Ocean climate influences on critical Atlantic salmon (Salmo salar) life history events

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Abstract: Ocean climate and ocean-linked terrestrial climate affect nearly all phases of Atlantic salmon (Salmo salar) life history. Natural mortality in salmon occurs in two main phases: juvenile stages experience high mortality during freshwater residency and pre-adult salmon experience high mortality in estuarine and ocean environments. Freshwater survivorship is well characterized and tends to be less variable than marine mortality. Sources of marine mortality are poorly known due to a lack of basic knowledge about post-smolt distributions and habits. Coherence patterns among regional and continental stock groups suggest broad scale forcing functions play a more important role in defining recruitment than mortality effects associated with individual rivers. The action of mesoscale regional environment is most prominent during the post-smolt year when survival, maturation, and migration trajectories are being defined. During the early weeks at sea, growth mediated survival defines recruitment patterns. A correlation between sea surface water temperature and survival has been observed for salmon stocks in the northeast Atlantic suggesting temperature either directly affects growth or modifies post-smolt behavior. Age at first maturity is controlled by environmental as well as genetic factors. The abundance of two seawinter spawners in North America is directly scaled to the size of overwintering thermal habitat in the northwest Atlantic, which suggests a link between maturation and environment.

Résumé : Le climat océanique et le climat terrestre lié à l’océan influent sur presque toutes les phases du cycle vital du saumon de l’Atlantique (Salmo salar). La mortalité naturelle du saumon se produit dans deux phases principales : les juvéniles connaissent une forte mortalité durant leur séjour en eau douce, et les pré-adultes meurent en grand nombre dans les milieux estuariens et océaniques. La survivie en eau douce est bien caractérisée et tend à être moins variable que la mortalité dans le milieu marin. Les causes de mortalité dans le milieu marin sont mal connues en raison de notre manque de connaissances de base concernant les répartitions et les morts des post-smolts. Les profits de cohérence entre les groupes de stocks régionaux et continentaux laissent penser que des phénomènes de forçage à grande échelle jouent un rôle plus important dans la détermination du recrutement que les facteurs de mortalité liés aux rivières prises individuellement. L’action du milieu régional à échelle moyenne est maximale durant l’année de post-smolt où la survie, la maturation et les trajectoires migratoires sont définies. Durant les premières semaines en mer, la survie liée à la croissance définit les profils de recrutement. On a observé une corrélation entre la température de l’eau de la surface de la mer et la survie chez les stocks de saumon du nord-est de l’Atlantique, ce qui laisse penser que la température affecte directement la croissance ou modifie le comportement des post-smolts. L’âge à la première maturité est déterminé par des facteurs tant environnementaux que génétiques. L’abondance des géniteurs dibermarins en Amérique du Nord est directement proportionnelle à la taille de l’habitat thermique hivernal dans le nord-ouest de l’Atlantique, ce qui laisse penser qu’il existe un lien entre la maturation et l’environnement.

Introduction

Survivorship in Atlantic salmon (Salmo salar) populations can be partitioned by mortality occurring in freshwater and mortality occurring during the marine phase. Mortality rates during the freshwater phase are estimated with a great deal of accuracy and precision because freshwater populations are accessible. Freshwater populations can be censused by fences or barriers that allow exact counts of migrating adults and juveniles. Marine mortality has been more difficult to assess. After salmon smolts migrate to sea they are usually uncensused until they appear in fisheries over a year later. For decades the life history of post-smolts was virtually unknown. Only recently have survey designs improved to allow characterization of post-smolt distribution, diet, and survivorship (Shelton 1997). These new surveys, in combination with indirect methods that make use of a variety of existing data, have allowed scientists to make new inferences about salmon in the sea.

