Fisheries and Oceans Canada / Pêches et Océans Canada
Science / Sciences

C S A S / **S C C S**

Canadian Science Advisory Secretariat / **Secrétariat canadien de consultation scientifique**

Research Document 2006/018 / **Document de recherche 2006/018**

Not to be cited without permission of the authors *

Ne pas citer sans autorisation des auteurs *

Perspectives on the marine ecology of Atlantic salmon (*Salmo salar*) in the Northwest Atlantic

Perspectives sur l'écologie marine du saumon atlantique (*Salmo salar*) dans l'Atlantique Nord-Ouest

D. G. Reddin

Dept. of Fisheries and Oceans
P.O. Box 5667
St. John's, NL A1C 5X1

* This series documents the scientific basis for the evaluation of fisheries resources in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Research documents are produced in the official language in which they are provided to the Secretariat.

This document is available on the Internet at:

* La présente série documente les bases scientifiques des évaluations des ressources halieutiques du Canada. Elle traite des problèmes courants selon les échéanciers dictés. Les documents qu'elle contient ne doivent pas être considérés comme des énoncés définitifs sur les sujets traités, mais plutôt comme des rapports d'étape sur les études en cours.

Les documents de recherche sont publiés dans la langue officielle utilisée dans le manuscrit envoyé au Secrétariat.

Ce document est disponible sur l'Internet à:

http://www.dfo-mpo.gc.ca/csas/

ISSN 1499-3848 (Printed / Imprimé)

Canada

FOREWORD

This document is a product from a workshop that was not conducted under the Department of Fisheries Oceans (DFO) Science Advisory Process coordinated by the Canadian Science Advisory Secretariat (CSAS). However, it is being documented in the CSAS Research Document series as it presents some key scientific information related to the advisory process. It is one of a number of contributions first tabled at a DFO-SARCEP (Species at Risk Committee / *Comité sur les espèces en péril*) sponsored workshop in Moncton (February 2006) to begin the development of a 'Conservation Status Report' (CSR) for Atlantic salmon. When completed in 2007, the CSR could form the basis for a Committee on the Status of Endangered Wildlife in Canada (COSEWIC) status report, recovery potential assessment and recovery strategy, and most importantly, enable DFO to implement pre-emptive management measures prior to engagement in any listing process.

AVANT-PROPOS

Le présent document est issu d'un atelier qui ne faisait pas partie du processus consultatif scientifique du ministère des Pêches et des Océans, coordonné par le Secrétariat canadien de consultation scientifique (SCCS). Cependant, il est intégré à la collection de documents de recherche du SCCS car il présente certains renseignements scientifiques clés, liés au processus consultatif. Il fait partie des nombreuses contributions présentées au départ lors d'un atelier parrainé par le MPO-SARCEP (*Species at Risk Committee* / Comité sur les espèces en péril) à Moncton (février 2006) en vue de commencer l'élaboration d'un rapport sur la situation de la conservation du saumon atlantique. Lorsqu'il sera terminé, en 2007, ce rapport pourrait servir de base à un rapport de situation du Comité sur la situation des espèces en péril au Canada (COSEPAC), à une évaluation du potentiel de rétablissement et à un programme de rétablissement mais, avant tout, il permettra au MPO de mettre en œuvre des mesures de gestion anticipées avant même de s'engager dans un processus d'inscription.

ABSTRACT

The ecology of Atlantic salmon (*Salmo salar*) in the Northwest Atlantic Ocean is reviewed. Atlantic salmon spend time in freshwater and in the sea and both habitats are consequently important to its life history and survival. The importance of the Labrador Sea as a nursery area for postsmolt salmon from stocks ranging along the entire length of its freshwater habitat in North America is idenfifed from research vessels fishing in the Labrador Sea and gannet feeding studies. All sea ages of salmon are shown to be present in the Labrador Sea and probably over-winter there as well. Salmon that will be multi-sea winter in age when they return to freshwater are found annually in abundance in the Greenland area. Also, there are documented migrations of North American salmon to the eastern side of the Atlantic, although the overall numbers are thought to be low. Temperature preferences of adult and postsmolt salmon are depicted from research vessel catch rates and temperature profiles. Postsmolts appear to select a much narrower range of temperatures at sea than do adults. Postsmolts preferred temperatures from 5 to 8°C; while adults were found abundantly from 4 to 10°C. The lack of any relationships between numbers of adult salmon or their return rates to counting facilities compared to the numbers of smolts leaving rivers suggests that carrying capacity in the Northwest Atlantic is not limiting salmon abundance. Studies with data storage tags show that salmon spend much of their time in the surface waters but also dive deeper in the water column probably in search of prey. Salmon are found closer to the surface at night then during the day. Migration routes to and from the Labrador Sea and Greenland area are shown. Migration in relation to surface currents in the North Atlantic is discussed. Many studies are available showing relationships between marine climate and salmon growth and survival in the sea. The North Atlantic Oscillation Index seems to be related to salmon abundance in the Northeast Atlantic but not in the Northwest.

RÉSUMÉ

Nous examinons l'écologie du saumon atlantique (*Salmo salar*) dans l'océan Atlantique Nord-Ouest. Le saumon atlantique passe du temps en eau douce et en mer, de sorte que les deux habitats sont importants pour son évolution biologique et sa survie. L'importance de la mer du Labrador en tant qu'aire de croissance des postsaumoneaux issus de stocks qui se trouvent dans tout son habitat d'eau douce en Amérique du Nord est évaluée à l'aide de navires de recherche qui pêchent dans la mer du Labrador, ainsi que d'études sur l'alimentation des fous de Bassan. Les études montrent que tous les groupes d'âge de saumons en mer sont représentés dans la mer du Labrador où ils passent aussi probablement l'hiver. Des saumons qui seront devenus pluribermarins à leur retour en eau douce sont observés chaque année en abondance dans la région du Groenland. De plus, on note que des migrations de saumon nord-américain vers l'Atlantique Est sont documentées, bien que leur nombre semble faible. Les températures que privilégient les saumons adultes et les postsaumoneaux sont déduites à partir des taux de prise des bateaux de recherche et des profils de température. Les postsaumoneaux semblent préférer une échelle de températures beaucoup plus restreinte en mer que les adultes. De fait, les postsaumoneaux évoluaient à des températures variant entre 5 et 8°C, tandis que les adultes étaient abondants entre 4 et 10 °C. L'absence de lien entre le nombre de saumons adultes et le taux de retour vers les installations de dénombrement par rapport au nombre de saumoneaux qui quittent les cours d'eau porte à croire que la capacité de charge dans l'Atlantique Nord-Ouest ne limite pas l'abondance du saumon. Des études réalisées à l'aide d'étiquettes enregistreuses montrent que le saumon passe une grande partie de son temps dans les eaux de surface, mais plonge aussi en profondeur dans la colonne d'eau, probablement en quête de proies. Le saumon est plus souvent proche de la surface la nuit que le jour. Les voies migratoires vers la mer du Labrador et le Groenland et en sens contraire sont indiquées. De plus, on étudie la migration par rapport aux courants de surface dans l'Atlantique Nord. Il existe de nombreuses études illustrant les relations entre le climat marin et la croissance du saumon, ainsi que son taux de survie en mer. L'indice d'oscillation atlantique nord semble avoir un lien avec l'abondance du saumon dans l'Atlantique Nord-Est, mais pas dans le Nord-Ouest.

INTRODUCTION

Atlantic salmon (*Salmo salar*) are renowned for their anadromous life history spending considerable time in both freshwater and marine environments. Initially, the population dynamics of salmon are set by events that take place in freshwater since that is where salmon are born and spend its juvenile phase. However, it is in the ocean that most of the growth, potential fecundity and a substantial portion of overall mortality occurs establishing the initial state for the next generation once the adults have returned to freshwater and spawn. The freshwater phase of the salmon's life has been more intensively studied then has the marine phase and so less is known about the life of salmon in the sea. However, there are a lot of general facts that we do know that show the importance to salmon of its life in the sea. For example, from survival rate time series, we know that overall mortality in the sea is high and variable (Dempson et al. 1998; Dempson et al. 2004; Hansen and Quinn 1998; Jonsson and Jonsson 2004b); although we do not know the source of the mortality. In fact, there are many factors that can effect the survival of Atlantic salmon while in the sea both man-made (Fairchild et al. 1999) and natural (Reddin and Friedland 1993; Friedland and Reddin 1993; Ritter 1989; Friedland 1998; Jonsson and Jonsson 2004a). However, we do not have specific information showing the source of these mortalities and their magnitude. This is partly because detailed information on migration routes and distribution is generally unavailable for specific stocks although it is thought that various life stages have varying migrations that can also overlap among stocks. For example, most North American potential two-sea-winter (2SW) salmon overlap in the summer of their first year at sea with their European cousins in the west Greenland/Davis Strait area.

The following is a summary of the marine ecology of Canadian salmon stocks in the Northwest Atlantic. More specific information on migration and distribution can be found in an excellent summary by Ritter (1989) as well as life history by Hansen and Quinn (1998) and environmental aspects by Saunders (1986) and Jonnson and Jonnson (2004b).

BACKGROUND

Salmon transition from freshwater to marine environment

The transition from freshwater to ocean life for Atlantic salmon smolts and kelts can be of serious consequence to an individual fish as well as being an important factor controlling year-class strength and abundance at the population level (McCormick and Saunders 1987, Levings 1994; Hansen and Quinn 1998; Jonnson et al. 1998; McCormick et al. 1998). It is generally thought that water temperature is the main controlling environmental variable for smoltification as the process of changing from freshwater to the sea is termed (Jonnson and Ruud-Hansen 1985); although photoperiod is also important (McCormick and Saunders 1987; Forsberg 1995). The smolt transformation process is accompanied by changes in metabolic rate (Hoar

1988) with increases in energy demands underpinning the need for the fish to immediately begin feeding. Levings (1994) has concluded that of all the variables influencing survival of postsmolt salmon, temperature is particularly important. That is because temperature influences all metabolic activities and their rates. If they are to survive, individual salmon must quickly adapt to their new physical environment and be able to flee predators and seek prey. Reddin et al. (2006, *In Press*) recorded temperature profiles collected by data storage tags applied to salmon smolts at Campbellton River that provided detailed information on the thermal habitat of postsmolts for periods ranging from a few days to about two months at sea. Temperatures recorded ranged from below 0 to nearly 20°C; although most ranged from 8 to 15°C.

The length of time spent inshore in or near the home estuary is thought to be brief. In spite of its brevity, life inshore may still be critical to postsmolt survival (Fried et al. 1978; Eriksson 1994; LaCroix and McCurdy 1996; Hansen and Quinn 1998; Jonnson and Jonnson 2004b; LaCroix et al. 2004; Finstad et al. 2005; LaCroix et al. 2005). Tytler et al. (1978) showed that the estuarine residence time could be as brief as one or two tidal cycles, which in some cases would presumably limit opportunities for predation and increase the chances of subsequent survival (LaCroix et al. 2004; LaCroix et al. 2005). LaCroix et al. (2004) also observed that most of the mortality even though low took place in the immediate vicinity of fish farms where potential predators were abundant. Hansen and Quinn (1998) reviewed Atlantic salmon migration summarizing movements of postsmolts outside of the estuary of their home rivers and concluded that movement to oceanic areas was very quick. This quick movement away from estuaries towards the open sea has been confirmed by tracking studies (Holm et al. 1982; Moore et al. 1995; Lacroix and McCurdy 1996; Holm et al. 1998; Moore et al. 2000) which additionally showed that migration was influenced by tidal currents and wind (LaCroix et al. 2005). One exception to this was in the Gulf of St. Lawrence where salmon postsmolts were caught as a bycatch in herring gear in a nearshore zone late in the summer presumably long after they had left their home rivers and estuaries (Dutil and Coutu 1988). On both sides of the Atlantic, movement of postsmolts once in the open sea seems to be generally northwards (Meister 1984; Reddin and Short 1991; Shelton et al. 1997; Hansen and Quinn 1998; Holm et al. 2000). Montevecchi et al. (1988) showed that the diet of northern gannets around the Funk Island, Newfoundland consisted of postsmolts, the river ages of which and presence of external tags suggested a southerly origin away from the island of Newfoundland as far as the state of Maine.

Current oceanographic conditions in the Northwest Atlantic

This section was reproduced from the Newfoundland and Labrador Region (DFO) Salmon Stock Status Update (DFO 2005). Ocean temperatures at Station 27 off St. John's, Newfoundland for the first eight months of 2005 were above normal with surface values during the summer (August) comparable to the record highs of 2004.

Oceanographic data collected during the spring and summer of 2005 on the Newfoundland Shelf generally showed above normal temperatures, particularly on the Grand Bank and off the south coast of Newfoundland. Observations from the mid-summer oceanographic survey indicated that the area of the cold-intermediate-layer (CIL <0°C) shelf water increased slightly over 2004 but was below normal for the 11th consecutive year off Cape Bonavista. In general, water temperatures on the Newfoundland and Labrador Shelf remained above normal during 2004 and the first half of 2005, continuing the warm trend that started during the late 1990s.

One of the best indicators of climate in the North Atlantic is the North Atlantic Oscillation Index (NAOI) (Dickson and Turrell (1999) which for 2005 was above normal. However, arctic outflow to the Northwest Atlantic was weaker-than-normal as the most significant pressure anomalies were shifted to the east. Air temperatures have been warmer than normal for six out of the past nine months up to September of 2005. Data on sea ice extent on the Newfoundland and Labrador Shelf for 2005 are not yet available. However, preliminary analysis indicates less-than-normal sea-ice extent and duration during the winter and spring of 2005.

Preliminary analyses have shown strong associations between marine environmental conditions and marine survival of salmon, adult salmon run timing and abundance of both large and small salmon (Martin and Mitchell 1985; Narayanan et al. 1995). For example, salmon run-times are significantly correlated with both sea-surface temperature in eastern Newfoundland waters and spring sea-ice cover with later run-times associated with cold conditions and extensive ice cover. There is insufficient information at present to quantify these relationships. However, based on historical data, the current marine environment in Newfoundland and Labrador waters is favorable for survival of Atlantic salmon.

Circulation patterns in the North Atlantic

An ocean current is a horizontal movement of water at the ocean's surface which is driven by wind circulation above surface waters (Hardy 1965). On a global scale, large ocean currents are constrained by the continents found bordering the three oceanic basins. Due to the continents creating a barrier, these currents develop an almost closed circular pattern called a gyre. Thus, each ocean basin has a large gyre located at approximately 30° North and South latitude in the subtropical regions. The atmospheric flow produced by the subtropical high pressure systems drives the currents that create these oceanic gyres. There are also smaller gyres that occur in the North Atlantic and Pacific Oceans centered at 50° North. Currents in these systems are propelled by the circulation produced by polar low pressure centers, a measure of which in the North Atlantic Ocean is the NAOI.

