March period, while the Rogers NAO index (Rogers, 1984) uses Azores to Iceland for the December to February period). The utilization of NAO indices in the context of understanding more local ecosystem impacts depends partly on the biogeographic area of interest - typically, the Hurrell index is more locally applicable to oceanic variability in the NE Atlantic

while the Rogers index may help to explain more of the local changes in the NW Atlantic (ICES, 2006).

NAO-related climate variability examples – through the alteration of pathways for moist air, precipitation over the N. Atlantic is strongly affected by the NAO. Thus, both precipitation and evaporation are correlated with the NAO (Hurrell, 1995). Figure 3.5.1 illustrates a composite precipitation/evaporation plot for the December to March period for the N Atlantic during a positive NAO phase (hatched areas denote significant correlation with the NAO and green denotes above average wetness). The patterns typically flip with a negative NAO.

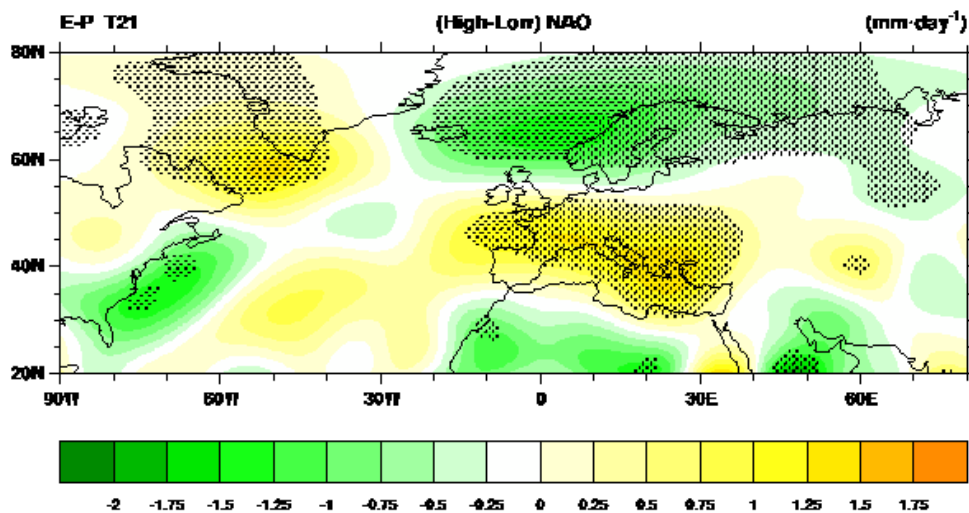


Figure 3.5.1. Precipitation/evaporation index for the N. Atlantic during a positive NAO phase for December to March (Figure courtesy J. Hurrell) (Hurrell, 1995).

Sea surface temperatures (SST) are also correlated with NAO. During a positive winter phase of the NAO, there is typically warming in parts of the NE Atlantic and North Sea with higher SSTs in these areas.

The Atlantic Multidecadal Oscillation (AMO) – provides an alternative measure of Atlantic climate variability to the NAO. This index is thought to be driven by the thermohaline circulation and is derived from the de-trended annual mean SST over the area 0°N to 75°N, 75°W to 7.5°W (Enfield *et al.*, 2001; <http://www.cdc.noaa.gov/data/timeseries/AMO/> for data download). The AMO provides a pattern of SST anomalies in the North Atlantic that appears to coordinate most of the Atlantic in a series of warm and cool phases that last for 20 to 40 years (Figure 3.5.2a; Sutton & Hodson, 2005). During the 20th century the index has oscillated between cool periods in 1905–1925 and 1965–1990 and warm periods in 1931–1960 and 1995–present, with the greatest SST anomalies just east of Newfoundland. The AMO appears to be a natural mode of operation of the climate in the North Atlantic and is possibly one of the connected processes that helps to create the NAO. Since the mid-1990s, the warm phase of the AMO is thought to have intensified, regionally, the long-term warming due to climate change; at other times it may obscure the climate change signal (Cannaby & Hüsrevoğlu, 2009) on a decadal timescale. The present warm phase of the AMO should dictate increasing summer droughts and warmer summers in North America, perhaps together with warmer and wetter summers in western Europe. However, the utility of forecasting climate by means of the AMO may alter as interactions with anthropogenic effects become apparent (Sut-

ton & Hodson, 2005). Given its apparent repeat patterns, the AMO may offer some prospect of application in a predictive capacity, but the forcing mechanisms behind this phenomenon are poorly known (Sutton & Hodson, 2005). Further, it has to be emphasized that this index embraces essentially all of the Atlantic north of the equator and yet clear differences in recent climate change between the western and eastern North Atlantic are well-documented (e.g. Hughes *et al.*, 2008; “*In situ* time series” below).

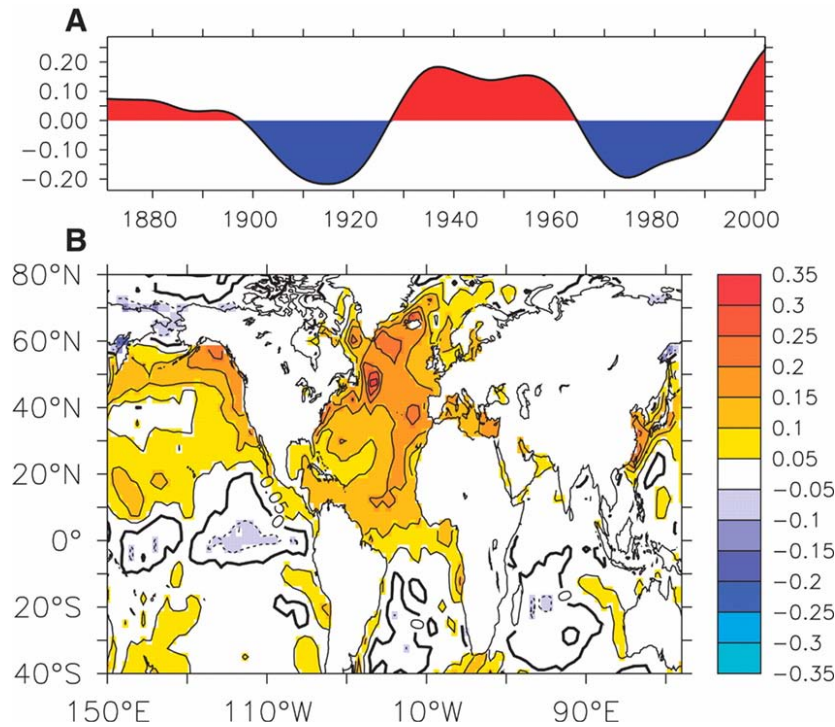


Figure 3.5.2 (a) AMO – the smoothed mean SST in the region 0°N to 60°N, 75°W to 7.5°W in deg C; (b) indicating that AMO is correlated to SST on a much wider scale than the region it is derived from. Figure from Sutton & Hodson (2005).

In respect of salmon recruitment, recent investigations suggest that the AMO is a more closely aligned climate forcing index than the NAO (Friedland *et al.*, 2009).

Gridded data sets – there are a number of sources for gridded SST and other meteorological variables. Some of these will be derived from model re-analyses, some interpolated data and some un-interpolated data. For instance, gridded model re-analyses are available for most ‘weather’ parameters (including: SST, air temperature, precipitation, light levels and wind speed) monthly back to 1948, with free web access (NOAA, Climate Diagnostics Center) and gridded SST products are available back to the 19th century (e.g. HadISST, Rayner *et al.*, 2003). Such data might give a good indication of regional differences for individual winters and thus may be useful in future hypothesis testing.

***In situ* time series** – the ICES Report on Ocean Climate (IROC) is produced annually by the ICES Working Group on Oceanic Hydrography (WGOH; Hughes *et al.*, 2008), and includes high quality *in situ* time series for both SST and salinity, covering much of the area of salmon distribution in the North Atlantic. These *in situ* records provide a direct measure of the historic evolution of conditions in the upper ocean experienced by, for example, the fish within it. The changes in the observed temperature and salinity record will be an integration of the combined impacts of changes in the

North Atlantic climate system itself including components of the signals from NAO, AMO, global warming and ocean circulation. Figure 3.5.3 illustrates the SST *in situ* records from IROC 2007 (Hughes *et al.*, 2008). There are evident differences between the western North Atlantic and the eastern North Atlantic and Nordic seas, the latter characterised by a period of warming in the last 10 to 15 years. The *in situ* time series also indicate higher salinity in recent years in Nordic Seas and the Faroes/Shetland Channel, with a period of low salinity in the Baltic Sea.

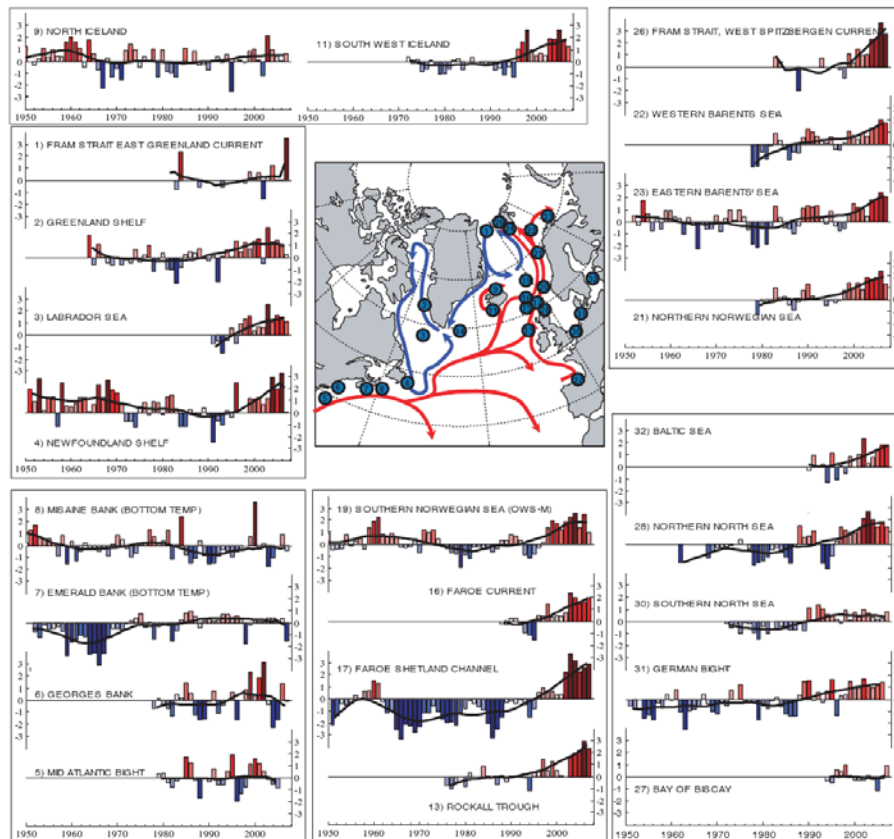


Figure 3.5.3. *In situ* SST records for sites around the N Atlantic (data from ICES Report on Ocean Climate 2007; Hughes *et al.*, 2008).

The Study Group noted the present lack of a clear understanding of the distribution of salmon at sea and the multiple possible migratory destinations of individuals within the same maturity grouping (e.g. southern European MSW fish migrating either to the Norwegian Sea only, or to the coasts of Greenland). This remained a constraint with regard to identifying the most appropriate environmental data sets, and it was recognised that clarifying specific data requirements or making efforts to link these with changes in biological characteristics would need to be refined once clear hypotheses could be developed in relation to, for example, observed changes in specific stocks or stock complexes. This would be more appropriate once provisional analyses had been completed and potential common patterns or trends identified.

4 Case Studies

The Study Group reviewed summary information from the Baltic Salmon Working Group and information available from a number of monitored stocks in the North Atlantic that have time series of data on biological characteristics of salmon or on changes in salmon abundance relative to environmental variables. These have loosely been grouped into a series of case studies and are described below.

4.1 Biological characteristics of the River Bush salmon stock – UK (N. Ireland)

The River Bush salmon project provides a long term study of the biological characteristics and stock recruitment dynamics of a typical whole river salmon stock from UK (N. Ireland). The project is based around annual full-river trapping census of returning adults and emigrating smolts at Bushmills in Co. Antrim. A range of biological data is recorded from smolts and adults to locally defined methodology as outlined below:

Smolts

Biological characteristics data: length, weight, (river) age, sex, run timing

Duration: 1973–2008

Quality: 400–800 samples yr⁻¹

Adults

Biological characteristics data: length, weight, (total & sea) age, sex, run timing

Duration: 1973–2008

Quality: average 250 samples yr⁻¹ (~14% of run)

The status of the population can be described through a number of potential mechanisms. The adult trap return provides a consistent annual metric from the initiation of the time series in 1973, but this can also be adjusted to provide an estimate of the total return to the river through integration of recorded in-river mortality such as angling exploitation. In addition, a coded wire tagging programme has been operational on the river since 1985, which has facilitated the calculation of the total return to the coast based around an annual screening programme of coastal commercial fisheries and the application of a run reconstruction model (Crozier & Kennedy, 1994b). River returns in the period 1980–1990 were significantly impacted by coastal commercial fisheries (Figure 4.1.1), with exploitation rates up to 80% in some years. In taking forward potential analysis of stock status in relation to biological and environmental data, the measures used to describe stock status will be a vital consideration. For example, while returns to the River Bush have been reasonably stable over the time series, there has been a very marked reduction in the overall returns to the coast (Figure 4.1.1). Such considerations will be particularly critical when groups of indicator rivers are considered together; utilisation of a standard status metric will ensure a more consistent, standard approach to any subsequent analysis.

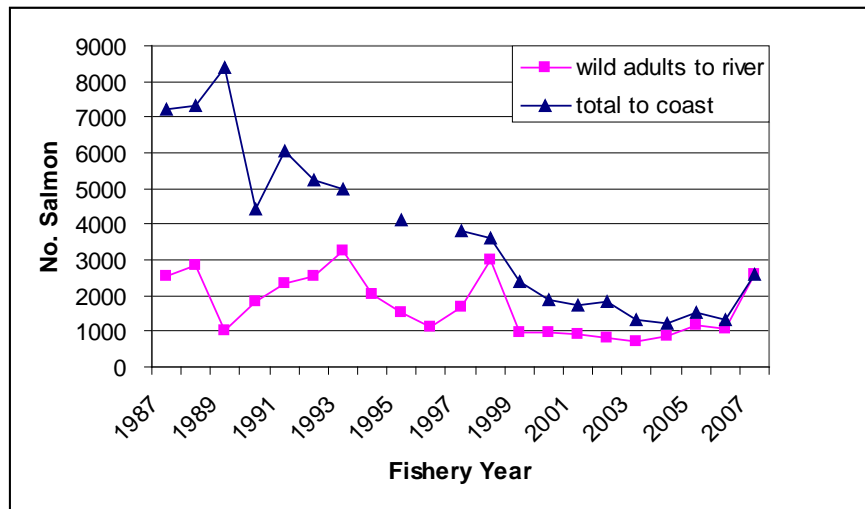


Figure 4.1.1. Comparison of returns of 1SW salmon to the River Bush and run reconstruction estimates of total numbers of 1SW salmon returning to the coast.

The river age of R. Bush smolts is determined from fish sampled at the downstream juvenile trap and annual scale reading analysis. Two-year-old smolts are most common, although the age structure is quite variable from year to year. There is no obvious trend over the time series; however, based on a five-year moving average there is a suggestion that the numbers of younger 1+ smolts may be increasing in the most recent years (Figure 4.1.2).

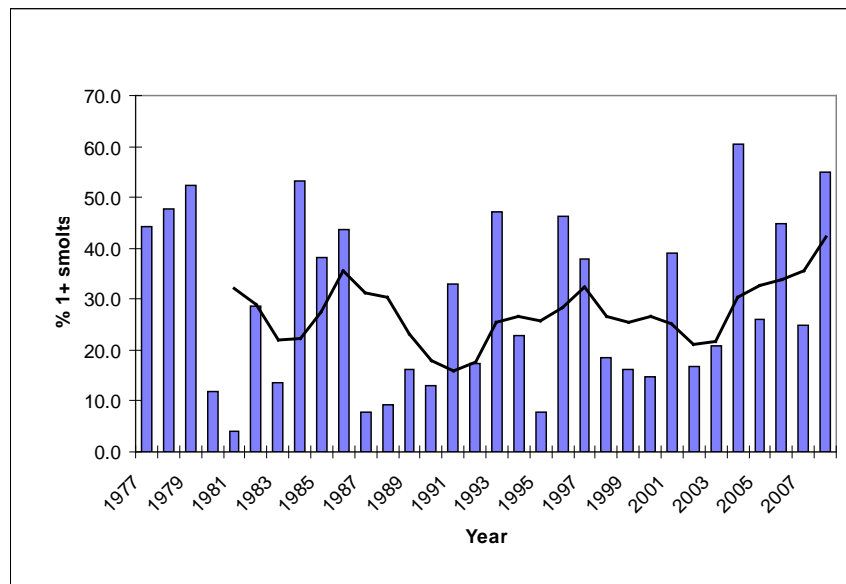


Figure 4.1.2. Percentage of 1+ smolts in annual wild smolt runs on the R. Bush, with 5 year moving average.

The mean lengths and weights of R. Bush smolts vary over the time series, but with little evidence of a discrete temporal trend. Figure 4.1.3 illustrates the mean annual length of 1+ and 2+ smolts and indicates relative stability for this biological characteristic between 1974 and 2008.

Previous work has indicated that the timing of smolt migration has shifted over the period, with increasing numbers of fish migrating earlier in the year (Crozier & Ken-

nedy, 2003). This has potential implications for subsequent survival, with some evidence that years of lower marine survival occur when there is a higher thermal discrepancy between river water and sea water at the time of the smolt migration.

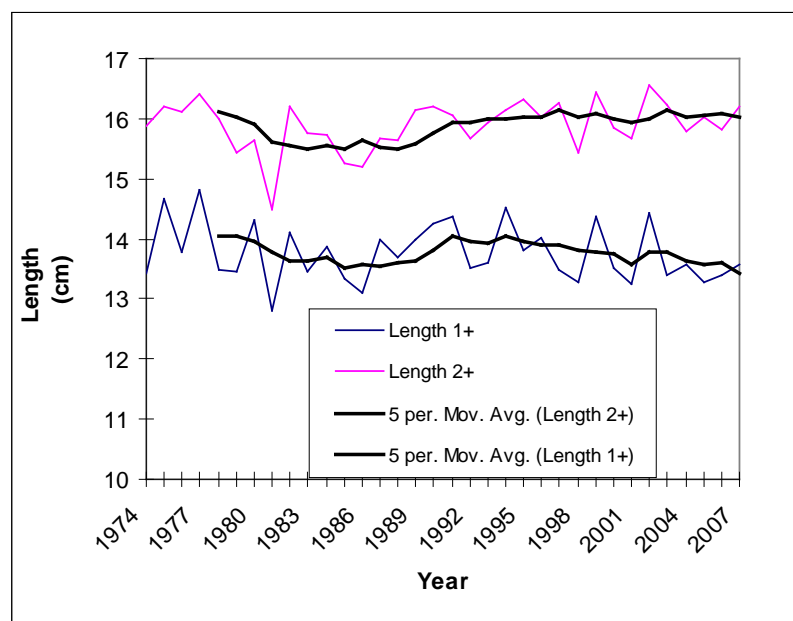


Figure 4.1.3. Mean annual length of 1+ and 2+ wild smolts on the R. Bush, with 5 year moving average.

The biological characteristics of adult salmon are collected from a representative sample of fish examined from the R. Bush salmon trap. Initial examination of the various characteristics across the time series has revealed several discrete trends in the stock. The sea-age composition of the stock has varied between years, but with 1SW fish comprising an increasing proportion of the adult run over the time series (Figure 4.1.4). In addition, the mean annual fork length of 1SW fish shows a significant reduction over the time series; there is no evident trend for MSW fish (Figure 4.1.5).

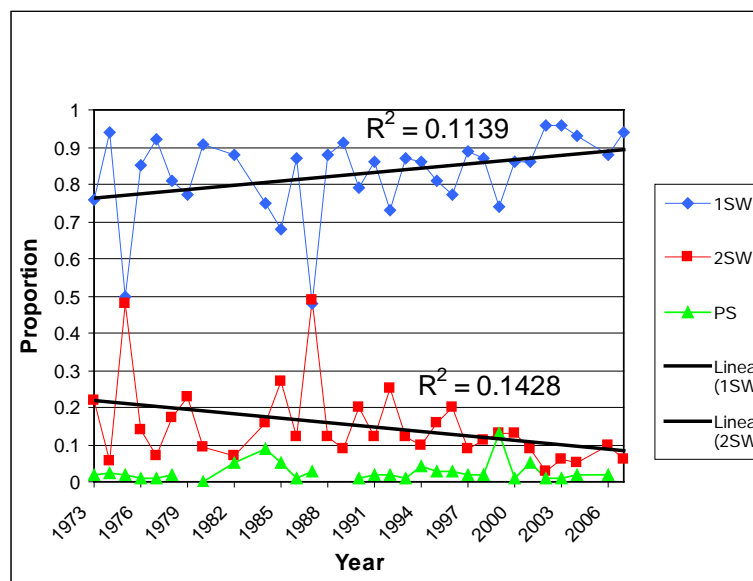


Figure 4.1.4. Proportional composition of total annual R. Bush wild salmon run according to sea-age.

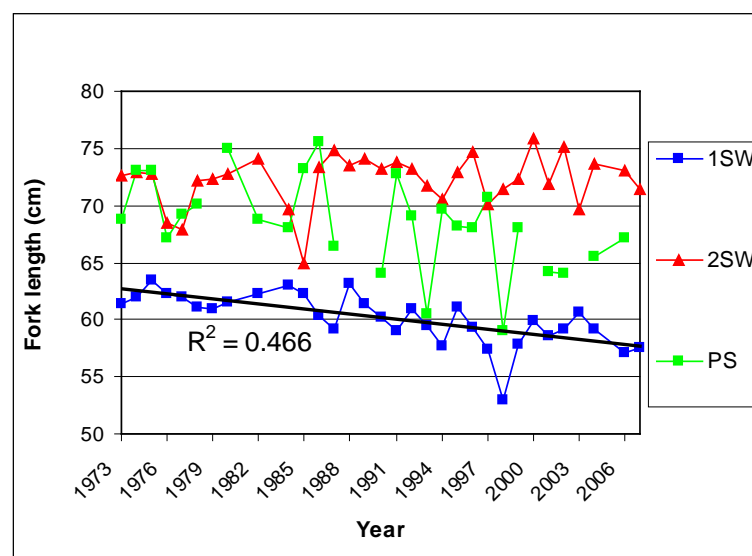


Figure 4.1.5. Mean annual length of 1SW, 2SW and previous spawners from the wild R. Bush salmon run.

4.2 Biological characteristics of salmon from the River Dee, North Wales and other monitored rivers in UK (England & Wales)

There are eight monitored rivers (Rivers Dee (Wales), Test, Itchen, Frome, Tamar, Fowey, Lune and Kent) in UK (England & Wales) which report Returning Stock Estimates (RSEs) for salmon to ICES (Cefas & Environment Agency, 2008). Monitoring programmes on most of these rivers are currently run by the Environment Agency - with the exception of the Frome programme which is run by the Centre for Ecology and Hydrology (CEH). [Separate 'case study' reports on two of these rivers – the Test and Frome - follow.]

Four rivers (Rivers Dee (Wales), Tyne, Tamar and Lune) are also identified as monitored 'index' rivers and are distinguished by having established or developing (par-

tial) adult trapping programmes to collect biological information (e.g. on age, size, sex, etc.) (Davidson, 2008). Collection of this type of information in UK (England & Wales) is now almost entirely confined to these rivers but is needed in order to partition RSEs into age and year class components and gain better insight into the response of populations to environmental change.

The above monitored/index rivers are spread around UK (England and Wales) and are broadly representative of the main salmon and sea trout producing regions. The group includes some of the leading 'chalk' rivers of southern England (e.g. Test, Itchen, Frome) as well as the more usual 'rain-fed' rivers of the west and north. While the monitoring programmes for individual rivers may differ in their detail, they share a number of common objectives in terms of the information collected and its application to management (Davidson, 2008).

Components of the River Dee programme

Partial adult trapping and the provision of RSEs (for sea trout as well as salmon) began on the Welsh Dee in 1991 at Chester Weir (a head-of-tide trapping site). This makes the Welsh Dee programme the longest running of all the index river trapping programmes. Unlike other monitored rivers where RSEs are based on resistivity fish counts, those for the Welsh Dee are derived from mark-recapture and, for salmon at least, rely on the support of anglers in reporting the capture of tagged fish. (This support is encouraged through the running of a logbook scheme and payment of tag rewards.)

Other elements of the Welsh Dee programme include:

- Net and rod fishery censuses to record catch, fishing effort, etc. On most of the main salmon rivers in UK (England and Wales) fishery statistics have been collected in a systematic manner since at least the 1970s (Russell *et al.*, 1995). On the Welsh Dee, records extend back to the early 1900s and include monthly and annual figures on the numbers and weight of fish caught as well as data on fishing effort. From the mid-1960s to the late 1980s, scales were sampled from Dee net caught salmon for ageing purposes accompanied by information on the length and weight of individual fish. Aside from some scale samples retained from the mid-1980s and individual fish records from around the same time, the resulting age and size composition data are now only available as monthly or annual summaries.
- Electrofishing (EF) surveys for juvenile salmon and trout. These are carried out annually on the Welsh Dee – sampling 80+ sites using timed (5-minute) techniques similar to those applied on the River Bush, N. Ireland (Crozier and Kennedy, 1994a). This provides information on spatial and temporal changes in abundance, age and size composition. Additional annual and 6-yearly surveys - using more conventional semi-quantitative EF methods - are undertaken on the Welsh Dee and most other salmonid rivers in UK (England & Wales) as part of a national sampling programme. In some cases, these build on historic data sets beginning in the 1970s.
- Partial trapping and Coded Wire Tagging (CWTagging) of salmon (and sea trout) smolts to estimate smolt-to-adult return rates (Figure 4.2.1). Smolts are trapped using Rotary Screw Traps deployed in spring on the lower main Dee and at a major tributary site. This work, and a similar programme on the Tamar, is carried out in collaboration with Cefas. On other monitored rivers – namely the Tyne, Test and Frome – smolt trapping and tagging or (in the case of the latter) PIT tagging and video methods, are used to estimate the size of the smolt run.

Current status and historic trends

RSEs obtained on the Welsh Dee since 1992 indicate that numbers of returning salmon have remained relatively stable over the last 17 years – averaging around 5,700 fish at Chester (post in-river net fisheries and pre- the rod fishery). Current spawning stock levels are around 90% of the Conservation Limit.

1SW salmon comprise the majority of the run (~70%) with 2SW fish making up most of the remainder. Since the 1960s, the Welsh Dee, like many rivers across the North Atlantic, has seen a decline in overall catch – including a marked reduction in numbers of MSW salmon and particularly early run fish (Aprahamian *et al.*, 2008).

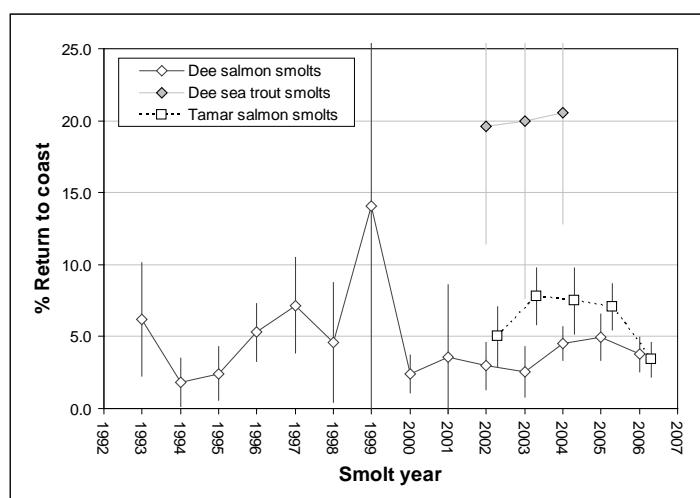


Figure 4.2.1. Return rates for CWTagged salmon and sea trout smolts on the Tamar and Welsh Dee, smolt years 1993-2006. [Error bars indicate 95% confidence limits]

Size composition data from net and trap caught salmon (pre and post 1991, respectively) indicate that the mean weight of 1SW fish has remained relatively stable over the last 40 years (Figure 4.2.2). However, the size of 2SW fish appears to have been increasing from the mid-1980s to the end of the 1990s, but has declined subsequently.

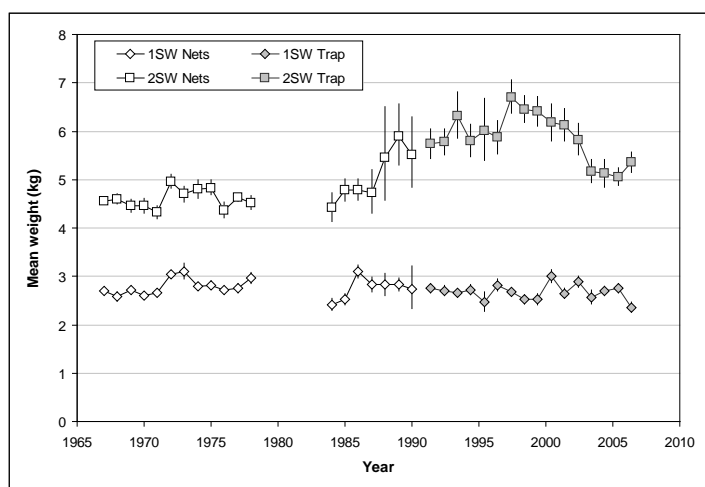


Figure 4.2.2. Geometric mean weights of 1SW and 2SW salmon on the Welsh Dee, June to August 1967-2006. [Error bars indicate 2 x SE.]

Annuli measurements from historic and recent scale samples have been used to back-calculate pre and post-smolt growth rates for salmon and explore the influence of environmental factors (e.g. freshwater and marine temperatures) on the patterns observed (Davidson and Hazlewood, 2005).

For example, growth rates among juvenile salmon on the Welsh Dee have been increasing over the last 20-30 years. This increase corresponds to a decline in the mean smolt age (judged from the scales of returning adults) – from ~2 years up to the late 1970s to around 1.6 years at present (most of this decline occurring over a decade or so). Similar changes in mean smolt age – in terms of timing and magnitude - have also been observed on the neighbouring rivers Wye and Severn (Davidson *et al.*, 2006; Aprahamian *et al.*, 2008).