One of the simplest and most effective uses of existing datasets has been to examine coherence patterns in abundance and catch time series data. Coherence, or synchrony, refers to the common response of fish stocks to environmental effects over broad spatial scales. Coherence has been observed in groundfish and pelagic species (Koslow et al. 1987; Zebdi and Collie 1995); however, the caveat that applies to other species, as well as salmon, is that the appropriate spatial scale of coherence is often difficult to estimate (Cohen et al. 1991; Myers et al. 1995). In Atlantic salmon, the strong stock and recruitment relationships that exist between egg deposition and juvenile production (Symons 1979; Chadwick 1982; Buck and Hay 1984) are often

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difficult to match in the eventual relationships that emerge between egg deposition and adult recruitment (Solomon 1985; Elliott 1993). Sea survival is generally more variable than freshwater survival (Chadwick 1987) and the emerging paradigm is that covariation among stocks is driven by broadscale climate fluctuations (Adkison et al. 1996). The action of mesoscale regional environment is most prominent during the post-smolt year when survival, maturation, and migration trajectories are being defined. However, the action of ocean driven environment on freshwater production and smolt migration play important roles as well.

Recruitment in Atlantic salmon populations is controlled by events that take place during their first year at sea (Scarnecchia et al. 1989; Salminen et al. 1995; Friedland et al. 1998a). Variation in recruitment translates directly into catches in commercial and recreational fisheries and spawning escapement. Thus, post-smolt mortality and the factors that control its annual variation are of paramount interest to scientists and managers. Furthermore, the highest marine natural mortality rates in salmonids are believed to occur during the first weeks to months at sea (Fisher and Pearcy 1988; Holtby et al. 1990; Eriksson 1994; Salminen et al. 1995). These mortality effects are believed to be growth mediated during this period due to either variation in ocean productivity, interspecific competition, or intraspecific interactions (Ricker 1962; Neilson and Geen 1986; L’Abee-Lund et al. 1993; Friedland et al. 1996). Therefore, broad scale processes that affect salmon growth are of great interest. However, in addition to mortality effects, annual variation in the rate of sexual maturity also influences recruitment patterns to fisheries and escapement at various ages. Both stock genetics and environmental effects pattern sexual maturation; the relative influences of these effects on maturation, especially as it relates to maturation after only a single year at sea, is still being actively researched (Thorpe 1994; Friedland and Haas 1996; Friedland et al. 1996). However, it is clear that stocks have different maturity schedules, often associated with latitude, and that age-at-maturity can change over time (Power 1981; Saunders 1981; Shearer 1990; Summers 1995).

Mortality and maturation mechanisms in salmon appear to be linked to ocean climate. Maturation, as evidenced by returns and survival of various aged salmon, has been shown to vary in correlation to a number of environmental signals such as temperature (Saunders et al. 1983; Scarnecchia 1983; Martin and Mitchell 1985; Scarnecchia et al. 1991; Friedland et al. 1993). However, in some cases ocean conditions associated with growth and maturation co-vary with conditions affecting the survival of smolts entering the sea (Scarnecchia et al. 1989). Survival of Pacific salmon species have been shown to vary with fluctuations in broadscale circulation patterns like ENSO events (Johnson 1988; Beamish and Bouillon 1993; Francis and Hare 1994) and more localized upwelling circulation that would be expected to impact local productivity and juvenile salmon growth (Fisher and Pearcy 1988; Kope and Botsford 1990). Even in confined systems like the Baltic Sea, the effects of temperature and circulation have been identified as determinants of growth and survival (Salminen et al. 1995).

In this paper, I will examine the general question of how climate impacts critical Atlantic salmon life history processes across freshwater and marine habitats, especially focusing on mortality and maturation. I will first review coherence patterns in regional stock groups of Atlantic salmon and consider what they suggest about the relative role of freshwater and marine mortality effects. I will then consider the effect of ocean-linked climate patterns on freshwater recruitment and growth and examine climate linkages to migration cues. Next, I will describe relationships between early post-smolt survival and ocean climate observed for Atlantic salmon populations in the northeast Atlantic. Finally, I will try to relate environmentally guided migration trajectories to the maturation process.