In the North Atlantic Ocean, there are two large gyres: the subpolar and subtropical gyres (Fig. 1). The subtropical gyre flows anticyclonic and is driven by the low-latitude trade winds and mid-latitude westerlies. On the western side of the Atlantic, subtropical waters are transported northward along the North American continent as the Gulf Stream up to Cape Hatteras at 36°N, where it changes direction to the east away from the North American continent. As the Gulf Stream approaches the Great Banks, the transport decreases as some of the water is re-circulated to the west. However, a considerable volume of water continues east and crosses the Atlantic as the Azores Current while the remainder forms the North Atlantic Current (NAC) that continues as a well-defined boundary current along the eastern slope of the Grand Banks. At about 51°N, the NAC moves to the east. As the waters flow eastward the NAC looses its well-defined structure, and the water is transported eastward in the Sub Polar Front (SPF), which is the boundary between the warm water in the subtropical gyre and the cooler and less saline water in the subpolar gyre to the north (Rossby 1996). The SPF makes a sharp turn toward the north at about mid-Atlantic and some of the warm water in the SPF eventually feeds the Irminger Current and some feeds the inflow of warm water to the Nordic Seas on either side of the Faroes Islands. The gyre in the Northwest Atlantic is bounded by the NAC on the eastern side, Irminger/West Greenland Currents to the north and Labrador Current on the western side. This gyre has been used as a possible explanation for the passive transport of salmon to the Greenland area (Stasko et al. 1973; Dunbar and Thomson 1979) and potentially to the eastern side of the Atlantic (Reddin et al. 1984).

DISTRIBUTION AND MIGRATION AT SEA

Postsmolts

Postsmolts were defined by Allan and Ritter (1977) as the juvenile stage in the ocean from the onset of the smoltification process to the end of the first winter at sea. The first directed capture of postsmolts at sea in the northwest Atlantic Ocean other than incidental captures in coastal areas (Caron 1983; Meister 1984; Dutil and Coutu 1988) was reported by Reddin and Short (1991). It was shown that postsmolts were distributed over much of the Labrador Sea in the autumn of all study years viz. 1987-89 and 1991 (Fig. 2). More recently, research vessels have caught postsmolts in the Labrador Sea in 1998, 2001 and 2005. Reddin and Short (1991) concluded that postsmolts are found annually in the Labrador Sea. Postsmolts were more abundant between 56° and 58° N than in other locations. In comparison to adult distribution in autumn, postsmolts were found over a smaller area. Montevecchi et al. (1988) and Montevecchi et al. (2002) reported gannets feeding on postsmolts in the vicinity of the Funk Island, Newfoundland in mid-summer.

Reddin and Short (1991) have concluded, based on river ages of postsmolts (*see text table, Biological Characteristics section*) and Carlin tagged postsmolts caught during their study, that those in the Labrador Sea originated from rivers over much of the geographical range of salmon in North America. Based on high catch rates of one-sea-winter (1SW) salmon in the Labrador Sea in spring and because water temperatures suitable for salmon occur there over the winter, Reddin (1985, 1988) concluded as did Ritter (1989) that some postsmolts likely over winter in the southern Labrador Sea and Grand Banks areas. However, the corroborative evidence from directed research or indirectly by commercial vessels fishing during the winter is lacking. Also, Dutil and Coutu (1988) observed postsmolts that were caught as bycatches in herring gear in the northern Gulf of St. Lawrence late in summer. It is not known if all of these postsmolts exited the Gulf later in the year or if some remain there over-winter. Ritter (1989) concluded that postsmolts from inner Bay of Fundy rivers, first reported by Jessop (1976) because of a lack of tag recoveries from outside the immediate area, also over-wintered in the Bay of Fundy and surrounding area.

The movement of postsmolts into the Labrador Sea from their rivers of origin in eastern North America has been discussed by Belding and Prefontaine (1938), Belding (1939), Caron (1983), Meister (1984), Dutil and Coutu (1988); Reddin and Short (1991), Montevecchi et al. (1988) and Ritter (1989) who postulated from tag recaptures that postsmolts from rivers in Maine, the Bay of Fundy, the Atlantic coast of Nova Scotia, and some rivers in Newfoundland and Labrador migrate off eastern Newfoundland, arriving near the Funk Islands (southern Labrador Sea) in late July-early August. Caron (1983) and Dutil and Coutu (1988) concluded that salmon of some Gulf of St. Lawrence stocks exit the Gulf through the Strait of Belle Isle, and that at least some postsmolts remained in the Gulf of St. Lawrence until late autumn (Dutil and Coutu 1988). Dutil and Coutu (1988) suggested that the movement of postsmolts out of the Gulf of St. Lawrence may be related to environmental factors, especially sea temperature, and the presence/absence of prey. Friedland et al. (1999) suggested that the Gulf of St. Lawrence acted variously in some years as a nursery area but that the presence of over-wintering salmon was unlikely due to cold water. Caron (1983) showed that the northerly Gulf of St. Lawrence stocks exited the Gulf through the Strait while a portion of the southwesterly salmon stocks used the Cabot Strait to the south of Newfoundland. Irrespective of which strait they exited the Gulf of St. Lawrence, they arrived in the Labrador Sea to northern Grand Banks area sometime in late summer to early fall.

Many postsmolt salmon are found in the Labrador Sea within four months of leaving their home rivers suggesting that this area is important nursery habitat during their early marine life. The available evidence from tag recaptures and river age distributions (*see text table in Biological characteristics section*) shows that postsmolts from many stocks can be found mixed in the Labrador Sea (Moller Jensen and Lear 1980; Meister 1984; and Montevecchi et al. 1988; Reddin and Short 1991), including salmon of North American and European origin (Lear and Sandeman 1980). Food resources and environmental conditions in the Labrador Sea during the winter months may influence postsmolt survival and growth as suggested by Reddin (1988). Scarnecchia (1983, 1984) showed that for Icelandic stocks, sea temperatures in the early months that salmon are at sea are correlated with the number returning one and two years later; as well as with their age at maturity. Trophic interactions (predator-prey) between postsmolts and seabirds

(Montevecchi et al. 2002) indicate that, besides causing significant mortalities in freshwater, avian predators may also cause significant mortalities of postsmolts at sea. Avian predators can capture postsmolts at sea suggesting that postsmolts spend at least some of their time in the upper part of the water column. More knowledge of these causes of mortality is important as they also would influence the numbers of returning adults. Montevecchi et al. (2002) showed that gannets shifted diet to other species including salmon postsmolts when capelin were in reduced abundance. These shifts in trophic dynamics, annual variations in environment and annual variability in survival rates could influence 1SW to multi-sea winter (MSW) salmon ratios of returns to home rivers if postsmolts destined to return at different sea ages are distributed at different locations at sea (Saunders et al. 1983; Scarnecchia 1984; Martin and Mitchell (1985); Meerburg 1987). Jonnson and Jonnson (2004a) showed the marine environmental conditions as measured by the NAOI influenced the age of maturity of some European stocks.

The size of the population of postsmolts in the Labrador Sea is also of interest. Reddin and Short (1991) could not directly estimate the population size but noted that the mean catch rate for postsmolts in the Labrador Sea in the fall of 1988 was about 50% of the average catch rate at Greenland, suggesting that the population in the Labrador Sea is quite large, especially considering the large area involved.

Adults

Templeman (1967, 1968), May (1973) and Lear (1976) reported that salmon were found in the spring in surface waters of the Northwest Atlantic from the southern edge of the Grand Bank to slightly south of Cape Farewell, Greenland (Fig. 3). As May (1973) observed, the most westward positions where salmon were caught closely follow the edge of the Arctic pack ice in spring. Reddin and Shearer (1987) and Reddin (1988) reported that salmon were usually found at sea in relatively cool water between 3°C and 8°C, indicating that they may be actively selecting water of this temperature. There are two locations where salmon have been found in abundance during spring. One location lies about 300 miles east of the Strait of Belle Isle. The other lies slightly to the east of the 200 m isobath (depth contour) along the eastern edge of the Grand Bank (Fig. 3).

Reddin (1985) presented some evidence based on smolt ages suggesting that salmon stocks in the Labrador Sea may be different from those along the eastern edge of the Grand Bank. The lower smolt ages of salmon caught to the east of the Grand Bank suggested that these stocks there were more southerly in origin than those in the Labrador Sea where smolt ages were higher. It is also known that stocks from Europe also occur in the Labrador Sea and Irminger Sea areas (Møller Jensen and Lear 1980; Reddin et al. 1984; Reddin and Lear 1990) and a clinal longitudinal distribution with continent of origin has been noted by several authors extending out into the Labrador Sea from the Greenland coast (Møller Jensen and

Lear 1980; Lear and Sandeman 1980). Thus, the salmon population in the Labrador Sea consists of more North American salmon further to the west.

The presence of immature salmon of sea age 1 in the Labrador Sea-west Greenland area that will not mature until the year following as 2SW salmon has been documented by Idler et al. (1981). There were no non-maturing salmon found along the south and west coasts of Newfoundland suggesting that the Labrador Sea (Idler et al. 1981) is an area of over-wintering for non-maturing 1SW salmon originating along the entire coast of North America. In late summer and autumn, non-maturing 1SW salmon are found inshore along the northeast Newfoundland and Labrador coasts, at West Greenland, in the Labrador Sea and in the Irminger Sea including the east Greenland coast (Idler et al. 1981).

Specifically, salmon are concentrated along the West Greenland coast from the inner coastal fjords to between 45 and 60 km offshore. These are potential multi-sea winter salmon that in their 2nd summer at sea have not started to mature and will spend another winter at sea before returning to their home river. Relatively good catches have occurred, as well, in the Labrador Sea north of 55°N. Salmon also have been caught by research vessels in the Irminger Sea and in commercial nets in east Greenland but catch rates were not nearly as high as at Greenland or in the Labrador Sea (Møller Jensen and Lear 1980). No sets have been made in summer/autumn in the Grand Bank area and undoubtedly there are other locations that are currently outside the survey area where salmon can be found in abundance, viz. the Gulf of St. Lawrence.

Few sets have been made for salmon during the winter months and these were all to the east of the Grand Bank of Newfoundland in 1985 (Fig. 3). The zero to low catch rates in the area of the Grand Bank suggest that they were located elsewhere at this time. These results suggest, since salmon were found in the Labrador Sea in the fall and then in the following spring, that adult salmon of North American origin probably overwinter there.

Reddin and Shearer (1987) discussed regional variations in abundance in the Northwest Atlantic by summarizing catch rates from research surveys and commercial fishing. Mean catch rates in the Greenland fishery were highest, those in the Labrador Sea and east of the Grand Bank were 55% less than those at Greenland, and catch rates on the Grand Bank and Irminger Sea were about 75% lower than those in the Labrador Sea and east of the Grand Bank (Table 1). Therefore, salmon were found concentrated in abundance in the spring off the eastern slope of the Grand Bank and less abundantly in the southern Labrador Sea and over the Grand Bank. During summer to early fall, salmon were concentrated in the West Greenland area and less abundantly in the northern Labrador Sea and Irminger Sea.

The exception to the above distributions seems to be for salmon from the inner Bay of Fundy as few are caught outside of the bay itself Jessop (1976). Ritter (1989) concluded that inner Bay of Fundy salmon remain as adults in the Bay of Fundy and surrounding areas. Another specialized area is the Ungava Bay where salmon from local rivers are known to over-winter (Power et al. 1987). Thus, there are three known over-wintering (nursery) areas for Canadian salmon in the northwest Atlantic.

Intercontinental migrations of salmon in the North Atlantic

Reddin et al. (1984) first provided information on the migration of salmon from Europe to North America and the reverse which they labelled as intercontinental migrations. While overall numbers were rather low, based on the number of tag recaptures, there being only less then twelve from either side of the Atlantic, it did provide evidence of salmon straying on the outside of their migration pathways. Recently, there has been further documented evidence of Miramichi River salmon present in the fishery at Faroes from salmon tagged at Faroes (Hansen and Jacobsen 2003). Hansen and Jacobsen (2003) did a simulation based on tag returns which showed that Canadian origin salmon in the Faroes area were 6% of the overall population in the area. Tucker et al. (1999) showed based on Cesium-137 (^{137}Cs) levels in salmon returning to the St. Marguerite River in Quebec and from patterns of ^{137}Cs in the ocean, that 43% of grilse and MSW salmon sampled had levels consistent with their having spent time in the Faroes/Norwegian Sea area.

The high values of Tucker et al. (1999) are in sharp contrast to what is generally believed to be the case that inter-continental migrations are rather low. Overall, the number of tags recaptured in the northeast Atlantic from North America has been low compared to the 1000s tagged. In addition, based on scale characters and database from the discriminant analysis used for the West Greenland fishery (Reddin and Friedland 1998), Reddin (1987) concluded the number of North American salmon in the Faroes area was very low. The results of Tucker et al. (1999) were especially surprising in that grilse showed high levels of ^{137}Cs which would require the fish to travel across the Atlantic and return in some 12 to 14 months. The inter-continental migrations reported by Reddin et al. (1984) and Hansen and Jacobsen (2003) were putative MSW salmon based on the date they were captured and scale analysis. Resolution of this apparent contradiction could be done by DNA analysis of scale material collected during studies on Faroese long-line and Irish Sea fisheries.

Diurnal Rythms of Salmon in the Sea

Dutil and Coutu (1988) discuss the limited data in the literature concerning the daily rhythm of activity of salmon in the marine environment. Since salmon catch rates tend to increase at dawn and dusk in many fisheries, they concluded that salmon were more active then and tended to stay near to the surface. During studies in the Labrador Sea, postsmolts were caught more frequently at dusk than at any other time, while older salmon were caught more frequently than postsmolts at dusk and throughout the remainder of the day (Reddin and Short 1991). This suggests that diurnal rhythms of postsmolts are different from those of older salmon. These diurnal rhythms may be related to rates of activity, as suggested by Dutil and Coutu (1988), and also may result from vertical movements in the water column. Because postsmolts are readily caught in surface set gillnets is further evidence that they spend at least some time in the upper 3 m of the water column. Diurnal differences in water depth have been noted for postsmolts and adults from data storage tagging studies by Reddin et al. (2004, 2006) and (*Pers. Comm*. M. Holm in (Anon. 2005)). While both postsmolts and adults spend most of their time near to the surface, deep diving activities have been observed that may be related to feeding. They appeared to be nearer the surface at night then during the day Reddin (2006 *In Press*).