The causes of these changes in salmon smolt age composition and freshwater growth are the subject of ongoing investigations. These have focused on the role of increasing water temperatures in promoting faster growth (Davidson *et al.*, 2006), but have also noted changes in other potential influencing factors e.g. nutrient enrichment (Aprahamian *et al.*, 2008). The latter is known to have occurred in parts of the Dee catchment due to intensification of agriculture. Aprahamian *et al.* (2008) also explored links between freshwater and marine age and growth in Dee salmon and survival, maturation and fitness since the 1930s.

The influence of past and possible future temperature regimes (the latter linked to climate change scenarios) on freshwater growth and survival have been explored at a catchment level on the Welsh Dee and other rivers in UK (England & Wales) (Davidson *et al.*, 2006) – applying the temperature-growth models of Elliott *et al.* (1995) and Elliott and Hurley (1997). More recent investigations have applied the same temperature-growth models at a sub-catchment level to investigate growth variations in populations of late summer salmon fry sampled over the last 15 years (see Figure 4.2.3).

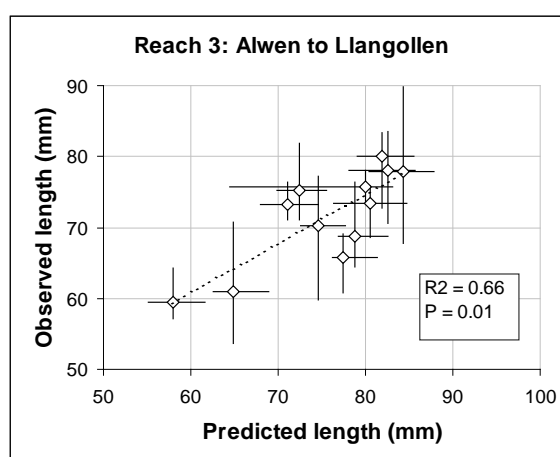


Figure 4.2.3. Observed and predicted mean lengths of salmon fry sampled from the middle reaches of the main River Dee. [Error bars indicate min and max estimates.]

Future work

Much of the Environment Agency's remit in terms of monitoring and managing migratory salmonids is concerned with in-river populations – whether juveniles or returning adults. Developing a better understanding of the links between environmental changes and the status and composition of stocks remains a priority –

this includes environmental changes associated with global warming, pollution, etc. Ongoing areas of work include:

- Further exploration on the Welsh River Dee of the past and possible future role of temperature (and other factors) in promoting faster freshwater growth and younger mean smolt ages in migratory salmonids. Assessing the implications of these changes for pre-smolt and post-smolt survival, adult return and the age and size composition of adult stocks, and what marine environmental effects might underpin these.
- More detailed examination of patterns and trends in biological characteristics within and between monitored river stocks and including assurance that related characteristics measured at different life-stages provide consistent signals. Compiling and comparing data sets from a number of rivers should aid understanding of geographical influences on the patterns observed and may provide clues as to the nature of underlying effects.
- Parallel investigations into the responses of resident or migratory trout to environmental change. Trout as resident fish or sea trout share common freshwater and estuarine/inshore marine habitats with salmon for at least part of their life-cycles and may prove valuable and possibly more sensitive indicators of the influence of environmental changes on biological process – particularly at a local scale.

4.3 Biological characteristics of salmon from the River Frome – UK (England & Wales)

The River Frome is at 50°N latitude. It is a chalk river and is representative of a group of similar river systems on the south coast of England. These rivers are characterised by stable flow and temperature regimes in comparison to upland rivers.

The long-term biological data have come from an adult salmon counter that has recorded hourly counts since 1973 and a collection of adult scales taken from angler catches and electro-fishing surveys from the 1960s. The collection of scales ceased in the mid-1990s when angling regulations restricted the season and anglers were encouraged to practice catch and release.

It is important to note the following:

- that the adult counts are generally difficult to split into age classes without the benefit of information from scales and in many years the numbers of collected scales are low.
- that the biological data derived from scales is from survivor information and therefore reflects all the factors that affect survival at sea, in particular any annual changes in size dependent mortality rate for smolts.

Adult returns measured by the adult counter fell heavily in the late 1980s early 1990s (Figure 4.3.1). At the same time there was general shift in the population towards a higher proportion of 1SW fish. 1SW fish decreased in size between 1965 and 1995, whilst during the same period 2SW fish increased in size (Figure 4.3.2). The median date of adult migration into the river has become later.

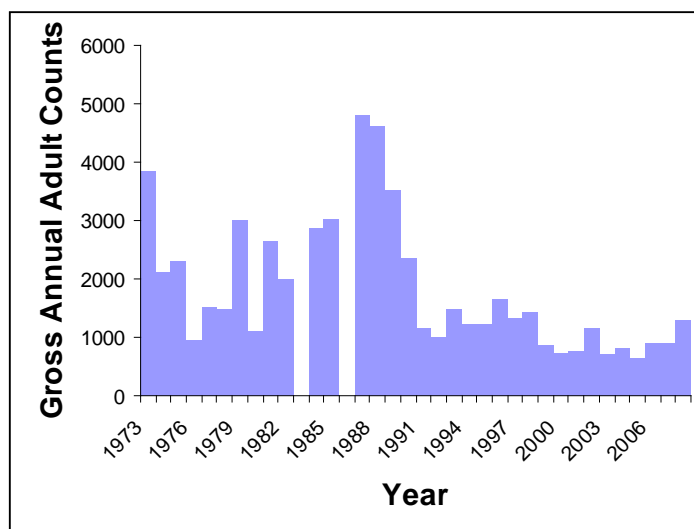


Figure 4.3.1. Gross annual counts of Atlantic salmon on the River Frome.

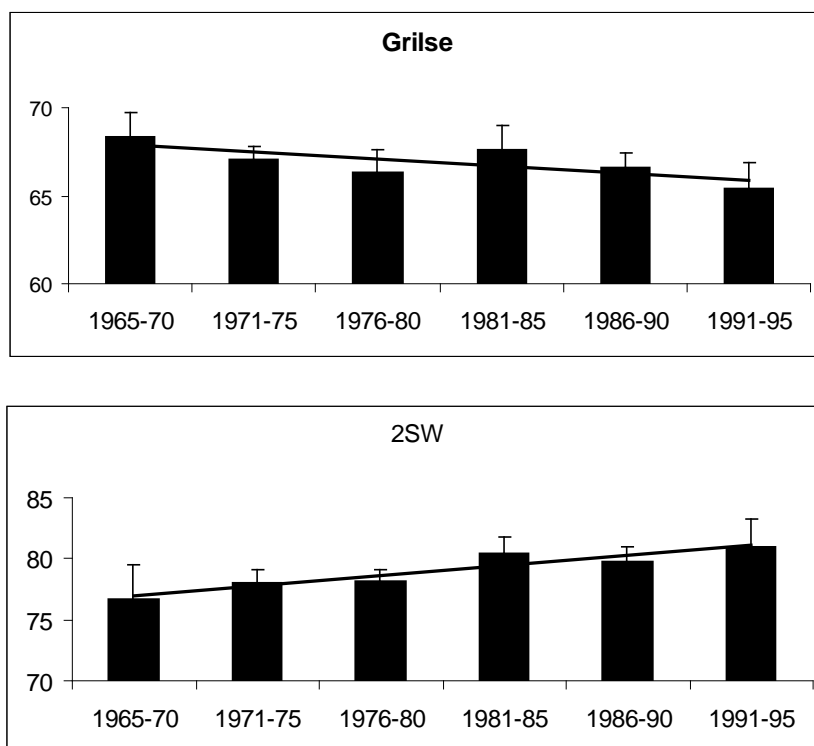


Figure 4.3.2. Mean sizes of 1SW and 2SW adult salmon returning to the River Frome (Note: y-axis is fork length in cm).

Using information derived from the scales of survivor adult returns to the river, the mean size of smolts seemed to increase post 1985 (Figure 4.3.3). At the same time the mean age of smolts declined, such that it is now close to 1 (Figure 4.3.4). Whilst, it is not certain whether the mean size of smolts has actually increased or whether this is simply the result of a change in the size dependent mortality rate, it is certain that the mean age of smolts has declined to 1, as very few 2 year old smolts are now produced.

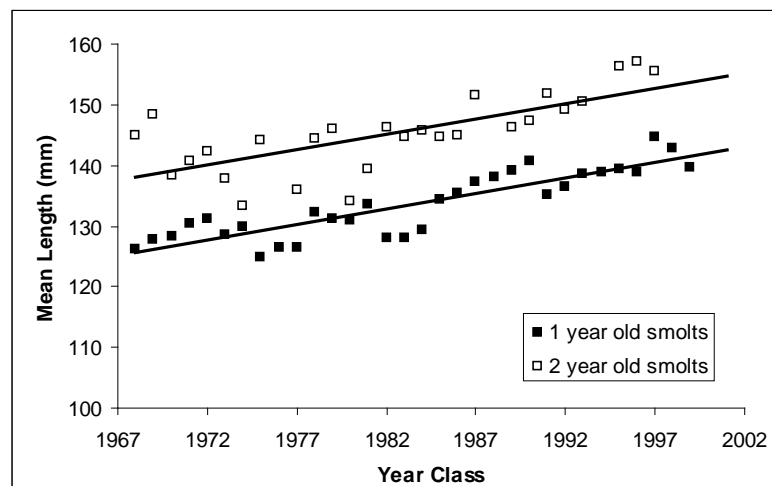


Figure 4.3.3. Mean smolt length of adult salmon returning to the River Frome.

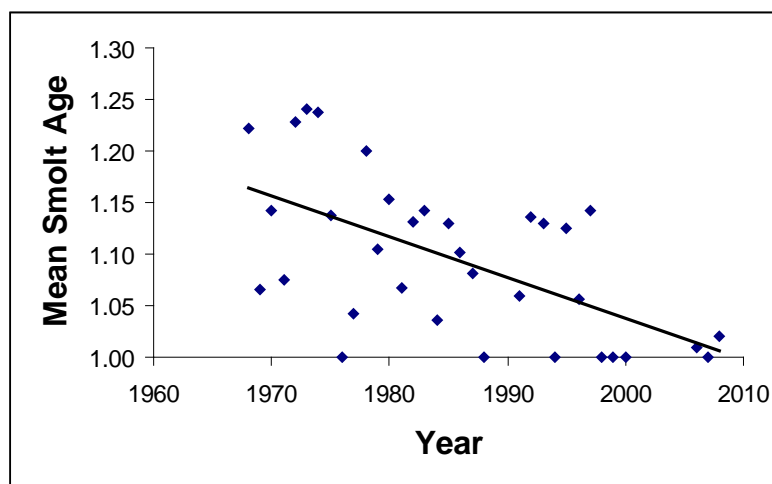


Figure 4.3.4. Mean smolt age of adult salmon returning to the River Frome.

Similarly, from the survivor data, there seems to be a strong link between the size of smolts and the number of years spent at sea. Small smolts have a lower probability of being 1SW fish than large smolts. When this was separated into sexes, this relationship appeared not to exist in males but was very strong in females (Figure 4.3.5).

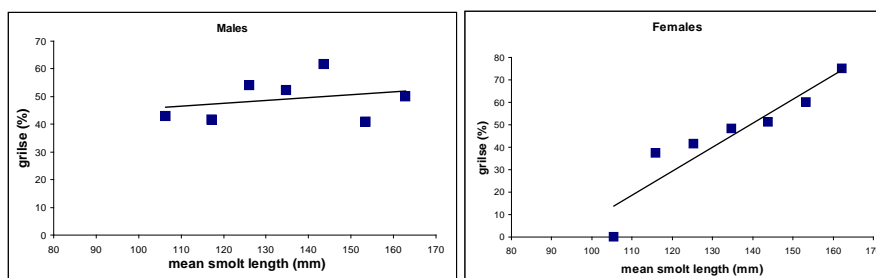


Figure 4.3.5. Percentage of smolt length classes returning as male and female adult 1SW fish in River Frome Atlantic salmon.

4.4 Biological characteristics of salmon from the River Test – UK (England & Wales)

Background

The Test is another of the group of southern England chalk rivers. Two fish counters and a smolt trapping programme form the basis of salmon stock monitoring on the river and have been ongoing since 1990 and 1992 respectively. High quality catch records are available since 1928 for some rod fisheries and for all major rod fisheries since 1952. Quality assured daily flow records are available for the lower river almost continuously since 1952.

No significant commercial fisheries have operated on the River Test for over fifty years. Rod exploitation rates were generally of the order 25–35% in the early 1990s when most fish caught were killed. Following the introduction of broodstock collection programmes from rod captures in the late 1990s all fisheries adopted a voluntary catch and release policy. Catch and release rates increased steadily until around 2001 when near 100% was achieved. This has continued to the present with only one or two fish a year being reported taken or which fail to recover on release.

There has been a marked shift in the age structure of the River Test salmon population from one dominated by MSW fish during the 1950s to one dominated by 1SW fish. Growth rates of the juveniles are known to be some of the fastest in the UK with over 90% of juveniles smoltifying at one year old.

In addition to the river discharge and salmon stock metrics available, a considerable amount of water temperature, suspended solids and other water quality data are available for almost a thirty year period. This dataset has enabled analysis of spawning success over the past eighteen years and may enable further evaluation over a thirty year span.

Spawning Success

Recent trends in egg deposition have indicated a steady increase in the percentage compliance based on a three year average (Figure 4.4.1).

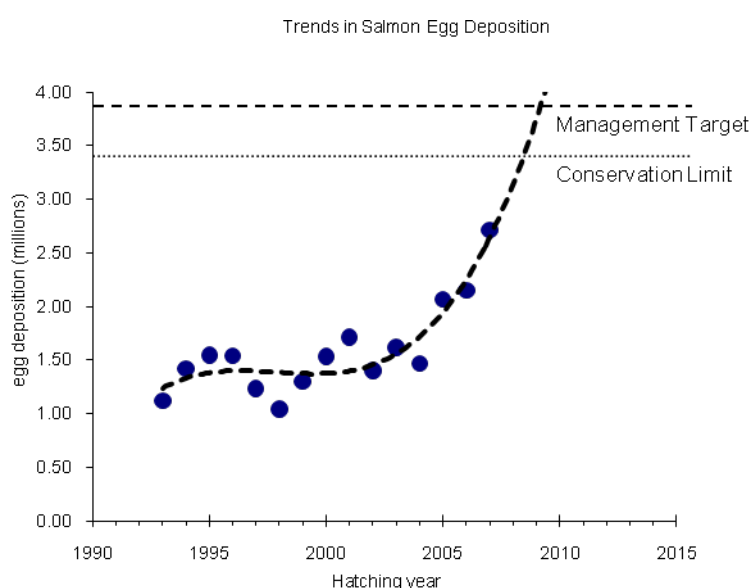


Figure 4.4.1. Trends in salmon egg deposition

It is notable that there have been marked contrasts in river discharge since the winter of 2000/1. The summers of 2003, 2005 and 2006 were characterised by unusually low discharge and high water temperatures. The summers of 2001, 2007 and 2008 have been characterised by unusually high discharge and low water temperatures.

In general the most seaward fisheries have done well since high rates of catch and release have been the norm. In years of low discharge the upper fisheries have not caught well and, by contrast, in years of high summer discharge the upper fisheries have experienced favourable catches.

Comparison of spawners with smolt output showed no relationship ($p = 0.945$; Figure 4.4.2) indicating that other environmental factors operating between spawning and smoltification may be influencing (obscuring) the stock-recruitment relationship. Comparison of a standardised measure of spawning success, smolts per spawner, with river discharge during incubation however indicated a negative trend with increasing river discharge (Figure 4.4.3).

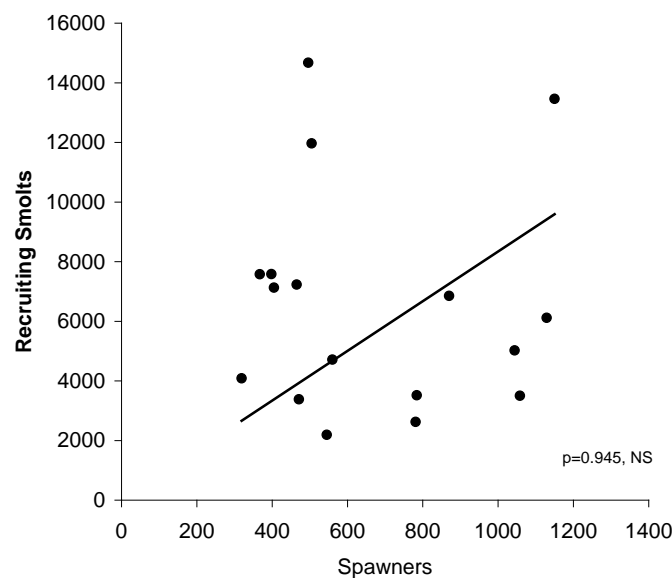


Figure 4.4.2. Stock Recruitment data for River Test

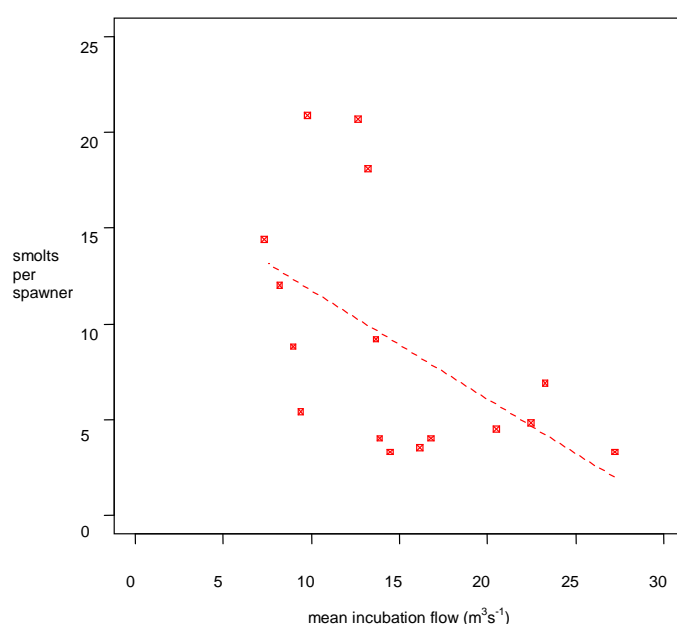


Figure 4.4.3. River discharge and spawning success

It was notable that the slope of the relationship between smolts per spawner and river discharge during incubation was negative, with moderate to high discharge leading to poor spawning success. There was some evidence that the relationship might be non-linear. Studies by Dr David Sear on the River Test and other local chalk streams suggested that the mechanism behind this observation involved the mobility of sediment during incubation. In short, during periods of low discharge although there may be a great deal of latent sediment in the river system very little was moved within the river and this could therefore not infiltrate a recently created redd. In contrast, during periods of moderate to high flow there was sufficient sediment mobility to infiltrate the redd and therefore compete for oxygen with salmonid eggs.

To investigate this hypothesis historic suspended solids and river discharge data were used to estimate the sediment transported for each season; incubation, summer and autumn. The relationship observed for the sediment transported during the incubation season was most striking and indicated an almost step like cap on spawning success if the sediment transported exceeded 200 t per season (Figure 4.4.4). Below 200 t and the spawning success could range from 5 to 22 smolts per spawner. Above 200 t and the spawning success only exceeded 5 smolts/spawner in one year (~7 smolts/spawner).

It was also hypothesized that water temperature during incubation might influence spawning success because average water temperatures were often close to the thermal limit for Atlantic salmon eggs. Winter water temperatures have been observed to rise faster than summer temperatures over the last thirty years (daily records from the adjacent River Itchen). No significant relationships were found between water temperature (max and mean) and spawning success either for the whole dataset or either the group above or below the 200 t sediment transported threshold.

Examination of the long term trends in suspended solids show a steady decline in suspended solids concentration over the last thirty years both in the upper and lower

catchments giving some cause for optimism. This equates to an average reduction in suspended sediment concentrations of approximately 20~25%. It should however be remembered that it is the mobility of this sediment that is the important factor and the high variability in spring discharge since the late 1980s suggests that this feature will continue to dominate the population dynamics of the River Test for the foreseeable future.

In summary, the environmental impact of diffuse pollution on the salmon population of the River Test appears to be substantial indicating a link between stock status and environmental factors operating in freshwater. These effects have been measured on a catchment scale and have implications for the management of salmon on this river as well as for the interpretation of stock recruitment data in general. Similar effects are likely to exist on other rivers.

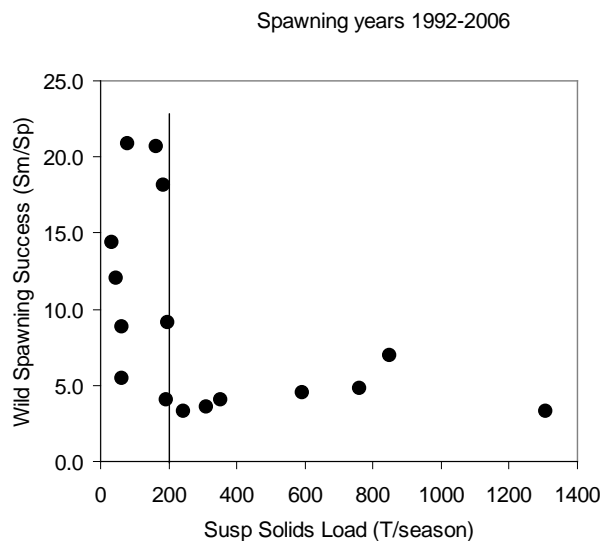


Figure 4.4.4. Spawning success and suspended solids load

4.5 Evidence for later age at maturity in Norwegian salmon stocks in recent years

There is much evidence for historic fluctuations in the age at maturity of Atlantic salmon. In the 1990s, there appeared to be a decrease in the age at maturity in many stocks. For example, the proportion of 1SW salmon has increased in North American stocks over the period 1970–1991 (Ritter, 1993), and in five UK rivers there was an increase in the 1SW proportion from 1930–1950 until ca. 1990 (Turrell & Shelton, 1993). However, analysis of longer time periods indicates that the 1SW proportion in salmon populations has also been high in earlier periods (Turrell & Shelton, 1993; Summers, 1995).

Common patterns in the proportions of 1SW fish indicate that similar forces may affect the timing of maturation over a wide geographic range. Experiments have shown that the age at maturity of salmon can be influenced by both genetic (Thorpe *et al.*, 1983; Gjerde, 1984) and other factors – for example, large smolt size may increase the chance of maturation after one year in the sea (Skilbrei, 1989).

Analysis of the pre-fishery-abundance (PFA) of Norwegian salmon stocks indicates a significant positive relationship between the number of 1SW salmon in one year and the number of 2SW salmon in the following year (Hansen *et al.*, in prep). The regres-

sion between PFA for 1SW salmon in year n and PFA of 2SW salmon in year $n+1$ shows positive residuals in the more recent years in three regions in Norway (Figure 4.5.1), suggesting that more salmon return as 2SW fish than expected from the number of 1SW fish the previous year.

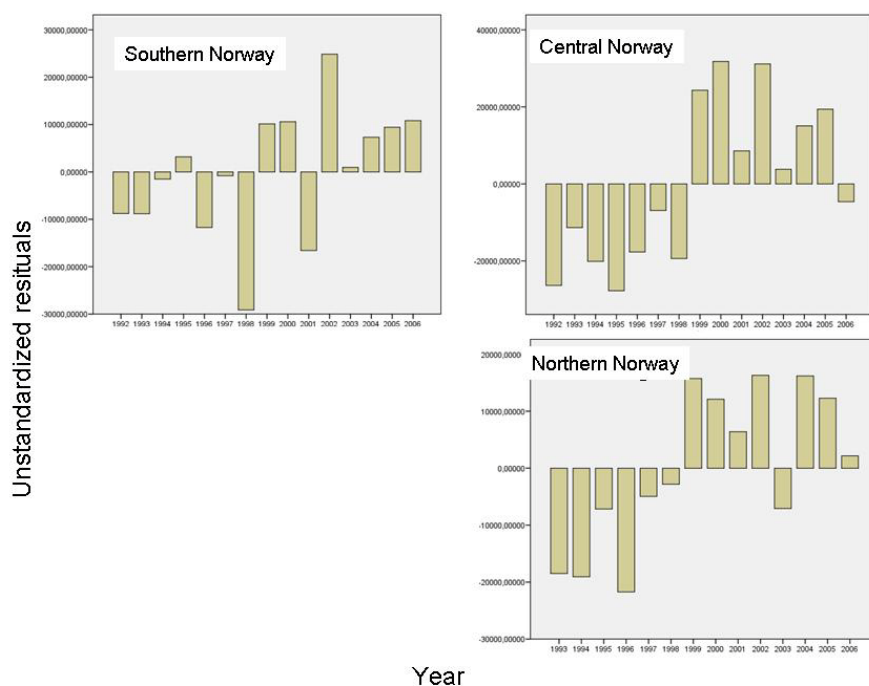


Figure 4.5.1. Unstandardised residuals from the regressions of PFA of 1SW salmon in year n and 2SW salmon in year $n+1$ in three Norwegian regions.

The 1SW component is typically male-dominated, and if there is a tendency for later maturity one would expect an increase in the male proportion among 2SW salmon. The apparent later age at maturity might be explained both by more salmon delaying age at maturity, or by survival in the second year at sea having increased relative to survival in the first year at sea. If the first hypothesis is true one might expect an increase in the proportion of male salmon among the returning 2SW fish, whereas the sex ratio among 2SW fish is more likely to be unchanged if the second hypothesis is more valid.

4.6 Baltic Sea – changes in post-smolt survival and the factors affecting it

The Study Group reviewed information on post-smolt survival arising from the work of the Baltic Salmon and Trout Assessment Working Group (WGBAST). WGBAST initiated preliminary analyses during their 2008 meeting to evaluate the possible reasons for the low at-sea survival of salmon stocks in the Baltic Sea. Further details are available in the working group report (ICES, 2008b), and work will continue during the WGBAST meeting in 2009.

Background

The post-smolt survival of salmon in the Baltic Sea is believed to have decreased in recent years, both for wild and hatchery-reared smolts (ICES, 2008b). According to post-smolt survival estimates generated from the assessment model, this decline

started in the mid 1990s and has continued since then. The reasons behind the observed decline are unclear, but at least two main hypotheses have been discussed.

- The “ecosystem hypothesis” states that changes in the Baltic Sea ecosystem have negatively affected salmon post-smolt survival rates by, for example changes in prey species abundances and increased competition or predation from other species. The Baltic Sea has undergone pronounced changes in the last two decades, characterised by several regime shifts in species composition (ICES, 2007). Climate changes affecting salinity, oxygen levels and temperature are believed to be the main drivers of this process, but fisheries and eutrophication also have impacts on the observed changes.
- The “smolt quality hypothesis” states that the increased mortality among hatchery-reared smolts is due to changed hatchery practices. The latter have been subject to continual improvements – for example, higher fat and energy contents of the feed, in combination with favourable river temperatures especially in autumn, have resulted in improved growth rates in hatcheries and increasingly large smolts. There is a general concern that the large size of reared smolts may have negative fitness consequences in the wild.

Preliminary analyses

Different estimates of survival were used in analyses as response variables, including post-smolt survival rates derived from the WGBAST assessment model, Carlin-tag recapture rates for Swedish hatchery stocks (see Section 4.7), and a more direct estimate of survival for two Swedish wild populations that was based on the relation between river production (parr densities) and the subsequent number of returning spawners.

Data on potential explanatory variables characterising the Baltic Sea ecosystem and the smolt hatcheries were collected from different data sources, including other ICES working groups which kindly agreed to let WGBAST have access to their data. In total, data on 102 predictor variables were obtained, including abundances of seal, cod, herring, sprat, phytoplankton and zooplankton, and salmon smolts. Information from hatcheries, and data on temperatures and salinity in different parts of the Baltic, were also included as predictor variables.

Initial analyses of single predictor variables were carried out using both traditional and Bayesian statistical methods. The working group then formulated more precise hypotheses focusing on factors that were judged, based on initial analyses, to be potentially important in describing variation in salmon sea survival. These hypotheses were tested using multivariate statistical procedures. It is important to note that significant associations do not necessarily indicate causal relationships between response and predictor variables.

Initial analyses showed that salmon survival was negatively correlated with seal abundance, indicating that predation by seals on salmon post-smolts (or older salmon) might be worth studying further. There was also a negative association between salmon survival and total smolt production (including both wild and hatchery smolts) in the Baltic Sea, suggesting that mortality at sea may be density dependent at some life stage. These results were further supported by the findings that the salmon survival index for two large Swedish populations correlated negatively with parr densities in these rivers, which may indicate density-dependence in the river and/or the sea. In addition, salmon survival correlated positively with herring abundance

and recruitment, indicating that herring may be an important, but limiting, food source affecting performance of salmon at sea.

Preliminary tests of hypotheses using multivariate analyses

WGBAST agreed on the following more specific hypotheses for testing with more refined multivariate analyses:

- **Competition hypothesis:** In this analysis, the idea was to test if intra-specific competition for food is important in explaining variation in post-smolt survival. In this case the survival of smolts would decrease when the smolt abundance increases.
- **Food availability hypothesis:** Young herring are considered important prey for young salmon in the Baltic Sea. Therefore, increased recruitment of 0+ herring in the smolt year should lead to higher survival if herring abundance is a limiting factor. This hypothesis is strongly connected to the competition hypothesis above. If herring recruitment directly affects post-smolt survival, then by definition, at-sea survival is density-dependent and should be affected by smolt production in rivers and hatcheries.
- **Seal predation hypothesis:** If salmon smolts are subject to substantial seal predation, then the increase in number of seals along the migration path of post-smolts should coincide with lower survival. If such a pattern is revealed, the predation hypothesis remains possible, but is not necessarily more likely than other hypotheses that might lead to similar predictions.
- **Smolt quality hypothesis:** This hypothesis is relevant only for hatchery-reared smolts and states that the increased mortality is due to changed practices in hatcheries. Pre-release factors suggested to be important include size, condition factor and fin damage.

These hypotheses are not mutually exclusive, i.e. all of them can be true at the same time. In order to analyse the relative credibility of the possible combinations of the first three hypotheses, a Bayesian approach was used to calculate the posterior probability for each combination. In addition to these biological hypotheses, there is uncertainty about whether post-smolt by-catch from pelagic trawling in the Bothnian Sea may decrease the survival of smolts. Consequently, each combination of biological hypotheses was analysed with and without such an assumption. The first three hypotheses were tested using recapture rates of hatchery-reared smolts from Swedish, Finnish and Latvian hatchery stocks as a response variable and the abundance of smolts, seals and herring recruitment as biological predictors. In addition, fishing effort in coastal and offshore fisheries was used in order to remove its effect on the tag return rate.

