

REPORT OF THE
WORKSHOP ON THE USEFULNESS OF SCALE GROWTH
ANALYSES AND OTHER MEASUREMENTS OF CONDITION IN
SALMON

Amherst, USA
5–10 July 1999

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1 INTRODUCTION

1.1 Main Tasks

Workshop on the Usefulness of Scale Growth Analyses and Other Measures of Condition in Salmon [WKUS].

At the 1998 Annual Science Conference (86th Statutory Meeting), ICES resolved that the above workshop will meet in Amherst, Massachusetts, USA from 5–10 July 1999 under the Co-Chairmanship of Mr J C MacLean (UK (Scotland)) and Dr K D Friedland (USA).

The Terms of Reference are as follows:

- a) evaluate data sets and methods to interpret ocean effects on salmon populations;
- b) design, if feasible, an experiment to test hypotheses concerning growth and condition effects in salmon.

1.2 Participants

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Courtemanche D.	Canada
Clarke L.	USA
Crabbe S.J.	Canada
Davidson I.	UK (England & Wales)
Desmarais D.	USA
Friedland K.D. (Co-Chair)	USA
Haas-Castro R.	USA
Herzig P.	USA
Letcher B.	USA
MacLean J.C. (Co-Chair)	UK (Scotland)
MacNeil P.	USA
O'Donnell M.	USA
Smithwood D.	USA
Sheehan T.	USA
Stokesbury M.	Canada
Yetter R.	USA

2 INTRODUCTION TO CONCEPTS AND CURRENT STATE OF KNOWLEDGE

2.1 Aging Salmon with Scales

Growth is an important aspect of the ecology and life history of fish and plays a major role in research and management. The most commonly used parameter is age. Aging salmon by scale analysis is a traditional technique that has been used to describe variations in patterns of development both between individuals and between populations in freshwater and marine phases of the salmon's life cycle. Procedures and nomenclature for aging Atlantic salmon from scales were standardised at a previous ICES Workshop (Anon, 1984).

Scales consist of a series of bands or circuli that are deposited in association with growth (Fukuwaka, 1988). The freshwater zone is identified as the innermost area where the circuli are closely spaced. The interpretation of age from the scale pattern relies on the observation that, in both the freshwater and marine phases, the diameter of scales and the number of circuli do not show parallel rates of change. This differential rate of growth promotes bands of alternating widely and narrowly spaced circuli. Recaptures of tagged salmon indicate that the series of narrow and widely spaced bands correspond to annual growth increments which have been loosely interpreted as "summer" and "winter" growth periods.

Freshwater ages range from 1 to 8 over the geographic range of Atlantic salmon. Much of this variation is associated with latitude: the more northerly populations producing older smolts than the southern populations. Less variation in age is observed in the marine phase with most salmon returning to freshwater after 1 or 2 years in the ocean although some remain for 3, or even 4, years in the ocean before returning.

2.2 Scales as Growth Indicators

Scale growth and the growth of other hard parts of fish such as bones and otoliths have been linearly associated with the length of fish. These relationships form the basis of backcalculation techniques to estimate sizes at age (Horppila and Nyberg, 1999) and have been applied to compute growth increments associated with specific developmental stages (Friedland et al. In press). Direct measurement of scale growth has been associated with fish growth and used to interpret factors affecting the marine survival of salmonids (Mathews and Ishida, 1989). In this study, the distances from the focus to the edge of the scale and annular rings were used as proxies of growth. With the availability of image processing, circuli spacings could be extracted from large numbers of scales and specimens. These circuli spacing patterns have been interpreted as indicators of seasonal growth. However, circuli spacing must be considered along with the deposition of the number of circuli during a given time period. Fukuwaka and Kaeriyama (1997) specifically dealt with the issue of growth and the development of microstructure in fish scales. Using path analysis they found that absolute growth was correlated with the increments of scale radius and in turn associated with the number of circuli deposited. Thus, both factors need to be considered when developing life stage or seasonal growth indices for salmon. Fisher and Pearcy (1990) also evaluated the rate of circuli deposition and circuli spacing patterns and found that the rate of circuli deposition was linearly related to growth, but that this rate relationship was different for different life stages. Thus, it is recommended that circuli spacing patterns should only be compared for the same development stage and that circuli deposition should also be taken into account either by measuring integrated distances or circuli counts.

2.3 Scale Growth Studies in the Northwest Atlantic

2.3.1 Growth Dynamics with Hatchery Stocks

Circuli spacing measurements have been made for a two hatchery stocks, the Penobscot and Connecticut River, from the southern part of the range of salmon in North America (Figure 2.3.1.1). The first stock the Workshop considered was the Penobscot River stock. The Penobscot is a hatchery dependant stock that mostly comprised of 2SW returns. Return rates have averaged 5.24 2SW returns per thousand released and 0.84 1SW returns per thousand released. Thus, approximate 10% of the cohort mature after one winter at sea. The variation in post-smolt growth as evidenced by circuli spacing patterns was compared to the patterns of return and maturation rates for the stock (Friedland and Haas, 1996). The circuli spacing of the post-smolt growth zone were extracted from samples of both age groups of returns (Figure 2.3.1.2). Circuli spacing patterns were similar for the two age groups through most of the post-smolt year; however, in winter circuli spacings were significantly higher in 1SW fish than in 2SW fish (Figure 2.3.1.3). In addition, the fraction of the cohort maturing early was significantly and positively correlated with late summer growth, suggesting that growth during that season is also pivotal in determining the proportion of a smolt class that matures early.

The second stock the Workshop considered was the Connecticut River stock, which was presented as a comparison to the Penobscot data (Friedland et al, 1996). The marine survival and sea-age of maturation for the two hatchery dependent stocks have been widely different over the past two decades. Return rates for 1SW and 2SW salmon have been significantly higher in the Penobscot stock; the Penobscot 2SW return rate has averaged nearly five times the Connecticut rate. In addition, the fraction of the smolt year class or cohort that matured as 1SW fish has been higher for the Penobscot stock. There are virtually no returns of 1SW fish to the Connecticut, so for all practical purposes it was considered that none of the Connecticut stock matured as grilse. The only meaningful comparison between the two stocks can be made for the circuli spacings of 2SW returns to the two rivers. Penobscot fish had wider spacing patterns during the summer season than did their Connecticut counterparts of the same smolt year (Figure 2.3.1.4). In addition, Penobscot fish tended to have more circuli pairs or more circuli deposited in the post-smolt growth zone contributing to larger post-smolt growth increments. These results suggest post-smolt growth was more robust for the Penobscot fish and that it may play a role in deciding the age-at-maturity and survival patterns for these two stocks.

2.3.2 Post-smolt Studies

There have been two significant collections of post-smolts in the Northwest Atlantic, one made in the Gulf of St. Lawrence during the early 1980s (Dutil and Coutu, 1988) and the other in the Labrador Sea during the late 1980s (Reddin and Short, 1991). Both sets of scales sample have been analyzed to see if they offer any insights on patterns of recruitment in salmon. Growth patterns varied significant for the three collection years for Gulf of St. Lawrence post-smolts (Figure 2.3.2.1). Friedland et al. (1999) go on to compare the growth patterns for Gulf of St. Lawrence post-smolts with those patterns for returns from three salmon stocks from the southern end of the range in North America. These data suggest that in some years, post-smolt growth in the Gulf is as robust as that observed for both the one seawinter (1SW) and two seawinter (2SW) returns to southern rivers. Post-smolts are believed to use oceanic nursery areas generally; thus, comparable growth between the two stock groups suggests that the Gulf may serve as an important part of the post-smolt nursery range in some years. The concept of the post-smolt nursery as a continuum

between neritic and oceanic areas is essential to evaluating ocean climate and productivity effects on salmonid recruitment.

The circuli spacing patterns for Labrador Sea post-smolts were very different from those for post-smolts in the Gulf of St. Lawrence. These collections are hypothesized to be from the juvenile nursery for post-smolts from the entire stock complex, which is supported by the distribution of river ages of fish in the samples. The first contrast to the Gulf samples is that the growth pattern for the three years from the Labrador Sea are nearly identical. Second, the growth patterns for the Labrador Sea post-smolts were very different from the growth patterns for the southern hatchery stocks for all three years we have data. This can be illustrated with data for the Penobscot River (Figure 2.3.2.2). For two of the three years, growth trajectories for fish from the Penobscot intersected the trajectories for post-smolts from the Labrador Sea collections after 4-5 circuli pairs. Since circuli pairs are laid down at a rate of approximately one per fortnight, the data suggests that distribution patterns for regional groups begin to overlap and stocks begin to experience similar environmental conditions by July of the post-smolt year or two months after their migration to sea. In some years, it would appear regional groups do not mix until fall. These data provide the first indication of the mixing processes between stocks and may be useful in understanding regional patterns of recruitment coherence in salmon versus coherence patterns associated with the entire North American stock complex (Friedland and Reddin, in prep.).

2.4 Scale Growth Studies in the Northeast Atlantic

2.4.1 Linkage to Environmental Effects

Factors affecting the recruitment of Atlantic salmon are of great interest due to the current decrease in indicators of stock abundance. Two recent papers (Friedland *et al.*, 1998; Friedland *et al.*, 1999) describe the relationship between survival for Northeastern Atlantic salmon stocks in relation to both sea surface temperatures and post-smolt growth in one of these stocks.

The North Esk in Scotland and the river Figgjo in Norway (Fig. 2.4.1.1) are similar in that they both drain into the ocean at similar latitudes. Furthermore, the emigrating smolts, which have been externally tagged since 1965 on both rivers, enter the ocean at approximately the same time (May). Comparisons of return rates to both rivers and for 1SW (one sea winter) and 2SW salmon are shown in figure 2.4.1.2. For both stocks, 1SW return rates are greater than 2SW return rates. Patterns of return rates for the North Esk are similar for both maturity groups and are characterised by a low period in the 1960s, a peak period in the early 1970s and thereafter a decline to the end of the time series. A similar pattern is observed for the 1SW return rates for the Figgjo stock. 2SW return rates for the Figgjo correspond to this pattern for the early part of the time series, thereafter remaining relatively high.

The relationship between return rates and indices of SSTs over an area considered to be relevant to post-smolts was investigated over 4 temperature bands (5-7°C, 6-8°C, 7-9°C and 8-10°C) for the months March through July. The results are highlighted in figures 2.4.1.3 and 2.4.1.4. 1SW return rates from both stocks, showed a significant positive correlation with variations in the 8-10°C temperature band in May and a significant negative correlation with variations in the 5-7°C temperature band also in May. The correlations highlighted for North Esk 2SW returns were similar to those of the 1SW returns, while the Figgjo 2SW returns correlated positively with variations in the 7-9°C temperature band.

Correlations of return rates with the 8-10°C temperature band were thought to be more ecologically significant than other associations as smolts from both the North Esk and the river Figgjo enter the ocean when SSTs are in this range. A composite illustration of the differences in SSTs during periods of high and low return rates (Fig. 2.4.1.5.) demonstrates that SSTs in the 8-10°C range are attained later in the year in periods of low returns.

Several authors (Ricker, 1962; Neilson and Geen, 1986; L'Abée-Lund *et al.*, 1993; Friedland *et al.*, 1996) have indicated that post-smolt mortality may be growth mediated by mechanisms related to ocean climate. To further investigate the link between return rate and SSTs, backcalculated growth increments for the 1st year of ocean life for the North Esk returns were derived by differencing the estimated length at the end of the 1st sea winter annulus from the estimated smolt length.

The increments for both 1SW and 2SW showed marked variation over the time series but remarkable correspondence on a year to year basis (Fig. 2.4.1.6). Furthermore, there is a significant correlation between return rate and growth (Fig. 2.4.1.7) strongly suggesting that changes in ocean climate, as measured by SSTs affects return rates through growth mediated responses in salmon.

2.4.2 Seasonal Effects

Current investigations (MacLean & Friedland, in prep.) in the northeast Atlantic have concentrated on assessing the coherence in growth patterns between two geographically separated stocks. Furthermore, fine scale analysis of the growth pattern in one of these stocks has allowed the critical period during the post-smolt year to be identified.

Material for the study was collected from the North Esk and the Girnock Burn, a tributary of the river Dee (Fig. 2.4.2.1). Scale samples have been collected from adults returning to the Girnock Burn since 1965 from a trap situated at the lower end of the tributary. In contrast to the North Esk data set where an overall measurement of post-smolt growth was obtained, a detailed growth profile of the post-smolt phase was derived by collecting intercirculi spacing information by means of an image processing system.

The growth profiles for the North Esk and the Girnock Burn, derived by different methods, show a remarkably similar pattern over the time series (Fig. 2.4.2.2) suggesting that these geographically distinct stocks are experiencing a common ocean environment during their first year at sea. As noted in section 2.4.1, the pattern of post-smolt growth for the North Esk stock mirrors that of the return rate. Figure 2.4.2.3A shows the reported catch in the north east region (which encompasses both study stocks) and Figure 2.4.2.3B shows the reported catch in the Dee district for all gears combined and for fixed engine gears. The catch pattern in these plots is similar to the two growth profiles and to the return rate index for the North Esk stock suggesting that catch information reflects both return rate and growth attained during the first year at sea. Scatter plots (Fig. 2.4.2.4 and Fig. 2.4.2.5) of growth increments in relation to both catch and return indices show a significant correlation at both sites.

For the Girnock Burn data set, the post-smolt growth increment was determined from a summation of circuli pair spacings to the appropriate circuli pair. Such detailed growth information makes it possible to investigate the relative contribution of particular periods during post-smolt phase to the overall growth increment. The post-smolt increments were divided equally firstly, into 4, then 6 and finally 8 periods and a principal component analysis was employed to examine the relationships between these fine scale growth indices and the overall post-smolt growth increment. The principal component factor loadings on the first two eigenvectors are shown in Fig. 2.4.2.5. For each series of divisions, the first fine scale growth increment consistently showed loadings more similar to the total post-smolt growth increment than any of the other fine scale growth indices. This highlights the immediate post-smolt period as being the most important period in determining subsequent growth and survival.

2.5 Relevance to Current Assessments of Salmon in the North Atlantic

The management of salmon fisheries, and of the stocks/populations underpinning the fisheries, across the north Atlantic is complex and involves many organisations and several different legal frameworks. The NASWG (North Atlantic Salmon Working Group) is an ICES working group that meets annually to address questions posed by NASCO (North Atlantic Salmon Conservation Organisation) on the status of salmon stocks. Representatives from nearly all Atlantic salmon producing and harvesting countries attend.