Biological characteristics of salmon caught in the Northwest Atlantic

The following text table shows the biological characteristics of salmon caught at sea including those of postsmolts prior to completion of their first full year. Details of fishing locations and gear are given in Reddin (1985) and Reddin and Short (1991). The biological characteristics of salmon caught by gill nets set from research vessels in the Northwest Atlantic:

Location	**Sea age**	**FL (cm)**	**WW (kg)**	**River age distribution %**							
				1	**2**	**3**	**4**	**5**	**6**	**7**	**N**
Labrador Sea	0	36 (2.9)	0.56 (0.13)	7	34	38	11	7	1	1	162
(All from fall)	1	65 (4.7)	2.97 (0.68)	12	31	27	17	8	4	0	312
	2	70 (5.0)	3.67 (0.97)	0	24	48	26	2	0	0	42
	3	66 (8.6)	3.29 (1.36)	15	0	31	31	23	0	0	13
Grand Banks	1	55 (4.4)	1.75 (0.24)	13	33	50	0	5	0	0	24
(All from spring)	2	74 (3.4)	4.3 (0.76)	0	19	59	22	0	0	0	32
	3	72 (3.0)	3.6 (0.57)	0	33	33	33	0	0	0	3

There is a clinal gradient in scale characters including river age increasing from south to north (Lear and Misra 1978) which can be used to generally infer the region of origin for salmon caught at sea. The river age distribution of salmon in the Labrador Sea and Grand Banks area shows the presence of salmon of non-Newfoundland and Labrador origin in the younger river age fish. Labrador mainly produces salmon of river age 4 and 5 while Newfoundland is 3 and 4. Thus, the presence of salmon of river age 1 and 2 indicates salmon originating from regions to the south of Newfoundland and Labrador. The sea age 0 salmon caught in the Labrador Sea indicates the presence of salmon of southern origin in the late summer and early fall. It is known from tagging in Maine, USA (Meister 1984) and Quebec (Caron 1983) that postsmolts migrate northwards along the Atlantic coast into the Newfoundland and then the Grand Banks/Labrador Sea area (Montevecchi et al. 1988). Caron (1983) also showed Quebec origin salmon exiting the Gulf of St.

Lawrence through the Strait of Belle Isle and Cabot Strait into the Northwest Atlantic. Some of these salmon would move northward to the Greenland area in the early summer as well as into inshore waters along the northern Newfoundland and Labrador coasts (Pippy 1982; Ritter 1989; Reddin and Lear 1990).

Marine ecology, relation to climate and salmon

Carrying capacity of the sea

Jonsson and Jonsson (2004b) concluded that mortality of salmon in the ocean is density independent based on analysis of returns to the River Imsa, Norway where the number of returning adults increased linearly with smolt production (Jonsson et al. 1998). They concluded that recruitment for salmon in the North Atlantic is currently below carrying capacity such that adult production will increase or decrease proportionately to the number of smolts. This was based on the knowledge that at one time there were a lot more salmon in the ocean than now and from this they assume that carrying capacity in the sea has not been reached and it is production from freshwater that is limiting current population levels.

As shown in Fig. 4aandb, there certainly is no linear relationship for returning salmon numbers versus the number of smolt leaving rivers in Newfoundland, at least based on the five rivers used in the analysis. Returning adult numbers are shown to vary four to five fold for a similar smolt output. Thus, good returns can result from low smolt output and poor returns can result from high smolt output and vice versa. This suggests that carrying capacity is not limiting the number of adults produced from a given smolt cohort and that survival is highly variable. In the Pacific, Peterman (1981) has shown that density independent factors seem to contribute significantly to production of Pacific species. There are many papers available for Pacific salmon showing climate effects on marine life but relatively fewer for Atlantic salmon (see Beamish 1995; Jonsson and Jonsson 2004a; Beaugrand and Reid 2003).

Sea surface temperature and salmon

Because temperature is easy to measure and record there is much more known about it in relation to salmon then many other environmental variables. The relationship between salmon abundance and SST was examined by relating catch rates to SSTs during research vessel cruises in the Northwest Atlantic area, 1965-2004 (Fig. 5). A plot of mean values for SSTs from adult salmon captures grouped by rounding to the nearest °C showed that catch rates were significantly related to SST ($F=3.15$, $P=0.001$). The results show variable catch rates depending on sea temperature with SSTs ranging between 3 and 13°C and a peak in abundance occurring at 7.5°C (Fig. 5). There have been no sets made at SSTs higher than 13.5°C but there should be to confirm whether salmon are found at higher SSTs. Previously published results in which it was stated that salmon in the Labrador Sea were more abundantly found in SSTs between 4-8°C are revised to 4-10°C (this range includes 80% of the salmon).

For postsmolts caught in the Labrador Sea from 1987 to 2004 there was no significant relationship between catch rates and sea temperatures (F=1.45, p=0.21). This was possibly due to the short range of temperatures over which catches occurred. There is an obvious peak in abundance at 6°C after which catch rates slowly decline (Fig. 5). Optimal range appears to be from around 5°C to 8°C.

Saunders (1986) has reviewed the thermal biology of Atlantic salmon and stated that for adults in the sea, there is a preference for areas with SSTs between 4°C and 12°C, with an optimal range of 4°C to 8°C. Furthermore, he has speculated that there is a metabolic adjustment associated with smoltification so that the best thermal range for feeding and growth of Atlantic salmon during its marine phase is lower than in its freshwater phase. This change in thermal optimum allows salmon to exploit both freshwater and marine habitats and achieve optimum growth in both. However, the difference between freshwater and marine thermal optimum requires that some time after smoltification the optimum shifts, which would require a transition phase from the higher to the lower regime. The transition could occur in the estuarine zone where water temperatures are cooler than in freshwater but not as cool as would be experienced later in the Labrador Sea and other offshore areas (Reddin et al. 2006, In Press). The fact that catch rates for postsmolts caught in the Labrador Sea in autumn were not correlated to temperature suggests that a shift in thermal regimes may have occurred three to four months after smoltification.

The significant relationship for SSTs and salmon catch rates suggests that adult salmon may modify their movements at sea depending on SST. Corroborative evidence for a change in distribution at sea according to thermal conditions can be discerned from the distribution of MSW salmon tagged and released as smolts in the Sand Hill River, Labrador, during 1969-72 in relation to SST (Pratt et al. 1974). Some fish from this stock were captured in the general vicinity of the home river in Labrador as well as along the northeast coast of Newfoundland. However, when plotted with the June 4°C isotherm, the distribution of tag recaptures suggested that some of the annual variability in the locations of recaptures was related to environmental conditions. In 1972, for example, MSW fish were recaptured considerably farther south than in either 1971 or 1973. The 4°C isotherm for June extended much farther southward in 1972 than in 1971 or 1973. The colder SSTs in 1972 may have occurred because of a more southerly distribution of sea ice and the concomitant cold water than in 1971 and 1973 (Reddin and Day 1980). Dunbar and Thomson (1979), Reddin and Shearer (1987), and Ritter (1989) provide evidence that other salmon stocks also distribute themselves at sea in relation to SST.

May (1973) first hypothesized that sea ice, the presence of which lowers SST, should also modify salmon movements which should be reflected in catches. Narayanan et al. (1995) showed that the relationship between salmon catches in the former commercial fishery on the south coast of Newfoundland and area of ice on the northeast coast was significant at less than the 5% level of significance (see Fig. 9 Narayanan et al. 1995, R^2=0.44, F=11.2, P=0.005). The correlation was positive indicating that as the area of ice increased on the northeast coast so did the catches on the south coast where there was no ice. It is known from tagging studies (Pippy 1982; Reddin and Lear 1990) that salmon migrating from the Labrador Sea southward to the Maritime Provinces and southerly Newfoundland rivers move into the Newfoundland coast in more northerly areas and then move coastwise in a southerly and then westerly direction along the Newfoundland coast. The increased catches with increased ice are consistent with salmon moving into coastal areas more southerly than normal to avoid ice and cold water (O'Connell et al. 1992). Thus, these fish would avoid exploitation in these areas and more salmon would be available to be caught in south coast areas.

Reddin et al. (2000) postulated that the relationship between ice and salmon catches suggests that the time when salmon move into coastal fishing areas around the Newfoundland coast may also be influenced by water temperature. They used a geographical model to analyze the relationship between mean week of catch and the week of first occurrence of the SST of 4°C in SFAs 1-14 from 1974-82. The results indicated a significant correlation between mean week of catch and the first week of occurrence of the 4°C isotherm. Both the geographical index and mean week of SST arrival contributed significantly to the relationship with catch (see Reddin et al. 2000, F=23.7, P<0.001, R^2=0.75). The migration of salmon in the coastal waters around Newfoundland and Labrador in relation to SSTs compares well with the findings of Ikonen (1986) in the Gulf of Bothnia and those of Westerberg (1984) who suggested that salmon orientate at least partly by following a thermal field. This is consistent with Dunbar and Thomson (1979) and Reddin and Shearer (1987) who related the occurrence and abundance of salmon to sea temperature and the location of the Iceland low pressure centre. In the Northeast Atlantic after leaving their home rivers, postsmolts move rapidly away from shore (Hansen and Jacobsen 2000) following northward flowing shelf currents into the southern Norwegian Sea and later more northerly areas (Holst et al. 2000). In contrast to distribution by ocean currents, Jakapstovu (1988) observed salmon in the Faroes area fishery were distributed by SST in relation to the subarctic front and that older fish would tolerate colder temperatures then younger ones. Undoubtedly, both temperature, prey and currents are important in determining the ocean distribution of salmon.

Sigholt and Finstad (1990) and Handeland et al. (2003) reported that lethal sea water temperatures for both wild and farmed salmon smolts adapting to seawater occurred at very low and high temperatures. At the lower end of the range, some mortalities for postsmolts newly introduced into sea cages occurred at 6-7°C while at the higher end, mortalities when temperatures exceeded 14°C, suggesting there may be environmental windows for successful smolt transition into the sea in locations other than at the extreme edges of the species distribution, as observed by Power et al. (1987). For adults, lethal temperatures occur when water is below 0°C (Fletcher et al. 1988) which is also the case for cod and other species where water temperatures are cold (Templeman 1965), especially if they come in contact with ice. Note that in the Northwest Atlantic, few postsmolts were found in water colder then 4°C while adults are. This may explain the tendency of salmon to avoid ice covered water reported by May (1973).

<u>Salinity and salmon</u>

Because salmon live in the sea, their physiology and survival is influenced by salinity. However, there is very little information on the salinity tolerances of wild Atlantic salmon at either the adult or postsmolt stages while free swimming in the ocean. In estuaries, there is a transition zone where the water changes from fresh to salt either abruptly or gradually depending on the topography. Handeland et al. (1996) showed that there was an approximate 48 hour period when postsmolts exhibited signs of osmotic stress while adjusting to the transition from fresh to seawater. It may result in increased predation as osmotic stress could impair their ability to avoid predators. However, in the Northwest Atlantic, salinities measured from research vessels where salmon frequent, ranged from 33.4 to 34.6 PPM. Salinity is not thought to be a problem for healthy salmon that have successfully made the transition. We conclude that the effects of salinity may be more important at a population level when salmon are entering the ocean as smolts and/or when returning to freshwater as adults.

<u>Depth of salmon in the ocean</u>

Until recently, there is little evidence available on the depths adult salmon inhabit at sea in the northwest Atlantic. Stasko et al. (1973) noted that stomach contents consisted primarily of organisms that are found at least part of the time in surface waters. Evidence from marine tagging experiments at Greenland suggested that because there is an inverse relationship between catch rate and the thickness of the homogenous upper layer, salmon must spend considerable time in the upper portion of the water column (Smed 1980; Christensen and Lear 1980; Reddin and Shearer 1987).

Fortunately, direct evidence of depth of salmon in the water column is now available from DST experiments for both postsmolts and adults. Reddin et al. (2006 *In Press*) showed temperature profiles from DST tagged postsmolts suggesting that while most of their time was spent near the surface (and nearer the surface at night), they undergo frequent deep dives probably in search of prey. Deeper diving activities have been reported previously for salmon kelts also from Campbellton River by Reddin et al. (2004). The observed tendency of postsmolts to be caught in the upper part of the water column is also evident from trawling for postsmolts at sea (Holm et al., 2000; Shelton et al., 1997; Rikardsen et al., 2004), by acoustic tracking of postmolts in fjords (Holm et al., 1982; Moore et al., 1998) and in net catches in surface waters (Dutil and Coutu, 1988; Reddin and Short, 1991; Thorisson and Sturlaugsson, 1995). Westerberg (1982aandb) noted during coastal tracking studies that salmon made dives to deeper depths that were of short duration similar to the results shown by Reddin et al. (2004).

Wada and Ueno (1999) listed three hypotheses to explain diving behaviour in Pacific salmon, viz. making orientation for homing migration, feeding, and controlling body temperature. Reddin et al. (2004) suggested a fourth hypothesis would be diving to avoid predators. They further pointed out that there may be an energetic advantage for salmon to seek prey in cooler deeper waters where prey are more abundant and then return to warmer surface waters where their food would be digested more rapidly. Our conclusion is that deep diving activities of salmon postsmolts shown by the DSTs to as deep as 50 m, due to their frequent nature, are probably related to prey seeking and feeding.

Marine climate and salmon population dynamics

Friedland (1998) reviewed ocean climate influences on salmon life history events including those related to age at maturity, survival, and growth. He concluded that ocean climate and ocean-linked terrestrial climate events affect nearly all aspects of salmon life history. For example, higher sea surface temperature has been implicated in increasing the ratio of grilse to MSW salmon (Saunders et al. 1983; Martin and Mitchell 1985; Jonsson and Jonsson 2004a), perhaps through growth rates (Scarnecchia 1983). Also, Scarnecchia (1984), Reddin (1987), Ritter (1989), Reddin et al. (1993), Friedland et al. (1993), Friedland et al. (1998, 2003aandb) showed significant correlations between salmon catches/production and environmental cues including those related to plankton productivity (Beaugrand and Reid 2003). Reddin and Shearer (1987) demonstrated that environmental conditions in the Labrador Sea influenced the abundance of salmon at West Greenland and this insight has been used to provide advice to fisheries managers through the North Atlantic Salmon Convention Organization (Anon. 2005). Assessments of the inner Bay of Fundy and Miramichi River stocks have also included environmental parameters thought to influence the survival during the early postsmolt stage and have been included in predictions of 1987 run sizes (Ritter 1989). However, the biological basis for these relationships is to date only speculative and deserves further study. But in spite of a lack of specific details on the underlying cause(s) of these apparent biological relationships, more recently, there have been several attempts to include environmental effects on recruitment of salmon in stock assessments (Friedland et al. 2003aandb; Chaput et al. 2005).