Coherent trends in regional population groups

Scale for coherence patterns

Coherence patterns in Atlantic salmon have been observed on continental and regional scales. Friedland et al. (1993) observed significant correlation among survival time series for five salmon stocks ranging geographically from Newfoundland to the northeast United States, which represents nearly the entire range of Atlantic salmon in North America. Coherence patterns can also be specific for sea age of return. Return rates for two sea-winter (2SW) salmon in the Penobscot and Saint John rivers in North America are highly correlated despite differences in the return rates for 1SW fish which comprise approximately 10% of the Penobscot stock and 60% of the Saint John runs (Friedland 1994). Correlation for groups of Icelandic rivers was demonstrated by examining catch time series (Scarnecchia et al. 1991). Grilse catch time series formed two clusters, one comprised of northeast coast rivers, the other northwest coast rivers. A stock clustering in central Europe is also evident from return rate data for wild stocks from southern Norway and western Scotland (Friedland et al. 1998a). Grilse return rates for the Figgjo and North Esk rivers, both of which empty into the North Sea, are highly correlated, whereas, the 2SW rates for the same rivers are less well correlated (Fig. 1). Population data for stocks outside the North Sea area suggest that survivorship varies regionally for other European stocks (Crozier and Kennedy 1993). Finally, correlation among catch time series for continental stock complexes suggests teleconnections may exist between the eastern and western North Atlantic. Fisheries have been largely unrestricted in North America and Europe for the period 1960–1995 with the exception of management measures implemented in recent years. The contrast in catch trends is large and can only be explained by changes in natural mortality and the recruitment process. The change in exploitation necessary to produce the observed change in catch is unrealistic and inconsistent with exploitation patterns observed from tagging experiments. Significant correlation between North American and southern European catches suggests a linkage between both complexes and a common environmental signal (Fig. 2C). However, this linkage is not as well developed between the northern European complex and either southern Europe or North American complexes, suggesting these stocks utilize different rearing areas and migrational pathways (Figs. 2A, 2B). Greenland and Faroese catches reflect the stocks harvested in the respective fishing zones.
From these analyses, it appears coherence is operating on continental and regional scales in Atlantic salmon. Despite the length of ocean migrations for the species, neighboring stocks appear to respond similarly to ocean conditions; thus we see many examples of allied river stocks with similar survival patterns. The scaling of these phenomena to the continental level suggests broadscale climate patterns, which simultaneously affect all regions of the ocean, are also at work.

**Spatial relationship and location for coherence**

A common pattern of catches and marine survival for any grouping of Atlantic salmon stocks suggests that factors controlling annual survivorship act nearly equally on all stocks in the group. This challenges conventional concerns about the natural mortality that occurs in river, estuary, or near-shore marine ecosystems proximate to natal rivers (Larsson 1985; Wood 1987; Hvidsten and Lund 1988; Magnhagen 1988). It is unlikely that riverine mortality could be synchronously linked with riverine mortality for fish emigrating from a river located in another geographic area. The correlation between survival rates suggests an important source of mortality acts on the stocks when they are in a common place or being acted upon by a common set of conditions. Since they are migrating from distinct locations, the longer they are at liberty, the greater the likelihood their distributions will begin to overlap. Under this scenario, more localized impacts may affect stocks if they share a common
migration destination. If on the other hand, the critical period for survival is early in the post-smolt year, there is a greater chance that the stocks will not be homogeneously mixed during the critical period. If coherence exists under these circumstances, it would argue for survival effects that act on broad spatial scales thus affecting stocks that may not overlap spatially.

**Land-sea interactions**

**Ocean-driven effects on freshwater production of juveniles**

Climate affects Atlantic salmon in freshwater through a number of physiological, behavioral, and feeding-related mechanisms. The main parameter defining spatial relationships and habitat suitability in freshwater is in-stream flow. In-stream flow, which is mediated by rainfall amounts, shapes spawning and juvenile habitats by mechanical means (Waters 1993). Production is further defined by the feeding opportunities and growth conditions associated with various habitats, again flow being a primary determinant (Gibson and Myers 1988; Mills 1989; Kennedy and Crozier 1993). Seasonal variations in mortality can be significant and are related to climate-mediated stress factors (Cunjak and Randall 1993). The migration from freshwater may be a source of significant mortality that can be ameliorated by river flows (Hvidsten and Hansen 1988). To the extent climate variation, both short-term variation and trend, are mediated by the same ocean-linked mechanisms affecting salmon during the marine phase, freshwater and marine productivity may also be linked.