Reference to Figure 2.5.1 (from Anon, 1999) shows that nominal catches throughout the north Atlantic have shown a considerable decrease since the 1960s. In response to this decrease progressively more and more severe restrictions, including closure in many instances, have been introduced to many fisheries. Current assessments of stock abundance, which are ultimately used to formulate advice on fisheries, first attempt to estimate the number of spawners required to ensure that the freshwater habitat is stocked to carrying capacity. This is termed the SER (Spawning Escapement Reserve). This value is then considered in relation to an estimate of the number of salmon available in the ocean at a time prior to any fisheries operating. This value is termed the PFA (Pre Fishery Abundance).

Although a great deal of progress has been achieved, such estimates are constrained by the paucity of available input data and consequently the derived figures pertain to large, geographic, groupings of many rivers. For North American rivers, 6 major groupings are considered and in Europe, rivers are grouped by country.

While management would be most appropriate at the level of the biological population, this is clearly not an attainable target given the scale over which genetic (Jordan *et al*, 1992; Jordan *et al*, 1997) and behavioural (Hawkins & Smith, 1986; Laughton & Smith, 1992) differences have been demonstrated to exist. On the other hand, it is clear that more finely tuned management, on smaller stock complexes than those currently employed, should be possible if methods of grouping stocks from small geographic areas could be developed. Section 2 has summarised studies, both in the north west and the north east Atlantic, which have indicated the scale at which stocks, originating from different locations, show similar patterns of growth. The workshop agreed that the degree of cohesiveness in growth patterns between different stocks could indicate more appropriate stock groupings for assessment purposes given that growth has been related to other important aspects of salmon biology.

3 INDICATOR STANDARDS

3.1 Scale-based Methods

It is important to ensure that all scale samples are being collected from the proper location on the fish. Martynov (1983) described the variability in scale characteristics for salmon with respect to the location of collection. Glenn and Mathias (1985) documented the development of scale circuli of young walleye, which was related to fish size and age, and the differential development of scales on the body. These studies indicated that the scales closest to the lateral line are laid down first and therefore will contain the most complete history of the fish's growth. Unfortunately, the lateral line area exhibits a high rate of regenerated scales. The workshop therefore supports the recommendation, made by the 1988 Report of the Second Atlantic Salmon Scale Reading Workshop (Shearer 1989), that scale collections are taken from the left hand side of the fish, 3-6 rows above the lateral line on a line extending from the anterior edge of the anal fin to the posterior edge of the dorsal fin.

Glen and Mathias (1988) concluded that back calculation and other scale generated data should be more accurate if the measured axis is along the long axis of the scale, due to the fact that lateral circuli are not deposited as regular as along the long axis. Unfortunately, there have been no peer reviewed publications of this type that have investigated these same processes for Atlantic salmon scales.

3.1.1 Back-calculated Increments

A general overview of the techniques commonly used for back calculating fish length from scale samples was presented. Accordingly, 2 main approaches were discussed; the "regression method", which relies on a regression of total length against scale length for a sample of fish and the "proportional method", which back calculates fish length for individuals. Often it is desirable to correct for the fact that many species do not begin scale formation until they are a few centimeters long (e.g. Atlantic salmon scales are formed at a length of 2-3 centimeters). It was noted that the regression method is rarely used for Atlantic salmon. For more information concerning these different methods please refer to Francis (1990) or Pierce et al. (1996).

A study investigating biases in back calculated lengths from the non-corrected proportional method for returning Scottish salmon (tagged as smolts) was presented. The back calculated lengths consistently underestimated the known fish length, although the differences were not significant. There also was a decrease in the bias as the back calculated smolt size increased. This type of study identifies the need for researchers to re-evaluate the tradition methods used and identify the biases that are introduced within the results obtained. There are currently studies underway which involve repeat sampling schemes that may help address and evaluate some of these concerns.

In support of the continued use of these back calculation methods, the results obtained to date have consistently paralleled other independently measured indices such as survival estimates and catch statistics for Atlantic salmon.

3.1.2 Circuli Spacing

A brief survey of the literature pertaining to the use of circuli spacing for the analysis of various growth and survival estimates was presented. Barber and Walker (1988) used circuli spacing to help piece together the ocean history of 2 stocks of Alaskan sockeye salmon. They concluded that the pattern of circuli spacing and annulus formation is in response to photoperiod and food availability during the fish's existence. They showed that circuli spacing patterns varied between stocks for various years at sea. Holtby et al. (1990) showed that intercirculi spacing was related to patterns of marine survival on an annual basis. Marine survival was strongly correlated with early marine growth encompassed within the first 5 marine circuli for returning adults. Both marine survival and ocean growth were also positively correlated with other environmental variables. Large smolt size did not guarantee high survival except in years when survival was relatively poor. Neither survival nor early ocean growth were correlated with smolt production.

Jaenicke *et al.* (1994) showed that the ratio of scale spacing parameters were positively correlated with commercial catches, while there was a negative correlation between fish weight and catch. They found that early post smolt growth patterns were positively correlated to survival while late post smolt growth was negatively correlated. The highest correlations occurred with the first few circuli. Healey (1982) was able to identify the timing and relative intensity of early marine mortality of chum salmon *Oncorhynchus keta* based on circuli number and spacing patterns.

It is recommended that the use of circuli spacing data for other species be surveyed to help fortify the work that has been done with Atlantic salmon. Investigations need to be conducted to help quantify the variability in circuli and annuli deposition for Atlantic salmon. It has been suggested that circuli appear to be deposited approximately every 2 weeks, but this most likely varies at different times of the year and at different life stages of the fish.

The workshop recommended that both the types of data and the processes involved in their collection should be standardised to facilitate comparisons between stocks and regions and that assumptions regarding back calculations and circuli spacings are validated.

3.2 Weight, Length and Condition

Several studies from various regions have linked data sets of weight, length, and condition factor to salmon survival. Ward and Slaney (1998) reported survival of steelhead trout was positively correlated with smolt length and weight. Reductions in size at maturity for Fraser River sockeye salmon was associated with increased sea surface temperatures (Cox and Hinch 1997). Bigler et al. (1996) reviewed size trends among North Pacific salmon (*Oncorhynchus* sp.) over an 18 year period. They reported decreased trends in sizes as abundance increased.

Parrish and Mallicoate (1995) reported decadal trends in mackerel condition factor to be correlated with environmental variables such as sea level, ambient temperature and salinity, and up-welling proxies. However, the condition factor of anchovy was much less correlated with environmental variables. Decadal changes in growth and recruitment of Pacific halibut were linked to oceanographic changes in the North Pacific (Clark et al. 1999).

The data sets presented originated from the Pacific coast, and although data sets are available on the east coast of North America, it was decided that there was no need to replicate studies using Atlantic salmon at the current time.

3.3 Chemistry of Body Parts

3.3.1 Otolith Composition

Elemental analysis of Atlantic salmon otoliths may provide a useful tool for the study of such things as growth, maturation and environmental histories of individual fish. Otoliths are useful due to their resistance to chemical remodeling and stability (Campana and Neilson 1985). It is believed that otoliths can provide new information about trends in maturation. While some studies have reported that Sr:Ca ratios can be a record of temperature and salinity in various species (Farrell and Campana 1996), it is believed that Sr:Ca ratios deposited in Atlantic salmon otoliths during the postsmolt year are a record of somatic growth and maturation (Friedland et al. 1998). This ability to detect sexual development and spawning events could be useful in examining variation that occurs between populations and individuals and it was suggested that there is a need for this to be applied to a wide range of Atlantic salmon populations.

Sr:Ca ratios measured during the freshwater phase of life reflect salinity and environmental availability of strontium. Sr:Ca ratios significantly increase as the fish enters the marine environment (Friedland et al. 1998). This is a possible tool for studying the environmental histories of individual fish. Data also suggested that Sr:Ca ratios deposited during the freshwater phase of life differ according to origin (Friedland 1998).

It was agreed that further studies need to be conducted on the various elemental signals found in otoliths. These signals could provide a wealth of information concerning life history events in Atlantic salmon.

3.3.2 Organic Isotopes

Stable isotope analysis of carbon and nitrogen may be useful in determining trends in food web structure. In freshwater systems, stable isotope analysis is an important means of assessing the importance of terrestrial and aquatic inputs into salmon streams. Carbon and nitrogen have proven to be useful in analyzing food web relationships. ^{13}C and ^{12}C are often used for identifying primary food sources because they are fixed during photosynthesis and are passed relatively unchanged through the food chain. A study involving wild juvenile Atlantic salmon in the Miramichi system, New Brunswick concluded that salmon found in the headwaters obtained most of their carbon from allochthonous sources, but downstream salmon relied equally on both allochthonous and autochthonous sources. This study also provided staple isotope data for a stream system that was beginning to undergo deforestation (Doucett et al. 1996). This could potentially serve as a means of evaluating changes in food webs due to environmental changes.

Stable isotope analysis has also provided information on the nutrient link between returning adult salmon and juveniles. The energy and nutrients transported from the ocean by the adult salmon can be released into the aquatic system when the carcass decays. Marine-derived nitrogen is the predominant source of nitrogen in some spawning streams (Kline et al. 1990). A study conducted on juvenile chum and pink salmon showed that harpacticoid copepods act as an intermediary between the adults and juveniles (Fujiwara and Highsmith 1997). It is believed that this nutrient link may influence population fluctuations of salmon.

The working group recommended that stable isotope analysis could be a useful tool in studying changing food trends of salmon in both marine and freshwater life stages.

3.4 Other Approaches

There are several other methods of assessing fish growth and condition. Three common methods include assessing relationships of otolith size at age, RNA-DNA ratios, and examining body composition. In a recent study with Atlantic cod both Otolith size at age and body size at age were highly correlated with year class strength (Campana 1996). Using data collected on otoliths rather than scales gives the researcher a way to examine growth at the daily level rather than examining circuli pairs. However, there are drawbacks to using otoliths in that preparing otoliths is time consuming and the fish needs to be sacrificed to remove the otoliths.

In a separate study with Atlantic cod recent growth of juveniles at two different sites was assessed by examining RNA-DNA ratios (Buckley and Lough 1987). This analysis proved that fish in sites that were stratified in terms of prey abundance (abundance above and below the thermocline) had higher RNA-DNA ratios than sites that the prey was well mixed. However, as with otoliths there are drawbacks to using RNA-DNA ratios as an indicator of growth or condition. The major drawback is that while it works well with larva and juvenile fish, the information collected on older fish may be spurious because of issues with DNA repair.

The final indicator of growth and condition, body composition, has been examined in Gulf menhaden (Deegan 1986). Data on lipid, water, protein, and energy content were collected to examine changes in body composition associated with metamorphosis. These data suggest that energy allocation may shift from protein growth to lipid storage as the fish grows. Additionally, there were variations in end of the lipid content that may be associated with environmental conditions such as temperature or salinity.

4 IMAGE PROCESSING APPLICATIONS

4.1 Scales

4.1.1 Collection and preparation

The Workshop agreed that scale samples should be obtained from the standardised location agreed at the 1984 and 1988 Atlantic Scale Reading Workshops (Anon, 1984; Shearer, 1989; see Sec. 3.1).

Scale samples are usually stored in paper envelopes until preparation for analysis. This storage technique also preserves some of the underlying epidermal material in which scales are embedded. Such material may be used for DNA extraction and analysis.

In general, 2 main methods have traditionally been used to prepare scales for conventional analyses (aging and back-calculation). The first method involves washing the scales in a mild detergent to clean them prior to mounting them between 2 glass microscope slides. The second method, requires the scale to be placed between 2 acetate strips and passed through a jeweler's press to create an impression of the scale on the acetate. This also has the additional benefit of not requiring the scales to be cleaned prior to the impression being prepared.

In the growth analyses undertaken to date (see Sec. 2), all scales have been mounted between glass slides. The rationale for the adoption of this procedure as opposed to using impressions has been that the pressure used to create an impression may result in distortions to the true dimensions of the scale. The Workshop discussed the relevant attributes of both preparations. While impressions were quicker to prepare than glass mounts there was a question mark over the accuracy of the impression in relation to the scale. It was felt that small distortions would have little or no bearing on aging or backcalculating processes but that any distortion could have a significant effect when fine scale measurements such as circuli spacings were being extracted. Preliminary investigations from UK (Scotland) indicated that the level of distortion along the 360° axis was <1%. The Workshop concluded that for growth analyses glass mounted preparations were preferable and that if impressions were to be used the effects of distortion should be investigated.

A method, described by Powers (1964) where scales are immediately mounted on a cellophane covered acetate slide, thus combining the collection and preparation of scales in a single process, was also discussed. The Workshop felt that such a technique was useful for aging and backcalculating scales but that the lack of a cleaning process precluded its use for obtaining fine scale growth measurements.

4.1.2 Location of measurements

Standardisation of the location on the scale from which circuli spacing measurements should be taken was discussed. To date, all measurements have been taken along the 360° axis. It was suggested that multiple axes on same scale could be measured to ascertain the degree of consistency exhibited from measurements along different axes. The Workshop also agreed that variation in scale characteristics among scales from the same individual should be addressed.

4.2 Shape Analysis

Differences in body shape among fish from various stocks, life history strategies and ages may reflect important variations in physiology, behaviour and habitat interactions. Truss networks of landmark points have been used successfully to identify shape differences and a new and often more powerful technique has been introduced and applied in the last 10.

years. Shape analysis based on thin plate spline techniques uses x,y coordinates of specific landmarks to describe the detailed morphometry of specimens. Subtle differences in shapes among groups or individuals can be revealed using the free shareware available at <http://life.bio.sunysb.edu/morph/morph.html>.

4.3 Fecundity and Egg Size

Measures of egg size and number (fecundity) have been used to explore the maturation process and spawning strategies among both Atlantic and Pacific salmon.

In a number of cases, relationships between body characteristics and egg size or fecundity have been described. For example, Quinn *et al.* (1995) correlated egg weight with snout length and body size in sockeye salmon (*Oncorhynchus nerka*), while Sutterlin and Maclean (1984) found that both absolute fecundity and egg volume were related to body weight in Atlantic salmon (*Salmo salar*).