Colbourne et al. (2003), Friedland et al. (2003a), and Downton and Miller (1998) and many others have examined relationships between environmental variables and abundance of Pacific and Atlantic salmon and other fish species with a view to providing forecasts of future abundance, but without any knowledge of what thermal habitat regimes the fish actually use. Colbourne et al. (2003) indicated that the goal of searching for relationships is important so that influences of the physical ocean environment can be included in forecasts of stock abundance and ultimately used in management plans for various fisheries (Bisbal and McConnaha, 1998; Friedland, 1998). This is currently the case for both North American and European Atlantic salmon which have been forecasted partly based on environmental information (Anon., 2005). Physical conditions in the ocean have been shown to be related to mortality and growth of some other species (Brander, 1995; Dutil et al., 1999; Watanabe and Yatsu, 2004). Blackbourn (1993) and Downton and Miller (1998) have suggested that freshwater survival rates for some species of Pacific salmon are even related to SSTs experienced by potential spawners while still at sea shortly before their return to freshwater. These studies and their importance clearly show the need for studies giving details on the physical oceanography and ecology of fish at sea.

Experimental fishing in the Northwest Atlantic has indicated that salmon are found most abundantly in water temperatures of 4 to 10°C (*See temperature and salmon abundance section, this paper*). Thermal conditions are important indices of abundance because they are factors influencing survival of both North American and European Atlantic salmon, especially for Norwegian and Scottish salmon in the early marine stage (Friedland *et al.*, 2000; and Reddin and Friedland, 1996). In the Pacific Ocean, sharp thermal limits restrict steelhead trout and Pacific salmon distribution at sea and may ultimately control overall productivity, further underscoring the need to collect data on thermal habitat and preferences (Welch *et al.*, 1995; Welch *et al.*, 1998). The Pacific studies suggest that global warming from greenhouse gases can possibly result in very strong limits to future productivity (Welch *et al.*, 1998). At present, our knowledge of thermal regimes for Atlantic salmon, including the results in this paper, suggest that, unlike Pacific salmon, no strict limits exist, although there still remain strong relationships between temperature, survival and abundance (Reddin and Friedland, 1993; Friedland, 1998; Friedland *et al.* 1998; Friedland *et al.* 2000). The collection of more information using data storage tags, especially if geo-location can be accurately determined, may show similar limits also exist for Atlantic salmon. However, our current information suggests that Atlantic salmon may be more resilient to increased water temperatures than their Pacific counterparts.

In the Pacific, shifts in ocean climate have been detected on a basin scale level (Beamish et al., 1997). In particular, it has been shown that Pacific salmon abundance trends were closely associated with changes in the ocean-climate environment and that these changes occurred throughout the distribution of Pacific salmon (Beamish and Bouillon 1993). For most stocks of Pacific salmonids, marine survival improved after the climate event in 1976-77 resulting in increased productivity and catches. Associated with these natural fluctuations is the concept of regimes and regime shifts, either towards higher productivity from low or the reverse (Hare and Francis 1995; Steele 2004; Beamish et al., 1997; Beamish et al., 1999). Beamish et al. (1997) noted that change can occur quickly and it can be large. For the northwest Atlantic, there is evidence that a basin-scale shift in productivity has also occurred for Atlantic salmon (Reddin et al. 2000; Chaput et al. 2005). Basin-scale events may also be linked to downturns in salmon abundance in the North

Atlantic similar to the Pacific through climate links to the ocean environment as indicated by recent changes to the NAOI (Dickson, 1997; Dickson and Turrell 2000; Boyland and Adams 2006); some of which have been linked to salmon (Beaugrand and Reid 2003; Jonnson and Jonsson 2004a; Chaput et al. 2005).

Recent downturns in salmon abundance in the late 1980s and 1990s are unprecedented in magnitude and once again have drawn attention to our lack of knowledge of life history during the marine phase. Current estimates indicate that 2SW North American salmon stocks are the lowest on record (Anon. 2005). Other North Atlantic salmon stocks are also in decline (Anon. 2005). For example, downturns in rod catches of Scottish spring salmon (springers) which began in the 1970s have continued into the 1990s with a marked increase in the rate of decline (Youngson 1996). Because declines in salmon abundance have been widespread, it has been concluded that the main cause lies within the ocean life phase (Reddin and Friedland 1993; Friedland et al. 1993). For many of the rivers where sea survival is measured, the lowest recorded values have occurred in recent years. These low survivals have coincided with greatly reduced marine exploitation achieved through massive reductions in effort or in some cases complete bans (Anon. 2005) leaving us with the conclusion that something other than exploitation is the main cause. Beaugrand and Reid (2003) have detected large scale changes in the biogeography of calanoid copepod crustaceans in the northeast Atlantic in relation to sea surface temperature. It seems that copepod assemblages associated with warm water have shifted about 10 degrees of latitude northwards. At the same time, a number of biological variables have been shown to be directly related to these changes including salmon which is in a decreasing mode. This regional temperature increase therefore appears to be an important parameter that is at present governing the dynamic equilibrium of northeast Atlantic pelagic ecosystems with possible consequences for biogeochemical processes and fisheries.

Salmon abundance and the North Atlantic Oscillation

Although it is not entirely understand or predictable, the many references to the importance of marine climate effects on salmon abundance and various life history characteristics suggest that marine environment may hold the key to the downturn in salmon abundance. The pattern of climate variability in the North Atlantic including ocean temperatures, current strength and direction, and other factors is contained in the North Atlantic Oscillation (NAO) which is a major driving force for climate in the North Atlantic (Hurrell 1995). An index for the North Atlantic Oscillation is measured as the difference between the normalized sea level pressure at Iceland and the normalized sea level pressure in the mid-Atlantic, variously measured at the Ponta Delgada, Azores or Gibralter on the Iberian Peninsula (Jones et al. 1997; Osborn 2004). Jonsson and Jonsson (2004a) showed that for the River Imsa, Norway salmon stock there is a strong correlation between the North Atlantic Oscillation Index and age at maturity. Because the NAO is particularly important in winter, the winter index is generally used as a measure of climate variability. I use it here to examine the relationships between salmon and the marine environment of the Northwest Atlantic.

The NAOI shows an upward trend from the 1960s to the early 1990s, but also that the trend has not been sustained in recent years and that there can be considerable year-to-year variability in the index (Fig. 7). In order to analyse the relationship between salmon and NAOI, an index or measure of salmon abundance is also required. Rago et al. (1993aandb) developed techniques for estimating the total number of potential 2SW salmon measured at the 1SW stage (termed prefishery abundance of non-maturing salmon) and 1SW maturing salmon (potential grilse). Since the techniques involved regional derivations of prefishery abundance the same information is also available for Labrador salmon. This is because there were no long-term data of returns to freshwater available for Labrador rivers and commercial catches expanded to total returns using exploitation rates were used instead, which also provides a number representing total recruits. Updates to the technique and current numbers are shown in Reddin (1998) and Anon. (2005). The winter NAOI was analysed in relation to North American and Labrador 1SW and 2SW prefishery abundance. The 2SW time series was shifted such that the year was when the fish were in their first sea winter which was compared to the NAOI from the same year. Also used was the percent of 2SW fish in the entire year class defined as the number of 2SW salmon divided by number of 1SW plus 2SW salmon. For both North American and Labrador salmon, neither abundance nor maturation as measured by percent 2SW salmon were significantly related to the NAOI (Fig.8). Dickson and Turrell (2000) and Jonsson and Jonsson (2004a) have shown that for some salmon metrics related to European salmon, there is a significant although weak relationship which they attribute to climate forcing of salmon abundance. There do not appear to be any relationships between either North American and Labrador salmon abundance and NAOI.

SUMMARY

This paper provides a summary of the ecology and life history of Atlantic salmon in the Northwest Atlantic Ocean and the ecological relationships of salmon to temperature, salinity, climate variables. While much is known about the life of salmon in the sea, there is much more to be learned. The survey information exists only for the Labrador Sea in the spring and fall and the Grand Banks area in the spring. Seasonal survey information for winter is lacking. There is no research vessel survey information for the Gulf of St. Lawrence where Dutil and Coutu (1988) showed there were salmon postsmolts caught as bycatch in herring gear. The extent that salmon migrate to the Northeast is unknown but thought to be low (Reddin 1987; Hansen and Jacobsen 2003); although Tucker et al. (1999) showed that it may be more extensive then previously thought. There is no experimental fishing during the winter in the Northwest Atlantic. Migration routes, distribution and abundance for specific stocks are completely unknown. Also, the reason(s) behind the current high mortality rates for Atlantic salmon which, although known to occur at sea, has no specific known cause(s). It is recommended that research vessel surveys should continue and be expanded to other areas of the Northwest Atlantic; that experiments with data storage tags especially with geo-location be initiated; and that inshore tracking experiments to determine mortality and sources also be initiated.

REFERENCES

Anon. 2005. Report of the Working Group on North Atlantic Salmon (WGNAS). 5-14 April 2005 Nuuk, Greenland. ICES C.M. 2005/ACFM:17, Ref. I.

Allan, I.R.H., and J.A. Ritter. 1977. Salmonid terminology. Journal du Conseil International pour l'Exploration de la Mer 37:293-299.

Beamish, R.J., and D.R. Bouillon. 1993. Pacific salmon production trends in relation to climate. Can. J. Fish. Aquat. Sci. 50:1002-1016.

Beamish, R.J. (ed.). 1995. Climate change and northern fish populations. Can. Spec. Publ. Fish. Aquat. Sci. 121: 739 p.

Beamish, R.J., C.-E.M. Neville, and A.J. Cass. 1997. Production of Fraser River sockeye salmon (*Oncorhynchus nerka*) in relation to decadal-scale changes in climate and the ocean. Can. J. Fish. Aquat. Sci. 54: 543-554.

Beamish, R.J., D.J. Noakes, G.A. McFarlane, L. Klyashtorin, V.V. Ivanov, and V. Kurashov. 1999. The regime concept and natural trends in the production of Pacific salmon. Can. J. Fish. Aquat. Sci. 56: 516-526.

Beaugrand, G. and P. C. Reid. 2003. Long-term changes in phytoplankton, zooplankton and salmon related to climate. Global Change Biology 9(6): 801-817.

Belding, D.L. 1939. Migration of the Atlantic salmon (Salmo salar) in the Gulf of St. Lawrence as determined by tagging experiments. Trans. Am. Fish. Soc. 69: 290-295.

Belding, D.L., and G. Prefontaine. 1938. Studies on the Atlantic salmon – II. Report on the salmon of the 1937 Port aux Basques (Newfoundland) drift net fishery. Contributions de l'Institut de Zoologie de L'Universite de Montreal – No. 3, 58 p.

Bisbal, G.A., and W.E. McConnaha. 1998. Consideration of ocean conditions in the management of salmon. Can. J. Fish. Aquat. Sci. 55:2178-2186.

Blackbourn, D.J. 1993. Sea surface temperature and the subsequent freshwater survival rate of some salmon stocks: a surprising link between the climate of land and sea. *In* Proceedings of the 9th Annual Pacific Climate (PACLIM) Workshop, 21-24 Apr. 1992. Edited by K.T. Redmond and V.L. Tharp. Tech. Rep. No. 34. California Department of Water Resources, Interagency Ecological Studies Program, Pacific Grove, p.23-32.

Boylan, P., and C.E. Adams. 2006. The influence of broad scale climatic phenomena on long term trends in Atlantic salmon population size: an example from the River Foyle, Ireland.

Brander, K.M. 1995. The effect of temperature on growth of Atlantic cod (Gadus morhua L.). ICES J. Mar. Sci. 52:1-10.

Caron, F. 1983. Migration vers l'Atlantique des post_saumoneaux (Salmo salar) du Golfe du Saint_Laurent. le Nat. Can., 110: 223-227.

Chaput, G., C.M. Legault, D.G. Reddin, F. Caron, and P.G. Amiro. 2005. Provision of catch advice taking account of non-stationarity in productivity of Atlantic salmon (Salmo salar L.) in the Northwest Atlantic. ICES Journal of Marine Science, 62:131-143.

Christensen, O., and W.H. Lear. 1980. Distribution and abundance of Atlantic salmon at West Greenland. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 176:22-35.

Colbourne, E. 2003. Physical oceanographic conditions on the Newfoundland and Labrador Shelf during 2002. DFO, CSAS Res. Doc. 2003/020, 57 p.

Dempson, J.B., D.G. Reddin, M.F. O’Connell, J. Helbig, C.E. Bourgeois, C. Mullins, T.R. Porter, G. Lilly, J. Carscadden, G.B. Stenson, and D. Kulka. 1998. Spatial and temporal variation in Atlantic salmon abundance in the Newfoundland-Labrador region with emphasis on factors that may have contributed to low returns in 1997. DFO Atlantic Fisheries Res. Doc. 98/114, 161 p.

Dempson, J. B., M. F. O’Connell, and C. J. Schwarz. 2004. Spatial and temporal trends in abundance of Atlantic salmon, Salmo salar, in Newfoundland with emphasis on impacts of the 1992 closure of the commercial fishery. Fisheries Management and Ecology 11: 387-402.

DFO. 2005. Assessment of Newfoundland and Labrador Atlantic Salmon. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2005/052.

Dickson, R.R., and W.R. Turrell. 2000. The NAO: the dominant atmospheric process affecting oceanic variability in home, middle, and distant waters of European Atlantic Salmon, pp. 92-115. In: Derek Mills (ed.) The ocean life of

Atlantic salmon: environmental and biological factors influencing survival. Proceedings of a Workshop Held at the Freshwater Fisheries Laboratory, Pitlochry, on 18th and 19th November, 1998. Blackwell Scientific, Fishing News Books. pp. 228.

Downton, M.W., and K.A. Miller. 1998. Relationships between Alaskan salmon catch and North Pacific climate on interannual and interdecadal time scales. Can. J. Fish. Aquat. Sci. 50:1002-1016.

Dunbar, M.J., and D.H. Thomson. 1979. West Greenland salmon and climatic change. Meddelelser om Gronland, 202(4):1-19.

Dutil, J.D., and J.M. Coutu. 1988. Early Marine Life of Atlantic salmon, Salmo salar, Postsmolts in the Northern Gulf of St. Lawrence. Fish. Bull. 86:197-211.