The model which included only the seal counts was assigned the highest probability (>0.4) as a predictor (Table 4.6.1). Models including estimated smolt abundance were assigned small probability compared to other combinations. One explanation for this might be that the competition and the food availability hypotheses are strongly connected, although these were analysed separately in this investigation. These two hypotheses should be combined in future analyses. A model with no predictors is equally likely with a model including seal counts and herring recruitment.

The smolt quality hypothesis was tested by including information on smolt size and condition factor, and was tested for two rivers separately, Luleälven and Umeälven. Multiple regressions, using tag-recapture rates from these rivers, total fishing effort in the Baltic Sea, and information on smolt length were used to test the effects of smolt

length on survival rates at sea. No significant effects of smolt length were observed for these rivers.

Relatively little data were available in relation to smolt condition factor, only covering the years 1998 to 2005. In analyses including total effort and smolt condition as predictor variables, no significant effects of condition factor (Fulton's index) were observed on tag recapture rate for these two populations. However, because of the low statistical power in these analyses, results should be viewed with caution.

Table 4.6.1. Explored combinations of potential covariates for tag return rate (survival index). Left column shows the probability of the combination of covariates. An empty cell indicates that the covariate is not included. "+" denotes a positive association and "-" indicates a negative association.

P (combination)	Covariates			
	Smolts	Seals	Herring	Trawl
0.446		-		
0.15				
0.144		-	+	
0.088		-		-
0.036		-	+	-
0.035	-	-		
0.025	-			
0.02				-
0.017	-	-	+	-
0.006	-	-		-
0.005			+	
0.005	-	-	+	-
0.004	-			-
0.001	-		+	
0.001	-		+	-
0			+	

Conclusions

Marine survival of post-smolts has varied with rather strong year effects across a range of stocks, suggesting that common factors are affecting all stocks in the same way. This supports a view that important causes behind the variation are Baltic-wide changes in environment or factors acting in the main feeding area. However, the variation between stocks is approximately equal to variation within stocks, which means that stock specific covariates (related to estuaries for example) should also be analysed further.

Results from preliminary analyses indicated that survival of post-smolts in the Baltic Sea may be density-dependent. Several survival indices were negatively correlated with the total production of wild and hatchery-reared smolts in the Baltic. Salmon survival also correlated positively with herring recruitment. Together, these results highlight the possible influences of ecosystem changes in the Baltic Sea because, following the logic of the competition/food availability hypotheses, changes in the ecosystem could potentially affect the sea carrying capacity for salmon, which may vary between years. Density-dependence at sea, combined with different carrying capacities in rivers, could lead to opposite developments in river stocks – while some in-

crease, others decrease. This may have implications for sensible management objectives and how to achieve them.

The results suggest that seals may affect survival of salmon. However, the available information on grey seal food preferences is limited, and much more information on seal ecology is necessary to evaluate these relationships. Further questions to explore include: 1) to what extent are seals feeding on smolts, post-smolts or larger salmon? 2) Is survival higher for stocks that are less exposed to seals? These require improved information on post-smolt migration routes and the spatial distribution of seals in spring and summer months.

With regard to the effects of rearing conditions on post-smolt survival rates, the available data are very limited, making it difficult to draw any general conclusions. There was no direct evidence for a negative association between body length of reared smolts and their survival at sea. However, more detailed studies of these relationships are necessary, including possible non-linear associations between these variables. Some further information on the effect of smolt condition on survival rates is included in the next section.

WGBAST recognised that future work on salmon survival rates in the Baltic should preferably include data on the biological characteristics of salmon stocks that may be associated with changes in sea survival, for example time series on growth, somatic condition and age composition of returning spawners. Such information would be valuable when formulating hypotheses and would also be important in identifying causal relationships between response and predictor variables.

4.7 Baltic Sea – review of Swedish tagging experiments and implications for estimating post-smolt survival

Following the construction of hydro-electric power plants in Sweden about a century ago, hatcheries were established to compensate for the loss of salmon (and sea trout) due to dam construction. The main objective at the outset was to produce fish for fisheries, although conservation has become an important goal more recently. In order to evaluate the success of the hatchery releases, a smolt tag was developed by Börje Carlin. This tag has been used in Sweden for the last 60 years in order to evaluate hatchery releases and is still in use today (Figure 4.7.1).



Figure 4.7.1. Carlin tags

The Study Group reviewed the information from a number of long-term Swedish tagging experiments carried out in the Baltic:

Data set I – This incorporates information from a number of tagging investigations and includes recoveries from commercial fishermen, anglers and hatcheries with details about the recapture site, and length, weight and the sex of the fish. This informa-

tion is now compiled in an Access database and contains in excess of 250,000 recaptures, most of them from Swedish rivers entering the Baltic Sea.

Data set II – For some tagging experiments conducted at the hatchery in Älvkarleby on the River Dalälven (60°38'35" N, 17°26'47" E) information on the condition of the tagged fish (marks, etc.) were recorded prior to release. These tagging details have been merged with the recapture details, so it is now possible to examine recapture information in relation to smolt condition. The data set contains 53,851 tagged fish of which 3,907 (7.26 %) were recaptured. Analysis of these data were split between three different recapture sites: Baltic Sea (where most of the fish were caught by commercial fishery), river (an 8km stretch of the river from the mouth to Älvkarleby, where most of the fish were caught by anglers), and hatchery (Figure 4.7.2).

Data set III – In some years wild smolts have also been caught and tagged on the River Dalälven allowing direct comparison of the recapture rate of wild and hatchery fish from the same strain.



Figure 4.7.2. Älvkarleby and River Dalälven. P = Hydroelectric power plant; H = adult salmon trap. The red line indicates the migration route of salmon and sea trout (also used before the construction of the power plant). Broodstock have been caught with different types of nets along this migration route, although angling is not allowed.

Results and discussion

Data set I

For all seven rivers in data set I with sufficient data for comprehensive analysis, the recapture rate has declined since the 1950s (linear regression: slope= -0.00128; $f=68.09$, $p=0.0389$) (Figure 4.7.3). Recapture rates for some tagging experiments were very

high. The reasons for this are unclear, but may reflect occasional large numbers of recaptures in herring nets.

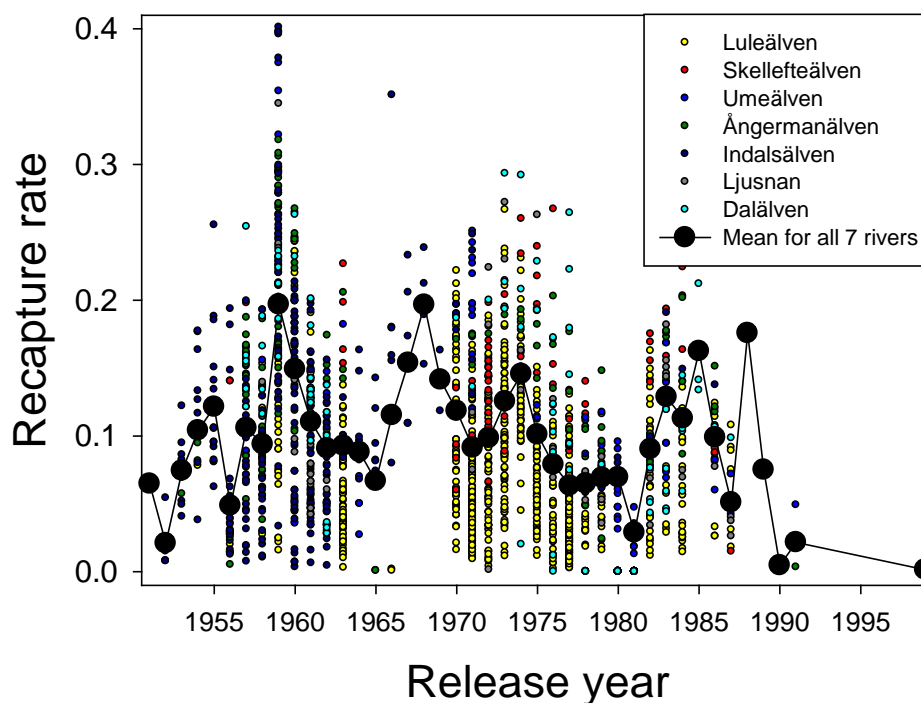


Figure 4.7.3. Recaptures of salmon tagged as smolts for seven rivers along the Swedish east coast.

Data set II

Recapture rates at different types of sites

The recapture rates of salmon have varied markedly between recapture sites, with the recapture rate of salmon in the Baltic Sea having decreased more than that for the hatchery trap and the river catches (Figure 4.7.4). The steeper decline in the Baltic Sea is not only due to increased mortality and changes in the Baltic Sea environment. There have been changes also in the commercial fishery, with a particular reduction in the use of drift nets. In addition, it is understood that the willingness of the fishermen to return tags has diminished in more recent years; interviews have confirmed that some fishermen do not return tags. In the river (anglers) and the hatchery trap the decrease in recapture rate is less dramatic and tag return rates and fishing pressure have remained reasonably consistent. Nevertheless, tag recapture rates have decreased significantly in all three recovery sites (Table 4.7.1).

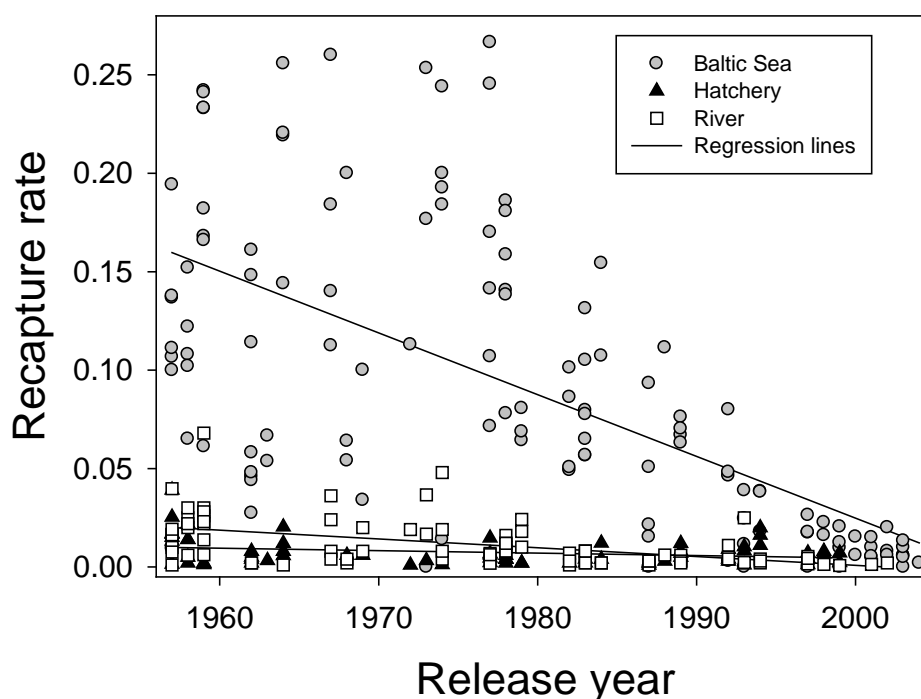


Figure 4.7.4. Recapture rate of salmon from the Baltic Sea, River Dalälven and hatchery trap. Only salmon tagged at the hatchery in Älvkarleby are included in this analysis.

Table 4.7.1. Changes in recapture rates over the last five decades for salmon tagged on the River Dalälven. The number of tagging experiments differ between experiments because some of those having very low recapture rates in the Baltic resulted in no returns in the river or in the hatchery.

Salmon recaptured in/at	No. tagging experiments	Intercept	Slope	R-square	F-value	P
Baltic Sea	127	6.30	-0.00314	0.399	82.86	<0.001
River	85	0.89	-0.000447	0.246	27.04	<0.001
Hatchery	69	0.26	-0.000126	0.068	4.89	0.0304

Recapture rates due to fish condition at tagging

Various categories of damage to the fish were recorded for some tagged batches; these were not noted in all years. These 'injuries' to the fish included: fin erosion, and/or damage/abnormalities to the operculum (gill cover), lower jaw and eyes (suspected blindness in one eye). Damage to paired structures (gill covers, pelvic and pectoral fins) were mostly not separated between left and right side, meaning that one or both sides could be injured. The level of fin erosion could vary from a small but visible wound to a totally eroded fin, but differing levels of severity were not included in the analysis. Overall, the frequency of occurrence of different 'injuries' was: dorsal fin 58.3 % of all tagged fish, caudal fin 2.6 %, pectoral fins 2.1 %, gill covers 1.7 %, pelvic fins 1.6 %, eye 0.17 %, and lower jaw 0.02 %.

The fish were categorised as in Table 4.7.3; release year, release date (Julian date) and length of fish at tagging were included as continuous variables. The data were first analysed with PROC LOGISTIC (SAS statistical software) in order to investigate the overall effect of the independent variables. The categories of injury indicated an overall difference in recapture rate; length at release, day and year of release also influenced recapture rate (Table 4.7.2).

Thereafter the data were analysed with PROC GENMOD (SAS statistical software), assuming binary response of recapture, in order to calculate least-square means for the categories and the differences between them. Fish with injuries to the dorsal fin were affected less than fish with other injuries.

Table 4.7.2. Logistic regression (response variable = recapture; 0 = not being recaptured, 1 = recaptured).

Effect	d.f.	Wald Chi-square	p
Fish injury category	3	42.25	<0.001
Release year	1	1765.0	<0.001
Release day	1	40.86	<0.001
Length at tagging	1	320.45	<0.001

Table 4.7.3. Least-square means (and standard error; see text for more information) for the wound categories. Means denoted with the same letter are not significantly different at the 0.05-level.

Fish injury category	Estimate (mean)	Standard error
Healthy (no injuries)	0.0604 ^b	0.0299
Just dorsal fin injured	0.0592 ^b	0.0264
Other fins injured	0.0358 ^a	0.1070
Dorsal fin and other fins injured	0.0392 ^a	0.0977

Data set III

Recapture rates of wild smolts were higher, on average, than recapture rates for hatchery fish from the River Dalälven (Figure 4.7.5). There was no significant correlation between the recapture rates of wild and hatchery fish, even though these originated from the same river ($p=0.435$).

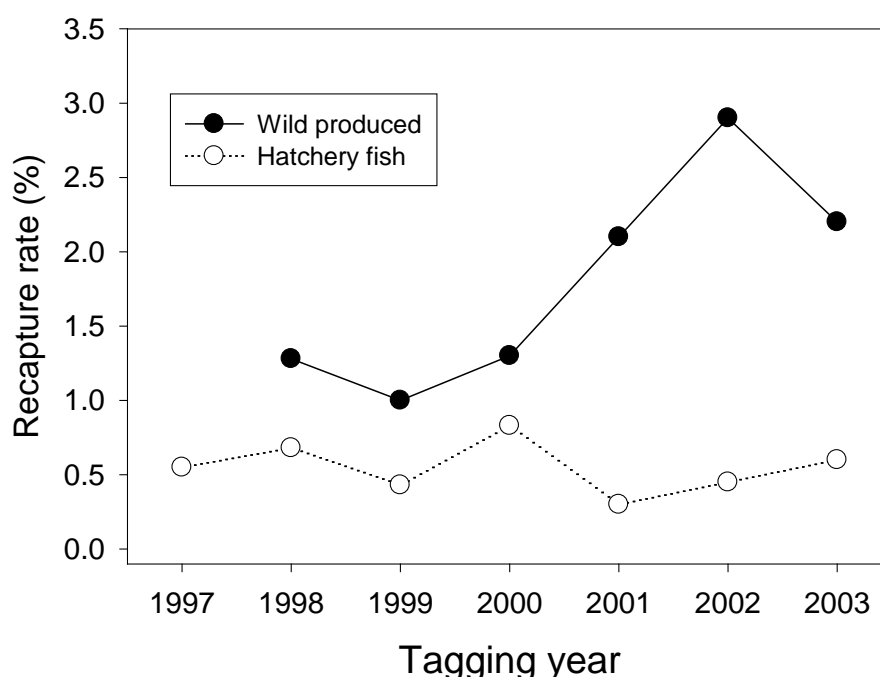


Figure 4.7.5. Recapture rates of wild and hatchery produced salmon in River Dalälven.

Conclusions

1. The results from tagging experiments need to be interpreted with caution and should take account of changes in fishing pressure, the willingness among different categories of fishermen to return tags and the type of recapture site.
2. Recapture rates for hatchery-reared smolts on many rivers have typically been lower than those for wild fish, indicating that hatchery fish have lower post-smolt survival. The injuries (fin damage, etc.) observed in many hatcheries might be one explanation for this, although not the only one.
3. Hatchery fish possess many characteristics which make them different from wild fish. Therefore comparison should be done with great caution.

4.8 Fecundity of Penobscot River broodstock

Information on long-term changes in broodstock fecundity for the Penobscot River (USA) was made available to the Study Group. This had been compiled as part of the task to identify life history characteristics that may have changed in response to changes in ocean survival. The available evidence indicated a decline in average fecundity (eggs/female) from the 1870s to 1921, and stable or increasing fecundity since a stock recovery programme commenced on the river in the 1960s (Figure 4.8.1).

Data on individual female fecundity were also compared. Data on individual female size (length) and eggs spawned were located for 1872, one of the first years that Craig Brook National Fish Hatchery (CBNFH) was in operation (Atkins 1873), and for 2002 and 2003 (Wilkie, 2006, unpublished data). No broodstock were collected on the Penobscot River from 1963 to 1966. However, during this period the fecundity of females from the Rivers Narraguagus and Machias was reported (Baum and Meister,

1971). Juveniles reared from these two stocks were used in the restoration programme on the Penobscot from 1963 to 1966 (Baum 1997), and are likely to represent the origins of the current Penobscot stock. These published fecundity relationships were therefore included in the comparison (Figure 4.8.2). Although spawning methods varied among the years, the slopes of the length fecundity regressions differed (ANCOVA $p < 0.05$) between 1872 and 2002-2003. In addition, the length fecundity regression for Machias and Narraguagus River salmon was similar to that determined in 1872.

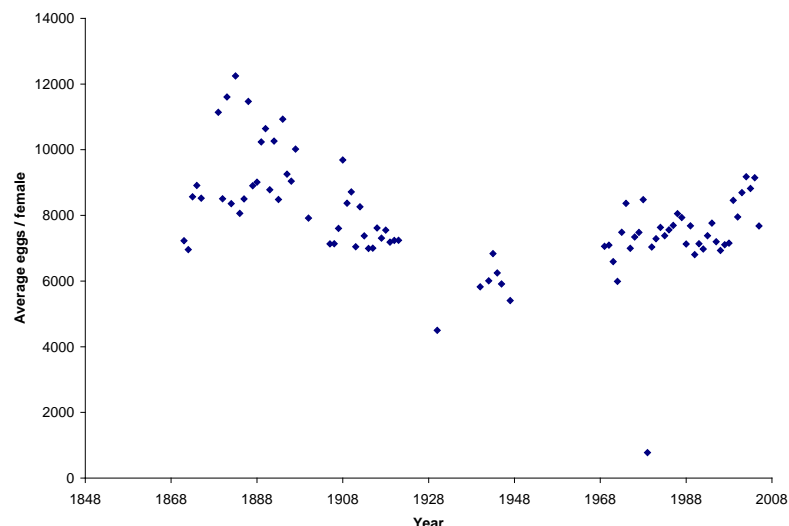


Figure 4.8.1. Average fecundity (eggs/female) based on total eggs produced and number of females spawned at Craig Brook National Fish Hatchery from 1871 to 2005. Data are from United States Atlantic Salmon Assessment Committee database.

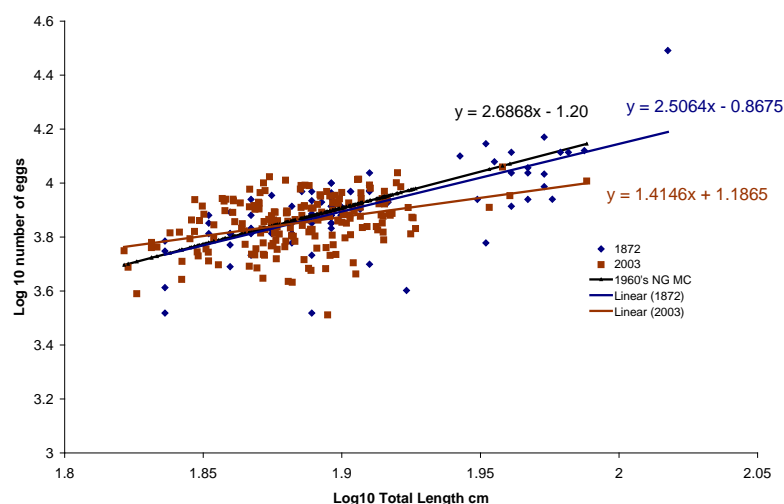


Figure 4.8.2. Fecundity of individual females measured by Wilkie (2002 & 2003) and Atkins (1872), and output of the regression from Baum and Meister (1963-1966) for broodstock from the Narraguagus and Machias rivers used to begin restoration of the Penobscot River.

The differences observed could be due to domestication (Heath *et al.*, 2003), freshwater growth rate (Jonsson *et al.*, 1996, Thorpe *et al.*, 1984), or the age composition of the

samples (Randall, 1989). It is thought that the age of the salmon sampled very likely affected the results and this is subject to ongoing investigation.

5 Exploratory analyses

The Study Group completed a number of exploratory analyses using the biological characteristics data sets described in Section 3.2.

5.1 Condition Factors – considerations in their application and use

For decades, fisheries biologists have used a range of simple statistical indices to measure and compare the “quality” of individual fish within a given population, and to express their size and “plumpness” as some form of condition index or condition factor. These various indices all are based on relationships between the observed weight of the fish and its observed length. Within any given fish species or population, a long, “thin” fish will have a low condition index and a short plump fish will have a high index. Marshall *et al.* (2004) have reviewed much of the recent literature pertaining to the range of condition indices available. Fulton’s K is given by $(W \cdot 1000 / L^3) \times 100000$, where W is the weight in kg and L the fork length in cm, and has been widely applied in fisheries biology. Its attraction is its very simplicity: it requires no “prior knowledge” of the weight-length relationship and can be calculated for any fish for which weight and length are known. Its problem also is its very simplicity, in that it assumes that fish grow isometrically according to the length cubed. If the actual weight-length allometry of a particular species, or series of populations, is >3 then K tends to increase with length. For exponents <3 , K tends to decrease with length. A considerable recent literature has accumulated on attempts to circumvent these difficulties and, as reviewed by Blackwell *et al.* (2000) and outlined below, perhaps the most appropriate means of assessing variation in fish condition is to calculate the relative mass index, W_R .

The relative mass index, W_R , appears to be the most useful condition factor for application in ecological studies of fish. In their comprehensive review of the computation and application of the most commonly used condition indices, Blackwell *et al.* (2000) affirmed that W_R may well provide a beneficial fisheries management tool in its use as a surrogate for body condition, biochemical reserves and overall fish health. They emphasised the importance of assessing the data for length-dependence prior to computation of a population mean W_R . Certainly, from inspection of regression residuals, one can readily ascertain if there is a systematic pattern to the departures of individual fish from the predicted weight (W_s) equation (see below) for fish of particular length. For example, if the length-related pattern of W_s decreases (or increases) and then increases (or decreases) due to intermediate-sized fish being of markedly lower (or higher) observed weight for their length, then W_R should not be used (Blackwell *et al.*, 2000). However, the problem still remains of distinguishing mathematical length-dependence – such as a consistent increase (or decrease) in W_R with length – from ecologically real increases (or decreases) in condition of longer and perhaps older fish. It is certainly plausible that larger fish might well have very different prey preferences and be plumper for their length than smaller fish. Notwithstanding the interpretational complexities presented by length-dependence, perhaps the greatest advantage of W_R is that by calculating the standard weight/length equation for W_s by means of the regression line percentile (RLP) method (see below), mathematical length-dependence can be effectively eliminated (Blackwell *et al.*, 2000).

W_R for individual fish is computed as the ratio between the observed weight (W) and the standard (that is, predicted) weight (W_s) for a fish of that length. W_s is estimated from a single regression model derived from multiple populations or samples. In treating each population separately, weight-length (log transformed) regressions are calculated for each population and back-transformed weights are then estimated for each cm grouping for the separate populations. The 75th percentiles across all populations for each cm grouping are then determined and these are converted to logarithms and regressed on the logarithm of each cm grouping. This final regression provides the W_s line for predicting weight of any individual fish from its known length. W_R then is simply the ratio of W to W_s .

Problems with W_R

In recognizing the problem of length-dependence of Fulton's K when the allometric exponent departs from the assumed value of 3, Jones *et al.* (1999) proposed a new index ($M = BL^2H$) which is based on measurements of body length (L) and height (H) (i.e. depth of the body measured at the anterior insertion of the dorsal fin) and includes the parameter B , which is derived by regression. B is estimated from the linear regression of M on L^2H . In testing their model with empirical data on Chinook salmon they could clearly show a better prediction of individual fish mass when using M than by using Fulton's K . The problem with applying their method is that salmon biologists typically measure only fork length and weight and therefore this index cannot be applied to contemporary data sets or historical time series. Sutton *et al.* (2000) also emphasised the shortcomings of condition indices based on isometric assumptions. Their focus of interest was on lipid reserves of Atlantic salmon parr and although they review a number of studies which indicate a high correlation between somatic condition and lipid content, they found that Fulton's index was only a poor correlate.

Condition factor also can change seasonally within a population, and Hansen & Nate (2005) addressed this specific problem for walleye in Wisconsin, USA. They found W_R to be highest in spring, lowest in early summer and intermediate in late summer/autumn and that for spring/early summer samples W_R was not an especially good predictor of condition. They accordingly proposed a new relative mass index which allowed incorporation of a seasonal adjustment factor.

Neff & Cargnelli (2004) compared four indices of condition factor for bluegill sunfish and found all to be highly correlated with one another, though only W_R and K correlated with observations of non-polar lipid density for individual fish. Their conclusion was that K was a good predictor of individual energetic state and overall quality during the breeding period.

Application of Condition Factors to recent studies of adult Atlantic salmon

Todd *et al.* (2008) investigated two independent time series (1993–2006) of 1SW salmon captured in Scottish net fisheries. The River North Esk is an estuarine seine net fishery and comprises fish that have mainly originated from the River North Esk. Strathy Point is a mixed stock bag-net fishery; tagging studies have shown that these nets exploit fish destined for rivers on the east, north and west coasts of Scotland and occasionally also Ireland. To circumvent the potential problem of length-dependence of condition indices, Todd *et al.* (2008) expressed the condition of each year-class (adult return year) of these salmon as the predicted weight (PWt) at standard length. Year classes of lower PWt are of poorer somatic condition. For the two time series,

the mean lengths of 1SW fish sampled over the study period were 58 cm (River North Esk) and 60 cm (Strathy Point).

Todd *et al.* (2008) recorded very similar results for the two time series (Figure 5.1.1). Both showed PWt peaking in 1997 but then declining steadily and precipitously to 2006. Subsequent monitoring in 2007 and 2008 indicate that condition factor has stabilized, or perhaps even risen slightly, above the 2006 nadir. PWt correlates very strongly with W_R : for Strathy Point (1993-2006) the correlation between PWt and mean W_R for the 14 year classes yielded a coefficient of 0.997 ($p < 0.001$). Clearly, either of year class PWt or mean W_R provide the same measure of average salmon condition factor. From these time series of PWt, and by utilizing the OISSTv2 dataset, correlations were drawn with de-trended residuals of sea surface temperature (SST) anomalies in the Norwegian Sea during the midwinter months prior to migratory return of these 1SW fish (Figure 5.1.1). The conclusion drawn was that recent warming of the North Atlantic had indirectly led to a decline in feeding conditions for these southern European 1SW salmon. It was suggested that in recent years, some 1SW salmon appear to have been effectively starving during their last few months at sea and were apparently catabolising their energy reserves before even re-entering freshwater to spawn.

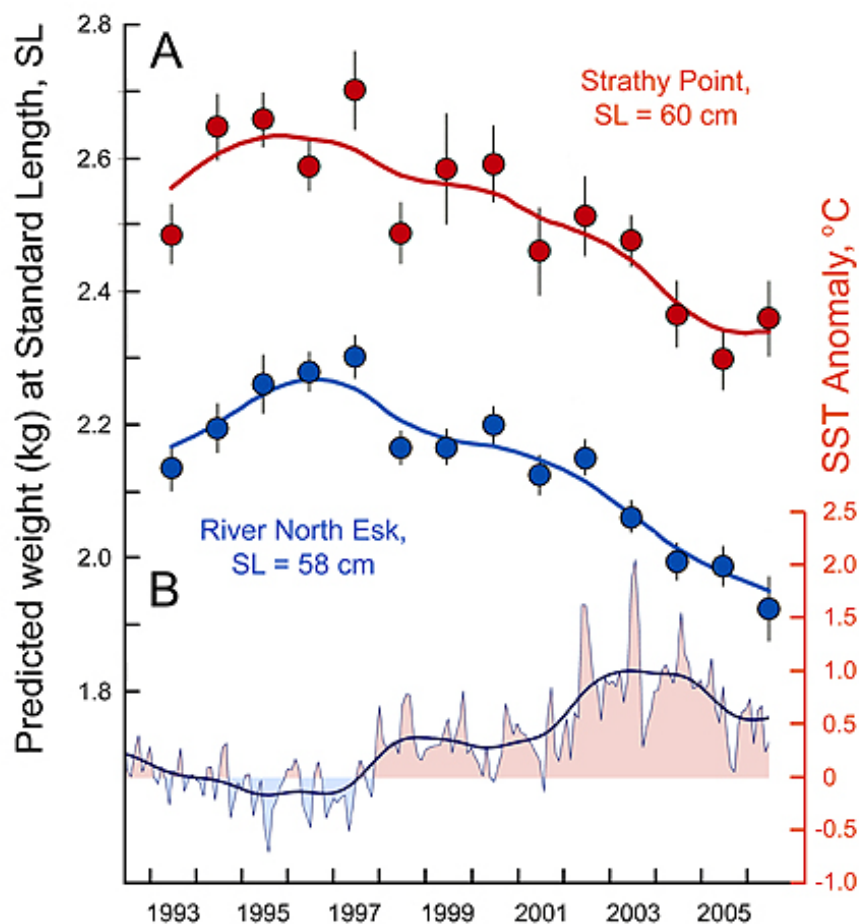


Figure 5.1.1. A. Predicted weight (PWt) $\pm 95\%$ CI at standard length (SL) for adult 1SW Atlantic salmon. B. Example mean monthly SST anomalies (OISST v2) for the eastern North Atlantic Ocean, calculated with a weighting kernel of $\sigma = 500\text{km}$ and centred on 64.5°N 4.5°E in the Norwegian Sea. For all time-series, weighted running means ($\sigma = 1$ year) were used to de-trend the data.