MacLean (pers. comm.) identified different relationships between body length and fecundity in early and late running Atlantic salmon on the North Esk, Scotland. These indicated that early entrants were less fecund than late entrants, although the former produced larger eggs and spawned in different areas of the catchment. Spatial differences in reproductive strategies were also noted by Sutterlin and Maclean (1984) in Atlantic salmon who found that egg size was positively correlated with the size of spawning substrates.

5 DATA SET INVENTORY FOR NORTH ATLANTIC SALMON POPULATIONS

Information on existing scale data sets was made available to the Workshop by participants by corresponding colleagues. Tables 5.1 and 5.2 and Figure 5.1 present the information for Europe and North America respectively. Each data set has been identified with respect to both country and region within country. In addition, the duration, details of ancillary data collected, comments on scale preparation and analysis to date for each data set have been noted. The map reference number allows the geographic position of each entry to be identified on the map shown in Figure 1. It is acknowledged that this inventory is not comprehensive and that other major data sets probably exist. For example, although details were not available to the Workshop it has been intimated that there are several data sets in Sweden, for both Atlantic and Baltic stocks, dating back to the 1940s. Furthermore, data sets that were of short duration and/or comprised a limited number of scale collections per year were omitted from the inventory. In general, the data sets have been listed by latitude in a north to south direction.

Tables 5.3 and 5.4 summarise the temporal and spatial dimensions of the data sets for Europe and North America. It is evident that data sets exist over most of the species range and that regional clusterings also occur allowing both global scale and regional scale hypotheses to be investigated.

6 EXPERIMENTAL DESIGNS

The inventory of data sets, detailed in section 5, is extensive and provides an opportunity to expand previous work (detailed in section 2). Specifically, the datasets that exist will allow spatial and temporal boundaries with respect to stock cohesiveness and environmental correlates to be delimited. The results of such studies should identify the appropriate stock complexes that could be used in assessment models and, in addition, may provide insights into the mechanisms affecting salmon growth in the ocean.

6.1 Regional Experiments

Hypotheses concerning the cohesiveness of growth signatures should be considered, in the first instance, at the within region level to determine at what spatial and temporal scales growth patterns between stocks are similar. The inventory compiled in section 5 offers more than adequate scope to do this within many regions. For instance, in Europe, there are clusters of stocks in Norway, Iceland, UK (Scotland), UK (England & Wales), Ireland, France and Spain. Similarly, in North America groups of stocks where scale samples exist have been identified in Newfoundland, the Gulf, Scotia-Fundy, New Brunswick and Maine regions. Over time, it is possible that growth signatures from all stocks could be extracted providing maximum resolution from the inventory.

The outcome of such analyses would allow a comparison of the spatial scales over which growth signatures are similar within and among regions. Areas showing different growth patterns could be delimited and potential mechanisms underlying these could be investigated in relation to patterns of environmental variables that could potentially be having an affect on growth. It was recognised that there will also be a genetic component in determining growth patterns.

The Workshop also considered the possible outcomes of such regional experiments in a temporal context. It was concluded that it was likely that comparisons of growth signatures within and among regions would reveal varying degrees of cohesion throughout the time series. Such an outcome could be investigated further with respect to co-varying environmental variables and would also highlight the relevance, or otherwise, of applying assessment models to spatially constant stock groupings throughout an extensive time series.

While encouraging such regional experiments, it should be pointed out that larger scale comparisons of growth signatures will rely on the amalgamation of appropriate (dependant on results) regional data sets. Therefore it is extremely important that all analyses should be performed in a standard manner that would ultimately allow regional data sets to be amalgamated.

6.2 Basin Wide Comparisons

The workshop considered that the correct time to undertake basin wide comparisons of growth signatures would be once conclusions from an informative number of within and among region comparisons had been reached. It would only be once such work had been undertaken that the most relevant hypotheses could be tested on a basin wide scale. However, it is already clear that the general from of questions to be investigated would include the following:

- Over what spatial and temporal scale are growth signatures similar?
- Does this scale vary in different areas of the species range?
- Do the discontinuities in growth signatures correspond to variations in either environmental parameters or variations in abundance indicators of Atlantic salmon?
- Is there sufficient cohesion, at any level, that would allow indicator stocks to be identified?

7 PLANNING AND ORGANISATION OF COOPERATIVE STUDIES

The workshop acknowledged that the most efficient way in which to proceed with cooperative studies was to coordinate future work through two regional coordinators, one for North America and one for Europe. It was suggested that the co-chairs of the meeting should act as coordinators for collaboration within their respective continents.

To further assist collaboration the Workshop agreed that a web page is set up. The initial structure of the page would include, among others, sections covering the report of this Workshop, key papers in the relevant areas, current collaborations and a message board to allow interested individuals and organisations to correspond with one another.

The Workshop recommended that a further workshop should be convened at a future, unspecified date, once significant progress had been achieved.

8 RECOMMENDATIONS

The Workshop made the following recommendations.

- 1) Scale collections should be taken from the left hand side of the fish, 3-6 rows above the lateral line on a line extending from the anterior edge of the ventral fin to the posterior edge of the dorsal fin as recommended by previous ICES Workshops (Anon, 1984; Shearer, 1988).
- 2) The type of growth data and the processes involved in their collection should be standardised to facilitate comparisons between stocks and regions.
- 3) Assumptions regarding back calculations and circuli spacings are validated.
- 4) Further investigation of stable isotope analyses as a tool in studying changing food trends of salmon in both marine and freshwater life stages.
- 5) Glass mounted scale preparations were preferable in growth analyses and that if impressions were to be used the effects of distortion should be investigated.
- 6) Multiple axes on same scale could be measured to ascertain the degree of consistency between measurements along different axes.
- 7) Variation in scale characteristics among scales from the same individual should be investigated.
- 8) The Co-Chairs (J. C. MacLean and K. D. Friedland) of the meeting should act as coordinators for collaboration within their respective continents.
- 9) A further workshop should be convened at a future, unspecified date, once significant progress had been achieved.

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Table 5.1 Scale samples and other data types for salmon stocks originating in the North East Atlantic.

Country	Region	District/ River	Data Types	Duration	Scale Preparation	Analysis to Date	Map Ref. No.
Finland	Lapland 69°N, 29°E	Tenojoki And tributaries	Scales, Length, Weight, Sex, GSI	1973 - 1999	Impressed	Age, Growth Increments	1
Finland	Lapland 70°N, 28°E	Naatanajoki And tributaries	Scales, Length, Weight, Sex	1976 - 1999	Impressed	Age, Growth Increments	2
Norway	North (Sub Arctic)	Repparfjordelv	Scales, Length, Weight	1962 - 1998		Age, Growth Increments	3
Norway	Central	Saltfaldselv	Scales, Length, Weight	1976 - 1998		Age, Growth Increments	4
Norway	Central	Vefsna	Scales, Length, Weight	1970 - 1987		Age, Growth Increments	5
Norway	South	Drammen	Scales, Length, Weight	1985 - 1999		Age, Growth Increments	6
Norway	South	Imsa	Scales (some), Length, Weight	1977 - 1999		Age	7
Norway	South	Figgjo	Scales (some), Length, Weight	1967 - 1999		Age	8
Iceland	North Central	Midfrardara	Scales, Sex, Length, Weight	1985 - 1999		Age	9
Iceland	North Central	Blanda	Scales, Sex, Length, Weight	1985 - 1999		Age	10
Iceland	North East	Vesturdalsa	Scales, Sex, Length, Weight	1983 - 1999		Age	11
Iceland	North East	Hofsa	Scales, Sex, Length, Weight	1987 - 1999		Age	12
Iceland	South West	Ellidaar	Scales, Sex, Length, Weight	1988 - 1999		Age	13
Iceland	South West	Olfusa	Scales, Sex, Length, Weight	1976 - 1999		Age	14
UK (Scotland)	North	Strathy	Scales, Sex, Length	1993 - 1998	Impressed	Age, Some Back Calculations	15

Table 5.1 continued.

UK (Scotland)	West	Several	Scales, Sex, Length	1993 - 1998	Impressed	Age, Some Back Calculations	16
UK (Scotland)	Moray Firth	Spey	Scales, Sex Length, Weight	1968 - 1993	Impressed	Age, Some Back Calculations	17
UK (Scotland)	North East	Dee (Gimnock Burn)	Scales, Sex, Length	1966 - 1998	Impressed	Age	18
UK (Scotland)	North East	Dee	Scales, Sex Length, Weight	1974 - 1986	Impressed	Age, Some Back Calculations	19
UK (Scotland)	North East	North Esk	Scales, Sex, Length, Weight	1962 - 1999	Impressed	Age, Back Calculations	20
UK (Scotland)	East	Tummel	Scales, Sex, Length, Weight	1968 - 1991	Impressed	Age	21
UK (Scotland)	East	Almond	Scales, Sex, Length, Weight	1969 - 1976	Impressed	Age	22
UK (Scotland)	East	Tay	Scales, Sex Length, Weight	1984 - 1996	Impressed	Age, Some Back Calculations	23
UK (Scotland)	East	Tweed	Scales, Sex Length, Weight	1962 - 1999 (most years)	Impressed	Age, Some Back Calculations	24
UK (Northern Ireland)	Co. Antrim	Bush	Scales, Length, Weight	1973 - 1999		Age, Some Back Calculations	25
Ireland	Eastern	Boyne	Scales	1944 - 1986 (some years)	Mounted (most)		26
Ireland	Southern	Blackwater	Scales	1981 - 1986 (some years)	Mounted (some)		27
Ireland	South Western	Lee	Scales	1944, 1945, 1956	Mounted		28
Ireland	Shannon	Shannon	Scales	1927 - 1994 (some years)	Mounted (some)		29
Ireland	Galway	Corrib	Scales	1968, 1985 - 1987	Mounted (some)		30
Ireland	North Western	Moy	Scales	1954 - 1989 (most years)	Mounted (most)		31

Table 5.1 continued.

UK (England & Wales)	North West	Eden	Scales, Weight	1991, 1993, 1994	Cleaned	Age	32
UK (England & Wales)	North West	Kent	Scales, Weight	1993 – 1999	Cleaned	Age	33
UK (England & Wales)	Welsh	Dee	Scales, Length, Weight	1984, 1986, 1987, 1991 – 1999	Cleaned	Age	34
UK (England & Wales)	Welsh	Tywi	Scales, Weight	1988 – 1990	Cleaned	Age	35
UK (England & Wales)	Welsh	Tawe	Scales, Weight	1991 – 1996	Cleaned	Age	36
UK (England & Wales)	Welsh	Wye	Scales, Weight	1985 – 1999	Cleaned	Age	37
UK (England & Wales)	Midlands	Severn	Scales, Weight	1988 – 1999	Cleaned	Age	38
UK (England & Wales)	Thames	Thames	Scales, Length, Weight	1983 – 1999	Cleaned	Age	39
UK (England & Wales)	Southern	Test	Scales, Weight	1991 – 1994	Cleaned	Age	40
France	Upper Normandy	Bresle	Scales, Length, Weight	1984 – 1999		Age	41
France	Lower Normandy	See	Scales, Length, Weight	1987 – 1999		Age	42
France	Lower Normandy	Selune	Scales, Length, Weight	1987 – 1999		Age	43
France	Brittany	Trioux	Scales, Length, Weight	1987 – 1999		Age	44
France	Brittany	Leguer	Scales, Length, Weight	1987 – 1999		Age	45
France	Brittany	Douron	Scales, Length, Weight	1987 – 1999		Age	46
France	Brittany	Penze	Scales, Length, Weight	1987 – 1999		Age	47
France	Brittany	Elom	Scales, Length, Weight	1987 – 1999		Age	48
France	Brittany	Aulne	Scales, Length, Weight	1987 – 1999		Age	49

Table 5.1 continued.

France	Brittany	Odet	Scales, Length, Weight	1987 - 1999	Age	50
France	Brittany	Aven	Scales, Length, Weight	1987 - 1999	Age	51
France	Brittany	Elle	Scales, Length, Weight	1987 - 1999	Age	52
France	Brittany	Scorff	Scales, Sex (1994-1999 only), Length, Weight	1987 - 1999	Age	53
France	Brittany	Blavet	Scales, Length, Weight	1987 - 1999	Age	54
France	Pays de Loire	Loire	Scales, Length, Weight	1987 - 1993	Age	55
France	Centre	Allier (Loire tributary)	Scales, Length, Weight	1987 - 1993	Age	56
France	Southern Gascony	Adour	Scales, Length, Weight	1984 - 1999	Age	57
France	South West	Gave Oloron (Adour tributary)	Scales, Length, Weight	1987 - 1999	Age	58
France	South Gascony	Nivelle	Scales, Length, Weight	1989 - 1999	Age	59
Spain	Cantabria	Deva	Scales, Length, Weight	1953-1961 (some years) 1987-1999	Age	60
Spain	Cantabria	Nansa	Scales, Length, Weight	1961-1963 1986-1999	Age	61
Spain	Cantabria	Pas	Scales, Length, Weight	1947-1964 (some years) 1987-1999	Age	62
Spain	Cantabria	Asón	Scales, Length, Weight	1948-1963 (some years) 1986-1999	Age	63

Table 5.2. Scale samples and other data types for salmon stocks originating in North America.