Juvenile salmon growth and habitat is largely determined by climate effects related to prevailing temperature regimes and flow conditions. Regier and Meisner (1990) outlined three main areas where climate change is likely to impact freshwater fish populations: temperature, water quantity, and water quality. Regional or seasonal temperature change would be expected to directly influence juvenile salmon growth and the age at which fish smoltify and mature. Minns et al. (1995) simulated the effect of temperature change on populations in eastern Canada by calibrating a model of smolt age that is based upon temperature and latitude. Model results suggested that smolt age would significantly decrease with increasing temperature. Mangel (1994) derived similar model results, but further illustrated the reach of ocean climate change by also showing the expected change in maturity schedules.

Increases in temperature also pose a direct threat to populations at the southern end of the species’ range. Some populations experience near lethal thermal conditions during summer making any further increase in temperature intolerable (Power 1990). Changes in rainfall patterns, especially as they relate to diminished flows in streams and rivers, may severely impact productivity of salmon populations. Minns et al. (1995) examined the effect of anticipated changes in flow on the concomitant change in the amount of suitable rearing habitat for Atlantic salmon in eastern Canada. These changes suggest that the production potential of regional salmon stocks could be severely limited.

Water quality encompasses a wide spectrum of effects from physical attributes of a system to its biological productivity. Climate change may shift nutrient loading patterns, cause oxygen stress, or actually shift the composition of the...
forage base for juvenile fish (Henderson et al. 1992). Modeling by historical analogy offers useful predictive tools to deal with anticipated climate changes (Neitzel et al. 1991). Additionally, it has been shown that river flows can be used effectively in models of combined marine–freshwater effects on salmon production (Scarnecchia 1981; Scarnecchia et al. 1989).

Migration timing

Among the many traits locally adapted in individual salmon stocks, cued migration behaviors are some of the most important. The two main cues identified in the initiation of smolt migrations are climate-related factors. Water temperature has been identified by numerous authors as a key factor stimulating smolt migration (Solomon 1978; Jonsson and Ruud-Hansen 1985; Jonsson et al. 1989). Stream and river water temperatures reflect regional weather patterns and thus would be correlated to annual production cycles in the coastal ocean. Response to temperature cues would reliably synchronize migration to a particular production event (Friedland and Haas 1988). In some river systems, there is insufficient contrast in spring water temperatures to reliably initiate smolt migration, thus the environmental cues are not as distinct (Osterdahl 1969; Hestagen and Garnás 1986). Smolts entering the ocean either too early or too late would begin their post-smolt year on migrational trajectories that could be less than optimal in respect to feeding opportunities, invading predator fields, or thermal stress. Therefore, the evolution of these proximate migration mechanisms is critical.

Ocean survival effects

Temperature distributions

The relationship between post-smolt survival of European salmon stocks and sea surface temperature distribution was first noticed by Friedland et al. (1993). A composite catch time series was used as a surrogate for post-smolt survival and population abundance. Most of the catch in the time series is from grilse catches; therefore, it is assumed that annual variation in maturation does not play a large role (Fig. 3A). Spring thermal habitat was highly correlated with population abundance, suggesting that warmer conditions in spring favored post-smolt survival in the northeast Atlantic area (Fig. 3B). However, regional survival signals were added to the time series; and for 1960–1990 all nations are included. Total nominal landing for the European stock is compared to the first principal component of spring habitat (B). Data are smoothed (from Friedland et al. 1993).

Emerged from this analysis. The survivals of Figgjo and North Esk 1SW fish were negatively correlated with the area of 5–7°C SST in May (Figs. 4A, 4E). These correlations are strongest using data from centering longitudes in the range 0–4°E. The second correlation was a positive relationship between survival and the area of 8–10°C SST also in May (Figs. 4D, 4H). The peak correlations were achieved with data from centering longitudes more to the west than for the cold water correlations. The positive correlations observed for the 5–7°C habitat data are only more weakly echoed in the 6–8°C data (Figs. 4B, 4F) and no significant correlations appeared in the 7–9°C data (Figs. 4C, 4G).