Further analyses of individual fish were undertaken and total lipids extracted. Since PWt can be computed only for an entire year class (or population), Todd *et al.* (2008) applied the relative mass index, W_R , in determining condition factor for individual fish of known (laboratory-extracted) lipid reserves. They showed that the relationship between condition factor and lipid content was sigmoid, and that poor condition fish in 2006 were returning as much as 30% underweight and yet with lipid reserves depleted by as much as 80% compared to a full condition individual. Such reductions in condition and lipid reserves will have marked influences on individual survivorship and fecundity. Moreover, as well as probably producing fewer eggs, it is likely that poor condition females will produce smaller or poorer quality offspring.

Subsequent analyses of lipid reserves and fatmeter monitoring (www.distell.com) of large samples of fish from Strathy Point in 2007 and two other net fisheries on the north coast of Scotland in 2008 have shown that the relationship between body condition and lipid reserves is not consistent among years. 2006 was the year of “skinny 1SW fish” from a number of locations in the British Isles, and lipid reserves at a given condition factor were lower in 2006 than in 2005 and 2007, despite W_R being closely similar for the three years. Clearly, therefore, it will not prove possible to hindcast lipid reserves for time series of observations based on length and weight alone. Condition factor can be calculated for these time series but in the absence of empirical observations no retrospective statements can be made concerning past lipid reserves. Future assessments of year-class variations in lipid reserves must be based upon continuing monitoring of commercial catches by means of fatmeter interrogations.

Future applications of condition factor analysis

The Study Group recognised that ecologically informative data pertaining to the health of wild salmon stocks and their performance at sea can be readily derived from time series analysis of condition factor variation, as apparent from Todd *et al.* (2008). It is important to emphasize here that measures of condition factor can be made that are independent of assessments of stock or population abundances. As long as population samples are representative of the maturity grouping(s), are seasonally defined and suitably large, then considerable insight can potentially be gained into the indirect effects of ocean climate change and regime shifts in plankton distributions and prey availability from analyses of condition factor. The concordance in temporal pattern for the two time series investigated by Todd *et al.* (2008) affirmed that the causal factor(s) is(are) attributable to the oceanic environment, and not a manifestation of freshwater conditions. Further, data such as these can be obtained and interpreted independently of any assessment of mortality rates. Todd *et al.* (2008) also found that condition factor was effectively “set” for the whole year class of 1SW salmon: condition factor did not change significantly during the June-August netting season. Therefore, even temporally constrained samples can provide informative and reliable data.

In taking forward possible analyses of condition factor, the Study Group recognised that a number of factors might need to be borne in mind:

- Analyses should be confined to net fisheries in near-shore or estuarine conditions. Rod caught fish are likely to be of limited value because of the difficulty in assessing how long fish have been in the river, during which time they will have been losing weight, declining in condition and catabolising reserves.

- The need for consistency and accuracy in measuring fish and in scale-reading.
- Recognising potential sampling biases. Fishing gear can be size selective and may not sample particular size classes of fish (e.g. a relatively large mesh has to be utilised in Norwegian bag nets and may therefore miss the smallest 1SW fish). However, since W_R is effectively independent of size it will still be plausible to apply this condition index to population data from those fisheries.

The initial studies of Todd *et al.* (2008) focused on 1SW 1SW fish in the expectation that this maturity grouping would show the clearest signal of any response to ocean climate change or alterations in planktonic prey availability. MSW fish are believed to migrate to ocean feeding grounds distinct from those exploited by fish destined to return as 1SW adults, and may therefore show complex responses to environmental variability. For example, how would the final adult condition factor of a 2SW fish that had a “good” first year at sea, but a “poor” second compare with one that had a “good” first year, but a “poor” second year?

The Study Group recommended that further efforts should be made to identify data sets for which condition factor can be assessed and extend such condition factor analyses to other stocks and to MSW fish. A comparison between Baltic populations and southern and northern European populations would be especially valuable, given their differing marine migratory trajectories and destinations. Furthermore, since it appears that stocks in northern Finnish rivers, which discharge into the Barents Sea, have not shown the same overall recent population declines as North Atlantic stocks (e.g. Niemälä *et al.*, 2004), a comparison of condition factor from time series in these locations would be especially valuable and informative.

The Study Group therefore encouraged collection of appropriate time series of data from stocks around the North Atlantic, noting:

- Any time series observations of weight, length and river/sea-age (from scale reading) can be of value in assessing trends in condition factor. Even short time series are of value when comparing the performance of the 1SW and MSW maturity groupings.
- The only data necessary are the date and place of capture, fork length (in cm, rounded down to the nearest 0.5 cm), fresh weight in kg (to the nearest 50 g) and the sea and river ages (scale reading).
- Information on sex is also very valuable, but if based upon external secondary sexual characteristics can be extremely unreliable for small 1SW fish (<55 cm) and for early-running 2SW “spring” fish (sampled in the UK). So-called 2SW summer salmon captured in June-September can usually be reliably sexed from external features, and since there is now very little netting of spring salmon data available from many places will be from this period.

5.2 Assessment of Fulton’s K versus Relative Mass Index, W_R

The Relative Mass Index, W_R , provides a reliable measure of condition factor for individual fish, and one which is largely free of length-dependence. Eliminating all influences of length-dependence with any condition index is quite probably impossible, if only because all indices include fish length in their computation. However, as discussed above, some indices are much more vulnerable to this mathematical problem than other indices.

Since much of the fish size information made available to the Study Group consisted of population mean lengths and weights for different sea-age classes, an assessment was required of the utility of computing a single index of condition factor (with no prior knowledge of length/weight allometry for fish of that population) and for whole year classes within a time series. The assumption is that only the annual mean length and mean weight of each year class within a time series are available. The assumption also is that those means are arithmetic – the raw data have not, for example, been transformed to logarithms to provide geometric means.

A number of time series providing length and weight data for individual fish, derived from sampling programmes in fisheries around the UK and Ireland, were made available to the Study Group. These included fish from fisheries mainly exploiting single river stock (e.g. Welsh Dee, River North Esk) and fish sampled in mixed stock fisheries (e.g. Strathy Point, NE England and Irish drift net fisheries) and ranged from exclusively wild fish (e.g. River North Esk, Wear) to stocks with a small hatchery component (e.g. Welsh Dee) to fish derived exclusively from hatchery tagging programmes (e.g. Rivers Tyne, Ogmere, Taff, etc.). These were used to compare the condition factors (Fulton's K), derived from the annual mean length and mean weight of each year class within a time series, against the alternative Relative Mass Index (W_R) for these stocks (Figures 5.2.1 and 5.2.2). Mean W_R is here derived from all individual fish within a year class and compared with K calculated from only the mean length and weight. Sample sizes for single year classes ranged from 10 to 1328 fish per year for given maturity groupings (only 1SW and 2SW fish were analysed).

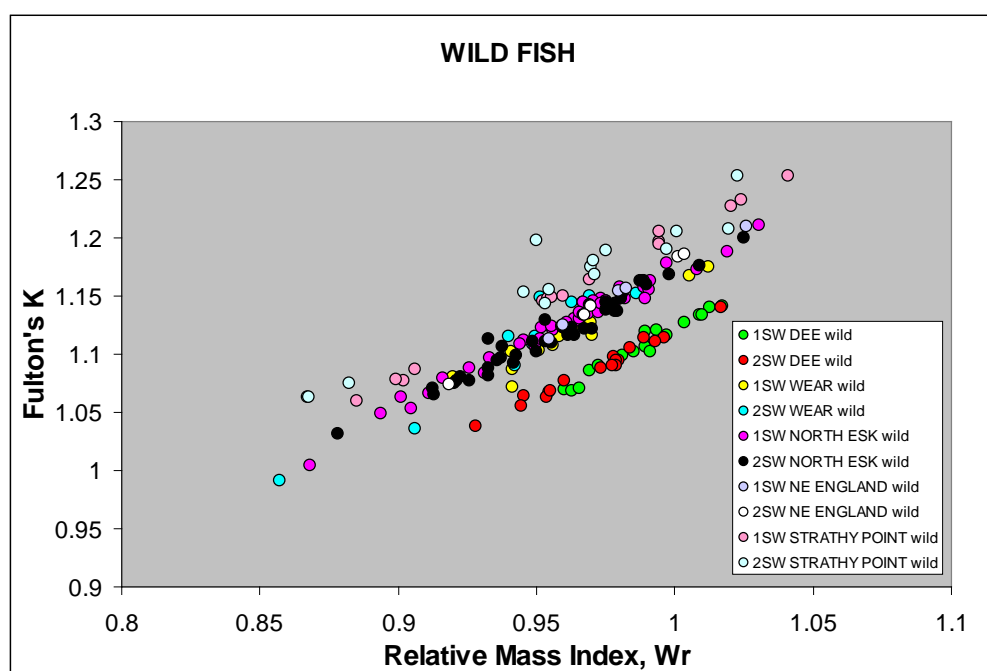


Figure 5.2.1. Scatterplots for wild (or presumed wild) 1SW and 2SW salmon captured in coastal or estuarine net fisheries. The exception is the River Dee (Wales), the data for which include a small proportion of hatchery-reared fish and for which all captures were from the trap at Chester (near the head of tide).

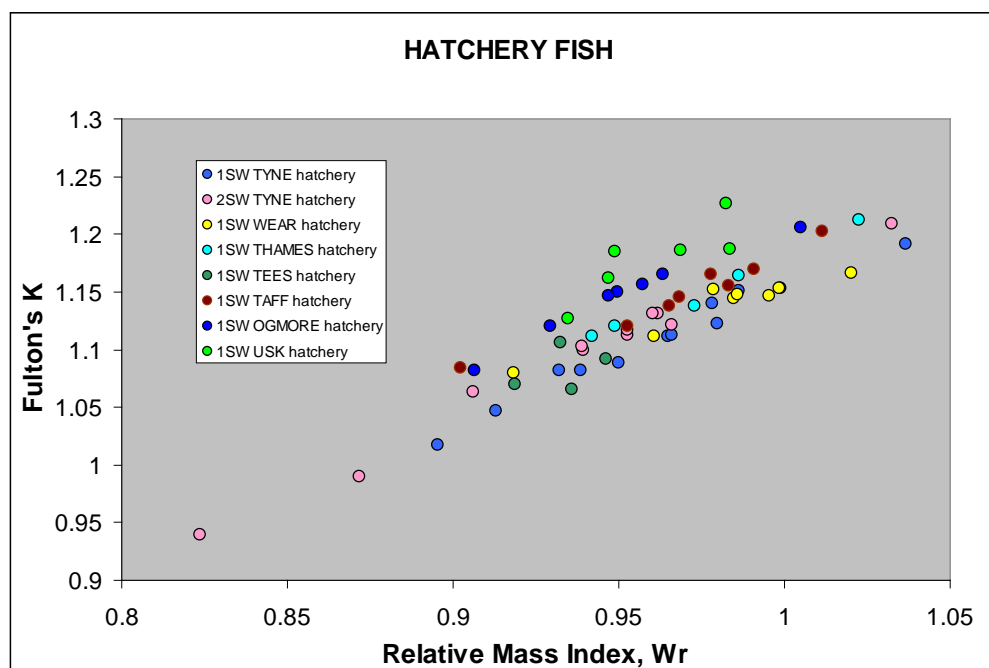


Figure 5.2.2. Scatterplots for hatchery-reared fish tagged. These samples were derived from fish of known river of origin (tagged with CWTs) and recovered in either or both the Irish and NE England coastal drift net fisheries.

Figures 5.2.1 and 5.2.2 illustrate the relationship between these two metrics for wild and hatchery-reared stocks respectively and show a clear and consistent pattern. It is evident that the simple condition factor (Fulton's K) derived from the mean length and weights for each year class within a population provides an adequate qualitative descriptor of variation in condition factor at the population level. The regression coefficients of the various data sets are very similar, and wild and hatchery-origin fish show the same overall morphometric relationship. It is also evident that even small sample sizes lead to the derivation of plausible measures of annual condition. However, the regression intercepts ("elevations") are population-dependent. This will be due to inherent differences in the shape of fish from different populations (e.g. River Dee fish are notably different to the remainder in Figure 5.2.1).

Thus, the simple condition factor, K , derived from mean length and weight data alone, can provide an objective, qualitative means of deciding whether or not a population time series is showing systematic increase, decrease, or no change in somatic condition. However, this approach has limitations and is of no quantitative value for between-stock comparisons.

5.3 Biological characteristics data sets – temporal trends

Preliminary examination of the various stock-specific biological characteristics data sets described in Section 3.2, using simple plots of these data against time over available time series, indicated substantial evidence of variability both over time and among stocks. Subsequently analysis of possible time trends was completed using the non-parametric Mann-Kendall statistic (Mann, 1945; Kendall, 1975) and the statistical programming environment R (R Development Core Team, 2007). One of the reasons this method was selected was that it does not assume any particular functional form for the trend (e.g. linear, exponential). These analyses were performed over a stan-

standardized time period starting from 1984 and extending to the most recently available data, typically 2007.

Essentially, the Mann-Kendall statistic assesses each data point and counts of the number of data points in future years that exceed it (assigned +1) and also the number that are less (assigned -1). These values are summed over all data points. Thus, if there are n observations in the time series Y_k ($k=1,\dots,n$) then the statistic is:

$$M = \sum_{k=1}^n \sum_{j=k+1}^n I(Y_k, Y_j)$$

where $I(\cdot)$ is an indicator variable defined by the sign of $D = Y_k - Y_j$. If D is positive then $I = 1$, if D is negative then $I = -1$, if $D = 0$ then $I = 0$.

The null distribution of the statistic M (i.e. assuming no trend) was calculated by Monte-Carlo simulation. The observations were re-ordered at random so that they were potentially assigned to different years and the value of M calculated. This was repeated 1000 times. These values of M under the null hypothesis were compared against the observed value of M to estimate the p-value (Manly, 2001).

The null hypothesis was that there is no trend. It was recognised that a potential problem with this approach is that it does not taken account of any correlation between successive or neighbouring years. The presence of such correlations might affect the p-values obtained and may require further consideration in future.

The results are presented in Table 5.3.1 Missing values indicate no time series available; 'o' indicates a non statistically significant trend ($P>0.05$); '-' is a negative trend ($p<0.05$); and '+' is a positive trend ($p<0.05$). It is evident that there are significant trends over time for many of the variables explored.

Table 5.3.1. Trends in biological characteristics over time: 'o' means not enough evidence at the 5% level to detect a trend. '+' is a positive trend ($p > 0.05$), '-' is a negative trend ($p < 0.05$).

Stock complex	Country	Stock	H/W	Time series	Latitude	Stock status	Median run date	Mean run date	Mean river age	Mean sea age	Prop. 1SW in run	Prop. 2SW in run	Prop. PS in run	1SW length	1SW weight	1SW condition	2SW length	2SW weight	2SW condition	PS length	PS weight	PS condition	Prop. female in 1SW	Prop. female in 2SW	Prop. female in PS	Prop. maiden spawners - 1SW	Prop. maiden spawners - 2SW
NAC (N)	Canada	Western Arm Brook	W	1984-06	51.2	+	-	o	-	+	o	o	o	+	+	+	-	o	o	+	+	o	o	o	o	o	o
	Canada	Middle Brook	W	1984-05	48.8	o	o	o	o	o	o	o	o	+	+	o	o	o	o	+	+	o	-	o	o	o	o
	Canada	Conne River	W	1984-06	47.9	-	o	o	o	+	-	o	+	+	+	o	o	o	o	o	o	o	o	o	o	-	+
	Canada	Miramichi	W	1984-07	47.0	-	o	o	-	+	o	o	+	+	o	-	+	o	o	+	+	o	-	+	+	o	o
NAC (S)	Canada	Nashwaak	W	1984-07	46.0	-	o	o	-	-	+	-	o	o	o	o	+	-	-	o	o	o	o	o	o	+	-
	Canada	St John (Mactaquac)	W	1984-07	45.3	-	-	-	-	o	+	o	o	o	o	o	-	-	-	o	o	o	o	o	o	o	-
	Canada	St John (Mactaquac)	H	1984-07	45.3	-	-	-	-	-	+	-	o	o	o	o	-	-	-	o	o	o	o	o	o	+	-
	Canada	La Have	W	1984-07	44.4	o	-	o	+	o	o	o	o	o	+	+	o	+	+	o	+	+	o	+	+	o	o
	Canada	La Have	H	1984-07	44.4	o	o	o	-	o	o	+	o	o	+	+	o	+	+	o	+	+	o	+	o	o	o
	USA	Penobscot	H	1984-07	44.5	-	-	-	o	-	+	o	o	o	+	+	o	o	+	+	o	o	-	o	o	+	o
N NEAC	Finland/Norway	Teno	W	1984-07	70.8	o	o	+	+	-	o	o	+	o	o	+	o	o	o	o	o	o	o	o	-	o	o
	Finland/Norway	Näätämöjoki	W	1984-06	69.7	o	o	+	+	-	+	o	o	+	o	o	o	o	o	o	o	o	o	o	-	o	o
	Russia	Tuloma	W	1984-08	68.9	o	o	+	-	-	o	o	o	o	o	o	-	-	o	o	o	o	o	o	o	+	o
	Norway	Årgårdsvassdraget	W	1992-07	64.3	o	o	o	o	+	o	+	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
	Norway	Gaula	W	1989-07	63.3	o	o	o	-	+	o	o	+	o	o	o	o	o	o	o	o	o	o	o	o	o	o
	Iceland (N&E)	Laxa í Adaldalur	W	1984-07	65.6	o	o	o	o	o	+	+	+	+	+	+	+	+	+	+	+	+	o	-	o	o	o
S NEAC	Iceland (N&E)	Hofsa	W	1984-07	65.4	o	o	o	o	o	+	+	+	+	+	+	+	+	+	+	+	+	o	+	o	o	o
	Iceland (S&W)	Nordura	W	1984-07	64.6	o	o	o	o	o	+	+	+	+	+	+	+	+	+	+	+	+	o	+	o	o	o
	Iceland (S&W)	Ellidaar	W	1984-07	64.1	o	o	o	o	o	+	+	+	+	+	+	+	+	+	+	+	+	o	+	o	o	o
	UK (Scot)	N. Esk	W	1984-07	56.7	o	o	o	o	o	+	+	+	+	+	+	+	+	+	+	+	+	o	+	o	o	o
	UK (NI)	Bush	W	1984-07	55.1	-	+	o	o	o	+	-	o	o	o	o	o	-	-	o	o	o	o	o	o	+	-
	UK (E&W)	Lune	W	1987-07	54.0	o	o	o	o	o	o	o	o	o	o	o	o	-	o	o	o	o	o	o	o	+	-
	UK (E&W)	Dee	W	1984-07	53.4	-	o	o	o	o	+	-	o	o	+	+	+	+	+	-	-	-	-	+	o	o	o
	UK (E&W)	Wye	W	1984-07	51.6	o	o	+	-	-	+	+	-	+	+	o	o	o	o	-	-	o	o	o	o	o	o
	UK (E&W)	Frome	W	1984-08	50.7	-	o	o	o	o	+	+	+	+	+	+	+	+	+	+	+	+	o	o	o	o	o
	France	Bresle	W	1984-08	50.1	o	o	o	o	o	+	+	+	+	+	+	+	+	+	+	+	+	o	+	o	o	o
Summary - all areas		No. of stocks for which data available				20	11	12	19	20	25	21	16	22	19	19	21	17	17	15	15	15	19	18	9	12	11
		% of stocks with significant declining trend				45	45	25	58	40	4	19	6	9	5	11	14	35	18	13	13	7	21	11	11	8	36
		% of stocks with significant increasing trend				5	9	17	11	25	48	14	25	27	42	32	19	18	24	20	33	13	5	33	22	42	9
		% of stocks with no significant trend				50	45	58	32	35	48	67	69	64	53	58	67	47	59	67	53	80	74	56	67	50	55

5.4 Biological characteristics data sets – spatial patterns

The Study Group examined two approaches for assessing patterns in the changes in biological characteristics over broader spatial scales. For these purposes the individual river stocks were allocated to different groupings. For the first approach, the conventional NAC (Canada and USA) and NEAC north (Russia, Norway, Finland, N&E Iceland) and NEAC south (British Isles, France and S&W Iceland) stock complexes were used. However, for the second analysis the NAC rivers were further subdivided into two groups based on a latitudinal split.

Standardised (z-score) analysis

The first approach used a standardised (z-score) analysis to examine the trend in mean smolt age. This analysis was restricted to wild stocks and extended over available time series. The length of the time series varied between stocks, extending as far back as 1911 (though not complete) for the River Wye (UK), the shortest was from the River Årgård (Norway) which started in 1992. Of the 18 wild stocks available, 6 were from Southern NEAC, 5 from Northern Neac and 7 from the NAC areas, respectively. In deriving the z-score, the data for year n were standardised in relation to the mean smolt age between 1983 and 1994 as follows:

$Z_n = (\text{Mean smolt age}_n - \text{mean smolt age}_{1983-94}) / \text{STD}_{1983-94}$, where STD = standard deviation.

The reference period of 1983–1994 was taken as this was +/- 5 years either side of 1988/9 which is the period when there was a marked change in marine mortality (ICES, 2008); 5 years also represents approximately one salmon generation. The trend in mean smolt age was examined by geographical area and for each geographical area the mean standardised smolt age was determined.

The results of this analysis are presented in Figures 5.4.1 to 5.4.3. and indicate that in the samples from the NAC area and the Southern NEAC area there has been a significant decline in mean smolt age from the 1970s and 1960s, respectively ($P < 0.05$). In contrast, for the samples from the NEAC Northern area smolt age has remained constant since the early 1970s ($P > 0.05$). For this area there is an indication of an increase in mean smolt age up until the late 1990s – early 2000s followed by a recent decline.

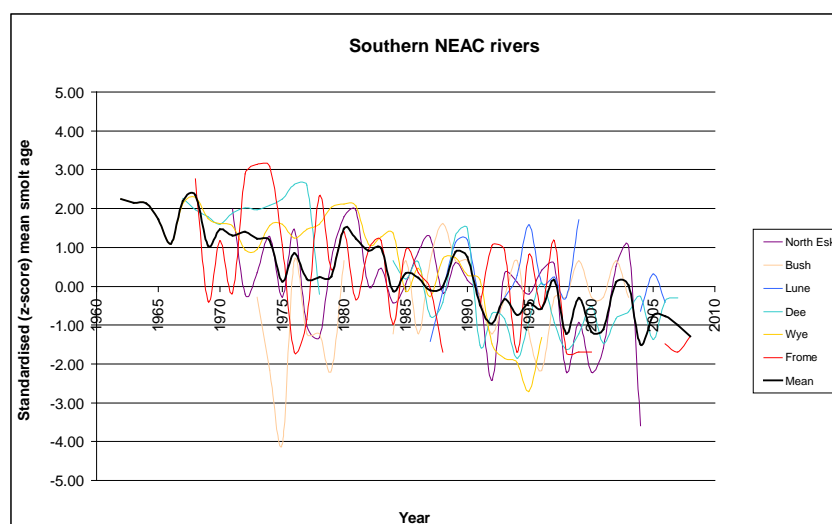


Figure 5.4.1. Standardised mean smolt age for stocks from the Southern NEAC area

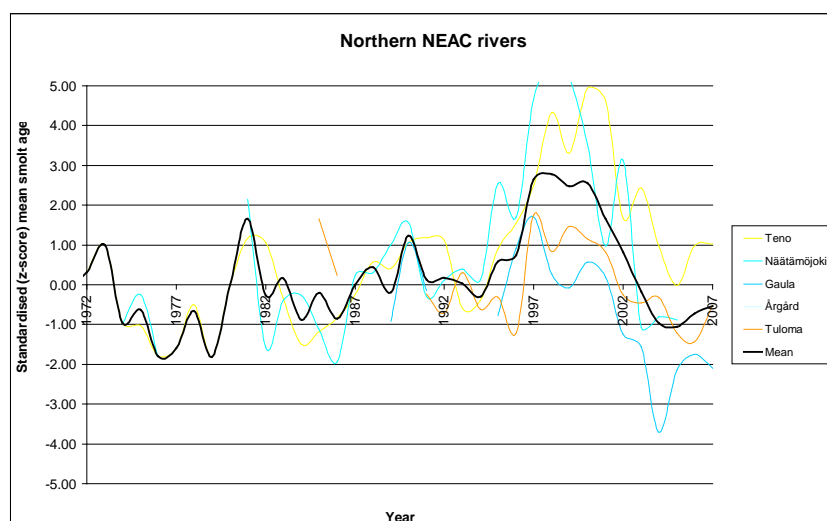


Figure 5.4.2. Standardised mean smolt age for stocks from the Northern NEAC area

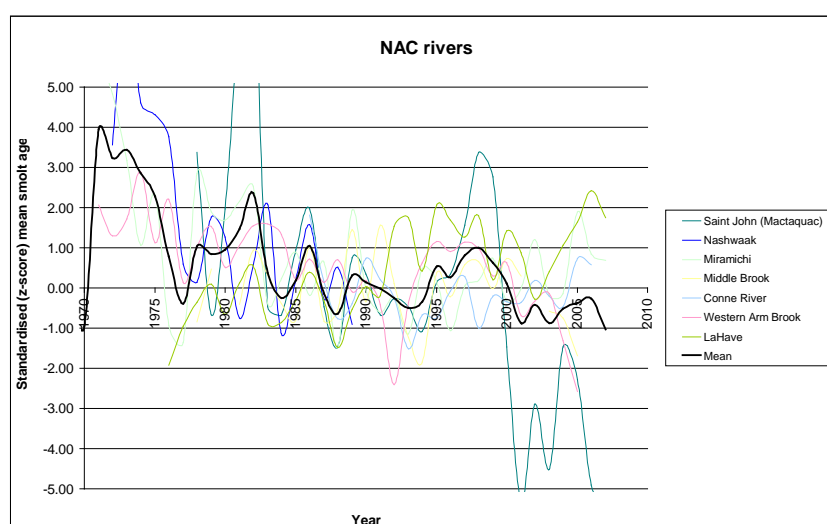


Figure 5.4.3. Standardised mean smolt age for stocks from the NAC area

The decline in mean smolt age may be the consequence of an increase in growth rate as the faster growing parr migrate to sea earlier (Metcalf *et al.*, 1989; Økland *et al.*, 1993). The increase in growth rate may relate to an increase in temperature (Elliott *et al.* 2000; Jonsson *et al.*, 2005), and/or an increase in growth as a result of density-dependent processes (Gibson, 1993; Jenkins *et al.*, 1999; Imre *et al.*, 2005; Lobón-Cerviá, 2005), and/or increased freshwater production. A possible consequence of the increase in growth rate and smolts migrating at an earlier age is to dampen the impact of an increase in marine mortality. This assumes that the higher survival rate to smolt for a one-year-old smolt (S1) is not outweighed by their higher marine mortality. A decline in smolt age may affect reproductive success as egg size is smaller for S1 as opposed to S2 smolts of the same sea-age and early survival (egg to swim-up) may also be lower (Moffett *et al.*, 2006).

These possible effects might be explored further to assess whether available data sources (adult and juvenile) tell a common story, to investigate possible implications for pre-smolt and post-smolt survival and adult return (perhaps even the age and

size composition of adult fish), and what marine environmental effects might influence this.

However, this relatively simple initial analysis of trends in mean smolt age within each geographical region has highlighted certain issues that may need to be considered in taking forward further analyses:

- The sample size in some years was as low as 3 fish (for this analysis all the data were included irrespective of sample size).
- The choice of reference period – in this analysis 1983–1994 was used, but this meant that there were few years of data for the reference period for some rivers. For example, there were only 3 years of data in the reference period for the River Gaula), and in the case of the River Årgård, where there was only one year of data available between 1983 and 1994, the river had to be excluded from further analysis.
- A statistically more robust approach may be more appropriate.
- Mean smolt age data have been derived from all returning monitored fish. The data make no allowance for possible differences in the seasons over which they were captured or for changes in the mix of different maturity groupings in the run. Given the potential link between smolt age and sea-age, examination of trends in smolt ages might usefully be completed for the separate maturity groupings.

Meta-analysis

The second approach used meta-analysis, which statistically combines the results of several studies (in this case different rivers) to address a shared research hypothesis. Just as individual studies summarise data collected from many participants in order to answer a specific research question (i.e., each participant is a separate data-point in the analysis), a meta-analysis summarises data from individual studies that concern a specific research question (i.e., each study is a separate data-point in the analysis).

This is normally done by identification of a common measure of effect size. An effect size is a statistical measure portraying the degree to which a given event is present in a sample (Cohen, 1969). The type of measure (e.g., standardized mean difference) is called the effect, and its magnitude is considered an effect size. Different measures of effect size are calculated for different types of primary data, commonly modelled using a form of meta-regression. In this instance, all effect sizes were calculated from Pearson correlation coefficients between a given variable and year. Resulting overall averages when controlling for study characteristics can be considered meta-effect sizes, which are more powerful estimates of the true effect size than those derived in a single study under a given single set of assumptions and conditions.

Fail-Safe Tests were also applied in these analyses. These tests are statistical methods for estimating the magnitude of the *publication bias* known as the *file-drawer problem* (Rosenthal, 1979). These techniques calculate the number of non-significant, unpublished studies that need to be added to a summary analysis in order to change the results from significant to non significant. A large fail-safe number indicates that many unpublished studies are required to change the statistical results, and thus one may be more confident in the results from the summary analysis.

This approach was used to explore relationships for most of the available biological characteristics and a selection of results appears in Figure 5.4.4. These provide the central tendencies (means) for four stock groups and the total effect – if the error bar

crosses the vertical zero-line the effect is non significant at the $p = 0.05$ -level. These analyses were performed over a standardised time period starting from 1984 and extending to the most recently available data, typically 2007. All available data were included, although the completeness of the data sets varied considerably for the different biological characteristics, as indicated in Table 3.2.1. Median and mean run dates were converted to day of the year prior to analysis.

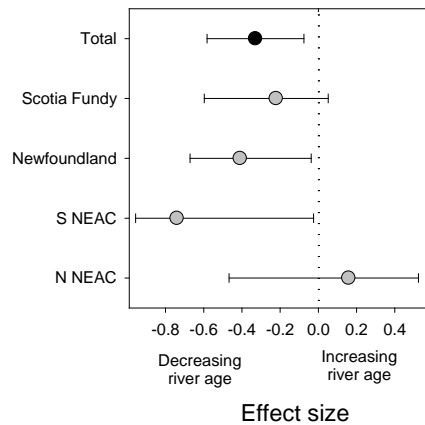
The following stock complex groupings were used in the meta analysis:

- NEAC north – rivers in Russia, Norway, Finland, Iceland (N&E).
- NEAC south - rivers in UK, France and Iceland (S&W).
- NAC north (denoted Newfoundland in Figure 5.4.4) - Rivers Western Arm Brook, Middle Brook, Conne and Miramichi.
- NAC south (denoted Scotia Fundy in Figure 5.4.4) - Rivers Nashwaak, St John (Mactaquac), La Have and Penobscot.