Country	Region	District/ River	Data Types	Duration	Scale Preparation	Analysis to Date	Map Ref. No.
Canada	Ungava Bay to Lower North Shore	Various rivers	Scales	1970-unknown			<u>1</u>
Canada	Newfoundland	Campbellton	Scales, weights, lengths	1993-1999	Impressions		<u>2</u>
Canada	Newfoundland	Exploits	Scales, weights, lengths, sex	1964-1999	Impressions or mounts	Ages	<u>3</u>
Canada	Newfoundland	Gander	Scales, lengths, some weights and sex	1951, 1975-1999	Impressions	Ages	<u>4</u>
Canada	Newfoundland	Terra Nova	Scales, lengths, some weights and sex	1978-1999	Impressions	Ages	<u>5</u>
Canada	Newfoundland	Western Arm Brook	Scales, weights, lengths	1972-1999	Mounted	Ages, Some Annular increments	<u>6</u>
Canada	Newfoundland	Highlands	Scales, lengths	1986-1999	Impressions	Ages	<u>7</u>
Canada	Newfoundland	Middlebrook	Scales, lengths, some weights and sex	1978-1999	Impressions	Ages	<u>8</u>
Canada	Newfoundland	Flat Bay Brook	Scales, weights, lengths, sex	1994-1997	Impressions or mounts	Ages	<u>9</u>
Canada	Newfoundland	Conne	Scales, weights, lengths, sex	1986-1999	Impressions	Ages	<u>10</u>
Canada	Newfoundland	Little	Scales, weights, lengths, sex	1989-1999	Impressions or mounts	Ages	<u>11</u>
Canada	Newfoundland	NE Placentia	Scales, lengths, some weights and sex	1978-1999	Impressions	Ages	<u>12</u>
Canada	Newfoundland	Piper' Hole River	Scales, weights, lengths, sex	1989, 1994-1996	Impressions or mounts	Ages	<u>13</u>
Canada	Newfoundland	NE Trepassey	Scales, lengths, some weights and sex	1984-1999	Impressions	Ages	<u>14</u>
Canada	Newfoundland	Rocky	Scales, weights, lengths, sex	1989-1999	Impressions or mounts	Ages	<u>15</u>
Canada	Newfoundland	Biscay Bay	Scales, lengths, some weights and sex	1983-1986	Impressions	Ages	<u>16</u>
Canada	Quebec	River de la Trinité	Scales, weight, length, sex	1984-99			<u>17</u>

Table 5.2 continued

Canada	Quebec	River Saint-Jean	Scales, weight, length, sex	1984-99			<u>18</u>
Canada	Gulf	Restigouche	Length, scales, some weight	1978-99		1978-87 scale circuli spacing extracted	<u>19</u>
Canada	Gulf	Miramichi, some tributary and specific sampling	Length, scales, some weights and sex	1971-1992		1978-87 scale circuli spacing extracted	<u>20</u>
Canada	Gulf	Northwest and Southwest Miramichi	Length, scales, some weight and sex	1992-1998			<u>21</u>
Canada	Scotia-Fundy	East River	Length, weight, scales	1983-99			<u>22</u>
Canada	Scotia-Fundy	Margaree	Length, scales	1985-96			<u>23</u>
Canada	Scotia-Fundy	North River	Length, scales	1991-98			<u>24</u>
Canada	Scotia-Fundy	Middle and Baddeck	Length, scales	1992-98			<u>25</u>
Canada	Scotia-Fundy	Grand	Length, scales	1989-98			<u>26</u>
Canada	Scotia-Fundy	Stewiacke River					<u>27</u>
Canada	Scotia-Fundy	LaHave River	Length, weight, scales	1983-99			<u>28</u>
Canada	Scotia-Fundy	Liscomb River	Length, weight, scales	1983-99			<u>29</u>
Canada	New Brunswick	Big Salmon					<u>30</u>
Canada	New Brunswick	Nashwaak	Length, scales	1972-73, 1975, 1993-98			<u>31</u>
Canada	New Brunswick	Petitcodiac	Length, scales	1956-1966			<u>32</u>
Canada	New Brunswick	Pollett tributary of the Petitcodiac	Length, scales	1952-64			<u>33</u>
Canada	New Brunswick	Saint John	Length, weight, scales	1967-1998		1975-92 scale circuli spacing extracted	<u>34</u>
Canada	New Brunswick	Magaguadavic	Lengths, scales	1983-85, 1988, 1992-98			<u>35</u>
Canada	New Brunswick	St. Croix	Length, scales	1981-91, 1993-98			<u>36</u>
United States	Maine	Aroostook	Lengths	1988-99			<u>37</u>
United States	Maine	Machias	Lengths, scales, some weights	1953-72 trap catches 1940s-90s angler catches			<u>38</u>
United States	Maine	Narraguagus	Lengths, scales, some weights	1962-74, 1991-99, trap catch 1940s-90s angler catches			<u>39</u>

Table 5.2 continued.

United States	Maine	Union	Lengths, Adult weights, scales	1974-99, trap catches, 1970s-90s angler catches			<u>40</u>
United States	Maine	Penobscot	Lengths, scales, some weights	1969-99, trap catches 1940s-90s angler catches	Whole mounts	1975-92 scale circuli spacing extracted	<u>41</u>
United States	Maine	Androscoggin	Length, scales	1983-99			<u>42</u>
United States	Maine	Saco	Lengths, scales, some weights	1986-91, 1993-99			<u>43</u>
United States	New England	Merrimack	Lengths, weights, scales	1977-99	Whole mounts	Aging, condition factors, back-calculations	<u>44</u>
United States	New England	Connecticut	Length, weight, scales	1978-99	Whole mounts	1978-92 scale circuli spacing extracted	<u>45</u>

Table 5.4. Time matrix for scale samples and other data types for salmon stocks originating in North America.

Country	Region	District/River
Canada	Ungava	Various
Canada	Nfld	Campbellton
Canada	Nfld	Exploits
Canada	Nfld	Gander
Canada	Nfld	Terra Nova
Canada	Nfld	W. Arm Brook
Canada	Nfld	Highlands
Canada	Nfld	Middlebrook
Canada	Nfld	Flat Bay Brook
Canada	Nfld	Conne
Canada	Nfld	Little
Canada	Nfld	NE Placentia
Canada	Nfld	Piper's Hole River
Canada	Nfld	NE Trepassy
Canada	Nfld	Rocky
Canada	Nfld	Biscay Bay
Canada	Quebec	River de la Trinité
Canada	Quebec	River Saint-Jean
Canada	Gulf	Restigouche
Canada	Gulf	Miramichi
Canada	Gulf	NW-SW Miramichi
Canada	S-F	East River
Canada	S-F	Margaree
Canada	S-F	North River
Canada	S-F	Middle/ Baddeck
Canada	S-F	Grand
Canada	S-F	Stewiacke River
Canada	S-F	LaHave River
Canada	S-F	Liscomb River
Canada	NB	Big Salmon
Canada	NB	Nashwaak
Canada	NB	Petitcodiac
Canada	NB	Pollert
Canada	NB	Saint John
Canada	NB	Maguadavic
Canada	NB	St. Croix
US	Maine	Aroostook
US	Maine	Machias
US	Maine	Narraguas
US	Maine	Union
US	Maine	Penobscot
US	Maine	Androscooggin
US	Maine	Saco
US	NE	Merrimack
US	NE	Connecticut

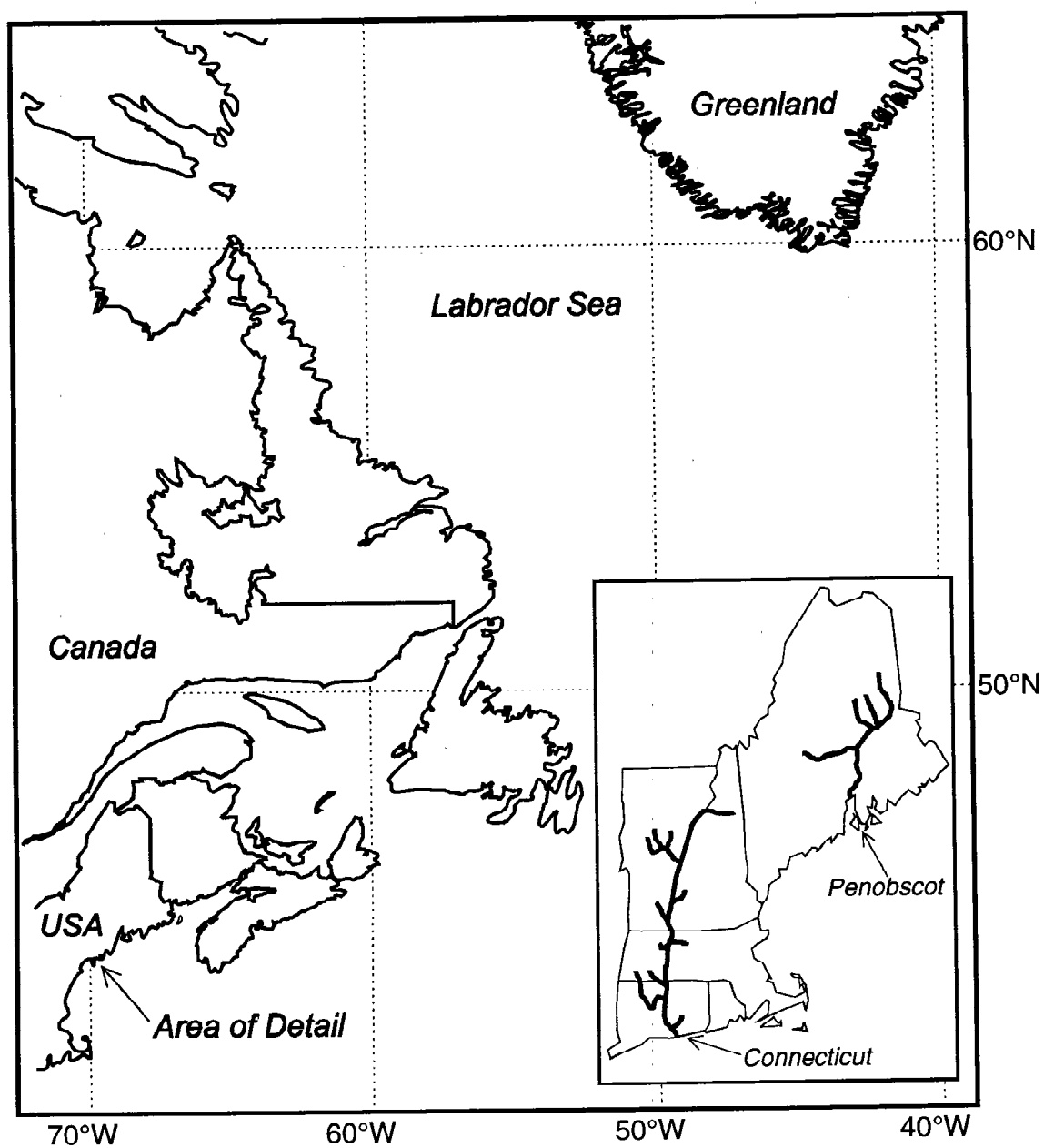
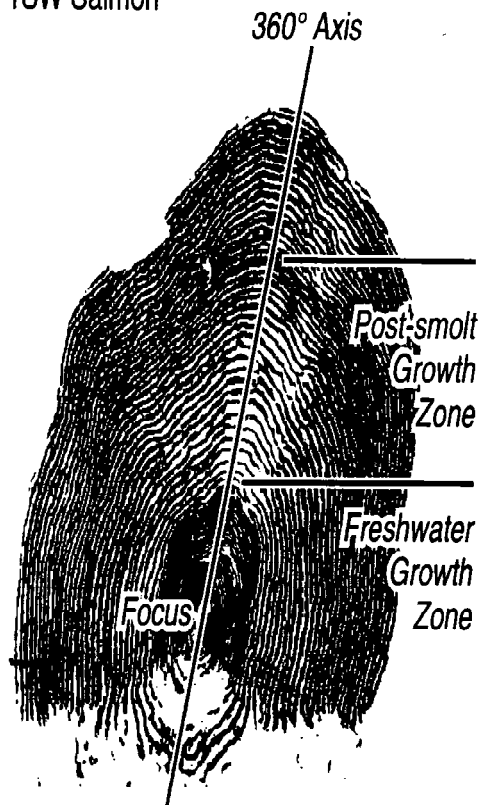


Figure 2.31.1. Map of Northwest Atlantic Area.

Illustrations of Atlantic Salmon Scales

1SW Salmon



Post-Smolt

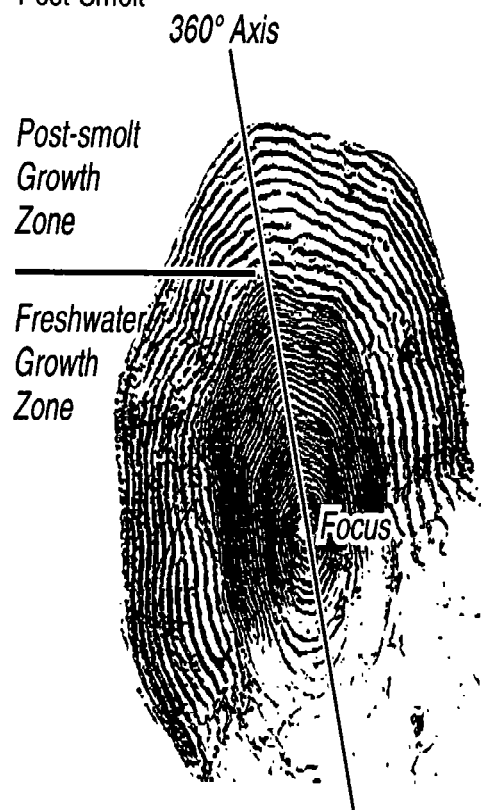


Figure 2.3.1.2. Atlantic salmon scales with growth zones marked.

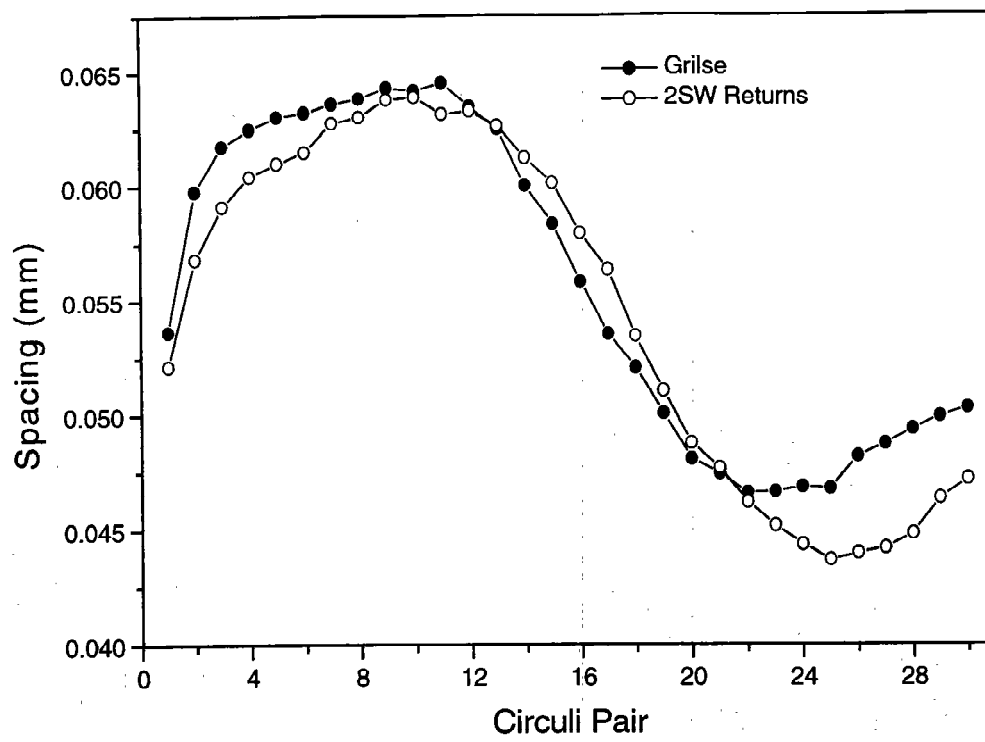


Figure 2.3.1.3. Circuli spacing patterns for 1SW and 2SW returns to the Penobscot River.