Eriksson, T. 1994. Mortality risks of Baltic salmon during downstream migration and early sea-phase: effects of body size and season. Nordic Journal of Freshwater Research 69: 100.

Fairchild, W. L., Swansburg, E. O., Arsenault, J. T., and Brown, S. B. 1999. Does an association between pesticide use and subsequent declines in catch of Atlantic salmon (Salmo salar) represent a case of endocrine disruption? Environmental Health Perspectives, 107: 349-357.

Finstad, B., F. Okland, E.B. Thorstad, P.A. Bjorn and R.S. McKinley. 2005. Migration of hatchery-reared Atlantic salmon and wild anadromous brown trout post-smolts in a Norwegian fjord system. J. Fish Biol. 66: 86-96.

Fletcher, G.L., M.H. Kao, and J.B. Dempson. 1988. Lethal freezing temperatures of Arctic char and other salmonids in the presence of ice. Aquaculture, 71:369-378.

Forsberg, O.I. 1995. Empirical investigations on growth of post-smolt Atlantic salmon (*Salmo salar* L.) in land-based farms. Evidence of a photoperiod influence. Aquaculture 133: 235-248.

Fried, S.M., J.D. McCleave, and G.W. LaBar. 1978. Seaward migration of hatchery-reared Atlantic salmon, Salmo salar, smolts in the Penobscot River estuary, Maine: riverine movements. J. Fish. Res. Board Can., 35:76-87.

Friedland, K. D., and D.G. Reddin. 1993. Marine survival of Atlantic salmon from indices of post-smolt growth and sea temperature. Ch. 6: pp. 119-138. In Derek Mills [ed.] Salmon in the sea and new enhancement strategies. Fishing News Books. 424 p.

Friedland, K.D., D.G. Reddin, and J.F. Kocik. 1993. Marine survival of North American and European salmon: effects of growth and environment. ICES J. Mar. Sci. 50: 481-492.

Friedland K.D., L.P. Hansen, and D.A. Dunkley. 1998. Marine temperature experienced by postsmolts and the survival of Atlantic salmon, Salmo salar L. in the North Sea area. Fisheries Oceanography 7: 22-34.

Friedland, K.D. 1998. Ocean climate influences on critical Atlantic salmon (Salmo salar) life history events. Can. J. Fish. Aquat. Sci. 55:119-130.

Friedland, K.D., J.-D. Dutil, and T. Sadusky. 1999. Growth patterns in postsmolts and the nature of the marine juvenile nursery for Atlantic salmon, Salmo salar. Fish. Bull. 97:472-481.

Friedland, K.D., L.P. Hansen, D.A. Dunkley, and J.C. MacLean. 2000. Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (Salmo salar L.) in the North Sea area. ICES Journal of Marine Science 57:419-429.

Friedland, K. D., D.G. Reddin, J.R. McMenemy, and K.F. Drinkwater. 2003a. Multidecadal trends in North American Atlantic salmon (Salmo salar) stocks and climate trends relevant to juvenile survival. Can. J. Fish. Aquat. Sci., 60: 563-583.

Friedland, K. D., D.G. Reddin, and M. Castonguay. 2003b. Ocean thermal conditions in the post-smolt nursery of North American Atlantic salmon. – ICES Journal of Marine Science, 60: 343-355.

Handeland, S.O., B.Th. Bjornsson, A.M. Arnesen, and S.O. Stefansson. 2003. Seawater adaptation and growth of post-smolt Atlantic salmon (Salmo salar) of wild and farmed strains. Aquaculture 220:367-384.

Hansen, L.P., and T.P. Quinn. 1998. The marine phase of Atlantic salmon life cycle, with comparisons to Pacific salmon. Can. J. Aquat. Sci. 55(Suppl. 1): 104-118.

Hansen, L.P., and J.A. Jacobsen. 2003. Origin, migration and growth of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in oceanic areas north of the Faroe Islands. ICES J. Marine Science, 60:110-119.

Hare, S.R., and R.C. Francis. 1995. Climate Change and Salmon Production in the Northeast Pacific Ocean. In: R.J. Beamish [ed.] Ocean climate and northern fish populations. Can. spec. Pub. Fish. Aquat. Sci. 121, pp. 357-372.

Hardy, Sir Alister. 1965. The Open Sea, its Natural History. Houghton Mifflin Co. Boston, 322 p.

Hoar, W.S. 1988. The physiology of smolting salmonids. In Fish physiology. Vol. XIB. Edited by W.S. Hoar and D.J. Randall. Academic Press, New York., pp. 275-343.

Holm, M., I. Huse, E. Waatevik, K.B. Døving, and J. Aure. 1982. Behaviour of Atlantic salmon smolts during the seaward migration. I. Preliminary report on ultrasonic tracking in a Norwegian fjord system. ICES CM 1982/M:7, 10 pp.

Holm, M., J.C. Holst, and L.P. Hansen. 1998. Spatial and temporal distribution of Atlantic salmon postsmolts in the Norwegian Sea and adjacent areas – origin of fish, age structure and releation to hydrographical conditions in the sea. ICES CM 1998/N:15, 8 pp.

Holm, M., J.C. Holst, and L.P. Hansen. 2000. Spatial and temporal distribution of post-smolts of Atlantic salmon. ICES Journal of Marine Science 57:955-964.

Holst, J.C., R. Shelton, M. Holm, and L.P. Hansen. 2000. Distribution and possible migration routes of postsmolt Atlantic salmon in the North-east Atlantic, pp. 65-74. In: Derek Mills (ed.) The ocean life of Atlantic salmon: environmental and biological factors influencing survival. Proceedings of a Workshop Held at the Freshwater Fisheries Laboratory, Pitlochry, on 18th and 19th November, 1998. Blackwell Scientific, Fishing News Books. pp. 228.

Hurrell, J.W. 1995. Decadal trends in the North Atlantic Oscillation and relationships to regional temperature and precipitation. Science 269: 676-679.

Idler, D.R., S.J. Hwang, L.W. Crim, and D.G. Reddin. 1981. Determination of sexual maturation stages of Atlantic salmon (Salmo salar) captured at sea. Can. J. Aquat. Sci. 38: 405-413.

Ikonen, E. 1986. Spawning migration of salmon (Salmo salar L.) in the coastal waters of the Gulf of Bothnia. Cons. Int. Explor. Mer, C.M. 1986/M:24.

Jakapsstovu, S.H. 1988. Exploitation and migration of salmon in Faroese waters. Chapter 25, p. 458-482. *In.* D. H. Mills and D. J. Piggins [Eds.] Atlantic salmon: planning for the future. Proceedings of the Third International Atlantic salmon Symposium, Biarritz, France, October 21-23, 1986. Croom Helm, London.

Jessop, B.M. 1976. Distribution and timing of tag recoveries from native and non-native Atlantic salmon (*Salmo salar*) released into the Big Salmon River, New Brunswick. J. Fish. Res. Board Can. 33: 829-833.

Jones, P.D., Jónsson, T., and Wheeler, D. 1997. Extension to the North Atlantic Oscillation using early instrumental pressure observations from Gibraltar and South-West Iceland. Int. J. Climatol. 17: 1433-1450.

Jonsson, B., and J. Ruud-Hansen. 1985. Water temperature as the primary influence on timing seaward migrations of Atlantic salmon (*Salmo salar*) smolts. Can. J. Fish. Aquat. Sci. 42: 593-595.

Jonsson, N., B. Jonsson, and L.P. Hansen. 1998. The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon. J. Anim. Ecol. 67: 651-672.

Jonsson, N., and B. Jonsson. 2004a. Size and age of maturity of Atlantic salmon correlate with the North Atlantic Oscillation Index (NAOI). J. Fish. Biol. 64: 241-247.

Jonsson, B., and N. Jonsson. 2004b. Factors affecting marine production of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 61: 2369-2383.

Karlsson, L., E. Ikonen, H. Westerberg, and J. Sturlaugsson. 1996. Use of data storage tags to study the spawning migration of Baltic salmon (Salmo salar L.) in the Gulf of Bothnia. ICES C. M. 1996/M:9, 15 p.

Lacroix, G.L., and P. McCurdy. 1996. Migratory behaviour of postsmolt Atlantic salmon during initial stages of seaward migration. J. Fish. Biol. 49: 1086-1101.

Lacroix, G.L., P. McCurdy, and D. Knox. 2004. Migration of Atlantic salmon postsmolts in relation to habitat use in a coastal system. Trans. Am. Fish. Soc. 133: 1455-1471.

Lacroix, G.L., and P. McCurdy. 2005. Survival and behaviour of post-smolt Atlantic salmon in coastal habitat with extreme tides. J. Fish. Biol. 66: 485-498.

Lear, W. H. 1976. Migrating Atlantic salmon (*Salmo salar*) caught by otter trawl on the Newfoundland continental shelf. J. Fish. Res. Board Can., 33: 1202-1205.

Lear, W. H., and R.K. Misra. 1978. Clinal variation in scale characters of Atlantic salmon (*Salmo salar*) based on discriminant function analysis. J. Fish. Res. Board Can. 35: 43-47.

Lear, W. H., and S.J. Sandeman. 1980. Use of scale characters and discriminant functions for identifying continental origin of Atlantic salmon. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 176:68-75.

Levings, C.D. 1994. Feeding behavior of juvenile salmon and significance of habitat during estuary and early sea phase. Nord. J. Freshwater Res. 69:7-16.

Martin J.H.A., and K.A. Mitchell. 1985. Influence of sea temperature upon the numbers of grilse and multi-sea winter Atlantic salmon (Salmo salar) caught in the vicinity of the River Dee (Aberdeenshire). Can. J. Fish. Aquat. Sci., 42: 1513-1521.

May, A.W. 1973. Distribution and migration of salmon in the northwest Atlantic. Int. Atl. Salmon Symp., 1972. Int. Atl. Salmon Found., Spec. Publ. 4: 372-382.

McCormick, S.D., and R.L. Saunders. 1987. Preparatory physiological adaptions for marine life in salmonids: osmoregulation, growth, and metabolism. Am. Fish. Soc. Symp. 1:211-229.

McCormick, S.D., L.P. Hansen, T.P. Quinn, and R.L. Saunders. 1998. Movement, migration and smolting of Atlantic salmon (Salmo salar). Can. J. Fish. Aquat. Sci. (Suppl. 1) 55:77–92.

Meerburg, D.J. [ed.]. 1986. Salmonid age at maturity. Can. Spec. Publ. Fish. Aquat. Sci. 89: 118 p.

Meister, A. L. 1984. The marine migrations of tagged Atlantic salmon (Salmo salar L.) of USA origin. Cons. int. Explor. Mer, C.M. 1984/M:27, 28 p.

Møller Jensen, J., and W.H. Lear. 1980. Atlantic salmon caught in the Irminger Sea and at East Greenland. J. Northw. Atl. Fish. Sci., 1: 55-64.

Montevecchi W.A., D.K. Cairns, and V.L. Birt. 1988. Migration of postsmolt Atlantic salmon, Salmo salar, off northeastern Newfoundland, as inferred by tag recoveries in a seabird colony. Can. J. Fish. Aquat. Sci., 45: 568-571.

Montevecchi, W.A., D.K. Cairns, and R.A. Myers. 2002. Predation on marine-phase Atlantic salmon (Salmo salar) by gannets (Morus bassanus) in the northwest Atlantic. Can. J. Fish. Aquat. Sci. 59:602-612.

Moore, A., G.L. Lacroix, and J. Sturlaugsson. 2000. Tracking Atlantic salmon post-smolts in the sea.

Moore, A., E.C.E. Potter, N.J. Milner, and S. Bamber. 1995. The migratory behaviour of wild Atlantic salmon (Salmo salar L.) smolts in the estuary of the River Conwy, North Wales. Can. J. Fish. Aquat. Sci. 52:1923-1935.

Moore, A., G.L. Lacroix, and J. Sturlaugsson. 2000. Tracking Atlantic salmon post-smolts in the sea. In The Ocean Life of Atlantic salmon – Environmental and Biological Factors Influencing Survival (Mills, D., ed.), pp. 49-64. Oxford: Fishing News Books.

Narayanan, S., J. Carscadden, J.B. Dempson, M.F. O'Connell, S. Prinsenberg, D.G. Reddin, and N. Shackell. 1995. Marine Climate off Newfoundland and its influence on Atlantic salmon (Salmo salar) and capelin (Mallotus villosus). In: Climate Change and northern fish populations. R.J. Beamish (ed.) Can. Spec. Publ. Fish. Aquat. Sci. 121 pp. 461-474.

O'Connell, M. F., J. B. Dempson, T. R. Porter, D. G. Reddin, E.G.M. Ash, and N. M. Cochrane. 1992. Status of Atlantic salmon (Salmo salar L.) stocks of the Newfoundland Region, 1991. CAFSAC Res. Doc. 92/22, 56 p.

Osborn, T.J. 2004. Simulating the winter North Atlantic Oscillation: the roles of internal variability and greenhouse gas forcing. Clim. Dyn. 22: 605-623.

Peterman, R.M. 1981. Form of random variation in salmon smolt-to-adult numbers relations and its influence on production estimates. Can. J. Aquat. Fish. Sci. 38:1113-1119.

Pippy, J. [Chairman] 1982. Report on the Working Group on the Interception of Mainland Salmon in Newfoundland. Can. MS Rep. Fish. Aquat. Sci., 1654: x + 196p.

Power G., Power M.V., R. Dumas, and A. Gordon. 1987. Marine migrations of Atlantic salmon from rivers in Ungava Bay, Québec. In: American Fisheries Society Symposium on Common Strategies in Anadromous/Catadromous Fishes, 1: 364-376.

Pratt, J. D., G. M. Hare, and G. M. Murphy. 1974. Investigations of production and harvest of an Atlantic salmon population, Sand Hill River, Labrador. Fish. Mar. Serv. Res. Dev. Branch Tech. Rep. Ser. No. NEW/T-74-1: iii+ 27p.

Rago, P.J., D.G. Reddin, T.R. Porter, D.J. Meerburg, K.D. Friedland and E.C.E. Potter. 1993a. A continental run reconstruction model for the non-maturing component of North Ameri-can Atlantic salmon: analysis of fisheries in Greenland and Newfoundland-Labrador, 1974–1991. ICES CM 1993/M:25.

Rago, P.J., D.J. Meerburg, D.G. Reddin, G.J. Chaput, T.L. Marshall, B. Dempson, F. Caron, T.R. Porter, K.D. Friedland, and E.T. Baum. 1993b. Estimation and analysis of pre-fishery abundance of the two-sea-winter population of North American Atlantic salmon (Salmo salar), 1974–1991. ICES CM 1993/M:24.