All the results arising from the meta analysis are provided in Table 5.4.1 (where 'o' denotes a non-significant relationship, '+' indicates a significant increase relative to the mean and '-' denotes a significant decrease). These analyses indicated a number of significant trends over time for certain variables at the stock complex level (Table 5.4.2). With respect to smolt age, the meta analysis provided results consistent with the earlier z-score approach, although with the latter approach a significant decrease was apparent only for the NAC Northern area (as opposed to the NAC area as a whole with the z-score approach).

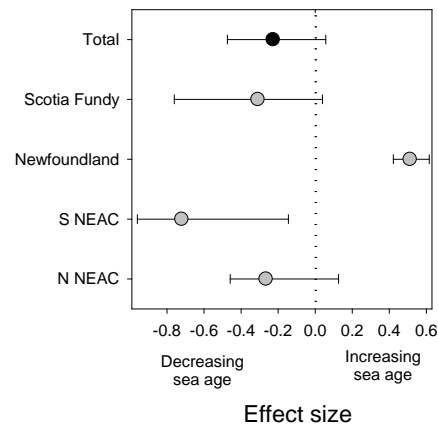
Figure 5.4.4. Example meta-analysis plots for selected biological characteristics – for stock groupings see text.

Mean river age



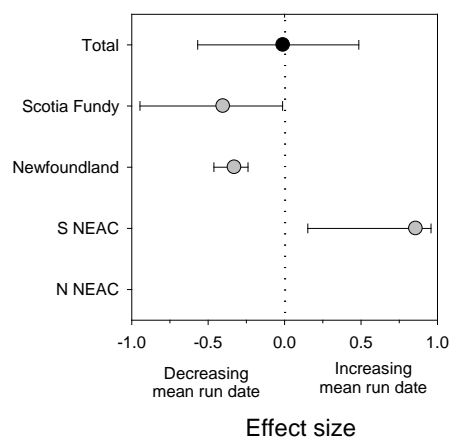
Fail safe number = 298.0

Mean sea-age



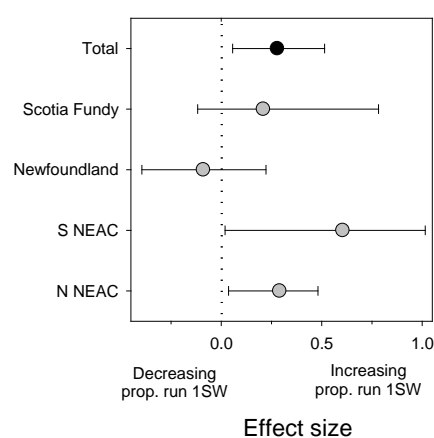
Fail safe number = 119.4

Mean (adult) run date



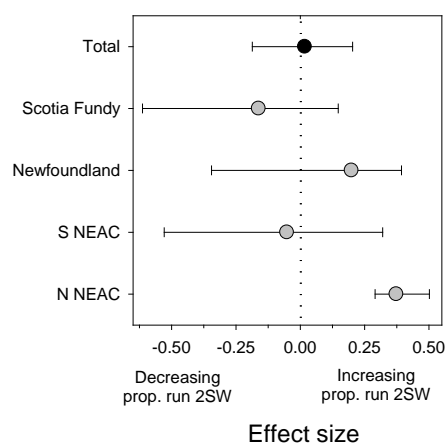
Fail safe number = 5.5

Prop. run – 1SW



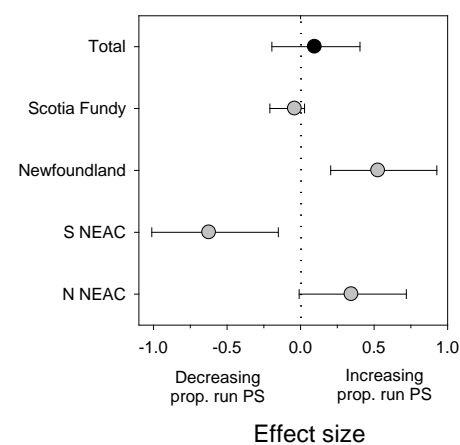
Fail safe number = 259.2

Prop. run – 2SW

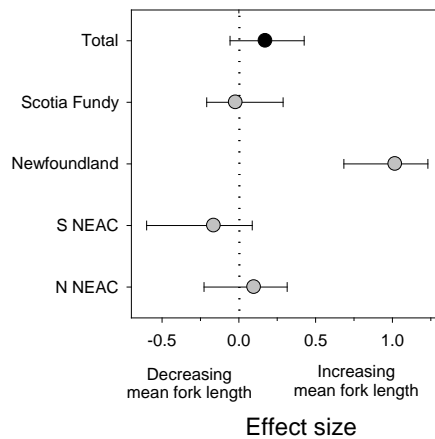


Fail safe number = 0

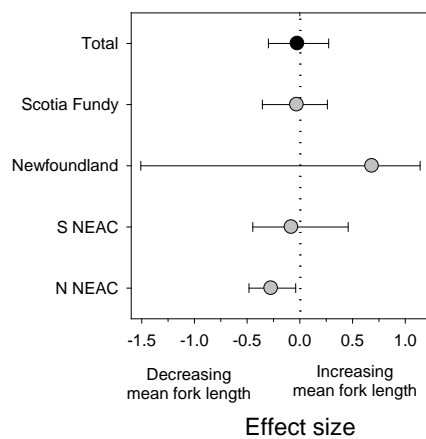
Prop. run – previous spawners



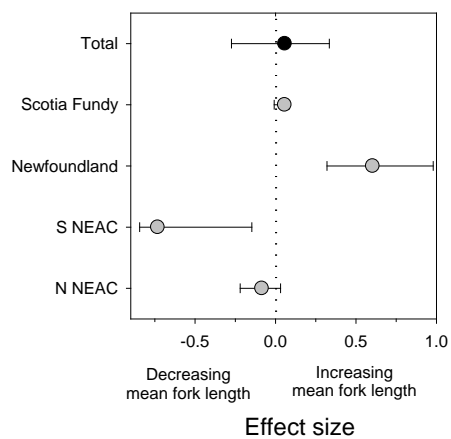
Fail safe number = 17.2

Mean length – 1SW

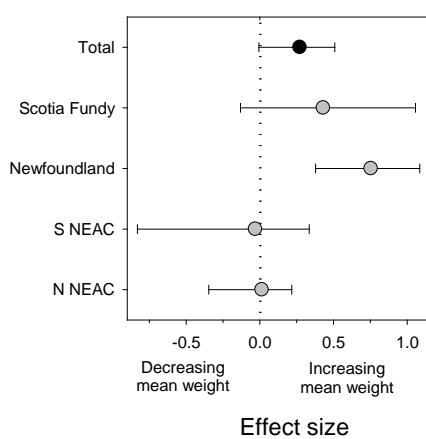
Fail safe number = 50.5

Mean length – 2SW

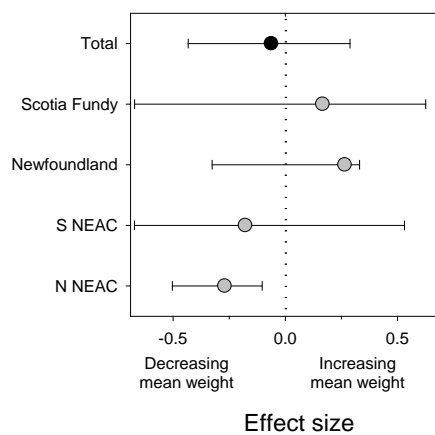
Fail safe number = 0

Mean length – previous spawners

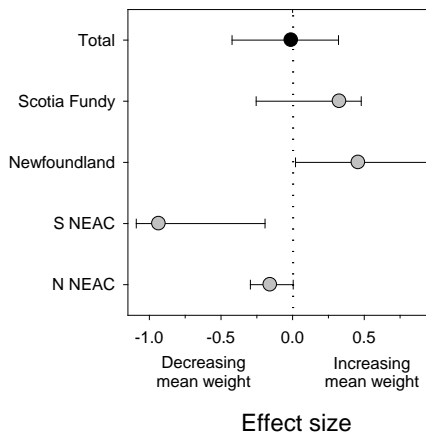
Fail safe number = 0

Mean weight – 1SW

Fail safe number = 94.4

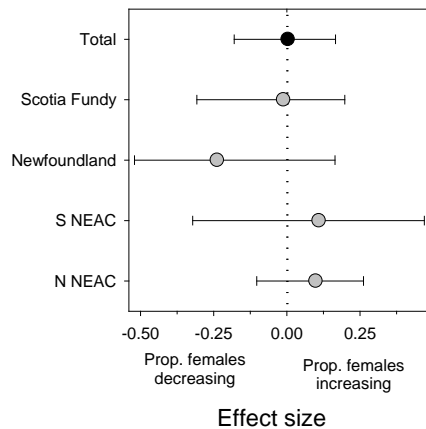
Mean weight – 2SW

Fail safe number = 9.7

Mean weight – previous spawners

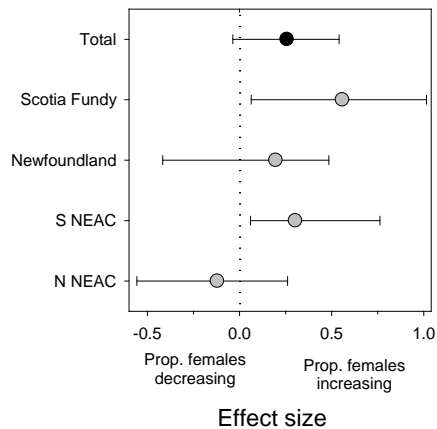
Fail safe number = 0

Prop. female – 1SW



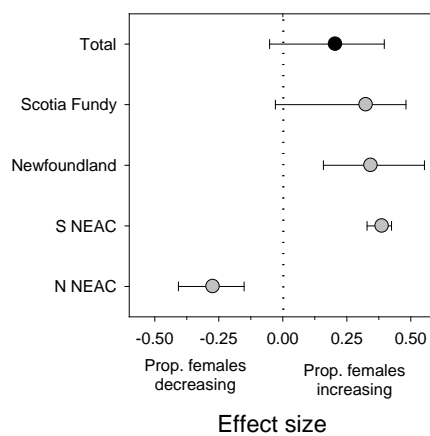
Fail safe number = 0

Prop. female – 2SW



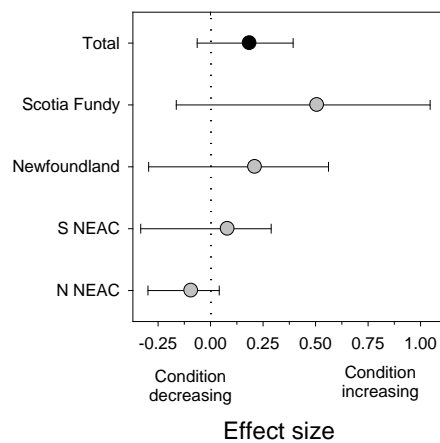
Fail safe number = 94.4

Prop. female – previous spawners



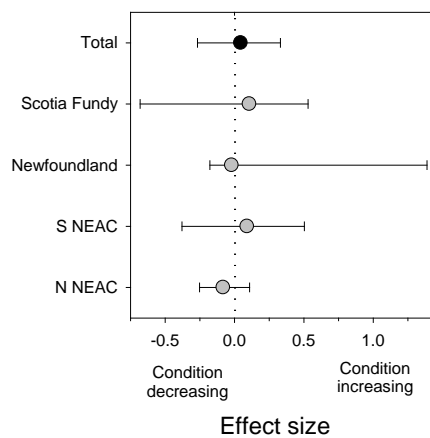
Fail safe number = 18.0

Condition factor – 1SW



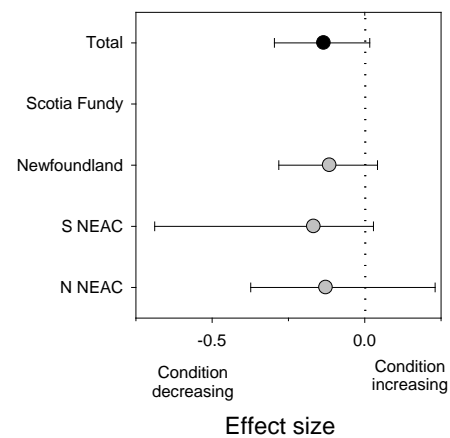
Fail safe number = 24.3

Condition factor – 2SW



Fail safe number = 0

Condition factor – prev. spawners



Fail safe number = 4.0

Table 5.4.1. Results of meta analysis at the stock complex level – indicating significant increase (+) or decrease (-) relative to the mean (o denotes non-significant relationship).

Stock complex	H/W	Time series	Latitude	Stock size - 1SW	Stock size - 2SW	Mean river age	Mean sea age	Mean total age	Median run date	Mean run date	Prop. 1SW in run	Prop. 2SW in run	Prop. PS in run	Mean length - 1SW	Mean weight - 1SW	Condition - 1SW	Mean length - 2SW	Mean weight - 2SW	Condition - 2SW	Mean length - PS	Mean weight - PS	Condition - PS	Prop. female in 1SW	Prop. female in 2SW	Prop. female in PS	Prop. maiden spawners - 1SW	Prop. maiden spawners - 2SW
All		1984-07		o	o	-	o	-	-	o	+	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
NAC (N)	W	1984-07	47.0 - 51.2	o	+	-	+	o	-	-	o	o	+	+	+	o	o	o	o	+	+	o	o	o	+	o	o
NAC (S)	H/W	1984-07	44.4 - 46.0	-	-	o	o	-	o	-	o	o	o	o	o	o	o	o	o	o	o	o	o	+	o	o	o
N NEAC	W	1984-07	65.4 - 70.8	+	o	o	o	o			+	+	o	o	o	o	-	-	o	o	o	o	o	o	-		
S NEAC	W	1984-07	50.1 - 64.6	o	o	-	-	-		+	+	o	-	o	o	o	o	o	o	-	-	o	o	+	+		

Table 5.4.2. Summary of significant trends in biological characteristics at the stock complex level derived from the meta analysis (PS = previous spawners).

Stock complex	Increasing trend	Decreasing trend
NAC (N)	Stock status - 2SW Mean sea-age Prop. PS in run Mean length & weight - 1SW Mean length & weight - PS Prop. Female in PS	Mean river age Mean run date (earlier) Median run date (earlier)
NAC (S)	Prop. Female in 2SW	Stock status - 1SW Stock status - 2SW Mean total age Mean run date (earlier)
N NEAC	Stock status - 1SW Prop. 1SW in run Prop. 2SW in run	Mean length & weight - 2SW Prop. Female in PS
S NEAC	Mean run date (later) Prop. 1SW in run Prop. Female in 2SW Prop. Female in PS	Mean river age Mean sea-age Mean total age Prop. PS in run Mean length & weight - PS

5.5 Overview of preliminary analyses of temporal and spatial trends

Preliminary analyses of the biological characteristics data sets available to the Study Group focused mainly on the 1SW and 2SW sea-age classes. Some data in respect of older sea-age classes were available to the Study Group, but these were restricted to relatively few stocks and sample sizes for these stock components were believed to be small. In light of these caveats, and given the time available at the meeting, the characteristics of these older stock components have not, as yet, been examined. However, some provisional analyses of fish categorised as previous spawners (PS) have been included in the following summary. For the purposes of this summary, the separate hatchery and wild data sets for the St John (Mactaquac) and La Have Rivers in Canada have been treated as separate stocks.

Stock status

Overall, 45% of the individual salmon stock data sets indicate a significant declining trend in the stock status variable (all sea-age groups combined) over the time series analysed (1984-2007). These stocks with declining trends are restricted to North America and the NEAC Southern area; there is not enough evidence at the 5% level to detect any negative trend for stocks in the NEAC Northern area. Only one of the stocks, the Western Arm Brook in Canada, shows a significant positive trend over the period. This is the most northerly of the North American stocks for which data are available.

Meta analysis at the stock complex level (for NAC, based on the arbitrary groupings described in Section 5.4) indicates a significant decrease in the stock status variable for both 1SW and 2SW salmon in the southern part of the NAC area, but a significant

increase in stock status for 1SW salmon in the NEAC Northern area and for 2SW salmon in the northern part of the NAC area.

Mean river age

The majority of the data sets (58%) indicate a significant decline in mean river (smolt) age over the standard time series (1984–2007), the largest percentage of stocks indicating a significant trend of all the variables examined. Relatively few stocks (11%) indicate a significant positive trend over the period and these are restricted to the NAC Southern area (only the La Have River - wild) and the NEAC Northern area (the two most northerly stocks for which data were available).

As indicated in Section 5.4, meta analysis at the stock complex level indicates a significant decrease in mean river age in the northern part of the NAC area and in the NEAC Southern area. The alternative z-score analysis, for wild fish only and over the entire available time series, also demonstrated significant negative trends in mean river age for both the whole NAC area (from the 1970s) and for the NEAC Southern area (from the 1960s). River age has remained constant in the NEAC Northern area since the early 1970s ($p > 0.05$), although there is an indication of an increasing trend up to the late 1990s / early 2000s, with a decline thereafter.

Mean sea-age

The majority of stocks demonstrate significant trends in mean sea-age since 1984, although patterns are variable. In total, 40% of the data sets indicate a significant decline in mean sea-age, 25% a significant increase and 35% no apparent trend. There appear to be marked differences between the NAC Northern area, where 3 of the 4 stocks demonstrate significant increases in mean sea-age and there are no declining trends, and the NAC Southern area where half of the stocks show significant decreases and there are no increasing trends. All of the stocks in the NEAC Northern area demonstrate significant trends, with three stocks decreasing and two increasing; the increases occur in the three most northerly stocks. It is not clear whether this might reflect some possible latitudinal effect. In the NEAC Southern area, two of the five stocks show a significant decline in mean sea-age and no stocks show a significant increase.

Meta analysis at the stock complex level indicates a significant increase in mean sea-age in the northern part of the NAC area and a significant decrease in the NEAC Southern area.

Mean/Median run date

Data on run timing are relatively sparse for stocks from the NEAC area. However, the available data suggest marked differences in the trend in run timing (data for all sea-age classes combined) between the NAC and NEAC area. Over half the stocks in the NAC area demonstrate significant negative trends (i.e. towards earlier running) in median adult run date (and one third of stocks for mean run date); no stocks demonstrate trends towards later running. In contrast, for the three stocks in the NEAC area for which such data are available, all indicate significant positive trends (i.e. later running) in either median or mean run date.

Meta analysis at the stock complex level indicates a significant decrease in mean run date in the NAC area (north and south) and a significant increase in mean run data in the NEAC Southern area.

Proportion of different sea-age classes in the run

The proportion of 1SW salmon in returning adult runs shows a significant increase in many stocks (48% of all stocks). A high proportion of the stocks in the NAC Southern area and in the NEAC Northern and Southern areas display similar positive trends. However, a different pattern is apparent in the NAC Northern area, where one stock, the Conne River in Canada, shows a significant negative trend in the proportion of 1SW salmon in the run and there are no stocks with positive trends. The Conne is the only stock among the available data sets to indicate such a negative trend. Meta analysis at the stock complex level indicates a significant increase in the proportion of 1SW salmon in the returning stocks for both the NEAC Northern and Southern areas. No significant relationships are apparent for the NAC areas.

There is less evidence for consistent patterns of change in the proportion of 2SW salmon in returning adult runs, with 67% of stocks showing no significant trend over the time period and evidence of both significant increasing (14% of stocks) and decreasing (19% of stocks) trends for different stocks. Meta analysis indicates a significant increase in the proportion of 2SW salmon in the returning stocks in the NEAC Northern area, but no significant relationships elsewhere. Evidence of significant positive trends in the proportion of both 1SW and 2SW salmon in the NEAC Northern area probably reflects declines in the proportion of older stock components in this area.

The analysis of the proportion of PS in returning stocks indicates that this is increasing over time for 25% of the available data sets examined; only one stock (6%) shows a significant declining trend. Increasing trends only occur in the NAC Northern and in the NEAC Northern area. There are no significant trends in the NAC Southern area and the only significant negative trend occurs in the NEAC Southern area. Meta analysis indicates a significant increase in the proportion of PS in the returning stocks in the NAC Northern area, a significant decrease in the NEAC Southern area, and no significant relationships elsewhere.

Mean length, weight and condition – 1SW salmon

The available data sets indicate differing patterns in the mean size of returning 1SW salmon both among stocks and over time. Significant increasing size trends are apparent for many of the stocks in North America, and particularly in the northern area where mean length is trending positively in all stocks. None of the stocks in the NAC Southern area show significant increasing trends in mean length, but a number do in respect of mean weight and condition factor; there are no negative trends in either length or weight in the NAC area. In a number of instances significant increases in length for a particular stock are matched by significant increasing trends in weight and sometimes condition factor, but this is variable. For the River Miramichi, while the mean length of 1SW salmon shows a significant increasing trend, the condition factor shows a significant decrease over time.

There is little evidence for trends over time in the NEAC Northern area, although there are significant increases in the mean length of 1SW salmon returning to one river and the mean condition factor of 1SW salmon in another. These are the two northernmost rivers in the area. There is greater variability in the NEAC Southern area, with some stocks showing significant decreases in fish size, while others in relatively close geographic proximity show significant increases.

Meta analysis indicates a significant increase in the mean length and weight of 1SW salmon in the NAC Northern area, but no significant relationships in mean length or

weight in the NAC Southern area or in either of the NEAC areas. There are no statistically significant trends in the condition factor of 1SW salmon at the stock complex level.

Mean length, weight and condition – 2SW salmon

As with the 1SW fish, the available data sets indicate widely differing patterns in the mean size of returning 2SW salmon both among stocks and over time. Both significant increases and significant decreases in the size of 2SW fish are apparent for different stocks in North America, but with no clear geographical pattern. In the NEAC Northern area there are no significant trends in the size of 2SW fish apart from the River Tuloma (Russia), where there has been a significant decrease in the mean length and weight of 2SW salmon over the period. Once again, there is greater variability in the NEAC Southern area with some stocks showing significant decreases in the size of returning 2SW fish, while others show significant increases.

For some stocks, common significant trends are apparent in the size of both returning 1SW and 2SW fish. This applies to certain stocks in the NAC Southern area (increasing size trend) and in the NEAC Southern area (size of both 1SW and 2SW fish decreasing on the North Esk, Scotland, but increasing on the River Dee, Wales).

Meta analysis indicates a significant decrease in mean length and weight of 2SW salmon in the NEAC Northern area, but no significant relationships in the NEAC Southern area or in the NAC areas. There are no statistically significant trends in the condition factor of 2SW salmon at the stock complex level.

Mean length, weight and condition – Previous Spawners (PS)

There are significant increasing trends in the size of previous spawning (PS) fish for many of the stocks in the NAC area and there are no negative trends in either length, weight or condition factor. The pattern in trends in the NAC area appears to be consistent with that seen in the 1SW salmon, the dominant sea-age group in many of these stocks. There are no significant trends in the size of PS fish returning to the NEAC Northern area. Size data for PS are only available for three stocks in the NEAC Southern area and these indicate no apparent trend in one instance, but decreasing size trends in the other two stocks.

Meta analysis indicates a significant increase in the mean length and weight of PS in the NAC Northern area, and a significant decrease in the mean length and weight of PS in the NEAC Southern area. There are no statistically significant trends in the condition factor of PS at the stock complex level.

Proportion of female fish

The available data sets indicate differing patterns in the proportion of female fish in the returning 1SW, 2SW and PS fish over the period from 1984. For each stock component, the majority of stocks indicate no detectable trend in the proportion of females (1SW 74%, 2SW 56% and PS 67% respectively). However, while trends among the remaining stocks tend to be negative (fewer females) for 1SW salmon, they tend to be positive for 2SW salmon and PS.

For 1SW salmon, three of the stocks (30%) in the NAC area indicated a significant decrease in the proportion of females and there were no positive trends. There were no significant trends in the NEAC Northern area, while in the NEAC Southern area the proportion of females increased for one stock, but decreased for another.

In contrast to the 1SW fish, three of the stocks (33%) in the NAC area indicated a significant increase in the proportion of females among the 2SW salmon and there were no negative trends. Trends were more variable in the NEAC Northern area, with two stocks indicating a significant decrease in the proportion of female 2SW salmon, while one showed an increase. In the NEAC Southern area, there was a significant increase in the proportion of females for two stocks and no negative trends.

Relatively few data sets are available in respect of PS. These indicate increasing trends in the proportion of females for two stocks (50%) in the NAC area, decreasing trends in one stock in the Northern NEAC area (33%) and no apparent trends in the NEAC Southern area.

Meta analysis indicates no significant trends in the proportion of females in returning 1SW salmon. However, there is a significant increase in the proportion of female fish in returning 2SW salmon in the NAC Southern area and in the NEAC Southern area. For PS, the proportion of females is increasing significantly in the NAC Northern area and in the NEAC Southern area, but decreasing significantly in the NEAC Northern area.

Proportion of different sea-age groups among maiden spawners

Information on the proportion of different sea-age class fish among the maiden spawners (fish returning to spawn for the first time) was largely confined to North American stocks, and broadly reflects the proportions of different sea-age fish in the run (see above). In respect of the proportion of 1SW salmon among the maiden fish, positive trends were evident for half of the stocks in the NAC Southern area, while in the NAC Northern area one stock shows a significant negative trend and there are no stocks with positive trends. Where data were available for the NEAC area (one in the Southern area and one in the Northern area), these both indicated a positive trend in the proportion of 1SW salmon.

There was an increasing trend in the proportion of 2SW salmon among the maiden spawners in one stock (Conne River) in the NAC Northern area, and decreasing trends were evident for half of the stocks in the NAC Southern area. There was no apparent change for the one stock in the NEAC Northern area, while there was a decrease in the proportion of 2SW salmon among the maiden spawners for the one stock in the NEAC Southern area.

No significant trends in the proportions of maiden spawners were detected at the stock complex level using meta analysis.

5.6 Exploration of two-way relationships

The Study Group completed some preliminary analyses to investigate potential inter-relationships between selected stock characteristics for each river, over the standardised time period from 1984. Simple linear regression models were used to test each relationship since the analyses were essentially exploratory in nature. In the majority of cases, this model seemed reasonable. In a few cases, a more complicated model may have been more appropriate; such refinements might be incorporated in future analyses. The relationships investigated were:

- 1SW weight v 2SW weight (fish sampled in the same year)
- 1SW weight (in year 'n') v 2SW weight (in year 'n + 1')
- 1SW condition factor v 2SW condition factor (fish sampled in the same year)

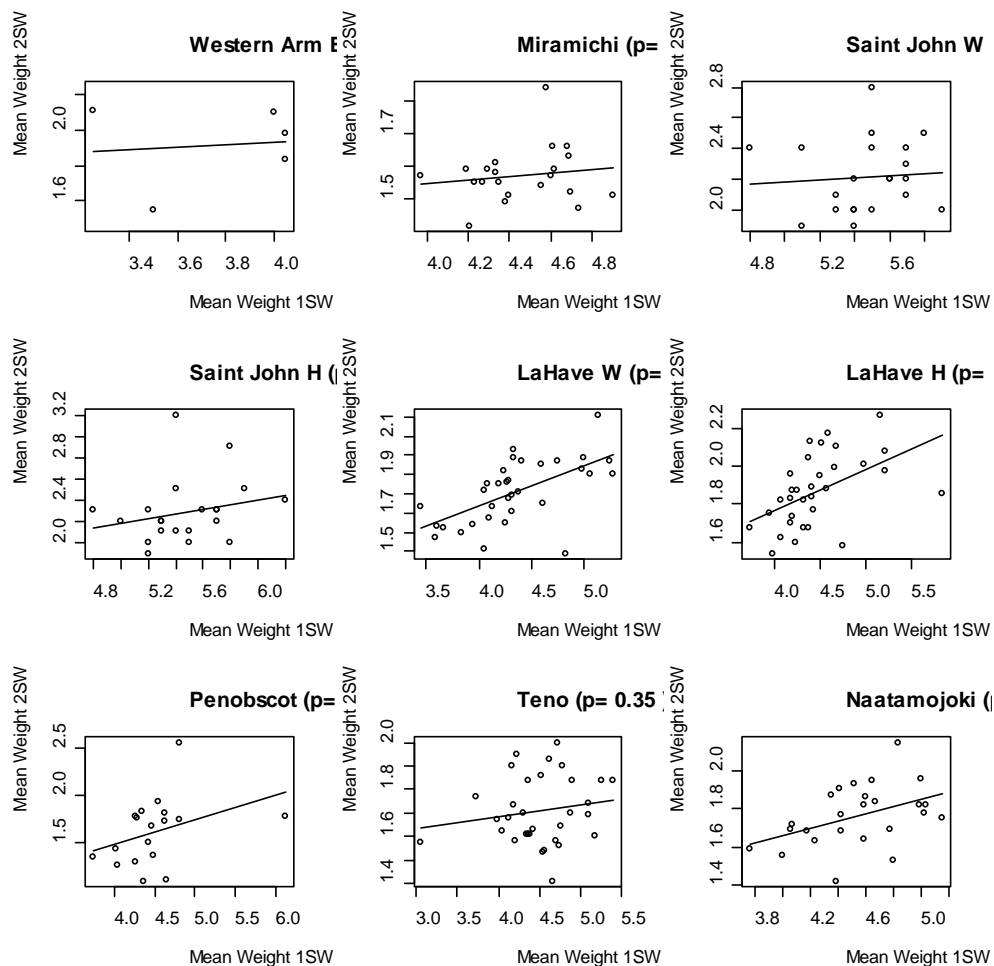
- 1SW condition factor (in year 'n') v 2SW condition factor (in year 'n + 1')
- Mean river age v mean sea-age
- 1SW length v 1SW weight
- 2SW length v 2SW weight
- Mean river age v 1SW weight
- Mean river age v 2SW weight
- 1SW weight v total run size
- 2SW weight v total run size
- 1SW weight v 1SW run size
- 2SW weight v 2 SW run size

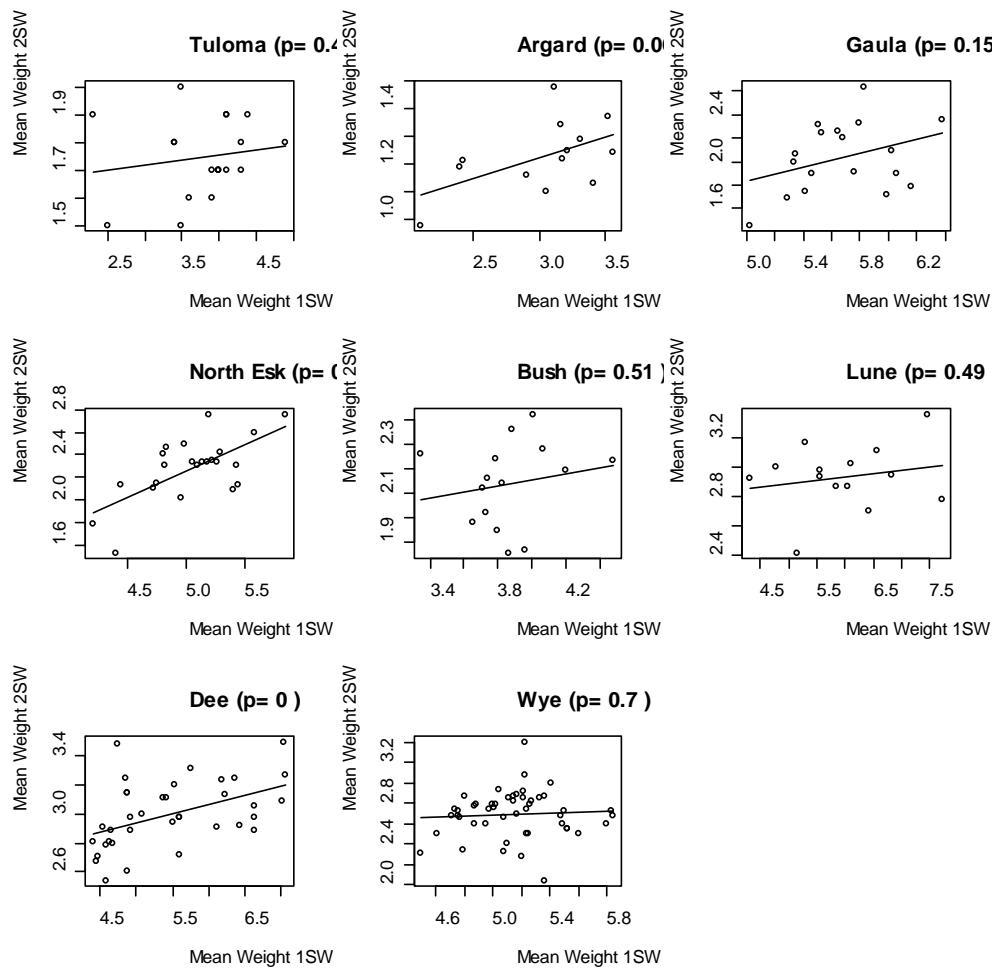
A series of plots were produced for each of the above relationships for each stock for which appropriate data were available (Figure 5.6.1 provides two examples). Each of the individual river plots also includes the p-value to assess the statistical significance of the slope of the linear regression model. The Study Group noted that even if this p-value is not small it does not necessarily mean that there is no relationship – only that we are unable to detect it with these data. Table 5.6.1 summarises the results of the linear regression models for each of the above relationships - 'o' means that there was not enough evidence at the 5% level to detect a trend; '+' denotes a positive trend ($p > 0.05$), and '-' denotes a negative trend ($p < 0.05$).