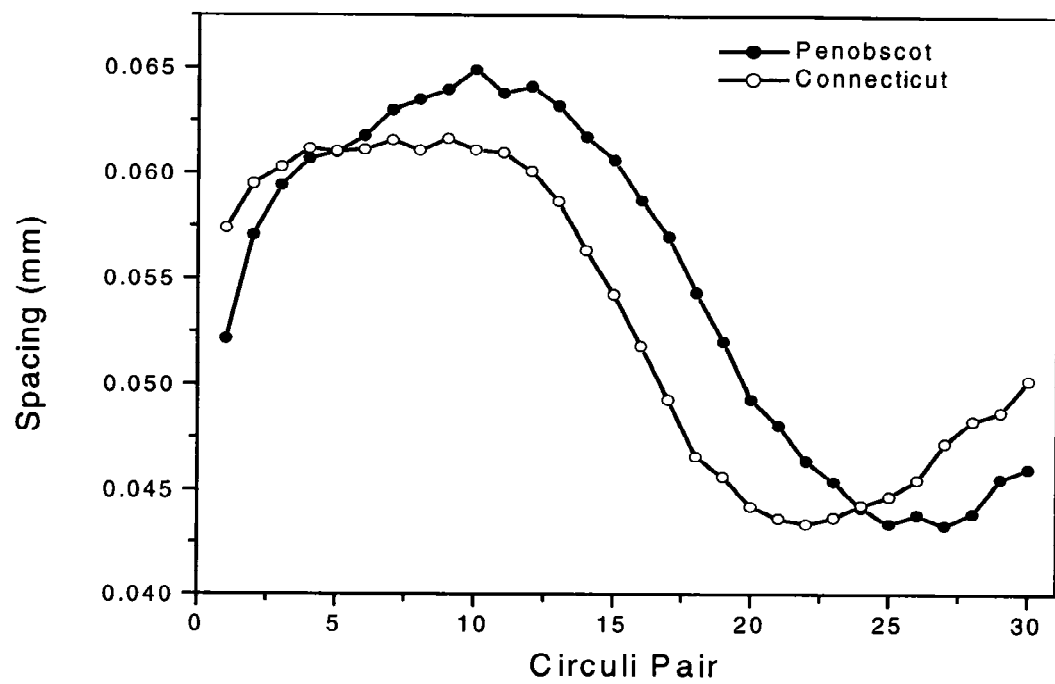


Figure 2.3.1.4. Circuli spacing patterns for Penobscot and Connecticut river 2SW salmon.

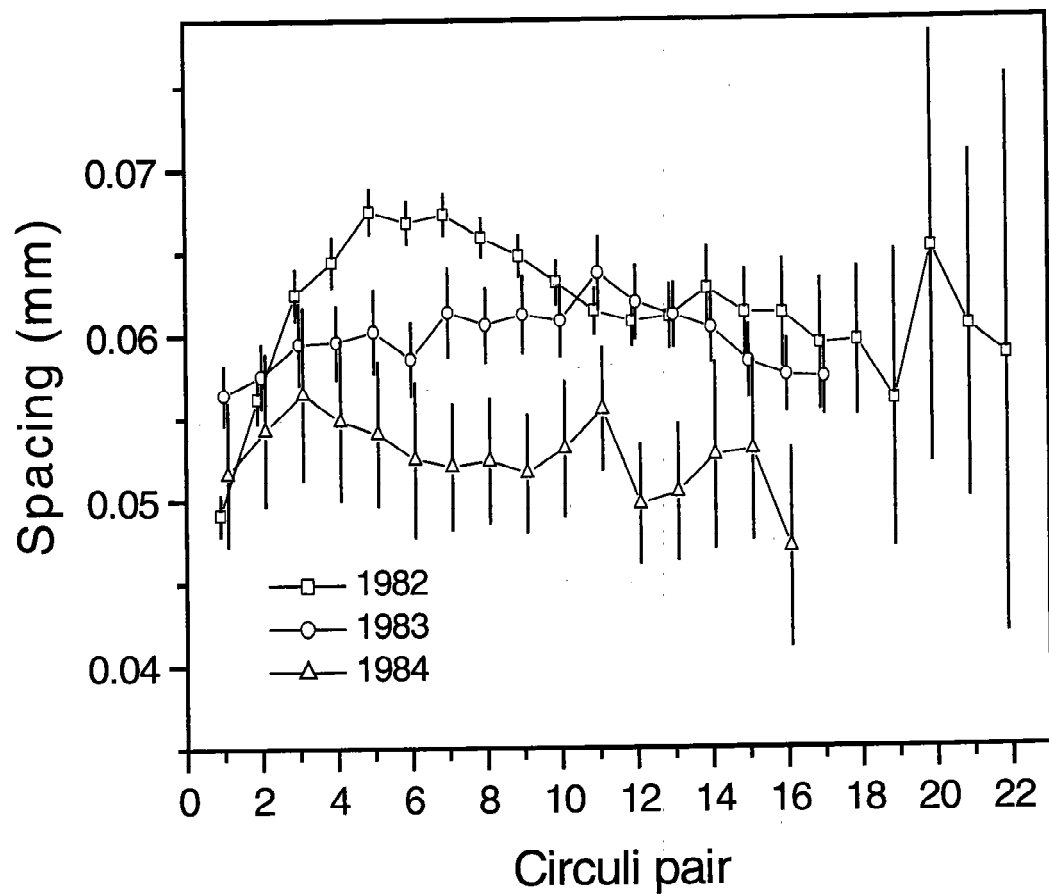


Figure 2.3.2.1. Circuli spacing of Gulf of St. Lawrence post-smolts.

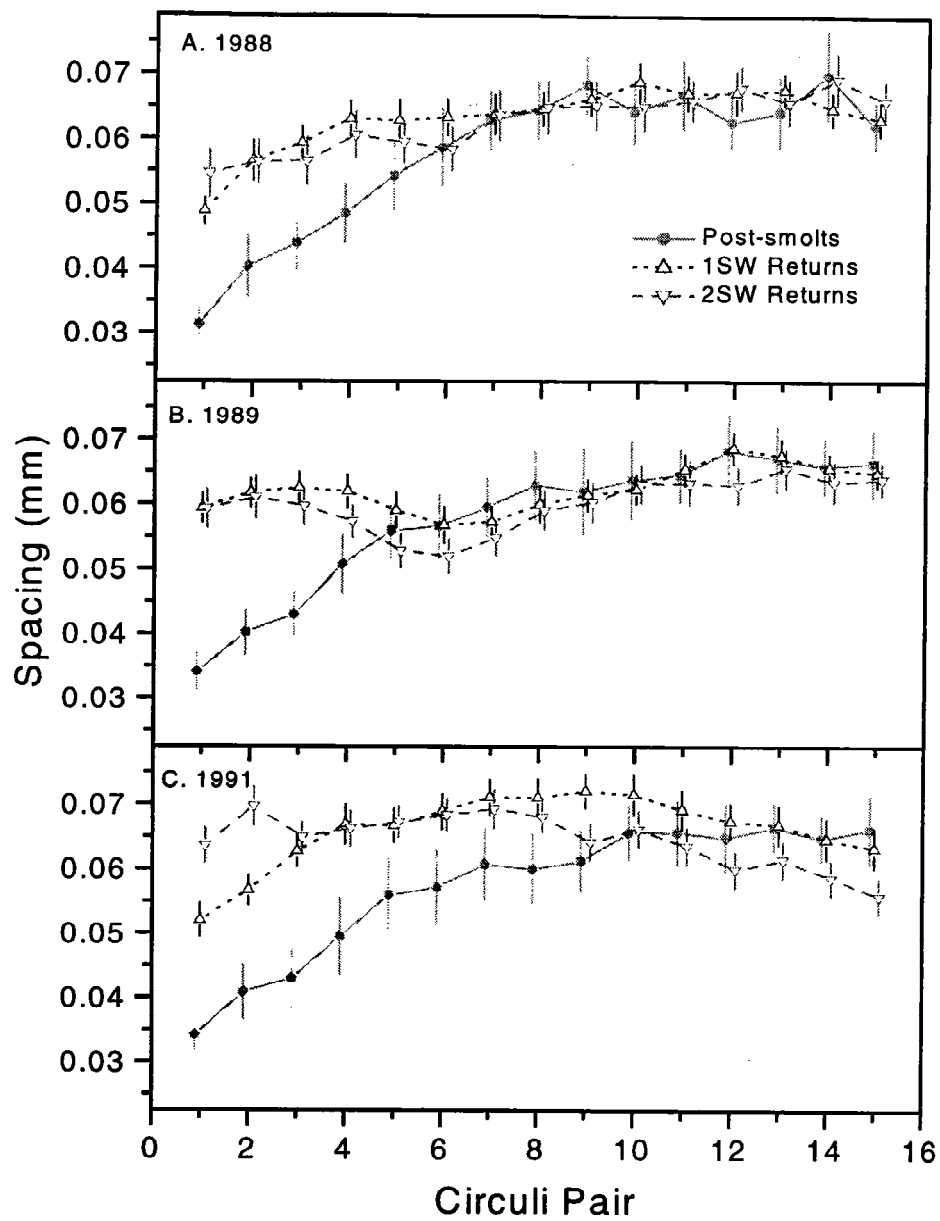


Figure 2.3.2.2. Circuli spacing of Labrador Sea post-smolts and Penobscot River 1SW and 2SW returns.

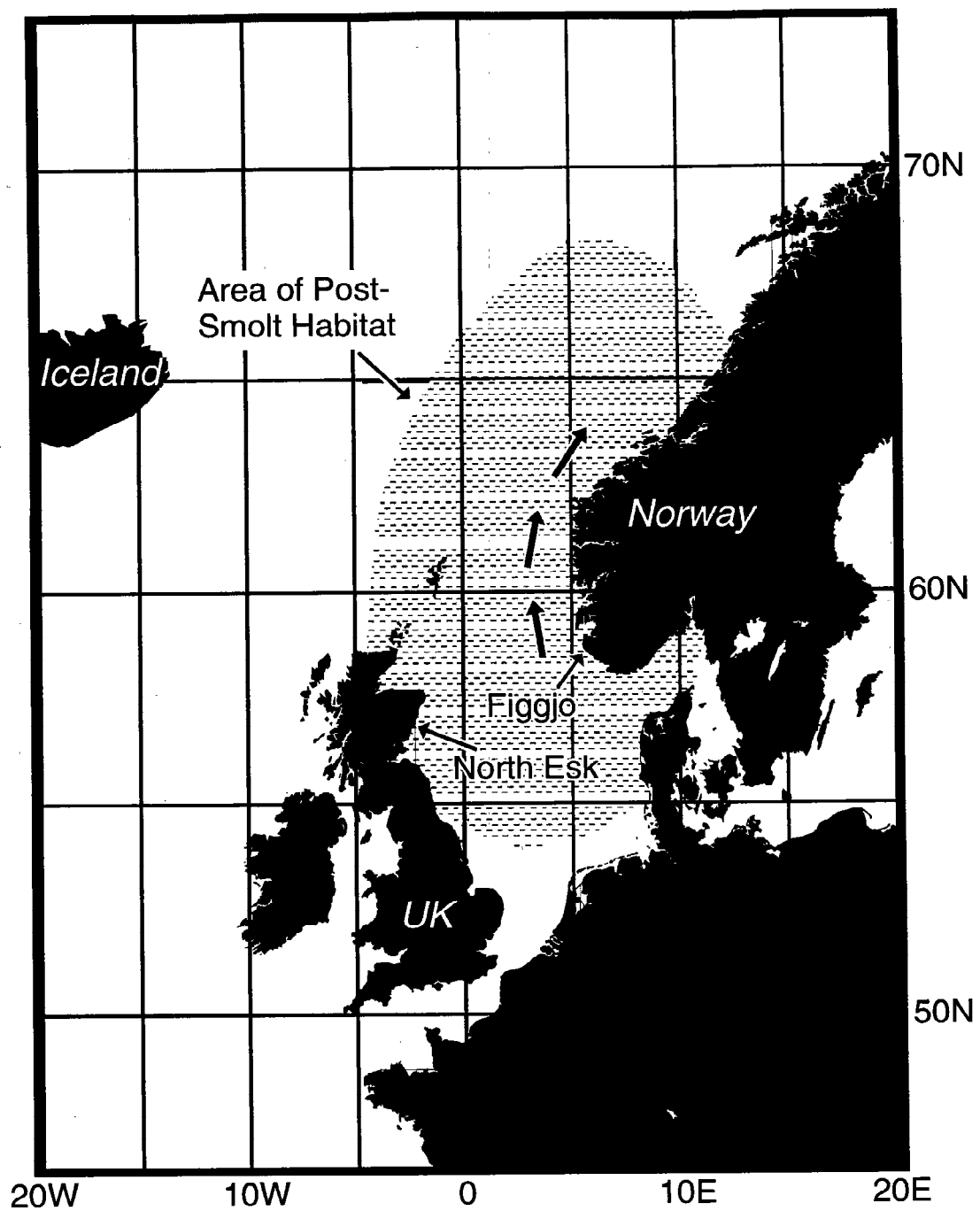


Figure 2.4.1.1. Map of Northeast Atlantic area with rivers Figgjo and North Esk indicated and general area of post-smolt habitat marked with hatching. Large arrows show general direction of Norwegian coastal current.