Reddin, D.G. 1985. Atlantic salmon (Salmo salar) on and east of the Grand Bank. J. Northwest. Atl. Sci. 6:157-164.

Reddin, D.G. 1987. Contribution of North American salmon (Salmo salar L.) to the Faroese fishery. le Naturaliste Canadien. 114(2): 211_218.

Reddin, D.G. 1988. Ocean life of Atlantic salmon (Salmo salar L.) in the Northwest Atlantic. Chapter 26, p. 483-511. *In.* D. H. Mills and D. J. Piggins [Eds.] Atlantic salmon: planning for the future. Proceedings of the Third International Atlantic salmon Symposium, Biarritz, France, October 21-23, 1986. Croom Helm, London.

Reddin, D.G. Estimation of the Labrador component of prefishery abundance of North America Atlantic salmon (Salmo salar L.) in 1998. DFO, CSAS Res. Doc. 99/91, 21 p.

Reddin, D.G., and F.A. Day. 1980. 1969-72 Newfoundland and Labrador Atlantic salmon (*Salmo salar*) commercial catch data. Can. Data Rep. Fish. Aquat. Sci. 220: iv + 55 p.

Reddin, D.G., W.M. Shearer, and R.F. Burfitt. 1984. Inter-continental migrations of Atlantic salmon (Salmo salar L.). Cons. Int. Explor. Mer, C.M. 1984/M:11, 9 p.

Reddin, D.G., and J.B Dempson. 1986. Origin of Atlantic salmon (Salmo salar L.) caught at sea near Nain, Labrador. le Naturaliste Canadien. 113: 211-218.

Reddin D. G., and W.M. Shearer. 1987. Sea_surface temperature and distribution of Atlantic salmon in the Northwest Atlantic Ocean. For: American Fisheries Society Symposium on Common Strategies in Anadromous/Catadromous Fishes, 1: 262_275.

Reddin D.G., and W.H. Lear. 1990. Summary of marine tagging studies of Atlantic salmon (Salmo salar L.) in the northwest Atlantic area. Can. Tech. Rep. Fish. Aquat. Sci., 1737: iv + 115 p.

Reddin, D.G., and P.B. Short. 1991. Postsmolt Atlantic salmon (Salmo salar) in the Labrador Sea. Can. J. Fish. Aquat. Sci. 48:2-6.

Reddin, D.G., and K. D. Friedland. 1993. Marine environmental factors influencing the movement and survival of Atlantic salmon. Ch. 4: pp. 79-103. In Derek Mills [ed.] Salmon in the sea and new enhancement strategies. Fishing News Books. 424 p.

Reddin, D.G., and K.D. Friedland. 1996. Declines of Scottish spring salmon and thermal habitat in the northwest Atlantic. How are they related?, pp. 45-66. In: Derek Mills (ed.) Enhancement of Spring Salmon. Proceedings of a One-day Conference Held in the Rooms of the Linnean Society of London. 26 January 1996. The Atlantic Salmon Trust, Pitlochry, Scotland.

Reddin, D.G., and K. D. Friedland. 1998. A history of identification to continent of origin of Atlantic salmon (Salmo salar L.) at west Greenland. Fisheries Research 43(1-3): 221-235.

Reddin, D.G., J. Helbig, A. Thomas, B.G. Whitehouse, and K.D. Friedland. 2000. Survival of Atlantic Salmon (Salmo salar L.) related to marine climate, pp. 89-91. In: Derek Mills (ed.) The ocean life of Atlantic salmon: environmental and biological factors influencing survival. Proceedings of a Workshop Held at the Freshwater Fisheries Laboratory, Pitlochry, on 18th and 19th November, 1998. Blackwell Scientific, Fishing News Books. pp. 228.

Reddin, D.G., K.D. Friedland, P. Downton, J.B. Dempson, and C.C. Mullins. 2004. Thermal habitat experienced by Atlantic salmon kelts (Salmo salar L.) in coastal Newfoundland waters. Fish. Oceanography 13:24-35.

Reddin, D.G., K.D. Friedland, and P. Downton. 2006. Early marine use of thermal habitat by Atlantic salmon smolts (Salmo salar L.). Fish. Bull. In Press.

Rikardsen, A.H., M. Haugland, P.A. Bjorns, B. Finstad, R. Knudsen, J.B. Dempson, J.C. Holst, N.A. Hvidsten, and M. Holm. 2004. Geographical differences in marine feeding of Atlantic salmon post-smolts in Norwegian fjords. J. of Fish Biol. 64:1655-1679.

Ritter, J.A. 1989. Marine migration and natural mortality of North American Atlantic salmon (Salmo salar L.). Can. MS Rep. Fish. Aquat. Sci. No. 2041. 136 p.

Rossby, T. 1996. The North Atlantic Current and surrounding waters: at the crossroads. Rev. Geophys., 34, 463-481.

Saunders, R.L. 1986. The thermal biology of Atlantic salmon: influence of temperature on salmon culture with particular reference to constraints imposed by low temperature. Inst. Freshw. Res. Drottningholm, Rep., 63:68-81.

Saunders, R.L., E.B. Henderson, B.D. Glebe, and E.J. Loundenslager. 1983. Evidence of a major environmental component in determination of the grilse:larger salmon ratio in Atlantic salmon (Salmo salar). Aquaculture, 33:107-118.

Scarnecchia, D.L. 1983. Age at sexual maturity in Icelandic stocks of Atlantic salmon (Salmo salar). Can. J. Fish. Aquat. Sci., 40:1456-1468.

Scarnecchia, D.L. 1984a. Climatic and oceanic variations affecting yield of Icelandic stocks of Atlantic salmon (Salmo salar). Can. Fish. Aquat. Sci., 41: 917-935.

Shelton, R.G.J., J.C. Holst, W.R. Turrell, J.C. MacLean, I.S. McLaren, and N.T. Nicoll. 1997. Records of post-smolt Atlantic salmon, Salmo salar L., in the Faroe-Shetland Channel in June 1996. Fisheries Research 31:159-162.

Sigholt, T., and B. Finstad. 1990. Effect of low temperature on seawater tolerance in Atlantic salmon (Salmo salar) smolts. Aquaculture, 84: 167-172.

Smed, J. 1980. Temperature of the waters off southwest and south Greenland during the ICES/ICNAF experiment in 1972. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 176: 18-21.

Stasko A.B., A.M. Sutterlin, S.A. Rommel, and P.F. Elson. 1973. Migration-orientation of Atlantic salmon (Salmo salar L.). International Atlantic Salmon Foundation Special Publication, Series 4: 119-137.

Steele, J.H. 2004. Regime shifts in the ocean: reconciling observations and theory. Progress in Oceanography 60: 135-141.

Sturlaugsson, J. 1995. Migration Study on Homing of Atlantic salmon (Salmo salar L.) in Coastal Waters W-Iceland - Depth movements and sea temperatures recorded at migration routes by data storage tags. ICES C.M. 1995/M:17, 13 p.

Templeman, W. 1965. Mass mortality of marine fishes in the Newfoundland area presumably due to low temperature. Int'l Comm. Northw. Atl. Fish. Spec. Publ., 6: 137-147.

Templeman, W. 1967. Atlantic salmon from the Labrador Sea and off West Greenland taken during A.T. Cameron Cruise, July-August 1965. Research Bulletin of the International Commission for Northwest Atlantic Fisheries, 4: 5-40.

Templeman, W. 1968. Distribution and characteristics of Atlantic salmon over oceanic depths and on the banks and shelf slope areas off Newfoundland. Research Bulletin of the International Commission for Northwest Atlantic Fisheries, 5: 62-65.

Thorisson, K., and J. Sturlaugsson. 1995. Postsmolt of ranched Atlantic salmon (Salmo salar L.) in Iceland: IV. Competitors and predators. ICES C.M. 1995/M:12, 9 p.

Tucker, S., I. Pazzia, D. Rowan, and J.B. Rasmussen. 1999. Detecting pan-migration in Atlantic salmon (*Salmo salar*) using ^{137}Cs. Can. J. Fish. Aquat. Sci. 56:2235-2239.

Tytler, P., J.E. Thorpe, and W.M. Shearer. 1978. Ultrasonic tracking of the movements of Atlantic salmon smolts (*Salmo salar* L.) in the estuaries of two Scottish rivers. J. Fish. Biol. 12: 575-586.

Wada, K., and Ueno, Y. 1999. Homing behavior of chum salmon determined by an archival tag. NPAFC Doc. 425: 29 pp.

Watanabe, C., and A. Yatsu. 2004. Effects of density-dependence and sea surface temperature on interannual variation in length-at-age of chub mackerel (Scomber japonicus) in the Kuroshio-Oyashio area during 1970-1997. Fish. Bull. 102:196-206.

Welch, D.W., Chigirinsky, A.I., and Ishida, Y. 1995. Upper thermal limits on the oceanic distribution of Pacific salmon (Oncorhynchus spp.) in the spring. Can. J. Fish. Aquat. Sci. 52:489-503.

Welch, D.W., Y. Ishida, Y., and K. Nagasawa. 1998. Thermal limits and ocean migrations of sockeye salmon (Oncorhynchus nerka): Long-term consequences of global warming. Can. J. Fish. Aquat. Sci. 55:937-948.

Westerberg, H. 1982a. Ultrasonic tracking of Atlantic salmon (Salmo salar L.) - I. Movements in coastal regions. Institute of Freshwater Research, Drottningholm Report, 60: 81-101.

Westerberg, H. 1982b. Ultrasonic tracking of Atlantic salmon (Salmo salar L.) - II. Swimming depth and temperature stratification. Institute of Freshwater Research, Drottningholm Report, 60: 102-120.

Westerberg, H. 1984. The orientation of fish and vertical stratification at fine- and micro-structure scales. In Mechanisms of Migration in Fishes (eds J.D. McCleave, G.P. Arnold, J.J. Dodson and W.H. Neill), Plenum Publishing Corporation, New York, pp. 179-204.

Youngson, A. 1996. The decline of spring salmon, pp. 3-12. In: Derek Mills (ed.) Enhancement of Spring Salmon. Proceedings of a One-day Conference Held in the Rooms of the Linnean Society of London. 26 January 1996. The Atlantic Salmon Trust, Pitlochry, Scotland.

Table 1. Average catch rate (numbers per 100 nets) of salmon from research and commercial fishing with surface gillnets in various regions of the North Atlantic , 1969-91.
~ indicates catch rate from commercial fishery
* indicates data for post smolts only   ** indicates data for Adults
note: 1 net = 33 meters

Year	Month	West Greenland *a,b,c*	Irminger Sea *a*	Labrador Sea *c*	Grand Banks *b,c*	East of Gr. Banks *b,c*	Northeast Shelf *c*
1969	Sep-Oct	26.4		30.6			
1970	Apr			5.1			6.6
	Sep-Oct	10.4		10.5			
1971	May			9.7	4.2		13.9
	Sep	21.1		14.2			
1972	Apr			5.6		4.8	
	Aug-Sep	11.3		39.2			
	Aug-Oct	42.0 ~	0.7 ~				
1973	Jun				6.9		
	Aug	41.0 ~	5.7				
1974	Jul	44.0 ~	8.5				
	Aug	72.0 ~	2.1				
1975	Aug	111.0 ~	11.9				
1977	Oct			26.1			0.0
1978	Aug	116.0		67.5			
1979	May				1.0		
	Aug-Sep	21.8		6.4			
1980	May-Jun				10.0	20.8	11.3
	Aug-Sep	35.1					
1982	Aug-Sep	48.5					
1985	Feb					1.2	
	Nov-Dec				0.8		
1986	Oct-Nov			4.0	2.0		
1987	Sep-Oct**			17.7	0.0		0.4
	Sep-Oct*			3.1			0.0
1988	Sep-Oct**			16.4			0.3
	Sep-Oct*			25.5			7.3
1989	Sep-Oct*	10.9		13.1			
	Sep-Oct*	0.0		38.9			
1991	Oct**			10.6	0.0		0.0
	Oct*			16.6	4.0		4.3
Mean		40.8	5.8	19.0	3.2	8.9	4.4
SD		34.8	4.6	16.1	3.4		5.2

a From Moller and Lear (1980)
b From Reddin (1986)
c DFO database

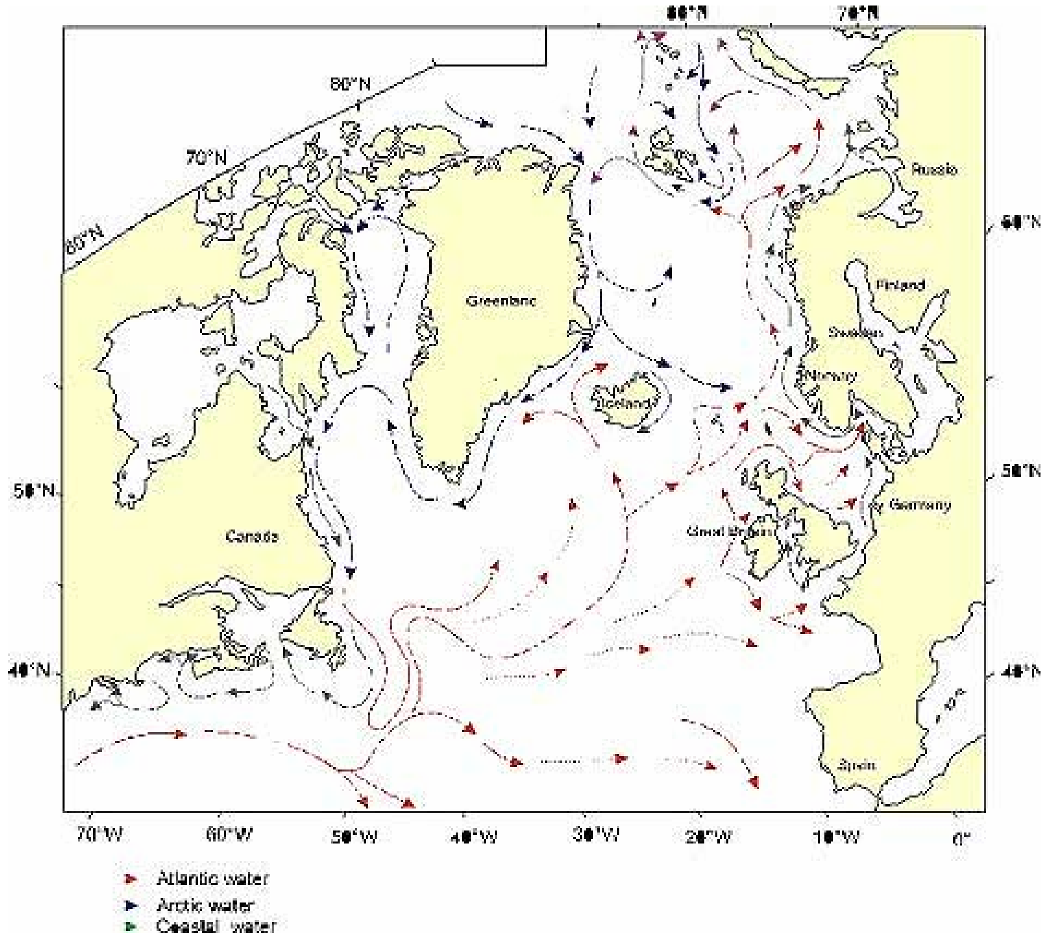

Fig. 1. Surface current patterns in the North Atlantic as described by Sundby at
http://www.mar-eco.no/learning-zone/backgrounders/deepsea_research/currents_in_the_north_atlantic