The results are discussed briefly below. The Study Group noted that further work is required to explore these and other relationships and to develop and explore possible hypotheses.

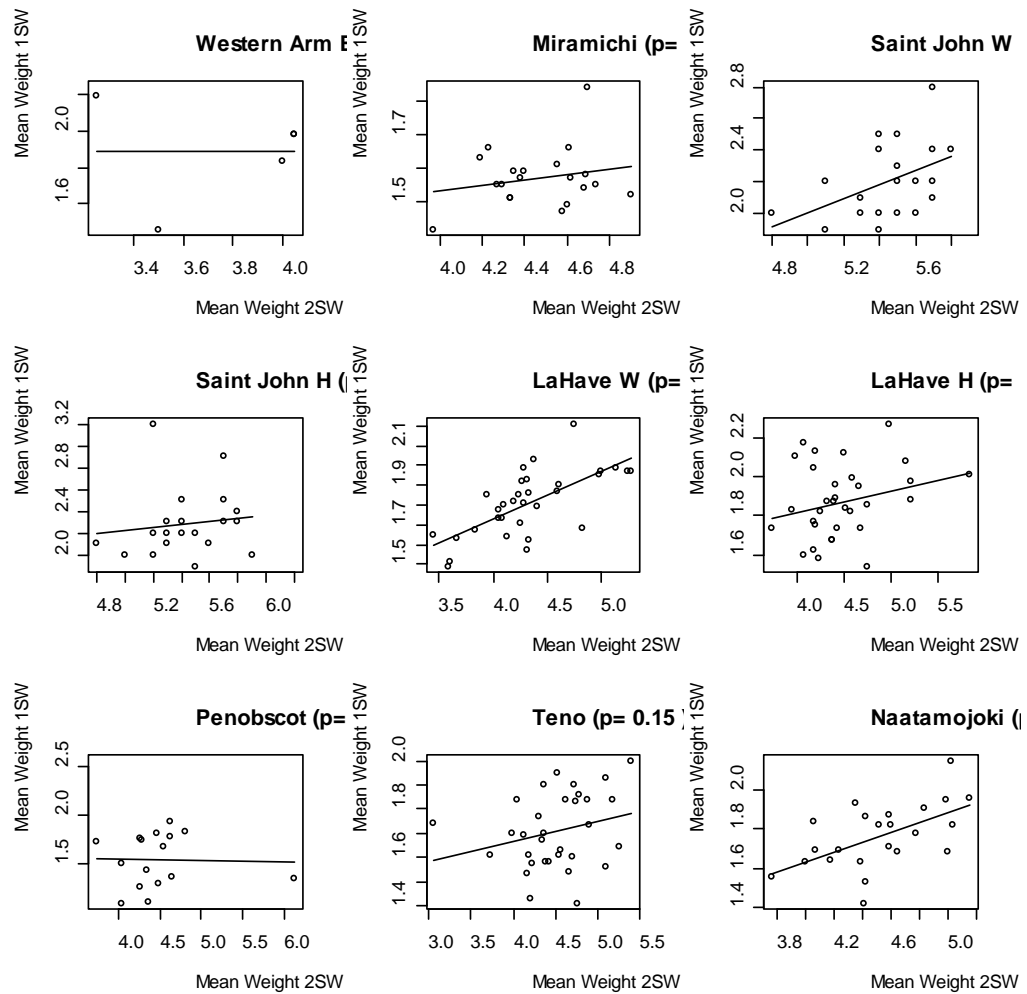
Figure 5.6.1. Example two-way plots for each individual stock of: (a) mean weight of 1SW salmon against the mean weight of 2SW salmon returning in the same year (i.e. from an earlier smolt cohort), and (b) mean weight of 1SW salmon against the mean weight of 2SW salmon returning in the following year (i.e. from the same smolt cohort). For stocks with both wild (W) and hatchery (H) stock components the data are plotted separately. The p-values provide the statistical significance of the slope of each linear regression model.

(a)





(b)



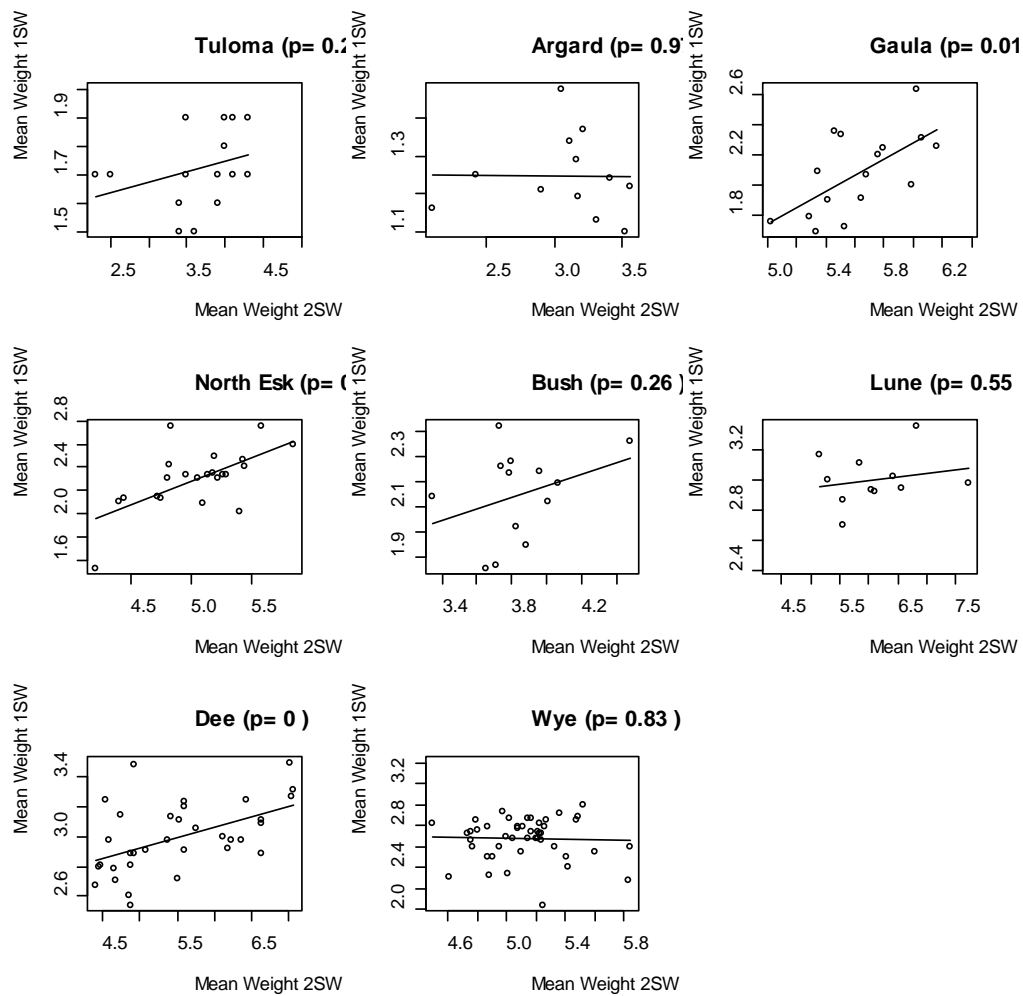


Table 5.6.1. Results of analysis of two-way relationships based on simple linear regression models: 'o' means that there was not enough evidence at the 5% level to detect a trend; '+' denotes a positive trend ($p>0.05$), '-' denotes a negative trend ($p<0.05$).

Stock complex	Country	Stock	H/W	Time series	Latitude	1SW wt (yr n) v 2SW wt (yr n)	1SW wt (yr n) v 2SW wt (yr n+1)	1SW CF (yr n) v 2SW CF (yr n)	1SW CF (yr n) v 2SW CF (yr n+1)	River age v Sea age	1SW Length v 1SW Wt	2SW Length v 2SW Wt	River age v 1SW Wt	River age v 2SW Wt	1SW wt v Total Run	1SW wt v 1SW Run	2SW wt v Total Run	2SW wt v 2SW Run
NAC (N)	Canada	Western Arm Brook	W	1984-06	51.2	o	o	o	o	-	+	o	-	o	+	+	o	o
	Canada	Middle Brook	W	1984-05	48.8					+	+				o	o		
	Canada	Conne River	W	1984-06	47.9					o	+		o		o	o		
	Canada	Miramichi	W	1984-07	47.0	o	o	o	+	o	+	+	o	o	o	o	o	o
NAC (S)	Canada	Nashwaak	W	1984-07	46.0					+								
	Canada	St John (Mactaquac)	W	1984-07	45.3	o	+	o	+	o	+	+	o	o	o	o	o	o
	Canada	St John (Mactaquac)	H	1984-07	45.3	o	o	o	o	o	+	+	o	o	o	o	o	+
	Canada	La Have	W	1984-07	44.4	+	+	+	+	o	+	+	+	+	o	o	-	-
	Canada	La Have	H	1984-07	44.4	+	o	+	+	-	+	+	o	o	-	-	o	o
	USA	Penobscot	H	1984-07	44.5	o	o	o	o	o	o	o	+	o	o	o	o	o
N NEAC	Finland/Norway	Teno	W	1984-07	70.8	o	o	+	o	-	+	+	o	o	o	+	o	o
	Finland/Norway	Näätämöjoki	W	1984-06	69.7	+	+	o	o	o	+	+	o	o	+	o	o	+
	Russia	Tuloma	W	1984-08	68.9	o	o	o	+	o	+	+	o	o	o	o	o	o
	Norway	Årgårdsvassdraget	W	1992-07	64.3	o	o	o	o	o	+	+	o	o	o	o	o	+
	Norway	Gaula	W	1989-07	63.3	o	+	o	o	o	+	+	o	o	o	o	o	o
	Iceland (N&E)	Laxa í Adaldalur	W	1984-07	65.6													
S NEAC	Iceland (N&E)	Hofsa	W	1984-07	65.4													
	Iceland (S&W)	Nordura	W	1984-07	64.6													
	Iceland (S&W)	Ellidaar	W	1984-07	64.1													
	UK (Scot)	N. Esk	W	1984-07	56.7	+	+	+	+		+	+						
	UK (NI)	Bush	W	1984-07	55.1	o	o	o	o	o	+	+	o	o	o	o	o	+
	UK (E&W)	Lune	W	1987-07	54.0	o	o	o	o	o	o	+	o	o	o	o	-	o
	UK (E&W)	Dee	W	1984-07	53.4	+	+	o	o	+	+	+	-	-	o	o	-	-
	UK (E&W)	Wye	W	1984-07	51.6	o	o	+	o	+	+	+	-	o	o	o	o	o
	UK (E&W)	Frome	W	1984-08	50.7													
	France	Bresle	W	1984-08	50.1													
Summary - all areas		No. of stocks for which data available				17	17	17	17	19	19	17	18	16	18	18	16	16
		% of stocks with significant declining trend				0	0	0	0	16	0	0	17	6	6	6	19	13
		% of stocks with significant increasing trend				29	35	29	35	21	89	88	11	6	11	11	0	25
		% of stocks with no significant trend				71	65	71	65	63	11	12	72	88	83	83	81	63

The size and condition of 1SW and 2SW fish returning in the same year

It is evident that for a number of stocks (29%) there is a significant positive relationship between the weight of 1SW and 2SW salmon returning in the same year (i.e. derived from different smolt cohorts). In no instances are significant negative trends identified, and all the plots in Figure 5.6.1 suggest positive trends even if the relationships are not significant. Significant positive relationships are evident in the NAC Southern area and in both the NEAC Northern and Southern areas. A very similar pattern is evident for mean condition factor. These common patterns of larger (or smaller) 1SW fish coinciding with larger (or smaller) 2SW fish in returning stocks in any year are consistent with common factors operating on the fish from the two sea-group groups during their return migration. However, it should be noted that there was also evidence of a correlation between size and condition of 1SW fish in year 'n' and 2SW fish returning in the following year ('n+1') suggesting common influences in the early part of the marine phase (see below). The Study Group recognised that further analysis of such data would be valuable to explore temporal and spatial patterns.

The size and condition of 1SW in year 'n' and 2SW fish returning in the following year ('n+1')

Similar positive relationships are also evident for many stocks (35%) between the weight of 1SW returning in one year and the weight of 2SW salmon returning in the following year (i.e. derived from the same smolt cohort). As with fish returning in the same year, there is no evidence of any negative relationships (Table 5.6.1 and Figure 5.6.1), and similar patterns are evident for mean condition factor. Significant positive relationships are evident all areas. These concurrent patterns for particular smolt cohorts suggest that common factors operating in the first period at sea may have a large influence on growth and size at maturity of returning adult fish. Again, the Study Group recognised that further analysis of such data would be valuable.

For some stocks, significant positive relationships are apparent between the weight/condition factor of returning 1SW salmon and the weight/condition factor of returning 2SW salmon in both the same and the following year. For other stocks, significant relationships were only evident in one case.

Mean river age v mean sea-age

Analysis indicates very different relationships between river age and sea-age for different stocks. In some rivers, significant positive relationships apply (i.e. older smolts tend to produce older adults). However, significant negative relationships are evident for some other stocks. Viewed spatially, there appears to be more evidence of variability in these relationships in the NAC area, where significant positive and negative relationships are evident, even in stocks in relatively close geographic proximity. The only significant relationship identified in the NEAC Northern area is negative, while only significant positive relationships (2) are evident in Southern NEAC. The link between smolt size and the sea-age of returning adults for Southern NEAC stocks is explored further in Section 5.7.

Length v Weight

Unsurprisingly, the length and weight of returning 1SW and 2SW fish are positively correlated. In most, but not all, instances these relationships are significant.

Mean river age v size of returning adults

The age of smolts (aged from adult scales) and the size of returning 1SW and 2SW adults was compared to see whether there were any consistent patterns between the age, and by inference the size of smolts, and the subsequent size (weight) of the returning adults. A number of significant, but variable, relationships were apparent. In the NAC Northern area and the NEAC Southern area significant negative relationships were apparent for some stocks – i.e. older/larger smolts tended to result in smaller returning adults. This is consistent with other evidence that smolt size can influence the subsequent growth rate of salmon, with larger smolts showing slower growth at sea (Jonsson & Jonsson, 2007). Such negative relationships were evident for 1SW salmon for one stock in the NAC Northern area and for both 1SW and 2SW salmon in the NEAC Southern area. However, while there was a negative relationship between smolt age/size and the weight of both 1SW and 2SW salmon in one example, this applied only to 1SW salmon in the other.

No significant relationships between smolt age/size and the weight of returning adults was apparent for any of the stocks in the NEAC Northern area. However, in the NAC Southern area some positive relationships occurred, indicating that

older/larger smolts tended to result in larger returning adults. This was evident for returning fish in two stocks - for both 1SW and 2SW fish in one and just 1SW returns in the other. This observation would appear to be at odds with the hypothesis that larger smolts have slower growth at sea.

Size of returning fish v stock status variable

Provisional analyses were also completed to investigate possible links between the size (weight) of returning adult 1SW and 2SW fish in any year and the stock-specific status variable for that year. For these purposes, relationships were explored with the total stock status (all sea-age groups) and an age-specific stock status derived from the total figure and the estimated proportion of each sea-class in the returning stock. The latter is expected to be more informative. The Study Group recognised that these analyses should be treated with caution given the concerns noted previously (Section 3.3), perhaps in particular with regard to the robustness of the stock status variable.

Considering only the comparisons between fish size and the age-specific stock status variables, a relatively small number of significant relationships are apparent; these are both positive (i.e. fish of larger mean size associated with better stock status) and negative (i.e. fish of smaller mean size associated with better stock status). Only positive relationships apply for the NAC Northern area and the NEAC Northern area, while both positive and negative relationships are evident in the other two areas.

5.7 Effect of smolt size and sex on sea-age of returning adult salmon

Section 5.6 noted the variable relationships that exist between river age and sea-age among the various data sets explored. Intuitively, one might expect that the physical condition of smolts entering the sea will have some impact on an individual's subsequent growth rate and thus possibly the length of time it spends at sea before returning to freshwater to spawn. This impact may also differ depending on the sex of the fish. Although, an examination of this effect would best be done with known individuals, these data are not readily available across a large number of rivers. However, there are scale archives of returning adults from many rivers and, although these represent data only from survivors, the Study Group considered it was worth examining these for evidence of some relationship between smolt size and returning adult sea-age and whether this might be affected by the sex of the fish.

The Study Group were able to explore a small subset of such data for the Rivers Frome and Dee, UK (England & Wales). Readily available data for these rivers were analysed using a Generalised Linear Model, with the dependent variable being sea-age (1SW or MSW) and smolt size, sex and river as independent variables. In both the Frome and Dee, smolt size had a significant ($p < 0.05$) positive impact on the proportion of female fish returning as 1SW fish (Figure 5.7.1). That is larger female smolts had a higher probability of returning as 1SW fish than smaller female smolts. For the River Frome, smolt size also had a significant positive effect in males and there was a non-significant positive effect in the River Dee (Figure 5.7.1).

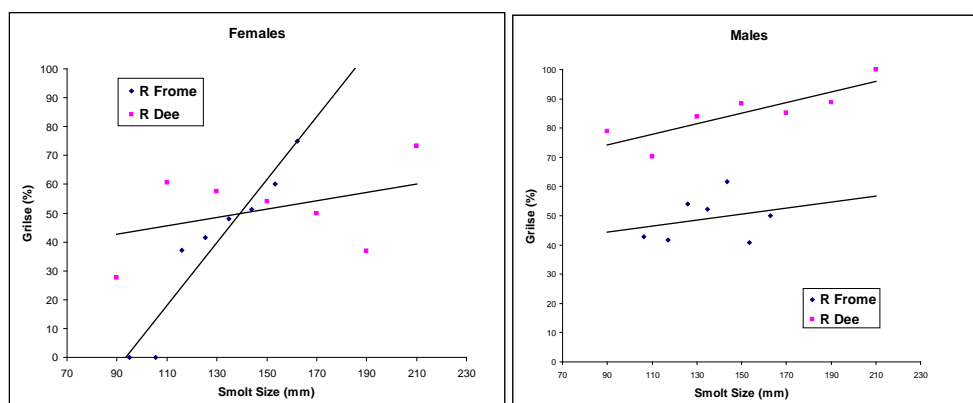


Figure 5.7.1. Proportion of each male and female smolt size class returning to the river as 1SW fish, from a subset of data from the River Frome and the River Dee.

These data require cautious interpretation given that they derive from survivors and from a small sub-set of data from just two rivers. There may also be size-dependent mortality effects that cannot be accounted for using these data. There was a suggestion from these data that the relationship may have changed over time, possibly reflecting changing growth conditions in the marine environment or changes to a size-dependent mortality rate. The Study Group considered that testing this hypothesis further using data from more rivers over a wider geographical spread would be beneficial.

6 Overview and recommendations

The Study Group consider that the work completed to date, and detailed in this report, should be regarded as preliminary. Progress has been made with compiling data sets and analysing data, and it is readily apparent that the biological characteristics of Atlantic salmon stocks are changing markedly across the geographical range of the species. Various, sometimes conflicting, hypotheses were identified in the literature review, and a number of issues were explored in the various analyses completed by the Group. However, the Study Group recognised that the time available did not allow a detailed appraisal and prioritisation of hypotheses based on the data currently available, and that further data sets were believed to be available that would facilitate this process. Thus, the Group believes that further work is necessary to better explore temporal and spatial trends, investigate possible common patterns or regional groupings, and develop and test hypotheses.

The Study Group noted the importance of monitoring programmes to collect age, growth and other biological data from salmon stocks and the need for these to be continued. Such studies are important for examining variations in marine recruitment and links with environmental conditions. Changes in freshwater or marine growth may be among the first signs that climate is having an unusual effect on salmonid populations and can be useful in understanding and explaining fluctuations in abundance and informing fisheries management in a period of potentially unprecedented environmental change. However, the Study Group further recognised that such data need to be better utilised and reported.

The Study Group made the following recommendations; this includes the various recommendations made earlier in the report:

- i) A similar Study Group should be held sometime in 2009/2010 to continue compilation and analysis of available data sets, and the development and testing of appropriate hypotheses. It is hoped that participation in the Group can be extended to provide wider expertise relative to different stock complexes and disciplines.
- ii) The next Study Group should continue to include oceanographers to assist with describing the salmon distributions and relating them to the ocean environment and that consideration be given to extending this to biological oceanographers
- iii) The collection and collation of data sets should be extended to include freshwater stages (e.g. smolt age, smolt size, growth at age, etc.). The Study Group noted that the available data were restricted largely to biological data on adults, that freshwater data had been largely ignored and that there was increasing evidence that freshwater influences might be instrumental to what subsequently happens in the sea.
- iv) In taking forward analyses, and possibly extending these to additional data sets, the Study Group recognised the importance of addressing data quality issues and the need to standardise approaches. In particular, it was felt that information for different stocks should include a description of data sources and of the methodology used to record each variable to aid interpretation. The methods used to derive salmon abundance measures and/or salmon survival/mortality estimates also needed to be characterised according to the assessment and calculation methods used. Further, an email address of an appropriate person able to provide a more detailed description of each data set should be appended to the spreadsheet.
- v) Further efforts should be made to identify data sets for which condition factor can be assessed and to extend such condition factor analyses to other stocks and to MSW fish. A comparison between Baltic populations and southern and northern European populations, including rivers that discharge into the Barents Sea, would be especially valuable, given their differing marine migratory trajectories and destinations.
- vi) The existing biological data sets merit further examination, but further efforts should also be made to extend the existing data sets by filling gaps and by adding data from other stocks to aid in the examination of spatial patterns and the development of appropriate hypotheses. This should, ideally, include data from the Baltic as well as the North Atlantic.
- vii) Data sets with less than 15 year time series should be included in the analyses where this provides greater spatial scale or allows comparison with other available datasets. The Study Group recognised that requests for additional data sets, and specifically for the raw data behind the annual mean values, should ideally be made in response to specific lines of enquiry and where worked examples/case studies suggested useful lines to pursue.

- viii) Relationships between mortality (freshwater and marine) and growth, and resulting biological characteristics, should be explored through the application of appropriate life history models.

With the exception of the recommendation for a further meeting later in 2009 (planned to be held at ICES Headquarters in November – see Annex 4), which ICES will need to note and approve, these recommendations are addressed largely to the Study Group and to members of WGNAS and WGBAST to whom specific data requests will be made.

Annex 1: List of participants

Name	Address	Phone/Fax	Email
Miran Aprahamian	Environment Agency Richard Fairclough House Knutsford Road Warrington WA4 1HG United Kingdom	TEL: +44 1925 542713 FAX: +44 1925 415961	miran.aprahamian@environment-agency.gov.uk
Jon Barry	Cefas Lowestoft Laboratory Lowestoft Suffolk NR33 0HT United Kingdom	TEL: +44 1524 844113	jon.barry@cefas.co.uk
Johan Dannewitz	Institute of Freshwater Research Swedish Board of Fisheries SE-178 93 Drottningholm Sweden	TEL: +46 8 69 90 656 FAX: +46 8 69 90 650	johan.dannewitz@fiskeriverket.se
Ian Davidson	Environment Agency Chester Road Buckley Flintshire CH7 3AJ United Kingdom	TEL: +44 1244 894520 FAX: +44 1244 550144	ian.davidson@environment-agency.gov.uk
Stephen Dye	Cefas Lowestoft Laboratory Lowestoft Suffolk NR33 0HT United Kingdom	TEL: +44 1502 524508 FAX: +44 1502 513865	stephen.dye@cefas.co.uk
Adrian Fewings	Environment Agency Colvedene Court, Colden Common, Winchester, Hampshire SO21 1WP United Kingdom	TEL: +44 7771 527299	adrian.fewings@environment-agency.gov.uk
Peder Fiske	Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway	TEL: +47 73 80 1522 FAX: +47 73 80 14 01	peder.fiske@nina.no
Anton Ibbotson	CEH Wallingford c/o River Laboratory, East Stoke, Wareham BH20 6BB United Kingdom	TEL: +44 1929 401895	ati@ceh.ac.uk
Richard Kennedy	River Bush Salmon Station, 21 Church Street, Bushmills, Co Antrim BT57 8QJ United Kingdom	TEL: +44 28 20731435	richard.kennedy@afbini.gov.uk

Julian C. MacLean	FRS, FL, Field Station Inchbraoch House, South Quay, Ferryden, Montrose, Angus DD10 9SL United Kingdom	TEL: +44 1674 677070 FAX: +44 1674 672604	j.c.maclea@marlab.ac.uk
Erik Petersson	Institute of Freshwater Research Swedish Board of Fish- eries SE-178 93 Drottning- holm Sweden	TEL: +46 8 69 90 602 FAX: +46 8 69 90 650	Erik.Petersson@fiskeriverket.se
Ted Potter	Cefas Lowestoft Laboratory Lowestoft Suffolk NR33 0HT United Kingdom	TEL: +44 1502 524260 FAX: +44 1502 513865	ted.potter@cefas.co.uk
Ian Russell (Chair)	Cefas Lowestoft Laboratory Lowestoft Suffolk NR33 0HT United Kingdom	TEL: +44 1502 524330 FAX: +44 1502 513865	ian.russell@cefas.co.uk
Chris Todd	Scottish Oceans Institute University of St Andrews, St Andrews, Fife KY16 8LB United Kingdom	TEL: +44 1334 463454 FAX: +44 1334 463443	cdt@st-andrews.ac.uk

Annex 2: List of working documents and data sets

- Dannewitz J. Overview of preliminary work completed by the Baltic Salmon and Trout Assessment Working Group (WGBAST) in relation to the low at-sea survival of salmon in the Baltic Sea.
- Davidson, I & Aprahamian M. Overview of stock status and biological characteristics of salmon from the Rivers Dee, Wye and Lune, UK (England & Wales).
- Dye S. Overview of oceanic environmental variables – spatial and temporal scales.
- Fewings A. Overview of stock status and biological characteristics of salmon from the River Test, southern England.
- Fiske, P. Examination of relationships between returns of 1SW and 2SW salmon for two Norwegian rivers and correlation with pre-fishery abundance (PFA).
- Ibbotson A. Overview of stock status and biological characteristics of salmon from the River Frome, southern England.
- Kennedy, R. Overview of stock status and biological characteristics of salmon from the River Bush, UK (N. Ireland).
- Petersson E. Examination of Swedish historic salmon tagging data for the Baltic and the potential application of Meta analysis for examination of biological characteristics datasets from different stocks.
- Russell I. Provisional analysis of salmon biological characteristics datasets from the North Atlantic.
- Russell I., Riley W., Privitera L., Moore A. & Potter E. Biological characteristics of Atlantic salmon – review of background literature and bibliography.
- Todd C. Relationships between oceanic conditions and growth condition of Atlantic salmon – evidence from two time series in UK (Scotland).
- Trial, J. Fecundity of Penobscot River (USA) broodstock.

Data sets

- Amiro P. & Gibson, J. Salmon biological characteristics data for the La Have River (wild and hatchery-origin) (1970-07) - Canada, Scotia Fundy Region.
- Chaput, G. Salmon biological characteristics data for Miramichi River (1971-07) - Canada, Gulf Region.
- Davidson I., Aprahamian M. & Russell I. Salmon biological characteristics data for the Rivers Wye (1910-07), Dee (1937-07) and Lune (1987-07) – UK (England & Wales).
- Erkinaro J. Salmon biological characteristics data for the River Teno (1972-07) and River Naatamojoki (1975-06), Finland/Norway.
- Euzenat G. Salmon biological characteristics data for the River Bresle (1984-08) – France.
- Fiske P. Salmon biological characteristics data for the River Gaula (1989-07) and River Argard (1992-07), Norway.
- Gudbergsson G. Salmon biological characteristics data for Rivers Laxa i Aldaldalur (1974-07), Hofsa (1971-07), Ellidaar (1949-07) and Nordura (1968-07) - Iceland.
- Ibbotson A. Salmon biological characteristics data for the River Frome (1968-08) – UK (England & Wales).