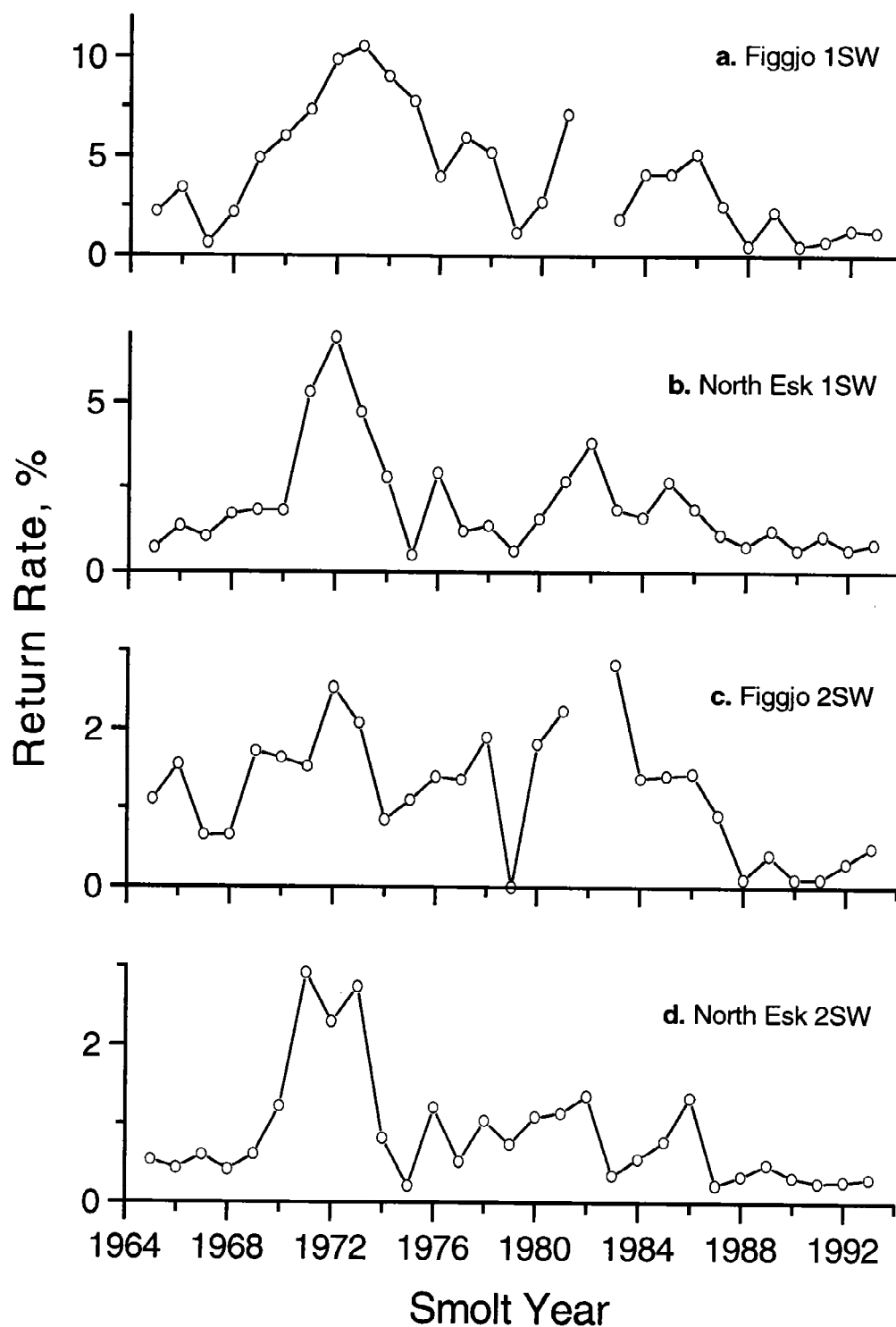


Figure 2.4.1.2. Tag recovery rate for 1SW and 2SW salmon to the rivers Figgjo and North Esk versus smolt year: (a), tag recovery rate for 1SW salmon to the river Figgjo; (b), tag recovery rate for 1SW salmon to the North Esk; (c), tag recovery rate for 2SW salmon to the river Figgjo; and (d), tag recovery rate for 2SW salmon to the North Esk.

Figure 2.4.1.3. Correlation between ISW return rate for Figgjo and North Esk salmon and thermal habitat versus month. Thermal habitat computed for four thermal ranges: 5-7°C (a); 6-8°C (b); 7-9°C (c); and, 8-10°C (d). Grid lines at $r=0.4$ represents the approximate location of significance at $p=0.05$.

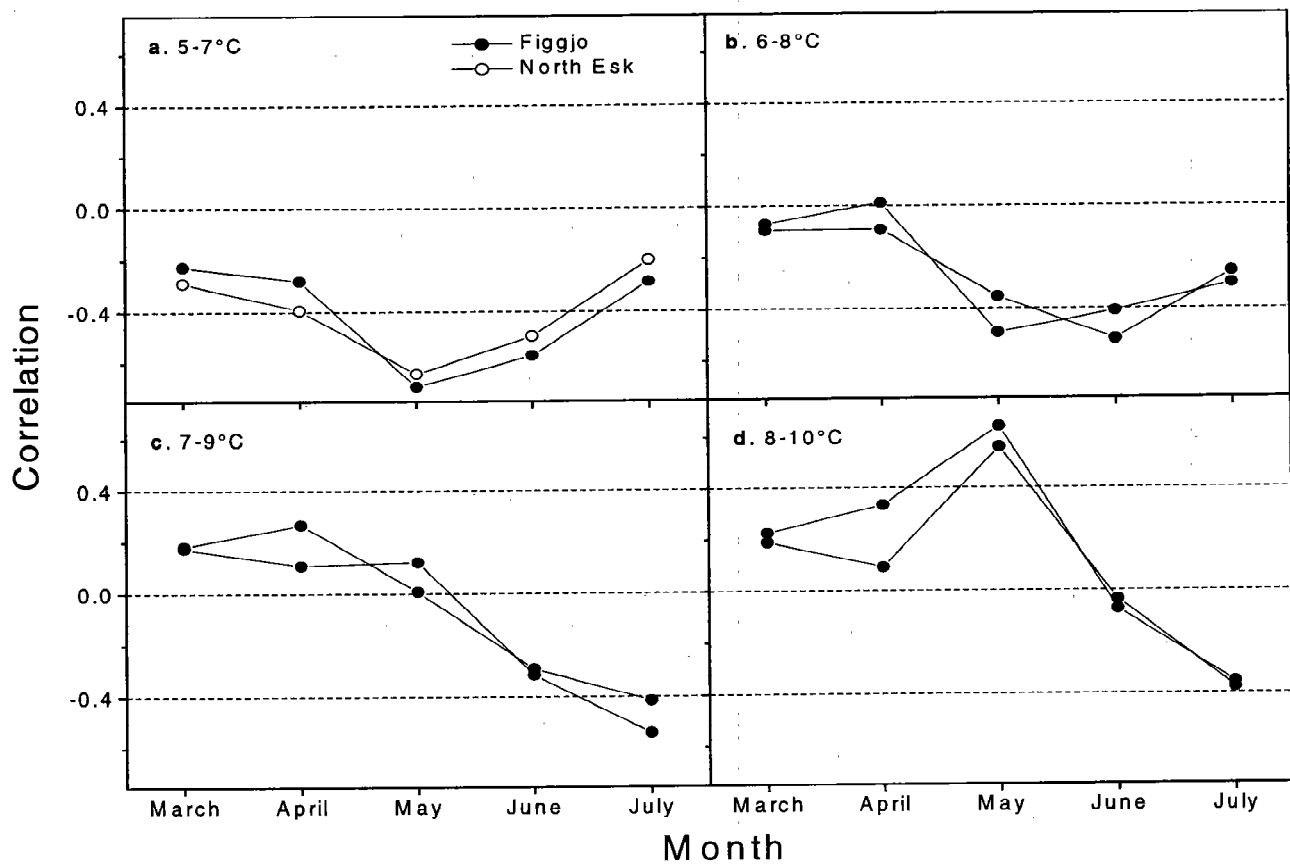


Figure 2.4.1.4. Correlation between 2SW return rate for Figgjo and North Esk salmon and thermal habitat versus month. Thermal habitat computed for four thermal ranges: 5-7°C (a); 6-8°C (b); 7-9°C (c); and, 8-10°C (d). Grid lines at $r=0.4$ represents the approximate location of significance at $p=0.05$.

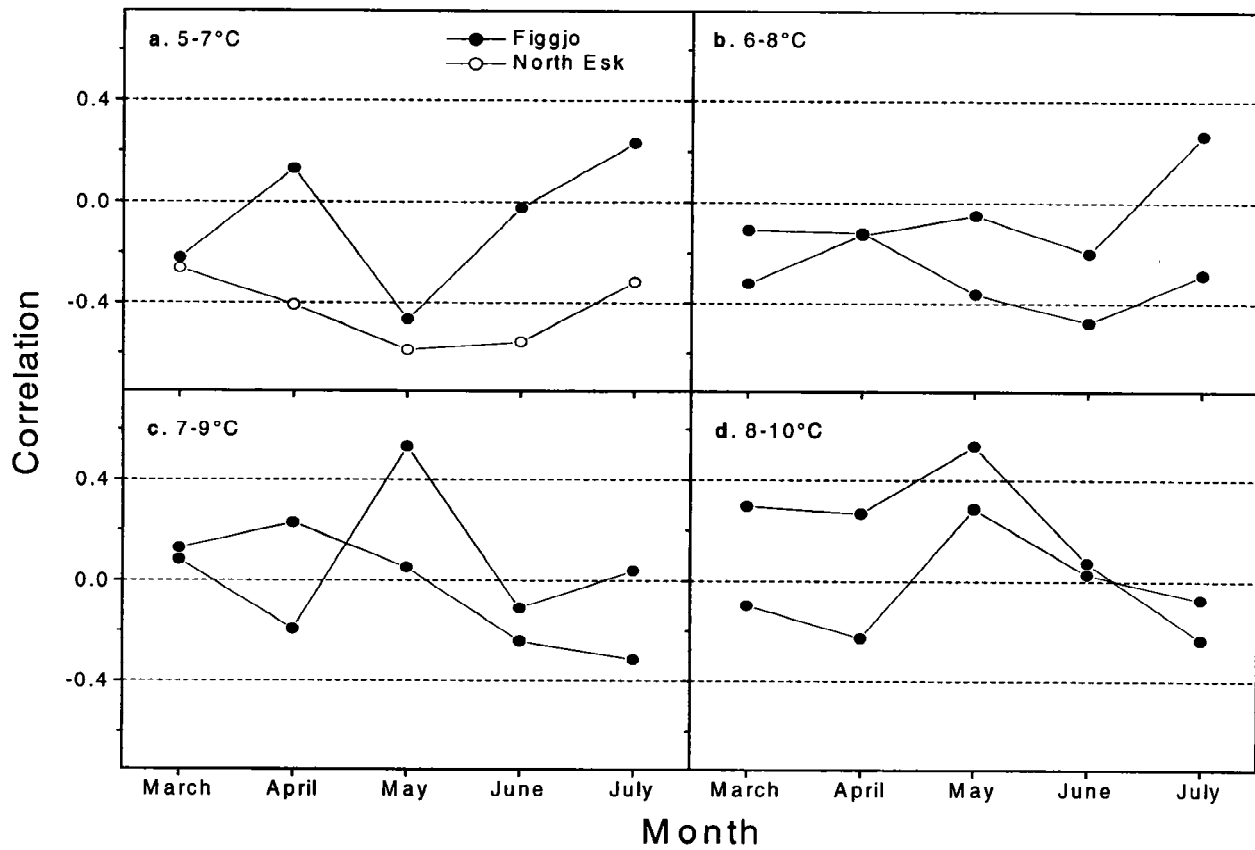


Figure 2.4.1.5. Sea surface temperature maps of the Northeast Atlantic area with the SST area of 8-10°C marked with hatching for two time periods 1971-74 and 1985-88, over the months: March (a); April (b); May (c); and, June (d).

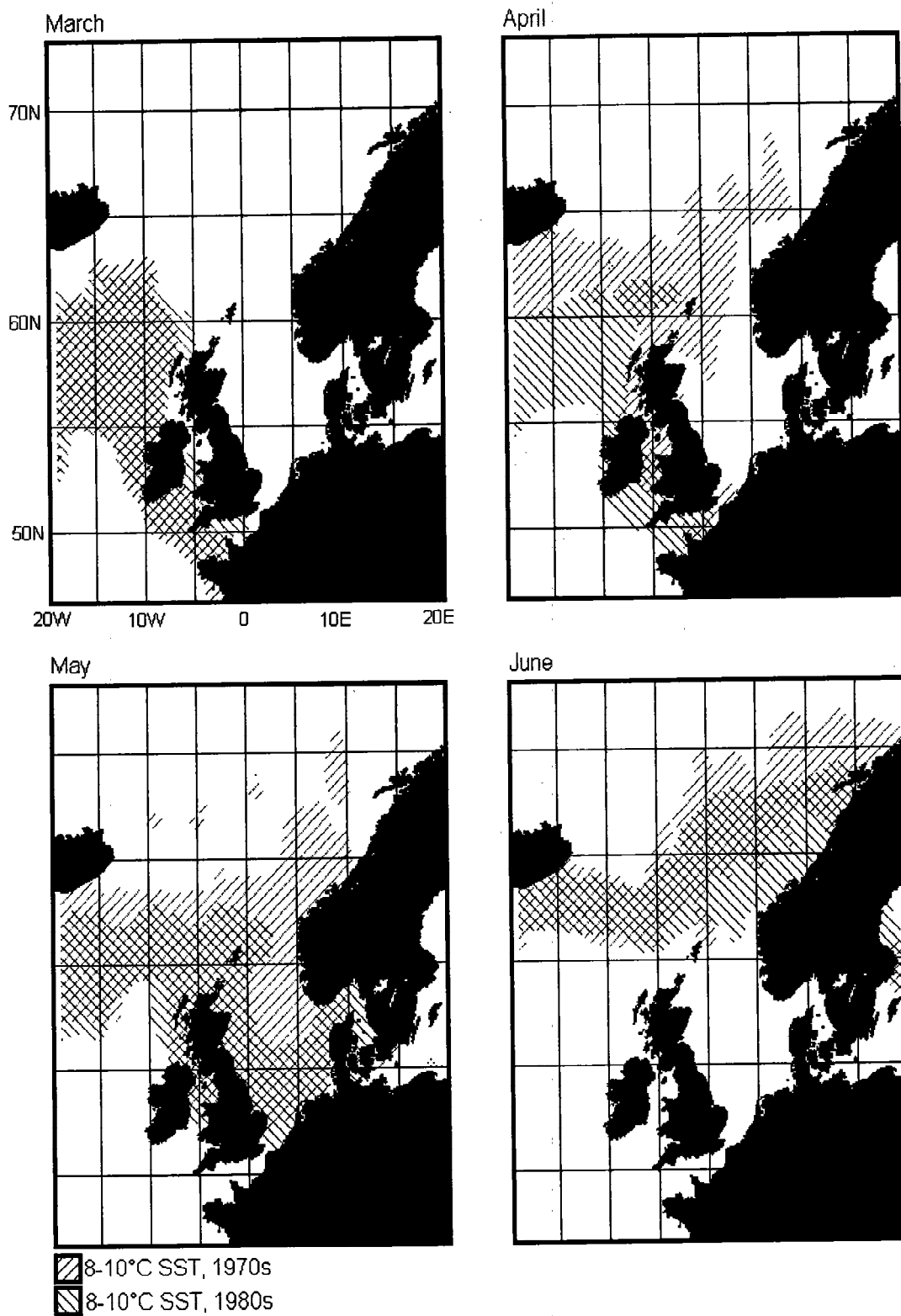


Figure 2.4.1.6. Post-smolt growth increment versus smolt year for 1SW and 2SW returns to the North Esk.