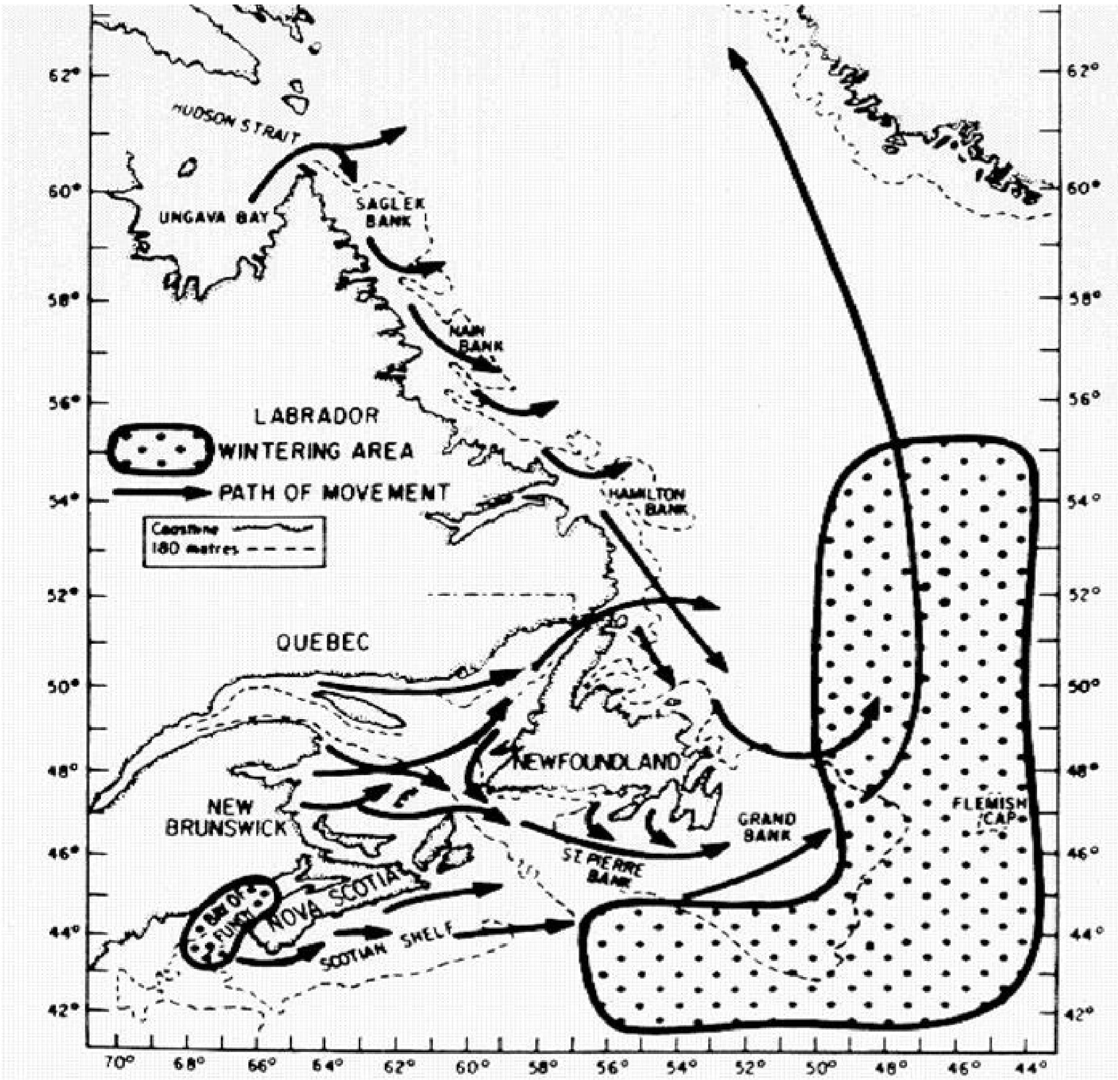

Fig. 2. Movement of Atlantic postsmolts away from home rivers into the Northwest Atlantic reproduced from Reddin (1988).

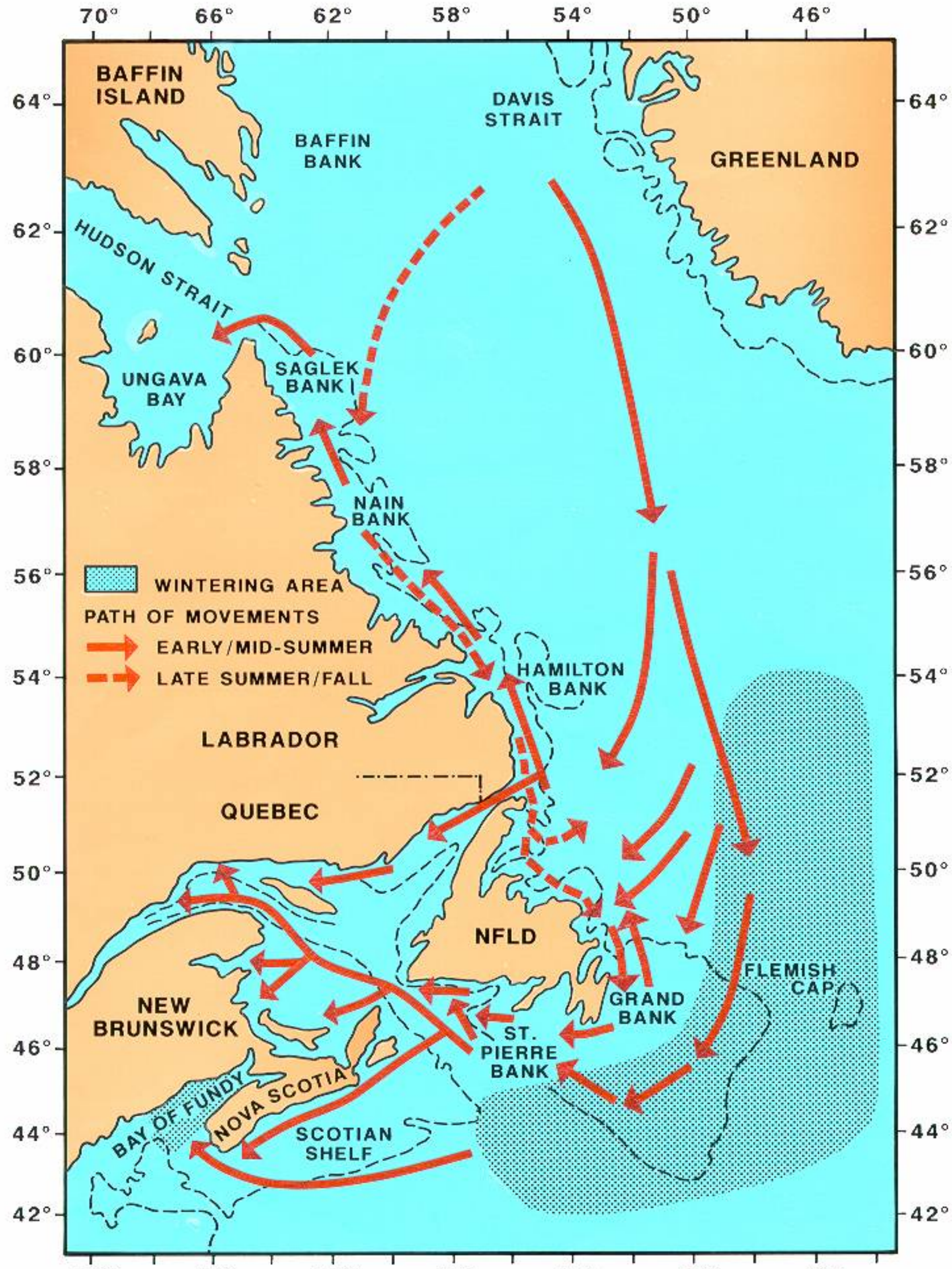

Fig. 3. Migration of Atlantic from the Labrador Sea and west Greenland area to home waters reproduced from Reddin (1988).

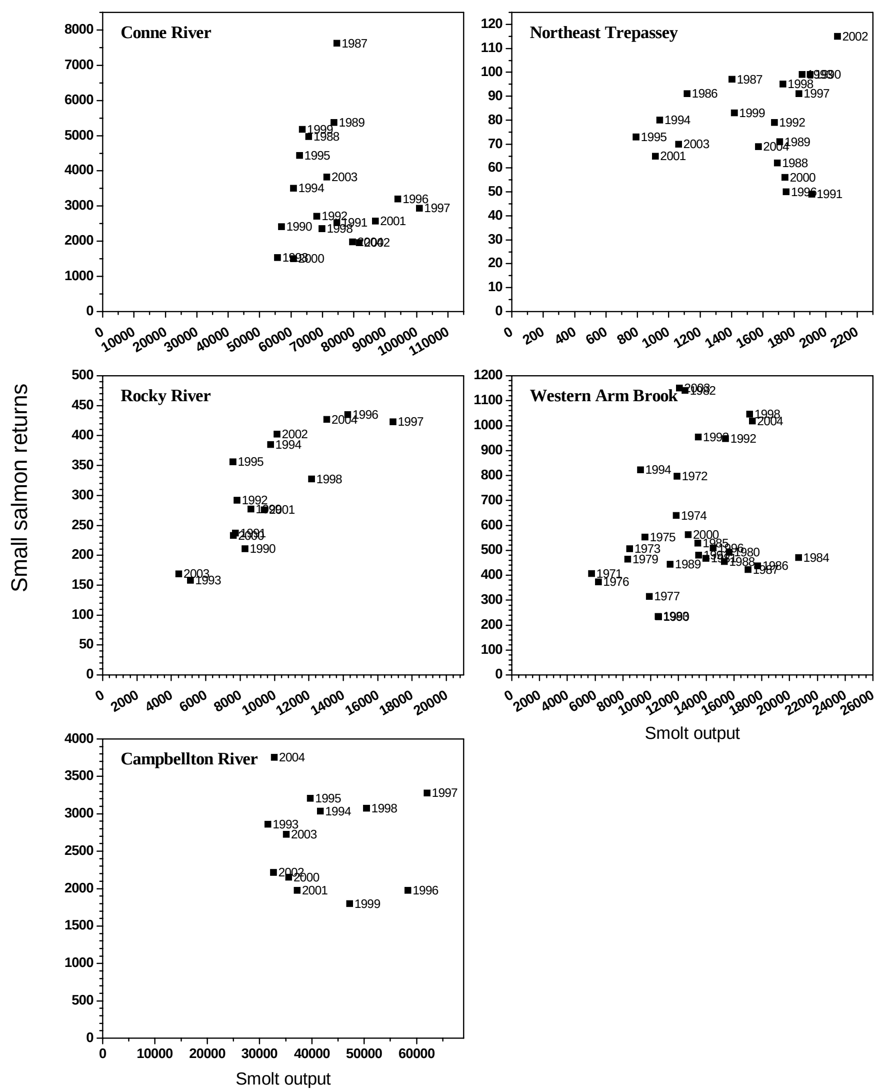

Fig. 4a. Adult salmon returns versus smolt output for five rivers in Newfoundland.

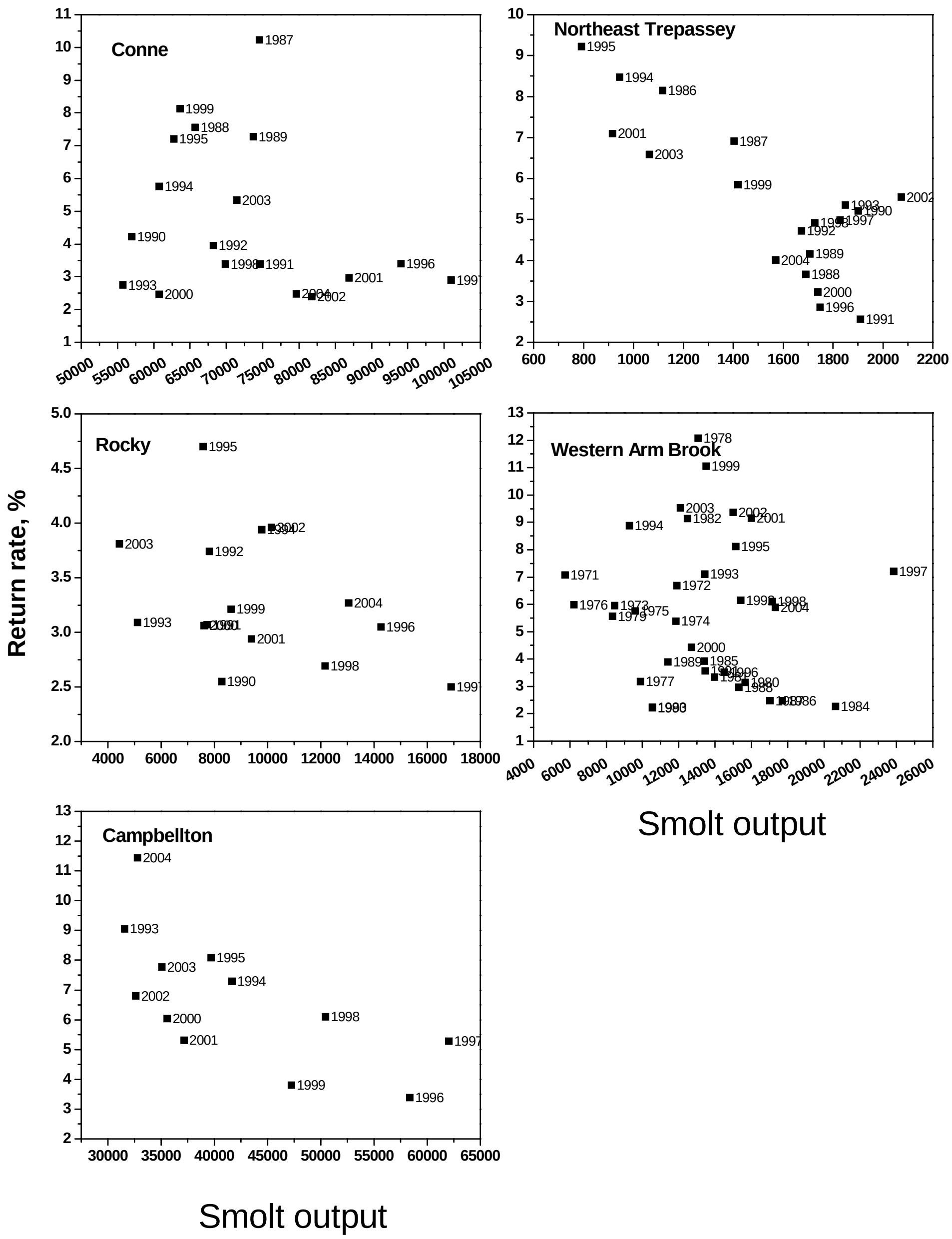

Fig. 4b. Adult salmon return rates (%) versus smolt output for five rivers in Newfoundland.