These correlations are related to variation in sea surface temperature distribution in the North Sea and along the coast of Norway during spring. Spring warming during the period of high survival rates was more rapid than during the more recent period of lower survival. These differences can be most easily traced by following the area of 8–10°C water through the spring period, which is also biologically significant to juvenile salmon because it’s the temperature at which post-smolts typically first enter the marine environment. In March during the 1970’s period, 8–10°C SST was distributed west of Ireland and the United Kingdom and south of 63°N (Fig. 5A). This band of SST expanded north and eastward during April (Fig. 5B) and May (Fig. 5C) until the...
Fig. 4. Correlation between thermal habitat and recovery rate of 1SW salmon versus the center longitude used to calculate the thermal habitat time series. Each correlation is for data from a 22° longitude range. Data for the Figgjo stock and thermal habitat ranges of 5–7°C (A); 6–8°C (B); 7–9°C (C); 8–10°C (D). Data for the North Esk stock and thermal habitat ranges of 5–7°C (E); 6–8°C (F); 7–9°C (G); 8–10°C (H). Coordinates are labeled with numerical month of the year (from Friedland et al. 1998a).

North Sea and coastal waters off southern Norway were all in excess of 8°C. By early summer, 8–10°C water was distributed in the coastal waters off northern Norway and well into the Norwegian Sea (Fig. 5D). This is in contrast to the average distribution of SST during the 1980’s period. March 8–10°C SST distribution was almost identical to the 1970’s distribution (Fig. 5E); but, differences emerged by April when 8–10°C water extended much closer to the Norwegian coast than during the 1970’s period (Fig. 5F). Likewise, in the May SST distributions, 8–10°C water did not reach the Norwegian coast and the northern North Sea remained cool (Fig. 5G). June distributions were generally similar to the 1970’s period, except that the 8°C isotherm stayed below 70°N in the 1980’s distribution (Fig. 5H).

Survival of salmon stocks from the North Sea area appear to be affected by the distribution of spring water temperatures in the northeast Atlantic. Survival fluctuated similarly for both 1SW and 2SW salmon for both index stocks, thus the contribution of maturation mechanisms to the observed return rates can be discounted. Survival for 1SW fish is recorded as the rate of return of tags versus the number released. The tagged fish were at liberty for the post-smolt year before being recovered, therefore, there is no way to know at what point the highest mortalities occurred during the post-smolt year. Eriksson (1994) reported the results of tagging experiments in the Baltic Sea in which post-smolt recoveries allowed for the estimation of weekly mortality rates for post-smolts. These rates were as high as 28% during the first two weeks at sea and declined rapidly thereafter. These results generally confirm the suspicions held by most salmon researchers that the highest mortality rates occur during this time period. The rates for the balance of the year are elevated as compared to those observed for adults, but they were nonetheless lower than the spring mortalities. This draws our focus to the time period when Figgjo and North Esk salmon would first be entering the marine environment, which is also addressed by the sea surface temperature correlation analysis.

The strongest correlations between survival rate and areal extent of thermal habitat occurred during the month of May. In both stocks, correlation with warm water habitat (8–10°C) was restricted to May; whereas, correlations with cold water habitat were also observed for June data. The distribution of sea surface temperature, which in essence is driving these correlations, was found to be ecologically significant. Sea surface temperature distributions for periods of good versus poor salmon survival showed that when cool surface waters dominated the Norwegian coast and North Sea during May, salmon survival was poor. Conversely, when the 8°C isotherm extended northward along the Norwegian coast during May, survival was good. Thus, it is the variation in temperature conditions for this segment of the Norwegian coast that presents the greatest challenge to the post-smolts.