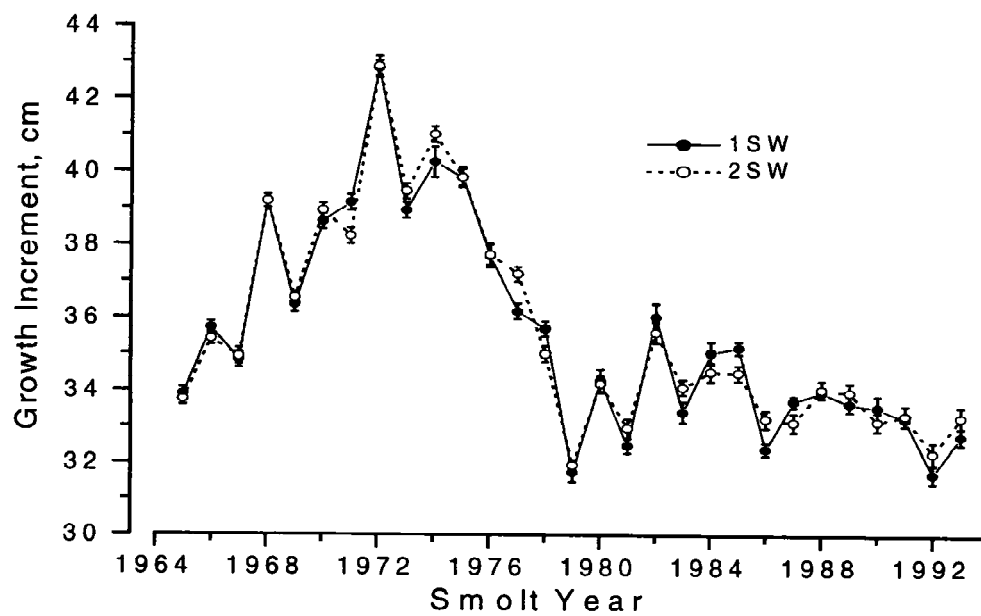
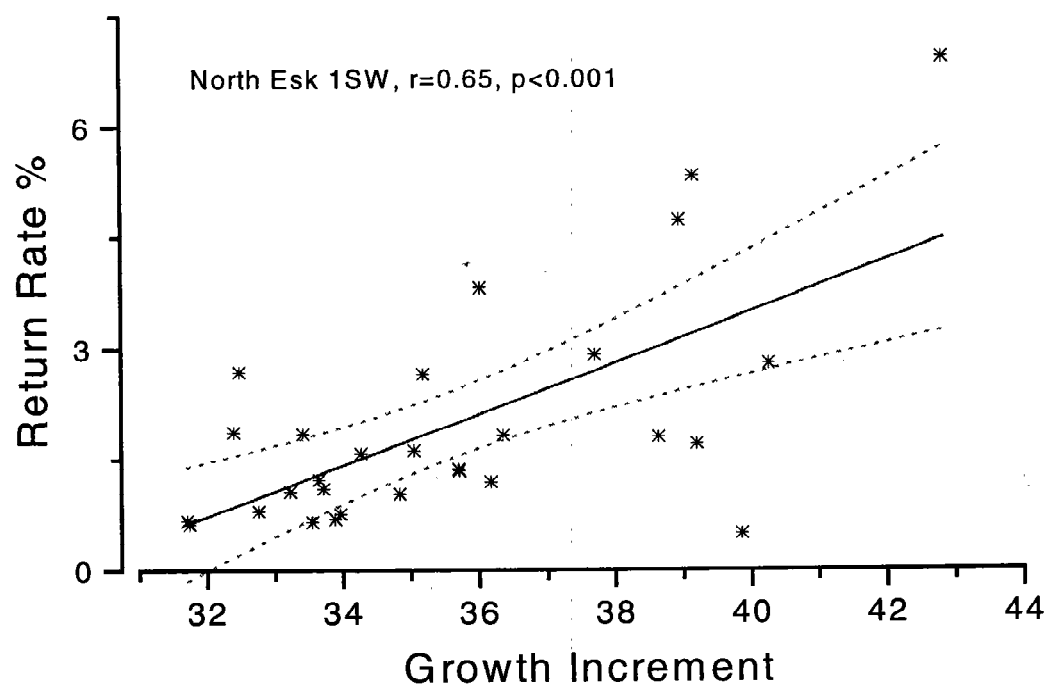


Figure 2.4.1.7. Scattergram and regression between 1SW return rate and post-smolt growth increment. Dashed line represents 95% confidence interval.



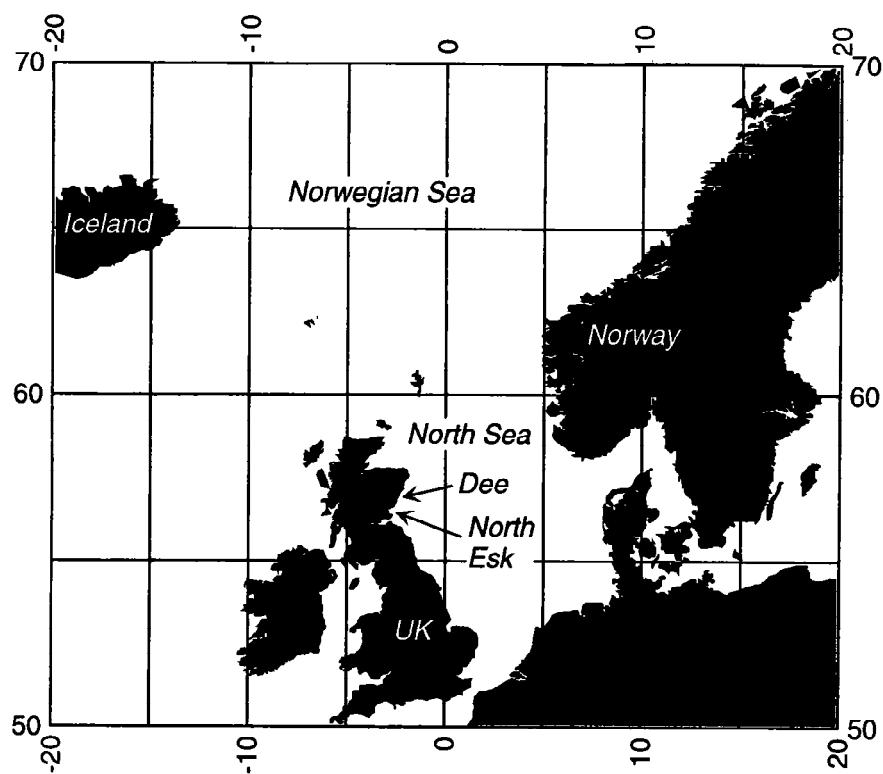


Figure 2.4.2.1. Map of Northeast Atlantic area showing the rivers Dee and North Esk.

Figure 2.4.2.2 Back-calculated post-smolt growth increment for returns to the North Esk and scale measurement growth increment for returns to the Girnock Burn versus smolt year.

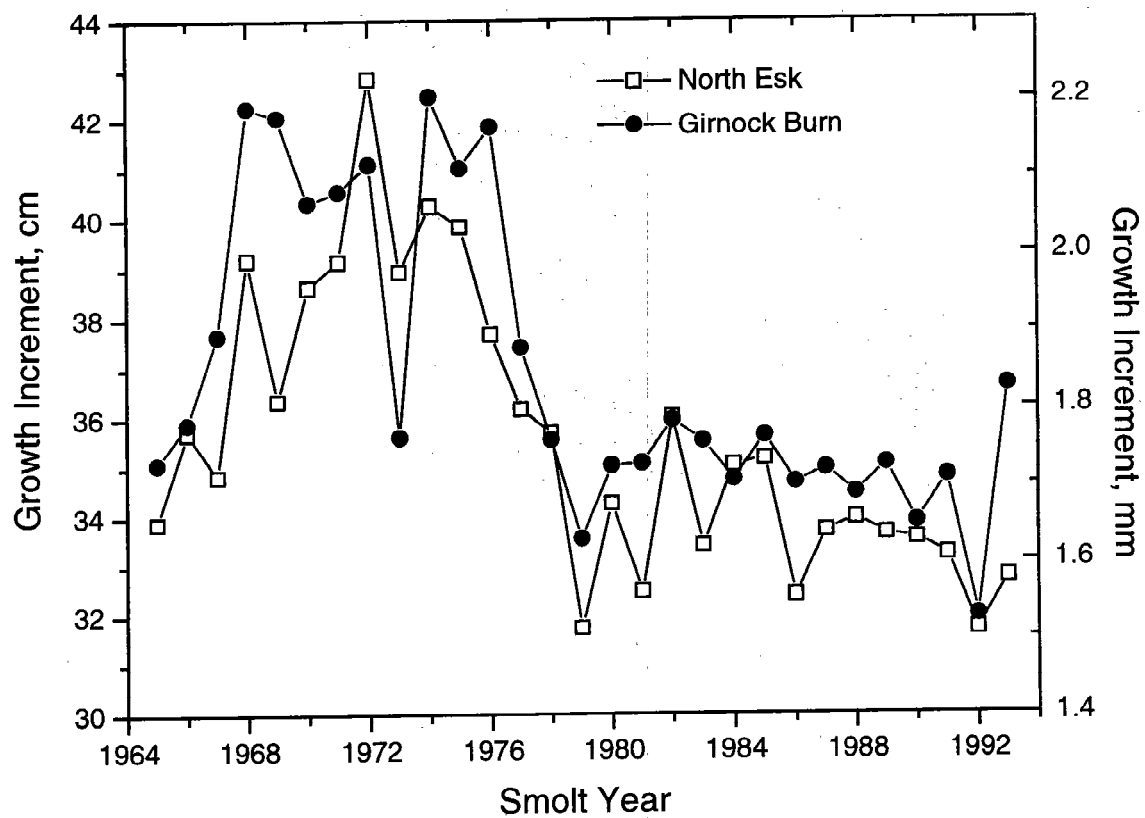


Figure 2.4.2.3. Time series trends in catch in the rivers North Esk (A) and Dee (B) made by all gears and by fixed engine only.

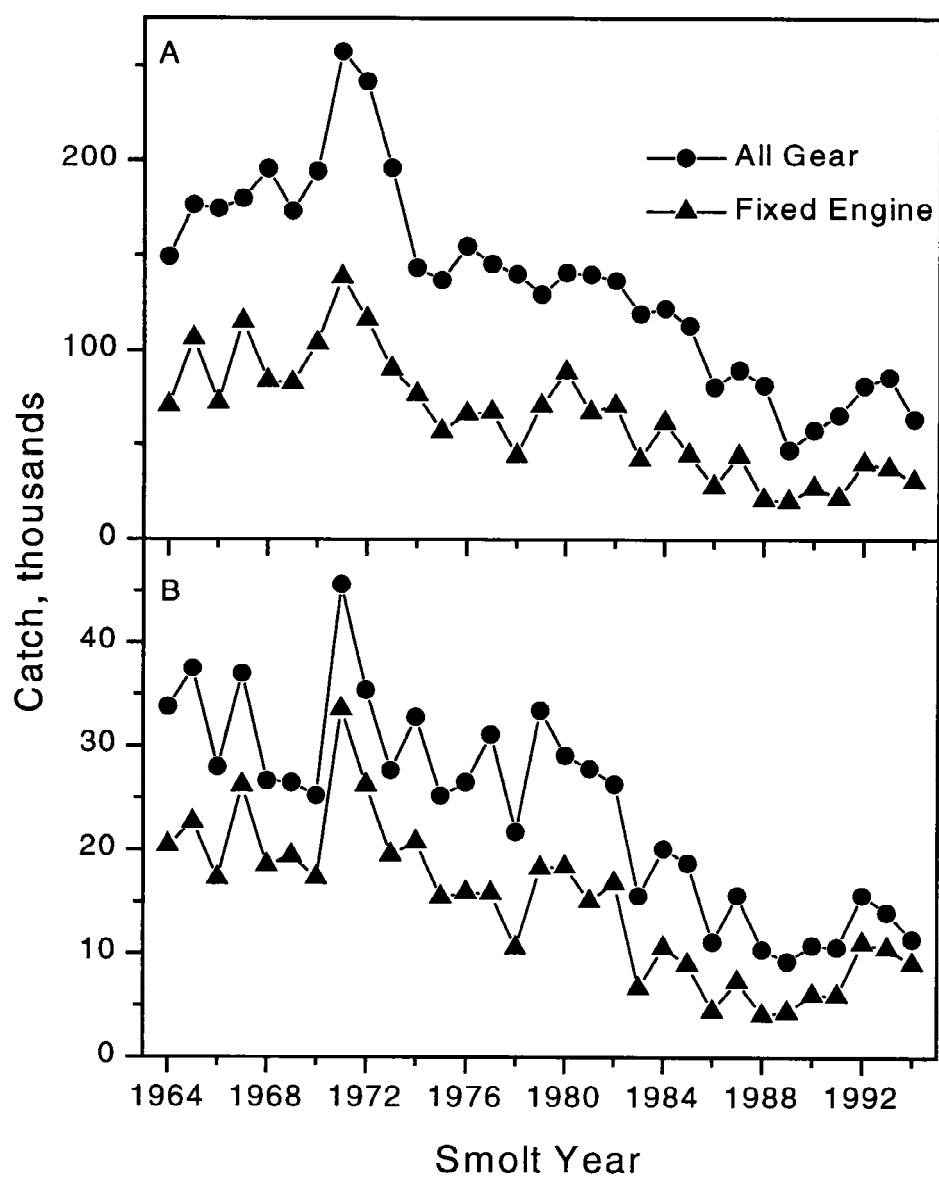


Figure 2.4.2.4. Z scores of North Esk total return rate index and total catch from all gears versus the North Esk post-smolt growth increment.