Jones R. Salmon biological characteristics data for the St John (Mactaquac) River (wild and hatchery-origin) (1978-07); and Nashwaak River (1972-07) - Canada, Scotia Fundy Region.

Kennedy R. Salmon biological characteristics data for the River Bush (1973-07) - UK (N. Ireland).

Maclean J. & Smith G. Salmon biological characteristics data for the River N. Esk (1981-07) – UK (Scotland).

Reddin D. Salmon biological characteristics data for Middle Brook (1975-05) and Western Arm Brook (1971-06) - Canada, Newfoundland.

Reddin D. & Dempson B. Salmon biological characteristics data for Conne River (1986-06) - Canada, Newfoundland/Labrador.

Sheehan T. Salmon biological characteristics - standardised spreadsheet.

Trial J. Salmon biological characteristics data for the Penobscot River (1978-07) - USA.

Zubchenko A. Salmon biological characteristics data for the River Tuloma (1983-08) – Russia.

Annex 3: References

- Amiro, P.G. (1998). The mystery of the missing inner Bay of Fundy salmon. *Atlantic Salmon Journal* **47**: 50-53.
- Andreasson, P.M.R., Martinussen, M.B., Hvidsten, N.A. & Stefansson, S.O. (2001). Feeding and prey selection of wild Atlantic salmon post-smolts. *Journal of Fish Biology* **58**: 1667-1679.
- Anon. (1994). Run timing of salmon. Report of the Salmon Advisory Committee. London, MAFF: 55pp.
- Aprahamian, M.W., Davidson, I.C. & Cove, R.J. (2008). Life history changes in Atlantic salmon from the river Dee, Wales. *Hydrobiologia* **602**: 61-78.
- Armstrong, J.D., Shackley, P.E. & Gardiner, R. (1994). Redistribution of juvenile salmonid fishes after local catastrophic depletion. *Journal of Fish Biology* **45**: 1027-1039.
- Armstrong, J.D., Kemp, P.S., Kennedy, G.J.A., Ladle, M. & Milner, N.J. (2003). Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fisheries Research* **62**(2): 143-170.
- Atkins, C.F. (1873). On the salmon of Eastern North America and its culture. Report of the Commission of Fish and Fisheries. pp 226-337.
- Baggerman, B. (1960). Factors in the diadromous migrations of fish. *Zoological Society Symposium I*: 33-60.
- Bagliniere, J.L., Denais, L., Rivot, E., Porcher, J.P., Prevost, E., Marchland, F. & Vaudlin, V. (2004). Length and age structure modifications of the Atlantic salmon (*Salmo salar*) populations of Brittany and Lower Normandy from 1972 to 2002. Rennes, Institut National de la Recherche Agronomique and Conseil Supérieur de la Pêche.
- Bardonnet, A. & Bagliniere, J.L. (2000). Freshwater habitat of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **57**: 497-506.
- Baum, E.T. & Meister A.L. (1971). Fecundity of Atlantic salmon (*Salmo salar*) from two Maine rivers. *Journal of the Fisheries Research Board of Canada* **28**(5): 764-767.
- Baum, E.T. (1997). Maine Atlantic Salmon: A national treasure. Atlantic Salmon Unlimited. 224 pp.
- Beall, E., Dumas, J., Claireaux, D., Barrière, L. & Marty, C. (1994). Dispersal patterns and survival of Atlantic salmon (*Salmo salar* L.) juveniles in a nursery stream. *ICES Journal of Marine Science* **51**: 1-9.
- Beamish, R.J. & Mahnken, C. (2001). A critical size and period hypothesis to explain natural and regulation of salmon abundance and the linkage to climate and climate change. *Progress in Oceanography* **49**: 423-437.
- Beamish, R.J., Mahnken, C. & Neville, C.M. (2004). Evidence that reduced early marine growth is associated with lower marine survival of coho salmon. *Transactions of the American Fisheries Society* **133**: 26-33.
- Beaugrand, G. & Reid, F.C. (2003). Long term changes in phytoplankton, zooplankton and salmon related to climate. *Global Change Biology* **9**: 801-817.
- Benoit, H.P. & Swain, D.P. (2008). Impacts of environmental change and direct and indirect harvesting effects on the dynamics of marine fish community. *Canadian Journal of Fisheries and Aquatic Sciences* **65**(10): 2088-2104.
- Bielak, A.T. & Power, G. (1986). Independence of sea-age and river-age in Atlantic salmon (*Salmo salar*) from Quebec North Shore Rivers. In: Meerburg D.J. (ed) 1986. Salmonid age at maturity. *Canadian Special Publications in Fisheries and Aquatic Sciences* **89**: 70-78.

- Bjornn, T.C. (1971). Trout and salmon movements in two Idaho streams as related to temperature, stream flow, cover and population density. *Transactions of the American Fisheries Society* **100**: 423-438.
- Boylan, P. & Adams, C.E. (2006). The influence of broad scale climatic phenomena on long term trends in Atlantic salmon population size: an example from the River Foyle, Ireland. *Journal of Fish Biology* **68**: 276-283.
- Brett, J.R. (1979). Environmental factors and growth. In: *Fish Physiology*, Vol VIII, pp 599-675. Eds W.S. Hoar, D.J. Randall & J.R. Brett. Academic Press, London.
- Buck, R.J.G. & Youngson, A.F. (1982). The downstream migration of precociously mature Atlantic salmon, *Salmo salar* L., parr in autumn; its relation to the spawning migration of mature adult fish. *Journal of Fish Biology* **20**: 279-288.
- Bujold, V., Cunjak, R.A., Dietrich, J.P. & Courtemanche, D.A. (2004). Drifters versus residents: assessing size and age differences in Atlantic salmon (*Salmo salar*) fry. *Canadian Journal of Fisheries and Aquatic Sciences* **61**: 273-282.
- Cairns, D.K. (2003). Temperature mortality relations in marine phase Atlantic salmon, (*Salmo salar* L.): the search for underlying mechanisms. In: *Marine mortality of Atlantic salmon: methods and measures* (ed. E.C.E. Potter, N. O'Maoileidigh & G. Chaput). Fisheries and Oceans Canada; Canadian Science Advisory Secretariat Research Document 2003/101, 150-160.
- Cannaby, H. & Hüsrevoğlu, Y.S. (2009). The influence of low-frequency variability and long-term trends in North Atlantic sea surface temperature on Irish waters. *ICES Journal of Marine Science* 10.1093/icesjms/fsp062.
- Cefas & Environment Agency (2008). Annual assessment of salmon stocks and fisheries in England and Wales 2007: Preliminary assessment prepared for ICES, April 2008 (ISBN 978 0 907545 25 4).
- Cohen, J. (1969). *Statistical power analysis for the behavioural sciences*. Academic Press, New York.
- Cragg-Hine, D., Bradley, D.C. & Hendry, K. (2006). Changes in salmon smolt ages in the Welsh River Dee over a 66 year period. *Journal of Fish Biology* **68**: 1891-1895.
- Crisp, D.T. & Carling, P. A. (1989). Observations on siting, dimensions and structure of salmonid redds. *Journal of Fish Biology* **34**: 119-134.
- Crisp, D.T. (1995). Dispersal and growth rate of 0-group salmon (*Salmo salar* L.) from point-stocking together with some information from scatter-stocking. *Ecology of Freshwater Fish* **4**: 1-8.
- Crisp, D.T. (1996). Environmental requirements of common riverine European salmonid fish species in fresh water with particular reference to physical and chemical aspects. *Hydrobiologia* **323**: 201-221.
- Crozier, W.W. & Kennedy, G.J.A. (1993). Marine survival of wild and hatchery reared Atlantic salmon (*Salmo salar* L.) from the river Bush, Northern Ireland. In: D. Mills (ed.) *Salmon in the Sea and New Enhancement Strategies*. Oxford: Fishing News Books, Blackwell Scientific Publications, pp. 139-162.
- Crozier, W.W. & Kennedy, G.J.A. (1994a) Application of semi-quantitative electrofishing to juvenile salmonid stock surveys. *Journal of Fish Biology* **45**: 159-164.
- Crozier W.W. & Kennedy G.J.A. (1994b). Marine exploitation of Atlantic salmon (*Salmo salar* L.) from the River Bush, N. Ireland. *Fisheries Research* **19**: 141-155.
- Crozier, W.W. & Kennedy, G.J.A. (1999). Relationships between marine growth and marine survival of one sea winter Atlantic salmon, *Salmo salar* L., from the River Bush, Northern Ireland. *Fisheries Management and Ecology* **6**: 89-96.

- Crozier, W.W. & Kennedy, G.J.A. (2003). Freshwater influences on marine survival of Atlantic salmon (*Salmo salar* L.): evidence from the River Bush, Northern Ireland. In: E.C.E. Potter, N. O'Maoileidigh, G. Chaput (eds.) Marine mortality of Atlantic salmon, *Salmo salar* L.: methods and measures. Research document, Canadian Science Advisory Secretariat 2003/101, pp124-129.
- Cunjak, R.A. & Chadwick, E.M.P. (1989). Downstream movements and estuarine residence by Atlantic salmon parr (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences **46**: 1466-1471.
- Cunjak, R.A., Caissie, D., El-Jabi, N., Hardie, P., Conlon, J.H., Pollock, T.L., Giberson, D.J. & Komadina-Douthwright, S. (1993). The Catamaran Brook (New Brunswick) habitat re-search project: biological, physical and chemical conditions (1990-1992). Canadian Technical Report of Fisheries and Aquatic Science **1914**.
- Dahl, J., Dannewitz, J., Karlsson, L., Petersson, E., Löf, A. & Ragnarsson, B. (2004). The timing of spawning migration: implications of environmental variation, life history, and sex. Canadian Journal of Zoology **82**: 1864-1870.
- Dalley, E.L., Andrews, C.W. & Green, J.M. (1983). Precocious male Atlantic salmon parr (*Salmon salar*) in insular Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences **40**: 647-652.
- Davidson, I.C. & Hazelwood, M.S. (2005). Effects of climate change on salmon fisheries. Science Report W2-047/SR, Environment Agency, Bristol, 52pp.
- Davidson, I.C., Hazlewood, M.S. & Cove, R.J. (2006). Predicted growth of juvenile trout and salmon in four rivers in England and Wales based on past and possible future temperature regimes linked to climate change. Proceedings of Biology and Management of Sea Trout Conference, 6-8 July 2004, Cardiff, Wales.
- Davidson, I.C. (2008). Index river monitoring for salmon and sea trout: A progress report on the monitoring programmes on the Tyne, Tamar, Dee and Lune, July 2008. Environment Agency Wales. GEWA 108BOTB-E-E.
- Dempson, J.B., Myers, R.A. & Reddin, D.G. (1986). Age at first maturity of Atlantic salmon (*Salmo salar*) - influences of the marine environment. In: Meerburg D.J. (ed) 1986. Salmonid age at maturity. Canadian Special Publication of Fisheries and Aquatic Sciences **89**: 79-89.
- Despatie, S.P., Castonguay, M., Chabot, D. & Audet, C. (2001). Final thermal preferendum of Atlantic cod: effect of food ration. Transactions of the American Fisheries Society **130**: 263-275.
- Dickson, R.R. & Turrell, W.R. (1999). The NAO: the dominant atmospheric process affecting oceanic variability in home, middle and distant waters of European Atlantic salmon. In: The Ocean Life of Atlantic Salmon (ed. D. Mills). Fishing News Books, Oxford, pp. 92-115.
- Dill, P.A. (1977). Development of behaviour of alevins of Atlantic salmon, *Salmo salar*, and rainbow trout, *Salmo gairdneri*. Animal Behaviour **25**: 116-121.
- Downton, P.R., Reddin, D.G. & Johnson, R.W. (2001). Status of Atlantic salmon (*Salmo salar* L.) in Campbellton River, Notre Dame Bay (SFA 4), Newfoundland in 2000. Canadian Science Advisory Secretariat Research Document: 73.
- Egglishaw, H.J. & Shackley, P.E. (1973). An experiment on faster growth of salmon *Salmo salar* L. in a Scottish stream. Journal of Fish Biology **5**: 197-204.
- Egglishaw, H.J. & Shackley, P.E. (1980). Survival and growth of salmon, *Salmo salar*, planted in a Scottish stream. Journal of Fish Biology **16**: 565-584.
- Einum, S., Thorstad, E.B. & Naesje, T.F. (2002). Growth rate correlations across life stages in female Atlantic salmon. Journal of Fish Biology **60**: 780-784.
- Elliott J.M. (1984). Numerical changes and population regulation in young migratory trout, *Salmo trutta*, in a Lake District stream, 1966-1983. Journal of Animal Ecology **53**: 327-350.

- Elliott J.M. (1991). Tolerance and resistance to thermal stress in juvenile Atlantic salmon, *Salmo salar*. *Freshwater Biology* **25**: 61-70.
- Elliott, J.M., Hurley, M.A. & Fryer, R.J. (1995). A new, improved growth model for brown trout, *Salmo trutta*. *Functional Ecology* **9**: 290-298.
- Elliott, J.M. & Hurley, M.A. (1997). A functional model for maximum growth of Atlantic salmon parr, *Salmo salar*, from two populations in northwest England. *Functional Ecology* **11**: 592-603.
- Elliott, J.M. & Hurley, M.A. (1998). An individual-based model for predicting the emergence period of sea-trout fry in a Lake District stream. *Journal of Fish Biology* **53**: 414-433.
- Elliott, J.M., Hurley, M.A. & Maberly, S.C. (2000). The emergence period of sea trout fry in a Lake District stream correlates with the North Atlantic Oscillation. *Journal of Fish Biology* **56**: 208-210.
- Elliott, J.M. (2001). The relative role of density in the stock-recruitment relationship of salmonids. In: E. Prevost, Chaput, G. (eds.) *Stock, recruitment and reference points - Assessment and management of Atlantic salmon*. Hydrobiologie et aquaculture, INRA, Paris, 25-66.
- Elo, K., Erkinaro, J., Vuorinen, J.A. & Niemela, E. (1995). Hybridization between Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) in the Teno and Naatamo River systems, northernmost Europe. *Nordic Journal of Freshwater Research* **70**: 56-61.
- Enfield, D.B., Mestas-Nunez, A.M. & Trimble, P.J. (2001). The Atlantic multidecadal oscillation and its relationship to rainfall and river flows in the continental US. *Geophysical Research Letters* **28**: 2077-2080.
- Englund, V., Niemela, E., Lansman, M. & Heino, M. (1999). Variations in Atlantic salmon, *Salmo salar* L., smolt age in tributaries of the River Teno, Finland. *Fisheries Management and Ecology* **6**: 83-86.
- Erkinaro, J., Dempson, J.B., Julkunen, M. & Niemela, E. (1997). Importance of ontogenetic habitat shifts to juvenile output and life history of Atlantic salmon in a large subarctic river: an approach based on analysis of scale characteristics. *Journal of Fish Biology* **51**: 1174-1185.
- Fairchild, W.L., Brown, S.B. & Moore, A. (2002). Effects of freshwater contaminants on marine survival in Atlantic salmon. *NPAFC*: 30-32.
- Field-Dodgson, M.S. (1988). Size characteristics and diet of emergent Chinook salmon in a small, stable, New Zealand stream. *Journal of Fish Biology* **32**: 27-40.
- Fleming, I.A. (1996). Reproductive strategies of Atlantic salmon: ecology and evolution. *Reviews in Fish Biology and Fisheries* **6**: 379-416.
- Friedland, K.D. & Reddin, D.G. (1993). Marine survival of Atlantic salmon from indices of post-smolt growth and sea temperature. *Salmon in the sea and new enhancement strategies*. D. Mills (ed.). Oxford, Fishing News Books. Blackwell Scientific Publications: 119-138.
- Friedland, K.D., Reddin, D.G. & Kocik, J.F. (1993). Marine survival of North American and European Atlantic salmon: effects of growth and environment. *ICES Journal of Marine Science* **50**: 481-492.
- Friedland, K.D. & Haas, R.E. (1996). Marine post-smolt growth and age at maturity of Atlantic salmon. *Journal of Fish Biology* **48**: 1-15.
- Friedland, K.D., Haas, R.E. & Sheehan, T.S. (1996). Post-smolt growth, maturation, and survival of two stocks of Atlantic salmon. *Fisheries Bulletin* **94**: 654-663.
- Friedland, K.D. (1998). Ocean climate influences on critical Atlantic salmon (*Salmo salar*) life history events. *Canadian Journal of Fisheries and Aquatic Sciences* **55** (supplement 1): 119-130.

- Friedland, K.D., Hansen, L.P. & Dunkley, D.A. (1998a). Marine temperature experienced by post-smolts and the survival of Atlantic salmon, *Salmo salar* L. in the North Sea area. *Fisheries Oceanography* **7**(1): 22-34.
- Friedland, K.D., Reddin, D.G., Shimizu, N., Haas, R.E. & Youngson, A.F. (1998b). Strontium:calcium ratios in Atlantic salmon (*Salmo salar*) otoliths and observations on growth and maturation. *Canadian Journal of Fisheries and Aquatic Sciences* **55**: 1158-1168.
- Friedland, K.D., Hansen, L.P., Dunkley, D.A. & MacLean, J.C. (2000). Linkage between ocean climate, post-smolt growth and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. *ICES Journal of Marine Science* **57**: 419-429.
- Friedland, K.D., Reddin, D.G., McMenemy, J.R. & Drinkwater, K.F. (2003a). Multidecadal trends in North American Atlantic salmon (*Salmo salar*) stocks and climate trends relevant to juvenile survival. *Canadian Journal of Fisheries and Aquatic Sciences* **60**: 563-583.
- Friedland, K.D., Reddin, D.G. & Castonguay, M. (2003b). Ocean thermal conditions in the post-smolt nursery of North American Atlantic salmon. *ICES Journal of Marine Science* **60**: 343-355.
- Friedland, K.D., Chaput, G. & Maclean, J.C. (2005). The emerging role of climate in post-smolt growth of Atlantic salmon. *ICES Journal of Marine Science* **62**: 1338-1349.
- Friedland, K.D., Clarke, L.M., Dutil, J.-D. & Salminen, M. (2006). The relationship between smolt and postsmolt growth for Atlantic salmon (*Salmo salar*) in the Gulf of St. Lawrence. *Fisheries Bulletin* **104**: 149-155.
- Friedland, K.D., MacLean, J.C., Hansen, L.P., Peyronnet, A.J., Karlsson, L., Reddin, D.G., Ó Maoiléidigh, N. & McCarthy, J.L. (2009). The recruitment of Atlantic salmon in Europe. *ICES Journal of Marine Science* **66**: 289-304.
- Garcia de Leaniz, C., Fraser, N. & Huntingford, F.A. (2000). Variability in performance in wild Atlantic salmon, *Salmo salar* L., fry from a single redd. *Fisheries Management and Ecology* **7**: 489-502.
- Gardner, M.L. (1976). A review of factors which may influence the sea-age and maturation of Atlantic salmon (*Salmo salar*). *Journal of Fish Biology* **9**: 289-328.
- Gee, A.S. & Milner, N.J. (1980). Analysis of 70-year catch statistics for Atlantic salmon (*Salmo salar*) in the River Wye and implications for management of the stocks. *Journal of Applied Ecology* **17**: 41-57.
- George, A.F. (1984). Scottish salmon and 1SW fish return-migration variations over 200 years. *Proceedings of the Institute of Fisheries Management 15th Annual Study Course*, Stirling University. Institute of Fisheries Management, Nottingham. A. H. Holden (ed.): 23-32.
- George, A.F. (1991). *Climate and the Salmon*. Salmon, Trout and Sea-trout. December 1991.
- Gibson, R.J. (1993). The Atlantic salmon in freshwater: spawning, rearing and production. *Reviews in Fish Biology and Fisheries* **3**: 39-73.
- Gjerde, B. 1984. Response for individual selection for age at sexual maturity in Atlantic salmon. *Aquaculture* **38**: 229-240.
- Good, S.P., Dodson, J.J., Meekan, M.G. & Ryan, D.A.J. (2001). Annual variation in size-selective mortality of Atlantic salmon (*Salmo salar*) fry. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 1187-1195.
- Gough, P.G., Winstone, A.J. & Hilder, P.G. (1992). *Spring salmon. A review of factors affecting spring salmon from the River Wye and elsewhere, and proposals for stock maintenance and enhancement*. Cardiff, National Rivers Authority: 57pp.
- Gudjonsson, S., Einarsson, S.M., Antonsson, Th. & Gudbergsson, G. (1995). Relation of 1SW fish to salmon ratio to environment changes in several wild stocks of Atlantic salmon (*Salmo salar*) in Iceland. *Canadian Journal of Fisheries and Aquatic Sciences* **52**: 1385-1398.

- Gurney, W.S.C., Bacon, P.J., Tyldesley, G. & Youngson, A.F. (2008). Process-based modelling of decadal trends in growth, survival, and smolting of wild salmon (*Salmo salar*) parr in a Scottish upland stream. *Canadian Journal of Fisheries and Aquatic Sciences* **65**: 2606–2622.
- Gustafson-Marjanen, K.I. & Dowse, H.B. (1983). Seasonal and diel patterns of emergence from the redd of Atlantic salmon (*Salmo salar*) fry. *Canadian Journal of Fisheries and Aquatic Sciences* **40**(6): 813–817.
- Handeland, S.O. Björnsson, B.T., Arnesen, A.M. & Stefansson S.O. (2003). Seawater adaptation and growth of post-smolt Atlantic salmon (*Salmo salar*) of wild and farmed strains. *Aquaculture* **220**: 367–384.
- Hansen, L.P. & Jonsson B. (1991). Evidence for a genetic component in the seasonal return pattern of Atlantic salmon, *Salmo salar* L. *Journal of Fish Biology* **38**: 251–258.
- Hansen, L.P. & Quinn, T.P. (1998). The marine phase of Atlantic salmon (*salmo salar*) life cycle, with comparison to Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **55**(supplement 1): 104–118.
- Hansen, M.J. & Nate, N.A. (2005). A method for correcting the relative weight (W_r) index for seasonal patterns in relative condition (K_n) with length as applied to walleye in Wisconsin. *North American Journal of Fisheries Management* **25**: 1256–1262.
- Haugland, M., Holst, J.C., Holm, M. & Hansen, L.P. (2006). Feeding of Atlantic salmon (*Salmo salar* L.) post-smolts in the Northeast Atlantic. *ICES Journal of Marine Science* **63**: 1488–1500.
- Heddell-Cowie, M. (2005). Importance of the River Teviot to Atlantic salmon, *Salmo salar*, rod catches in the River Tweed, Scotland. *Fisheries Management and Ecology* **12**: 137–142.
- Heggberget, T.G. (1988). Timing of spawning in Norwegian Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **45**: 845–849.
- Heinimaa, S. & Erkinaro, J. (2004). Characteristics of mature male parr in the northernmost Atlantic salmon populations. *Journal of Fish Biology* **64**: 219–226.
- Hodday, A.J. & Boehlert, G.W. (2001). The role of coastal ocean variation in spatial and temporal patterns in survival and size of coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 2021–2036.
- Holm, M., Holst, J.C. & Hansen, L.P. (2000). Spatial and temporal distribution of post-smolts of Atlantic salmon (*Salmo salar* L.) in the Norwegian Sea and adjacent areas. *ICES Journal of Marine Science* **57**: 955–964.
- Hubley, P.B., Amiro, P.G. & Gibson, A.J.F. (2008). Changes in scale circulus spacings of an endangered Atlantic salmon *Salmo salar* population: evidence of a shift in marine migration? *Journal of Fish Biology* **73**: 2321–2340.
- Hughes, S. & Turrell, W.R. (2003). Prospects for improved oceanic conditions. In: *Salmon at the edge*. D. Mills (ed.), Oxford, Blackwell Science Ltd.: 255–267.
- Hughes, S.L., Holliday, N.P. & Beszczynska-Möller, A. (eds.) (2008). *ICES Report on Ocean Climate 2007*. ICES Cooperative Research Report No. 291. 64 pp. ICES, Copenhagen, Denmark.
- Huntingford, F.A., Thorpe, J.E., Garcia de Leaniz, C. & Hay, D.W. (1992). Patterns of growth and smolting in autumn migrants from a Scottish population of Atlantic salmon, *Salmo salar* L. *Journal of Fish Biology* **41**: 43–51.
- Hurrell, J.W. & Dickson, R.R. (2004). Climate variability over the North Atlantic. In *Marine Ecosystems and Climate Variation*, N.C. Stenseth *et al.* (eds). Oxford, U.K.: Oxford University Press, 15–23.
- Hurrell, J.W., (1995). Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science* **269**: 676–679.

- Hutchings, J.A. & Jones, M.E.B. (1998). Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. Canadian Journal of Fisheries and Aquatic Sciences **55** (supplement 1): 22-47.
- ICES (2006). ICES Report on Ocean Climate 2005. ICES Cooperative Research Report No. 280. 47 pp.
- ICES (2007a). Report of the Working Group on North Atlantic salmon (WGNAS), ICES. International Council for the Exploration of the Sea. ICES CM 2007/ACFM:13. 253pp.
- ICES (2007b). Report of the Working Group on Integrated Assessments of the Baltic Sea. ICES CM 2007/BCC:04.
- ICES (2008a). Report of the Working Group on North Atlantic salmon (WGNAS), ICES. International Council for the Exploration of the Sea. ICES CM 2008/ACOM:18. 235pp.
- ICES (2008b). Report of the Baltic Salmon and Trout Assessment Working Group. ICES CM 2008/ACOM:05.
- Imre, I., Grant, J.W.A. & Cunjak R.A. (2005). Density-dependent growth of young-of-the-year Atlantic salmon *Salmo salar* in Catamaran Brook, New Brunswick. Journal of Animal Ecology **74**: 508-516.
- IPCC (2001) IPCC third assessment report: climate change 2001. Synthesis report (ed. R.T. Watson and the Core Writing Team). IPCC, Geneva, Switzerland , 184 pp.
- Jacobsen, J.A. & Hansen, L.P. (2001). Feeding habits of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in the Northeast Atlantic. ICES Journal of Marine Science **59**: 916-933.
- Jenkins, T.M.Jr., Diehl, S., Kratz, K.W. & Cooper, S.D. (1999). Effects of population density on individual growth of brown trout in streams. Ecology **80**: 941-956.
- Jensen, A.J., Johnsen, B.O. & Saksgård, L. (1989). Temperature requirements in Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), and Arctic char (*Salvelinus alpinus*) from hatching to initial feeding compared with geographic distribution. Canadian Journal of Fisheries and Aquatic Sciences **46**: 786-789.
- Jensen, A.J., Johnsen, B.O. & Heggberget, T.G. (1991). Initial feeding time of Atlantic salmon (*Salmo salar* L.) alevins compared to river flow and water temperature in Norwegian streams. Environmental Biology of Fishes **30**: 379-385.
- Jensen, A.J., Zubchenko, A.V., Heggberget, T.G., Hidsten, N.A., Johnsen, B.O., Kuzmin, O., Loenko, A.A., Lund, R.A., Martynov, V.G., Næsje, T.F., Sharov, A.F. & Økland, F. (1999). Cessation of the Norwegian drift net fishery: changes observed in Norwegian and Russian populations of Atlantic salmon. ICES Journal of Marine Science **56**: 84-95.
- Jensen, A.J. (2003). Atlantic salmon (*Salmo salar*) in the regulated river Alta: effects of altered water temperature on parr growth. River research and Applications **19**(7): 733-747.
- Jónasson, J., Gjerde, B. & Gjedrem, T. (1997). Genetic parameters for return rate and body weight of sea-ranched Atlantic salmon. Aquaculture **154**: 219-231.
- Jones, R.E., Petrell, R.J. & Pauly, D. (1999). Using modified length-weight relationships to assess the condition of fish. Aquaculture Management **20**: 261-276.
- Jonsson, N., Jonsson, B. & Hansen, L.P. (1990a). Partial segregation in the timing of migration of Atlantic salmon of different ages. Animal Behaviour **40**: 313-321.
- Jonsson, B., Jonsson, N. & Hansen, L.P. (1990b). Does juvenile experience affect migration and spawning of adult Atlantic salmon? Behavioural Ecology and Sociobiology **26**: 225-230.
- Jonsson, N., Hansen, L.P. & Jonsson, B. (1991a). Variation in age, size and repeat spawning of adult Atlantic salmon in relation to river discharge. Journal of Animal Ecology **60**: 937-947.
- Jonsson, N., Jonsson, B. & Hansen, L.P. (1991b). Energetic cost of repeat spawning in male and female Atlantic salmon (*Salmo salar* L.). Journal of Fish Biology **39**: 739-744.