It is important to consider the transport mechanisms at work on salmon juveniles when they first go to sea. The area utilized by Figgjo and North Esk post-smolts is dominated by a coastal current that travels to the northeast at mean seasonal rates of approximately 13–17 km·d⁻¹ (Hopkins 1991). Jonsson et al. (1993) reported that post-smolts in the same current had migratory speeds averaging 7.45 km·d⁻¹ and that the fish were rarely able to transport themselves southward against the prevailing currents. Thus, salmon post-smolts from the Figgjo and North Esk would be expected to occupy the thermally dynamic segment of the North Sea and Norwegian coast found to vary in correlation to survival. How might variation in thermal conditions affect the survival of post-smolt salmon? The rejoinder to this question is that there are many ways, but two main groups of factors are growth-mediated effects and production mechanisms.

**Growth-mediated effects**

Temperature has a direct effect on growth that will affect growth-mediated sources of mortality in post-smolts. Survival is inversely related to body size in pelagic fishes (Peterson and Wroblewski 1984). Growth-mediated survival, and especially how it relates to the ecology of early life history stages, is broadly identified as critical to the recruitment process (Anderson 1988; Pepin 1991). This has been seen in salmonids where growth-related mechanisms have been associated with mortality rates (Furnell and Brett 1986; Mathews and Ishida 1989; Holtby et al. 1990; L’Abee-Lund et al. 1993; Friedland et al. 1996). Post-smolt growth increases in a linear trend with water temperature up to a
maximum rate and then decreases at high temperatures (Brett 1979), thus making post-smolt growth-survival mechanisms temperature dependent. As described by Friedland et al. (1998a), post-smolts from the Figgjo and North Esk advected passively into the Norwegian coastal current would be affected by prevailing temperature conditions in a given year. In years where water temperatures were high enough to support rapid growth, the juvenile fish would be expected to attain body sizes large enough to avoid predation and survival for the cohort would be enhanced. Conversely, lower temperatures would depress growth and survival. This represents the most direct effect sea surface temperature distributions could have on post-smolts. Other factors, which co-vary with sea surface temperature trends, may be impacting growth and survival through indirect mechanisms. Contrasts in temperature regime are indicative of differences in weather patterns for a region. Since post-smolt growth is sensitive to changes in photoperiod (Forsberg 1995), the frequency of storms and changes in cloud cover could conceivably affect growth.

Production mechanisms

Primary production and the forage base for salmon post-smolts undoubtedly vary in association with temperature conditions. Recent findings with Pacific salmonids point to the importance of diet in the recruitment process, thus relating quality and abundance of prey to growth and survival (Healey 1991; Brodeur et al. 1992; Perry et al. 1996). Prey availability is often related to oceanographic processes and structural features in the water column (Levings 1994). Juvenile salmonids have been shown to modify their diet in response to feeding opportunities created by the concentration of food along fronts (Brodeur 1989; St. John et al. 1992) or restrictions imposed by thermal structure (Reddin 1985; Pearcy et al. 1988). It has also been hypothesized that variation in ocean productivity acts on post-smolts by shifting predation pressure from other species onto the post-smolts (Fisher and Pearcy 1988).

As a highly migratory species, salmon depend upon a number of orientation cues to successfully orient during their marine migration. The conditions first encountered by post-smolts may force additional swimming as the fish respond to migration cues (Salminen et al. 1994), thus creating energy deficits for the fish as they swim harder to avoid undesirable thermal conditions. In a more extreme case, post-smolts may face potentially lethal thermal conditions when they attempt to migrate from river to ocean environments, again underscoring the importance of climate variation (Narayanan et al. 1995).

Maturation schedules

Cohort differentiation

The linkage between maturation and climate can be seen in the relationship between stock abundance of North American Atlantic salmon stocks and winter temperature conditions in the northwest Atlantic area. Friedland et al. (1993) developed a composite catch time series of the North American stock complex during which catches were generally unrestricted by management measures and is thus taken as representative of stock size (Fig. 6A). This time series differs from the European catch time series in two important
ways. First, the differences in regional catches in North America are not as pronounced as in the European data (Fig. 3A). Second, the North American series contains a much higher proportion of nonmaturing (2SW) salmon in the catch. Therefore, this series is greatly affected by variation in maturation schedules for the contributing stocks to a much greater degree.