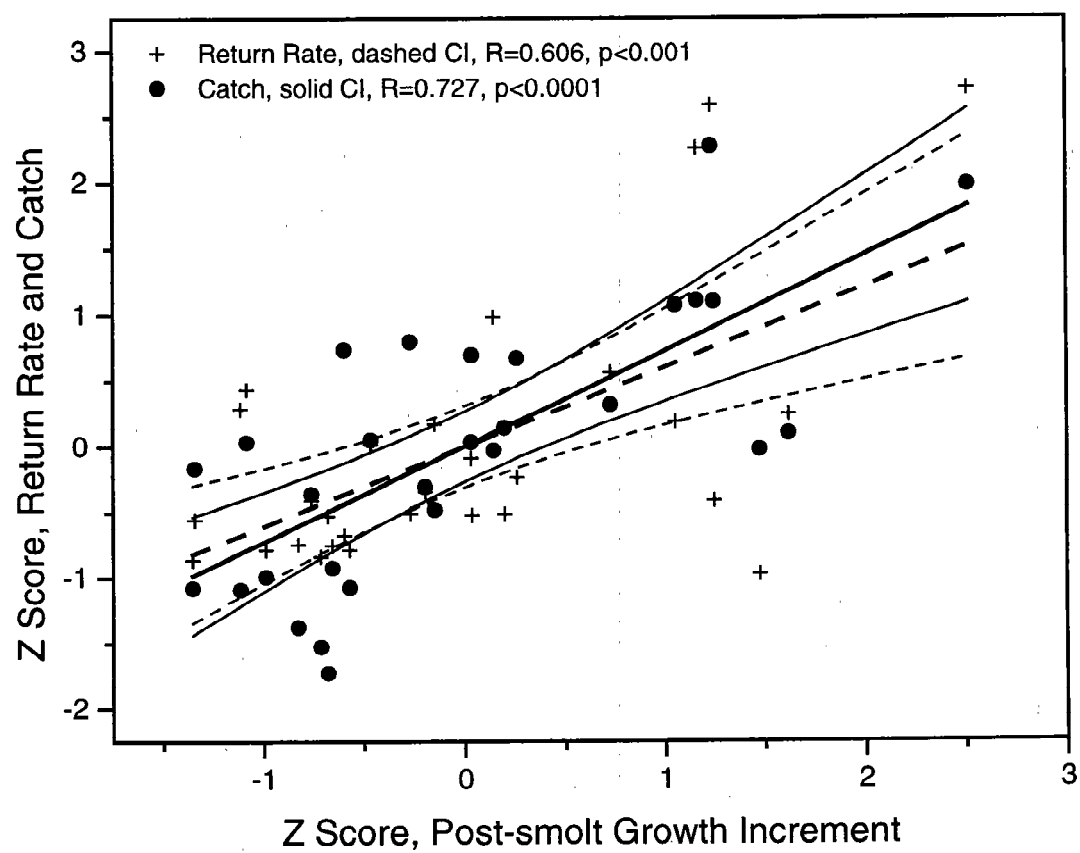


Figure 2.4.2.5. Z scores of Dee all gear and fixed engine total catches versus the Girnock Burn post-smolt growth increment.

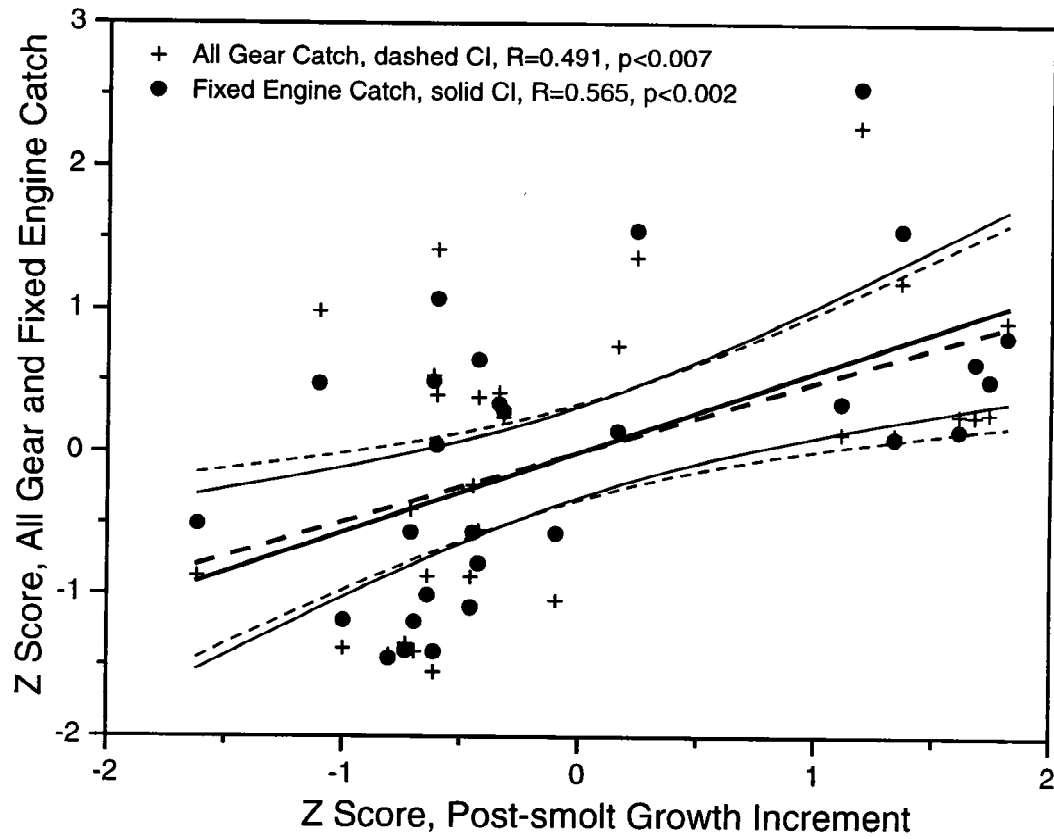


Figure 2.5.1. Nominal catches of Atlantic salmon 1960-1998.

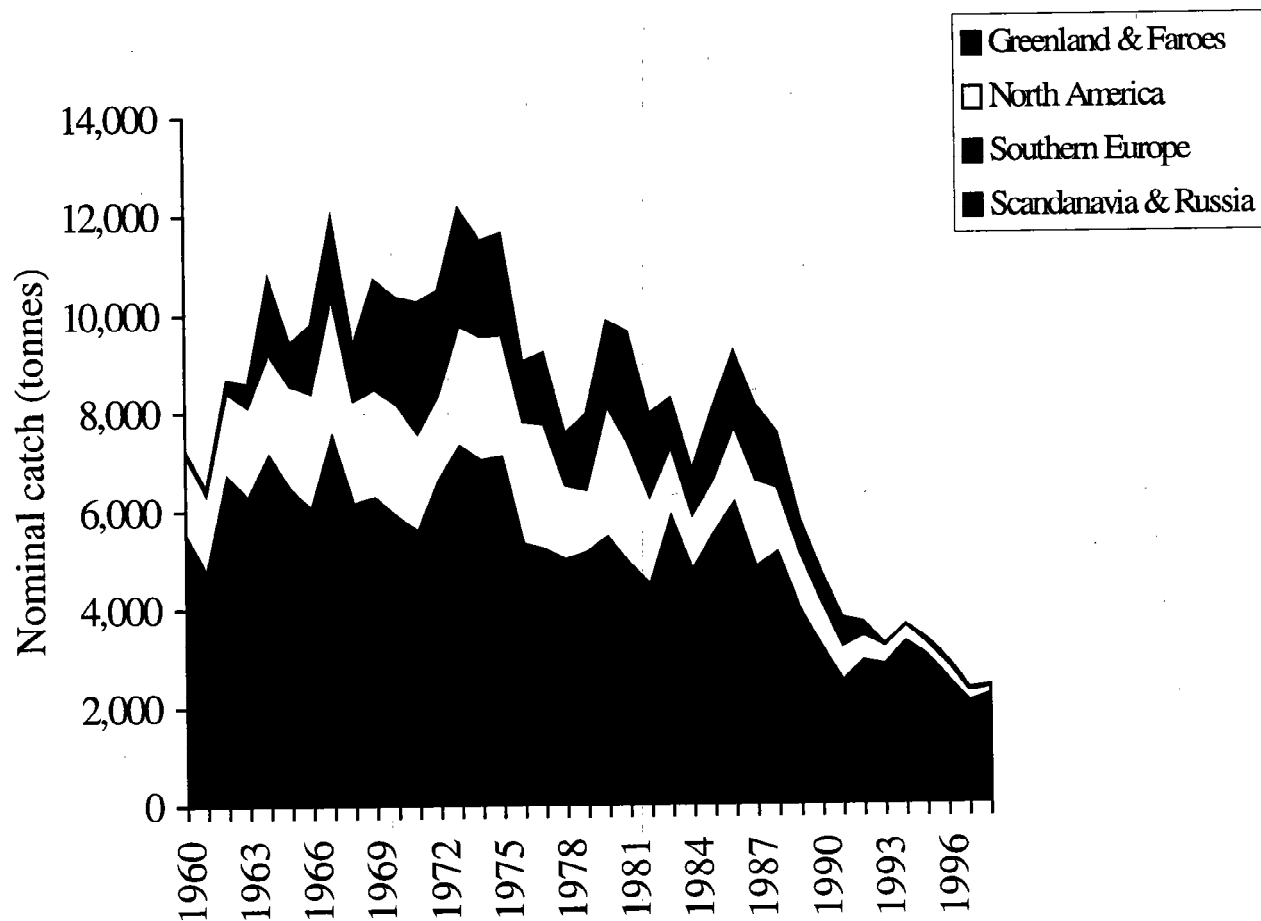
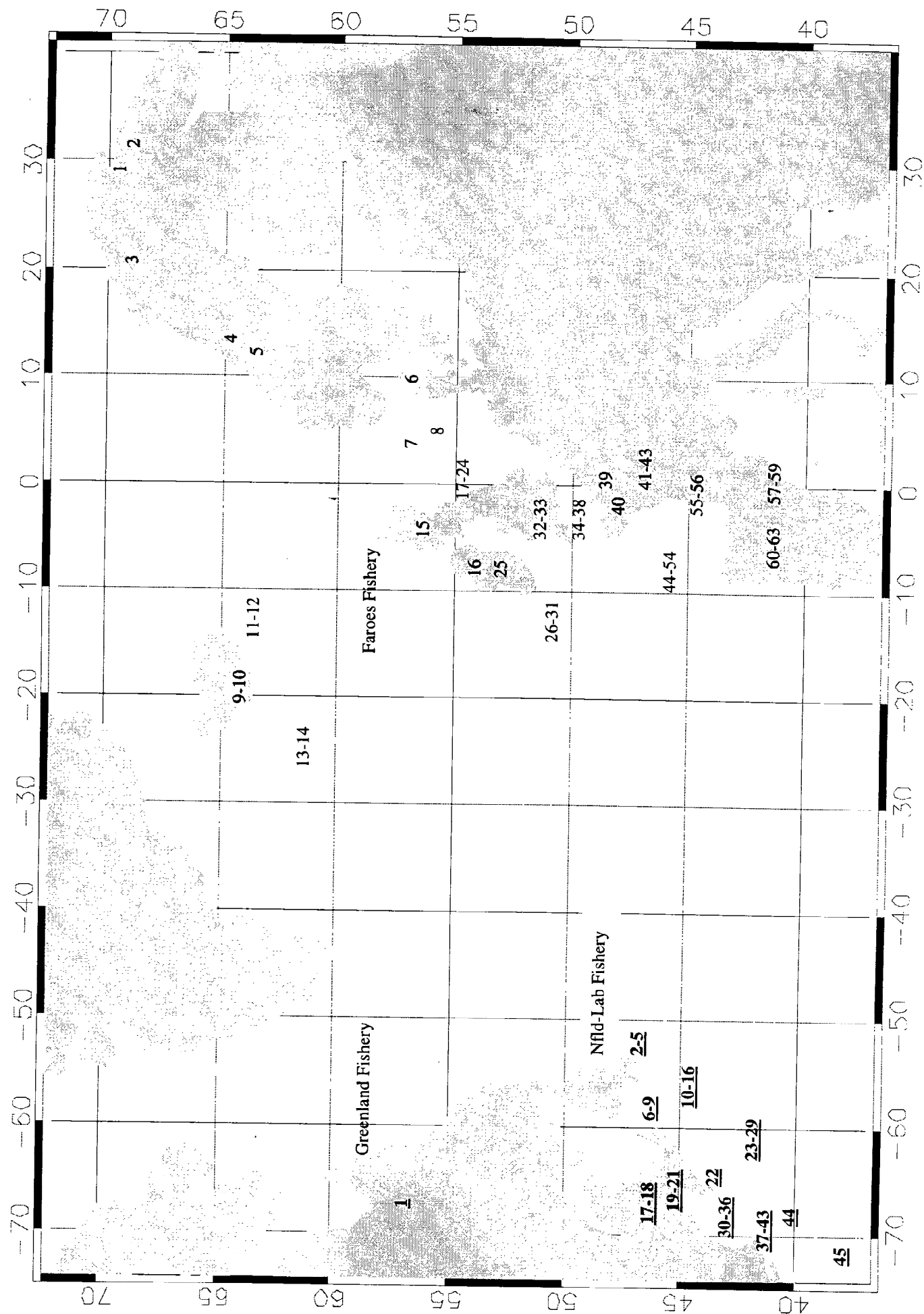


Figure 5.1. Map of the North Atlantic area showing the location of rivers from which scale samples are known to exist.





A4



Job separation sheet
Feuille de séparation des tâches
Auftrags-Trennblatt
Hoja de separación de tareas
Foglio di separazione lavori