- Jonsson, B. & Jonsson, N. (1993). Partial migration: niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries* **3**: 348-365.
- Jonsson, N., Jonsson, B. & Fleming, I.A. (1996). Does early growth cause a phenotypically plastic response in egg production of Atlantic salmon? *Functional Ecology* **10**: 89-96.
- Jonsson, N., Jonsson, B. & Hansen, L.P. (1997). Changes in proximate composition and estimates of energetic costs during upstream migration and spawning in Atlantic salmon *Salmo salar*. *Journal of Animal Ecology* **66**: 425-436.
- Jonsson, B., Forseth, T., Jensen, A.J. & Næsje, T.F. (2001). Thermal performance of juvenile Atlantic salmon, *Salmo salar* L. *Functional Ecology* **15**: 701-711.
- Jonsson, N., Jonsson, B. & Hansen, L.P. (2003). The marine survival and growth of wild and hatchery-reared Atlantic salmon. *Journal of Applied Ecology* **40**: 900-911.
- Jonsson, N. & Jonsson, B. (2004). Size and age at maturity of Atlantic salmon correlate with the North Atlantic Oscillation Index (NAOI). *Journal of Fish Biology* **64**: 241-247.
- Jonsson, N., Jonsson, B. & Hansen, L.P. (2005). Does climate during embryonic development influence parr growth and age of seaward migration in Atlantic salmon (*Salmo salar*)? *Canadian journal of Fisheries and Aquatic Sciences* **62**: 2502-2508.
- Jonsson, N. & Jonsson, B. (2007). Sea growth, smolt age at sexual maturation in Atlantic salmon. *Journal of fish Biology* **71**: 245-252.
- Juanes, F., Gephard, S. & Beland, K.F. (2004). Long-term changes in migration timing of adult Atlantic salmon (*Salmo salar*) at the southern edge of the species distribution. *Canadian Journal of Fisheries and Aquatic Sciences* **61**: 2392-2400.
- Juttila, E., Jokikokko, E. & Julkunen, M. (2005). The smolt run and post-smolt survival of Atlantic salmon, *Salmo salar* L., in relation to early summer water temperatures in the northern Baltic Sea. *Ecology of Freshwater Fish* **14**: 69-78.
- Juttila, E., Jokikokko, E. & Julkunen, M. (2006). Long-term changes in the smolt size and age of Atlantic salmon, *Salmo salar* L., in a northern Baltic river related to parr density, growth opportunity and post-smolt survival. *Ecology of Freshwater Fish* **15**: 321-330.
- Kallio-Nyberg, I., Juttila, E., Saloniemi, I. & Jokikokko, E. (2004). Association between environmental factors, smolt size and the survival of wild and reared Atlantic salmon from the Simojoki River in the Baltic Sea. *Journal of Fish Biology* **65**: 122-134.
- Kallio-Nyberg, I., Juttila, E., Jokikokko, E. & Saloniemi, I. (2006). Survival of reared Atlantic salmon and sea trout in relation to marine conditions of smolt year in the Baltic Sea. *Fisheries Research* **80**: 295-304.
- Karlsson, L. & Karlström, O. (1994). The Baltic salmon (*Salmo salar* L.): its history, present situation and future. *Dana* **10**: 61-85.
- Kennedy, G.J.A. & Strange, C.D. (1986). The effects of intra-specific competition on the distribution of stocked juvenile Atlantic salmon, *Salmo salar* L., in relation to depth and gradients in an upland trout, *Salmo trutta* L., stream. *Journal of Fish Biology* **29**: 199-214.
- Kendall, M.G. (1975). *Rank correlation methods*. Fourth edition, Charles Griffith: London.
- King, H.R., Pankhurst, N.W., Watts, M. & Pankhurst, P.M. (2003). Effect of elevated summer temperature on gonadal steroid production, vitellogenesis and egg quality in Tasmanian female Atlantic salmon. *Journal of Fish Biology* **63**: 153-167.
- King, H.R., Pankhurst, N.W. & Watts, M. (2007). Reproductive sensitivity to elevated water temperatures in female Atlantic salmon is heightened at certain stages of vitellogenesis. *Journal of Fish Biology* **70**: 190-205.
- Klemetsen, A., Amundsen, P.-A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F. & Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic

- charr *Salvelinus alpinus* L.: a review of aspects of their life histories. *Ecology of Freshwater Fish* **12**: 1-59.
- L'Abée-Lund, J.H. (1989). Significance of mature male parr in a small population of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **48**: 1015-1021.
- L'Abée-Lund, J.H., Vøllestad, L.A. & Beldring, S. (2004). Spatial and temporal variation in the grilse proportion of Atlantic salmon in Norwegian rivers. *Transactions of the American Fisheries Society* **133**: 743-761.
- Lacroix, G.L., & Knox, D. (2005). Distribution of Atlantic salmon (*Salmo salar*) postsmolts of different origin in the Bay of Fundy and Gulf of Maine and evaluation of factors affecting migration, growth, and survival. *Canadian Journal of Fisheries and Aquatic Sciences* **62**: 1363-1376.
- Lapointe, M.F., Bergeron, N.E., Bérubé, F., Pouliot, M.A. & Johnston, P. (2004). Interactive effects of substrate sand and silt contents, redd-scale hydraulic gradients, and interstitial velocities on egg-to-emergence survival of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **61**: 2271-2277.
- Letcher, B.H. & Terrick, T.D. (1998). Maturation of male age-0 Atlantic salmon following a massive, localized flood. *Journal of Fish Biology* **53**(6): 1243-1252.
- Lobón-Cerviá, J. (2005). Spatial and temporal variation in the influence of density dependence on growth of stream-living brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences* **62**: 1231-1242.
- Lower, N. & Moore, A. (2007). The impact of a brominated flame retardant on smoltification and olfactory function in Atlantic salmon smolts. *Marine and Freshwater Behaviour and Physiology* **40**: 267-284.
- Lundqvist, H., Clarke, W.C. & Johansson, H. (1988). The influence of sexual maturation on survival to adulthood of river stocked Baltic salmon, *Salmo salar*, smolts. *Holarctic Ecology* **11**: 60-69.
- Lundqvist, H., McKinnell, S., Fangstam, I. & Berglund, I. (1994). The effect of time, size and sex on recapture rates and yield after river releases of *Salmo salar* smolts. *Aquaculture* **121**: 245-257.
- MacCrimmon, H.R. & Gots, B.L. (1979). World distribution of Atlantic salmon, *Salmo salar*. *Journal of the Fisheries Research Board of Canada* **36**: 422-457.
- Manly B.F.J. (2001). Randomization, bootstrap and Monte Carlo methods in biology. Chapman and Hall/CRC, London, 399 pp.
- Mann, H.B. (1945). Non-parametric tests against trend. *Econometrica* **13**: 245-259.
- Marshall, C.T., Needle, C.L., Yaragina, N.A., Ajiad, A.M. & Gusev, E. (2004). Deriving condition indices from standard fisheries databases and evaluating their sensitivity to variation in stored energy reserves. *Canadian Journal of Fisheries and Aquatic Sciences* **61**: 1900-1917.
- Marshall, E.A., Quinn, T.P., Roff, D.A., Hutchings, J.A., Metcalfe, N.B., Bakke, T.A., Saunders, R.L. & LeRoy Poff, N. (1998). A framework for understanding Atlantic salmon (*Salmo salar*) life history. *Canadian Journal of Fisheries and Aquatic Sciences* **55** (supplement 1): 48-58.
- Martin, J.H.A. & Mitchell, K.A. (1985). Influence of sea temperature upon the numbers of grilse and multi-sea-winter Atlantic salmon (*Salmo salar*) caught in the vicinity of the river Dee (Aberdeenshire). *Canadian Journal of Fisheries and Aquatic Sciences* **42**: 1513-1521.
- Martinez J.L., Moran P., Perez J., De Gaudemar B., Beall E., & Garcia-Vazquez E. (2000). Multiple paternity increases effective size of southern Atlantic salmon populations. *Molecular Ecology* **9**: 293-298.
- Marty, C. & Beall, E. (1989). Modalities spatio-temporales de la dispersion d'alevins de saumon atlantique (*Salmo salar* L.) à l'émergence. *Revue des Sciences de l'eau* **2** : 831-846.

- Mason, J.C. (1976). Response of underyearling coho salmon to supplemental feeding in a natural stream. *Journal of Wildlife Management* **40**: 775-788.
- McCarthy, J.L., Friedland, K.D. & Hansen, L.P. (2008). Monthly indices of the post-smolt growth of Atlantic salmon from the Drammen river, Norway. *Journal of Fish Biology* **72**: 1572-1588.
- McCormick, S.D., Hansen, L.P., Quinn, T.P. & Saunders, R.L. (1998). Movement, migration, and smolting of Atlantic salmon (*salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **55** (supplement 1): 77-92.
- Metcalfe, N.B., Huntingford, F.A., Graham W.D. & Thorpe J.E. (1989). Early social status and the development of life-history strategies in Atlantic salmon. *Proceedings of the Royal Society London B* **236**: 7-19.
- Metcalfe, N.B. & Thorpe, J.E. (1990). Determinants of geographic variation in the age of seaward-migrating salmon, *Salmo salar*. *Journal of Animal Ecology* **59**: 135-145.
- Metcalfe, N.B. & Thorpe, J.E. (1992). Early predictors of life-history events: the link between first feeding date, dominance and seawater migration in Atlantic salmon, *Salmo salar*. *Journal of Fish Biology* **41**(supplement B): 93-99.
- Metcalfe, N.B., Taylor, A.C. & Thorpe, J.E. (1995). Metabolic rate, social status and life-history strategies in Atlantic salmon. *Animal Behaviour* **49**: 431-436.
- Mikheev, V.N., Metcalfe, N.B., Huntingford, F.A. & Thorpe J.E. (1994). Size-related differences in behaviour and spatial distribution of juvenile Atlantic salmon in a novel environment. *Journal of Fish Biology* **45**: 379-386..
- Moffett, I.J.J., Allen, M., Flanagan, C.F., Crozier W.W. & Kennedy, G.J.A. (2006). Fecundity, egg size and early hatchery survival for wild Atlantic salmon, from the River Bush. *Fisheries Management and Ecology* **13**: 73-79.
- Moore, A., Cotter, D., Rogan, G., Quayle, V., Lower, N. & Privitera, L. (2008). The impact of a pesticide on the physiology and behaviour of hatchery reared salmon smolts during the transition from the freshwater to marine environment. *Fisheries Management and Ecology* **15**: 339-345.
- Moore, A., Lower, N., Mayer, I. & Greenwood, L. (2007). The impact of a pesticide on migratory activity and olfactory function in Atlantic salmon (*Salmo salar* L.) smolts. *Aquaculture* **273**: 350-359.
- Moore, A. & Riley, W.D. (1992). A sexually mature female Atlantic salmon, *Salmo salar* L., smolt. *Aquaculture and Fisheries Management* **23**: 273-274.
- Moore, A., Scott, A.P., Lower, N., Katsiadaki, I. & Greenwood, L. (2003). The effects of 4-nonylphenol and atrazine on Atlantic salmon (*Salmo salar* L.) smolts. *Aquaculture* **222**: 253-263.
- Moore, A. & Waring, C.P. (1996). Electrophysiological and endocrinological evidence that F-series prostaglandins function as priming pheromones in mature male Atlantic salmon parr. *Journal of Experimental Biology* **199**: 2307-2316.
- Moore, D.S., Chaput, G.L. & Pickard, P.R. (1995). The effect of fisheries on the biological characteristics and survival of mature Atlantic salmon (*Salmo salar*) from the Miramichi river. *Water, Science and the Public: The Miramichi Ecosystem*. E.M.P. Chadwick (ed.), Special Publications of Canadian Journal of Fisheries and Aquatic Sciences **123**: 229-247.
- Myers, R.A. (1984). Demographic consequences of precocious maturation of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **41**: 1349-1353.
- Myers, R.A. & Hutchings, J.A. (1987). Mating of anadromous Atlantic salmon, *Salmo salar* L., with mature male parr. *Journal of Fish Biology* **31**: 143-146.
- Nagata, M. & Irvine, J.R. (1997). Differential dispersal patterns of male and female masu salmon fry. *Journal of Fish Biology* **51**: 601-606.

- Neff, B.D. & Cargnelli, L.M. (2004). Relationships between condition factors, parasite load and paternity in bluegill sunfish, *Lepomis macrochirus*. *Environmental Biology of Fishes* **71**: 297-304.
- Nicieza, A.G. & Braña, F. (1993). Relationships among smolt size, marine growth, and sea-age at maturity of Atlantic salmon (*Salmo salar*) in northern Spain. *Canadian Journal of Fisheries and Aquatic Sciences* **50**: 1632-1640.
- Niemelä, E., Erkinaro, J., Dempson, J.B., Julkunen, M., Zubchenko, A., Prusov, S., Svenning, M.A., Ingvaldsen, R., Holm, M. & Hassinen, E. (2004). Temporal synchrony and variation in abundance of Atlantic salmon (*Salmo salar*) in two subarctic Barents Sea rivers: influence of oceanic conditions. *Canadian Journal of Fisheries and Aquatic Sciences* **61**: 2384-2391.
- Niemelä, E., Erkinaro, J., Julkunen, M., Hassinen, E., Lämsmä, M. & Brørs, S. (2006). Temporal variation in abundance, return rate and life histories of previously spawned Atlantic salmon in a large subarctic river. *Journal of Fish Biology* **68**: 1222-1240.
- O'Connell, M.F. & Ash, E.G.M. (1993). Smolt size in relation to age at first maturity of Atlantic salmon (*Salmo salar*): the role of lacustrine habitat. *Journal of Fish Biology* **42**: 551-569.
- Økland, F., Jonsson, D., Jensen A.J. & Hansen L.P. (1993). Is there a threshold size regulating seaward migration of brown trout and Atlantic salmon? *Journal of Fish Biology* **42**: 541-550.
- Parrish, D.L., Behnke, R.J., Gephard, S.R., McCormick, S.D. & Reeves, G.H. (1998). Why aren't there more Atlantic salmon (*Salmo salar*)? *Canadian Journal of Fisheries and Aquatic Sciences* **55** (supplement 1): 281-287.
- Parsons, L.S. & Lear, W.H. (2001). Climate variability and marine ecosystems impacts. A north Atlantic perspective. *Progress in Oceanography* **49**: 167-188.
- Pauly, D. (1981). The relationship between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. *Journal du Conseil-Conseil permanent pour l'Exploration de la Mer* **39**: 251-282.
- Peyronnet, A., Friedland, K.D., O' Maoileidigh, N., Manning, M. & Poole, W.R. (2007). Links between patterns of marine growth and survival of Atlantic salmon *Salmo salar*, L. *Journal of Fish Biology* **71**: 684-700.
- Peyronnet, A., Friedland, K.D. & O'Maoileidigh, N. (2008). Different ocean and climate factors control the marine survival of wild and hatchery Atlantic salmon *Salmo salar* in the north-east Atlantic Ocean. *Journal of Fish biology* **73**: 945-962.
- Pinder, A.C., Riley, W.D., Ibbotson, A.T. & Beaumont, W.R.C. (2007). Evidence for an autumn seaward migration and the subsequent estuarine residence of 0+ juvenile Atlantic salmon *Salmo salar* L., in England. *Journal of Fish Biology* **71**: 260-264.
- Potter, E.C.E. & Crozier, W.W. (2000). A perspective on the marine survival of Atlantic salmon. In: *The Ocean life of Atlantic salmon: environmental and biological factors influencing survival*. D. Mills (ed.), Oxford, Fishing News Books, Blackwell Science: 19-36.
- Power, G. (1969). *The salmon of Ungava Bay*. Institute of North America: 72.
- Prevost, E., Chadwick, E.M.P. & Claytor, R.R. (1992). Influence of size, winter duration and density on sexual maturation of Atlantic salmon (*Salmo salar*) juveniles in Little Codroy River (southwest Newfoundland). *Journal of Fish Biology* **41**: 1013-1019.
- Quinn, T.P. (2005). *The behaviour and ecology of Pacific salmon and trout*. University of Washington Press, Seattle.
- Quinn, T.P., McGinnity, P. & Cross, T.F. (2006). Long-term declines in body size and shifts in run timing of Atlantic salmon in Ireland. *Journal of Fish Biology* **68**: 1713-1730.
- R Development Core Team (2007). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.

- Randall, R.G. (1989). Effect of sea-age on the reproductive potential of Atlantic salmon (*Salmo salar*) in eastern Canada. *Canadian Journal Fisheries and Aquatic Sciences* **46**: 221-2218.
- Rayner, N.A., Parker, D.E., Horton, E.B., Folland, C.K., Alexander, L.V., Rowell, D.P., Kent E.C. & Kaplan, A. (2003). Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late Nineteenth Century. *Journal of Geophysical Research* **108**, (D14), 4407. doi:10.1029/2002JD002670
- Riddell, B.E. & Leggett, W.C. (1981). Evidence of an adaptive basis for geographic variation of body morphology, and time of downstream migration of Juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*. **38**: 308-320.
- Riley, S.C. & Power, G. (1987). Age at maturity in landlocked and anadromous Atlantic salmon parr from two Quebec rivers. *Environmental Biology of Fishes* **19**: 223-228.
- Riley, W.D., Eagle, M.O. & Ives, S.J. (2002). The onset of downstream movement of juvenile Atlantic salmon, *Salmo salar* L., in a chalk stream. *Fisheries Management and Ecology* **9**: 87-94.
- Riley, W.D. (2007). Seasonal downstream movements of juvenile Atlantic salmon, *Salmo salar* L., with evidence of solitary emigration of smolts. *Aquaculture* **273**: 194-199.
- Riley, W.D., Ibbotson, A.T., Lower, N., Cook, A.C., Moore, A., Mizuno, S., Pinder, A.C., Beaumont, W.R.C. & Privitera, L. (2008). Physiological seawater adaptation in juvenile Atlantic salmon, *Salmo salar* L. autumn migrants. *Freshwater Biology* **53**: 745-755.
- Riley, W.D., Ibbotson, A.T. & Beaumont, W.R.C. (2009). Adult returns from Atlantic salmon, *Salmo salar* L., parr autumn migrants. *Fisheries Management and Ecology* **16**: 75-76.
- Rimmer, D.M., Paim, U. & Saunders, R.L. (1983). Autumnal habitat shift of juvenile Atlantic salmon (*Salmo salar*) in a small river. *Canadian Journal of Fisheries and Aquatic Sciences* **40**: 671-680.
- Rimmer, D.M., Paim, U. & Saunders, R.L. (1984). Changes in the selection of microhabitat by juvenile Atlantic salmon (*Salmo salar*) at the summer-autumn transition in a small river. *Canadian Journal of Fisheries and Aquatic Sciences* **41**: 469-475.
- Ritter, J.A. (1993). Changes in Atlantic salmon (*Salmo salar*) harvest and stock status in the North Atlantic. In: *Salmon in the sea and new enhancement strategies*, Mills, D.H. (ed.), Fishing News Books, Oxford, 3-25.
- Rivot, E., Perrier, C., Jouanin, C., Roussel, J-M., Riera, P. & Bagliniere, J-L. (Poster) Climate change may affect growth and life history in Atlantic salmon juveniles over the last 30 years.
- Roff, D.A. (1992). *The evolution of life history*. Chapman & Hall, New York & London.
- Rogers, J.C. (1984). The Association between the North Atlantic Oscillation and the Southern Oscillation in the Northern Hemisphere. *Monthly Weather Review* **112**: 1999-2015.
- Rosenthal, R. (1979). The "file drawer problem" and tolerance for null results. *Psychological Bulletin* **86**: 638-641.
- Rowe, D.K. & Thorpe, J.E. (1990). Suppression of maturation in male Atlantic salmon (*Salmo salar* L.) parr by reduction in feeding and growth during spring months. *Aquaculture* **86**: 291-313.
- Rowe, D.K., Thorpe, J.E. & Shanks, A.M. (1991). Role of fat stores in maturation of male Atlantic salmon (*Salmo salar*) parr. *Canadian Journal of Fisheries and Aquatic Sciences* **48**: 405-413.
- Russell, I.C., Ives, M.J., Potter, E.C.E., Buckley, A.A. & Duckett L. (1995) *Salmon and migratory trout statistics for England and Wales, 1951-1990*. MAFF Directorate of Fisheries Research, Data Report No. 38, 252 pp.

- Salminen, M. (1997). Relationships between smolt size and sea-age at maturity in Atlantic salmon ranches in the Baltic Sea. *Journal of Applied Ichthyology* **13**: 121-130.
- Salminen, M., Kuikka, S. & Erkamo, E. (1994). Divergence in the feeding migration of Baltic salmon (*Salmo salar* L.); the significance of smolt size. *Nordic Journal of Freshwater Research* **69**: 32-42.
- SALMODEL (2003) A coordinated approach towards the development of a scientific basis for management of wild Atlantic salmon in the north-east Atlantic. (Co-ordinator W.W. Crozier). Scientific Report. An EU Concerted Action. Quality of Life and Management of Living Resources Key Action 5: Sustainable agriculture, fisheries and forestry, and integrated development of rural areas including mountain areas. Contract No. QLK5-CT1999-01546.
- Saunders, R.L. & Schom, C.B. (1985). Importance of the variation in life history parameters of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **42**: 615-618.
- Scarnecchia, D.L. (1983). Age at sexual maturity in Icelandic stocks of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **40**: 1456-1468.
- Scarnecchia, D.L., Isaksson, A. & White, S.E. (1989). Effects of oceanic variations and the West Greenland fishery on age at maturity of Icelandic west coast stocks of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **46**(1): 16-27.
- Scarnecchia, D.L., Isaksson, A. & White, S.E. (1991). Effects of the Faroese long line fishery, other oceanic fisheries and oceanic variations on age at maturity of Icelandic north coast stocks of Atlantic salmon (*Salmo salar*). *Fisheries Research* **10**: 207-228.
- Schaffer, W.M. & Elson, P.F. (1975). The adaptive significance of variation in life history among local populations of Atlantic salmon in North America. *Ecology* **56**: 577-590.
- Simpson, A.L. (1992). Differences in body size and lipid reserves between maturing and non-maturing Atlantic salmon parr, *Salmo salar* L. *Canadian Journal of Zoology* **70**: 1737-1742.
- Skilbrei, O.T. 1989. Relationship between smolt length and growth and maturation in the sea of individually tagged Atlantic salmon (*Salmo salar*). *Aquaculture* **83**: 95-108.
- Solomon, D. J. (1978). Migration of smolts of Atlantic salmon (*Salmo salar* L.) and sea trout (*Salmo trutta* L.) in a chalkstream. *Environmental Biology of Fishes* **3**: 223-229.
- Solomon, D. & Lightfoot, G. (2007). Climate change and chalkstream salmon. Environment Agency, South West Region report. South Wessex Area, Environment Agency. V 1.5: 23pp.
- Staurnes, M., Sigholt, T., Asgard, T. & Baeverfjord, G. (2001). Effects of a temperature shift on seawater challenge test performance in Atlantic salmon (*Salmo salar*) smolts. *Aquaculture* **201**: 153-159.
- Stearns, S.C. (1992). The evolution of life histories. Oxford, Oxford University Press.
- Stewart, D. C., Smith, G. W. & Youngson, A. F. (2002). Tributary-specific variation in timing of return of Atlantic salmon (*Salmo salar*) to fresh water has a genetic component. *Canadian Journal of Fisheries and Aquatic Sciences* **59**: 276-281.
- Stewart, D.C., Middlemas, S.J. & Youngson A.F. (2006). Population structuring in Atlantic salmon (*Salmo salar*): evidence of genetic influence on the timing of smolt migration in sub-catchment stocks. *Ecology of Freshwater Fish* **15**: 552-558.
- Summers, D.W. (1995). Long-term changes in the sea-age at maturity and seasonal time of return of salmon, *Salmo salar* L., to Scottish rivers. *Fisheries Management & Ecology* **2**: 147-156.
- Sutton, S.G., Bult, T.P. & Haedrich, R.L. (2000). Relationships among fat weight, body weight, water weight, and condition factors in wild Atlantic salmon parr. *Transactions of the American Fisheries Society* **129**: 527-538.

- Sutton, R.T. & Hodson, D.L.R. (2005). Atlantic forcing of North American and European summer climate. *Science* **309**: 115-118.
- Swansburg, E., Chaput, G., Moore, D., Caissie, D. & El-Jabi, N. (2002). Size variability of juvenile Atlantic salmon: links to environmental conditions. *Journal of fish Biology* **61**: 661-683.
- Taranger, G.L. & Hansen, T. (1993). Ovulation and egg survival following exposure of Atlantic salmon, *Salmo salar* L., broodstock to different water temperatures. *Aquaculture and Fisheries Management* **24**: 151-156.
- Thorpe, J.E., Morgan, R.I.G., Talbot, C. & Miles, M.S. (1983). Inheritance of developmental rates in Atlantic salmon, *Salmo salar* L. *Aquaculture* **33**: 119-128.
- Thorpe, J.E., Miles, M.S. & Keay, D.S. (1984). Developmental rate, fecundity and egg size in Atlantic salmon, *Salmo salar* L. *Aquaculture* **43**: 289-305.
- Thorpe, J.E. (1989). Developmental variation in salmonid populations. *Journal of Fish Biology* **35** (supplement A): 295-303.
- Thorpe, J.E. (1990). Variation in life-history strategies in salmonids. *Polskie Archiwum Hydrobiologii* **37**(1-2): 3-12.
- Thorpe, J.E. (1994). Reproductive strategies in Atlantic salmon (*Salmo salar* L.). *Aquaculture & Fisheries Management* **25**: 77-87.
- Thorpe, J.E. (2007). Maturation responses of salmonids to changing developmental opportunities. *Marine Ecology Progress Series* **335**: 285-288.
- Todd, C.D., Hughes, S.L., Marshall, C.T., MacLean, J.C., Lonergan, M.E. & Biuw, E.M. (2008). Detrimental effects of recent ocean surface warming on growth condition of Atlantic salmon. *Global Change Biology* **14**: 1-13.
- Turrell, W.R. & Shelton, R.G.J. 1993. Climatic change in the north-eastern Atlantic and its impacts on salmon stocks. In: *Salmon in the sea and new enhancement strategies*, Mills, D.H. (ed.), Fishing News Books, Oxford, 40-78.
- UK Climate Impacts Programme (2002). Climate change scenarios for the UK: The UKCIP02 Briefing Report, April 2002.
- Watts, M., Pankhurst, N.W. & King, H.R. (2004). Maintenance of Atlantic salmon, (*Salmo salar*) at elevated temperatures inhibits cytochrome P450 aromatase activity in isolated ovarian follicles. *General and Comparative Endocrinology* **135**: 381-390.
- Webb, J.H. & McLay, H.A. (1996). Variation in the time of spawning of Atlantic salmon (*Salmo salar*) and its relationship to temperature in the Aberdeenshire Dee, Scotland. *Canadian Journal of Fisheries and Aquatic Sciences* **53**: 2739-2744.
- Webb, J.H. & Campbell, R.N.B. (2000). Patterns of run timing in adult Atlantic salmon returning to Scottish rivers - some new perspectives and management implications. In: *Managing wild Atlantic salmon: New challenges - New techniques*. F.G.J. Whoriskey & Whelan, K.E. (eds.), The Atlantic Salmon Trust, 100-138.
- Webb, J.H., Fryer, R.J., Taggart, J.B., Thompson, C.E. & Youngson, A.F. (2001). Dispersion of Atlantic salmon (*Salmo salar*) fry from competing families as revealed by DNA profiling. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 2386-2395.
- Wells, B.K., Grimes, C.B., Sneva, J.G., McPherson, S. & Waldvogel, J.B. (2008). Relationships between oceanic conditions and growth of Chinook salmon (*Oncorhynchus tshawytscha*) from California, Washington and Alaska, USA. *Fisheries Oceanography* **17**(2): 101-125.
- Welton, J.S., Beaumont, R.C. & Ladle, M. (1999). Timing of migration and changes in age structure of Atlantic salmon, *Salmo salar* L., in the River Frome, a Dorset chalk stream, over a 24-year period. *Fisheries Management and Ecology* **6**: 437-458.
- Whalen, K.G. & Parrish, D.L. (1999). Effect of maturation on parr growth and smolt recruitment of Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **56**: 79-86.

- Wilkie, N.F. (2006). Phenotypic and genetic variation within and among seven populations (six endangered) of Maine Atlantic salmon (*Salmo salar*). University of Maine MS Thesis, 65pp.
- Wootton, R.J. (1998). Ecology of Teleost Fish. Second edition, Kluwer, London.
- Youngson, A.F., Buck, R.J.G., Simpson, T.H. & Hay, D.W. (1983). The autumn and spring emigrations of juvenile Atlantic salmon, *Salmo salar* L., from the Girnock Burn, Aberdeenshire, Scotland: environmental release of migration. *Journal of Fish Biology* **23**: 625-639.
- Youngson, A.F., Jordan, W.C. & Hay, D.W. (1994). Homing of Atlantic salmon (*Salmo salar* L.) to a tributary spawning stream in a major river catchment. *Aquaculture* **121**: 259-267.
- Youngson, A.F., Malcolm, I.A., Thorley, J.L., Bacon, P.J. & Soulsby, C. (2004). Long-residence groundwater effects on incubating salmonid eggs: low hyporheic oxygen impairs embryo development. *Canadian Journal of Fisheries and Aquatic Sciences* **61**: 2278-2287.
- Zydlewski, G.B., Haro, A. & McCormick, S.D. (2005). Evidence for cumulative temperature as an initiating and terminating factor in downstream migratory behavior of Atlantic salmon (*Salmo salar*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences* **62**: 68-78.

Annex 4: Draft ToRs for proposed follow-up meeting

A Study Group on Biological Characteristics as Predictors of Salmon Abundance [SGBICEPS] (Chair: Ian Russell, UK) will meet at ICES HQ, Copenhagen, in November 2009 [dates to be determined] to:

- a) identify data sources and compile time series of data on marine mortality of salmon, salmon abundance, biological characteristics of salmon and related environmental information;
- b) consider hypotheses relating growth, mortality (freshwater and marine) and/or abundance trends for Atlantic salmon stocks with changes in biological characteristics of all life stages and environmental changes;
- c) conduct preliminary analyses to explore the available datasets and test the hypotheses.

SGBICEPS will report by 28 February 2010 for the attention of the WGNAS, ACOM, WGRECORDS and SCICOM.

Supporting Information

Priority:	In June 2009, NASCO asked ICES to 'continue the work already initiated to investigate associations between changes in biological characteristics of all life stages of Atlantic salmon, environmental changes and variations in marine survival with a view to identifying predictors of abundance'. WGNAS began work on this question but was unable to make significant progress due to other work pressures. A separate expert group [SGBICEPS] was therefore set up to take on this task and met for the first time in Lowestoft, England in March 2009, incorporating scientists working on both Atlantic and Baltic salmon. SGBICEPS completed preliminary analyses but recommends that work is continued in order to make further progress in addressing NASCO's request for advice.
Scientific Justification and relation to Action Plan:	<p>NASCO has indicated that there is interest in determining if declines in marine survival of Atlantic salmon coincide with changes in the biological characteristics of juveniles in freshwater or are modifying characteristics of adult fish (size at age, age at maturity, condition, sex ratio, growth rates, etc.) and with environmental change.</p> <p>WGNAS was unable to make significant progress on this request from NASCO due to lack of time. By addressing this topic within a Study Group it will be possible to provide the opportunity for scientists working on both Baltic and Atlantic salmon to contribute to the work.</p>
Resource Requirements:	Meeting facilities at ICES HQ in November 2009 (3 days) for about 20 people.
Participants:	Members of the WGNAS and WGBAST and other designated salmon experts.
Secretariat Facilities:	Final production of report.
Financial:	None. NASCO agreed to sponsor the attendance of up to two analytical experts at the first SGBICEPS meeting to expand the scope of the preliminary analyses already carried out by WGNAS. It is hoped that similar provisions will apply for future meetings.
Linkages To Advisory Committees:	The proposal originates from WGRECORDS but will have direct significance to WGNAS and ACOM in the context of the advice provided to NASCO.
Linkages To other	There are linkages with WGBAST, SCICOM and WGRECORDS in relation to improving scientific understanding of salmon and co-ordinating science on

Committees or Groups:	diadromous species.
Linkages to other Organisations:	NASCO