Total stock abundance was correlated to an index of winter thermal habitat in the northwest Atlantic. Winter thermal habitat, as represented by the first principal component of monthly 4–8°C thermal habitat for the months January–March, showed decadal trends similar to the estimate of stock abundance (Fig. 6B). A more refined analysis confirms this relationship by comparing the abundance of North American nonmaturing (2SW) stocks and winter thermal habitat; subsequently this relationship was used as the basis of management in mixed stock fisheries (Reddin et al. 1993).

The distribution of sea surface temperature data that is critical for Atlantic salmon appears to be related to the North Atlantic atmospheric oscillation. The position of the westerlies over the North Atlantic and the position of the Iceland low-pressure center define the oscillation (Dunbar and Thomson 1979; Mann and Lazier 1991). When the westerlies are in their northerly position, high pressure occurs in the north central Atlantic Ocean. When the westerlies are at their southern extreme, cold air from the Arctic invades the Labrador Sea and Greenland area. The atmospheric pressure difference between the Azores and Iceland during winter indicates the magnitude of the oscillation. Friedland et al. (1993) found that the oscillation is in negative phase with the area of 4–8°C winter habitat for North American stocks (Fig. 7). In comparing the distribution of 4–8°C water when the oscillation was high versus a period when it was low, it was found that the greatest differences occurred in the area of East Greenland and the Davis Strait area of the Labrador Sea (Fig. 8).

Migrational models

Friedland et al. (1998b) propose a hypothesis that migration may be a significant determinant of maturation in Atlantic salmon, which they support with data on elemental composition of otoliths, maturation trends, and the relationship between population abundance and ocean climate. Though the hypothesis is specified for southern North American salmon stocks, ones with age structures that include fish that mature at both 1SW and 2SW, it is intended as a general hypothesis applicable to all stocks. The principal aspect of the hypothesis is that fish that migrate more northerly as post-smolts are differentially affected by overwintering conditions and may also find themselves in a location, after winter, where they fail to receive cues related to sensing their home rivers. As a result, these fish feed and grow and join feeding migrations, as in the case of these
North American fish, in feeding areas in the Labrador Sea. As a consequence, they regress in their maturation state. Alternatively, fish that make a more southerly post-smolt migration experience different overwintering conditions and are closer to home rivers after winter. They are more likely to receive cues associated with their natal rivers, develop sexually, and invoke other behaviors to navigate home. This segment of the salmon’s migration is not well known; however, it is clear that homing salmon change behavior in response to cues associated with natal rivers (Hansen et al. 1993). Though not well studied, there is precedence for relating migration to maturity. Woodhead (1959) found that immature cod in the Barents Sea which follow different migration routes, showed different patterns of sexual development.

The relationship between the abundance of North American 2SW spawners and the areal extent of thermal habitat during their first seawinter is consistent with the migration-maturation hypothesis described above. A number of competing theories have been proposed to explain the relationship between winter thermal habitat and abundance (Friedland et al. 1993). Ideas based on competition or survival mechanisms have always been difficult to rationalize because post-smolts nearly achieve adult size by their first seawinter and thus are not as likely to experience predation rates as high as juvenile fish. Likewise, it is equally difficult to support mortality due to starvation. On the other hand, the concept that ocean climate simply influences a segment of the stock to take a more northerly post-smolt migration and thus not sexually mature after the first seawinter, offers a consistent, albeit still inconclusive, explanation for the observed phenomena.

Conclusions

An improved understanding of the linked mechanisms involved in controlling decadal climate response in the North Atlantic is emerging (Latif et al. 1996). Furthermore, climate predication models that could be used to feed back into biological models are under development (Griffies and Bryan 1997). As we learn more about the biological response of Atlantic salmon to environmental variation, we should be able to develop a unified model of survival and maturation for the marine phase that could be used to complement freshwater production models. Management policy that is predicated on freshwater production trends and political challenges and ignores decadal scale trends in ocean productivity is doomed to failure (Lawson 1993). It is critical that both environments be linked and that the life history of the salmon be viewed in its totality.

References


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