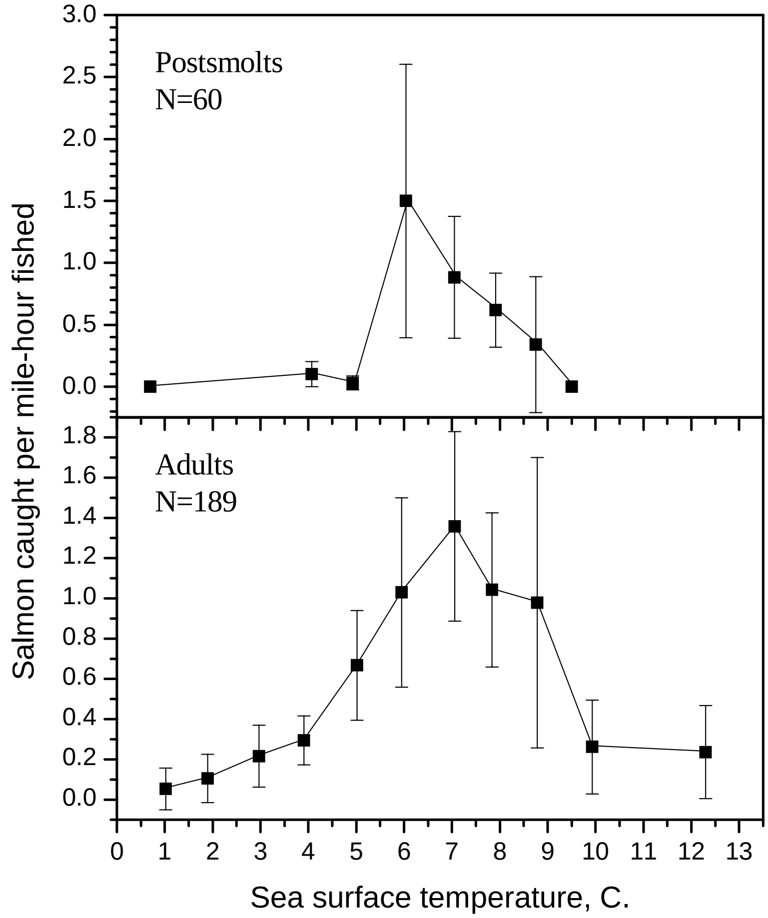

Fig. 5. The response to sea temperature by adult and postsmolt salmon in the Northwest Atlantic measured by catch rate in surface set gillnets, 1965-2001.

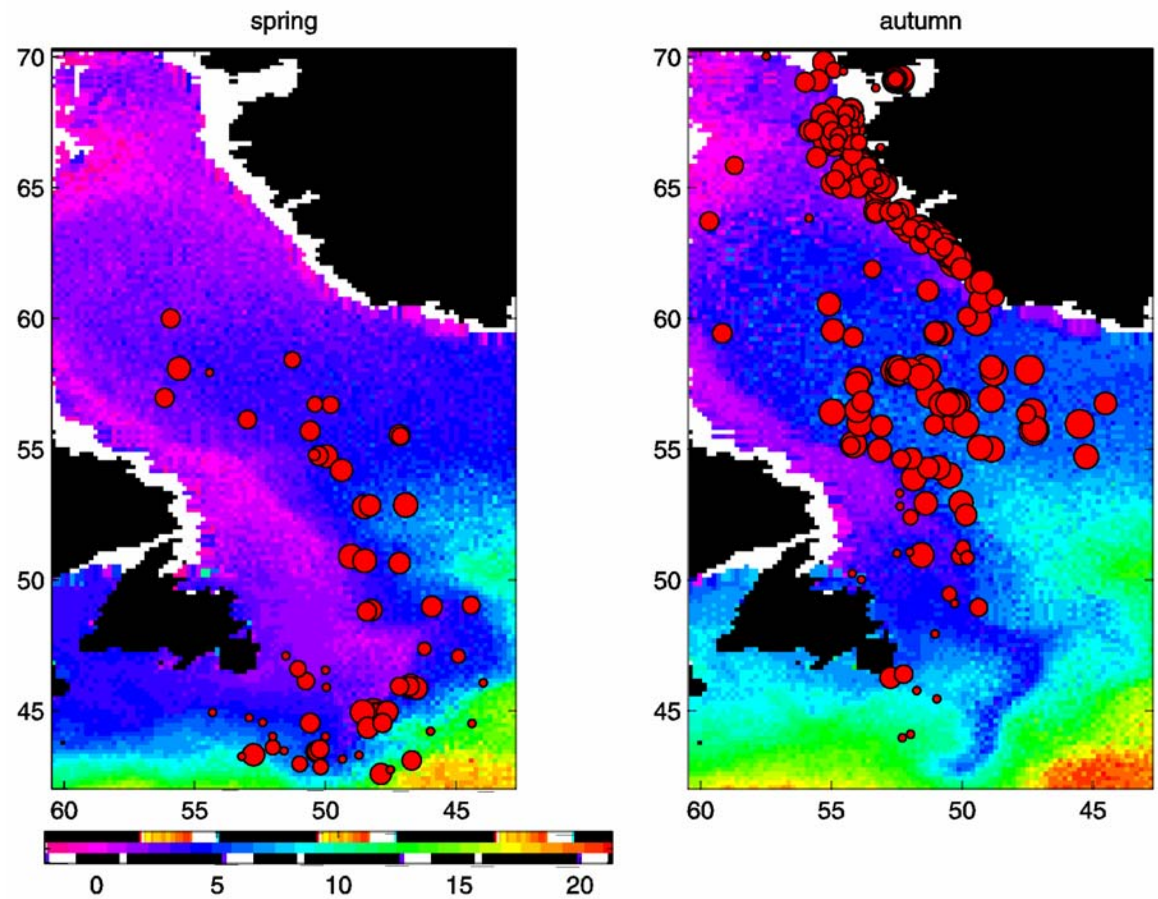

Fig. 6. Research vessel catch rates represented by circles as the log of salmon caught per mile-hour gear fished for Atlantic salmon in the northwest Atlantic and SSTs, 1965-2001.

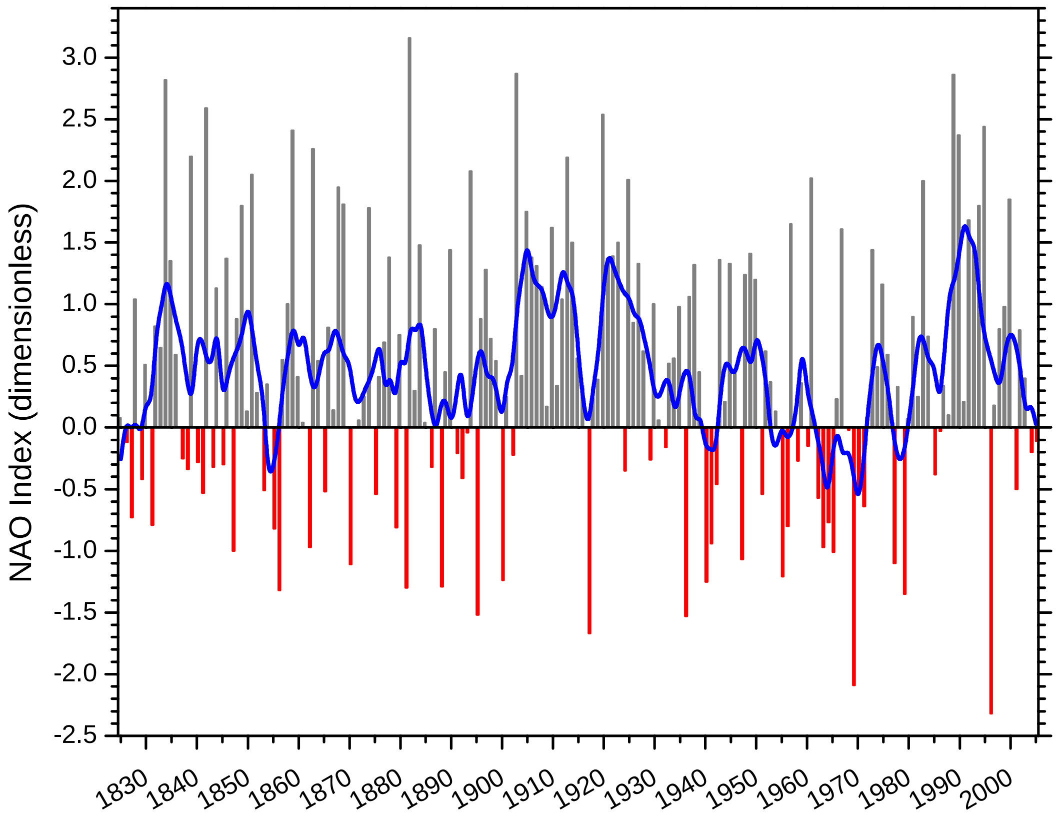

Fig. 7. The North Atlantic Oscillation Index for December to March measured as the average of the normalized sea level pressure difference between Iceland and Gibralter. Data from Jones et al. (1997) updated to 2004/2005 by Osborn (2004).

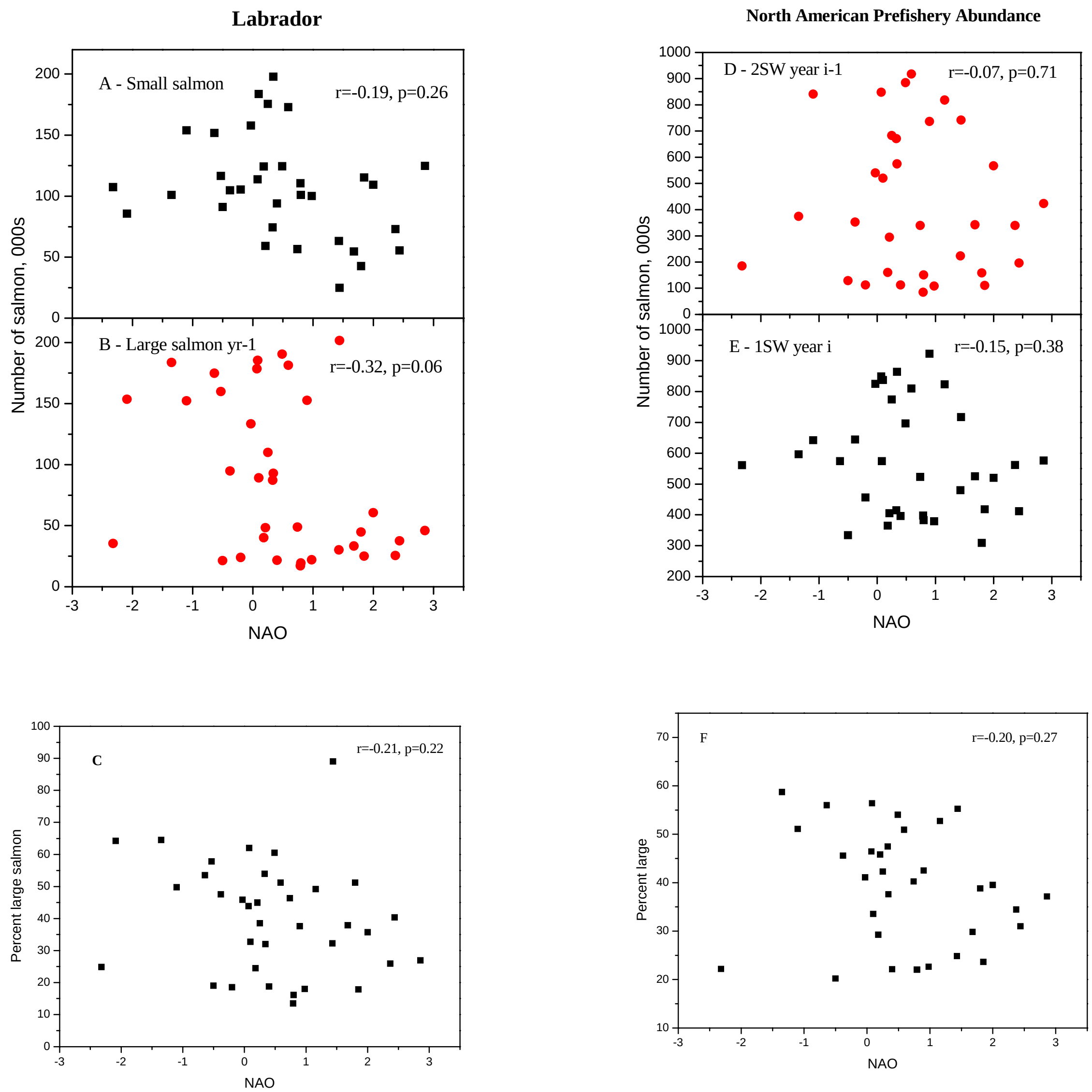

Fig. 8. The relationship between the North Atlantic Oscillation index and numbers of salmon prior to fisheries for Labrador (Panels A and B), Labrador large salmon by year class expressed as a percent (Panel C), North American recruits (Prefishery abundance, Panels D and E) and prefishery abundance by year class expressed as a percent (Panel F), 1971-2004.