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Aspects of the Life History, Biology, and Population Dynamics of Atlantic Salmon (*Salmo salar* L.) in Eastern Canada

Aspects du cycle, de la biologie et de la dynamique des populations de saumon atlantique (*Salmo salar* L.) dans l'Est du Canada

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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

A review of selected aspects of the life history, biology, and population dynamics of the Atlantic salmon of eastern Canada is presented. Information is provided on the following: life cycle and variability and plasticity in life history characteristics, size and growth in fresh water, biological characteristics of smolts, size and growth in marine water, survival in fresh water and at sea, and fecundity. A comprehensive list of references including those for major reviews of various topics is provided. The review is intended to provide pertinent resource material for the purpose outlined in the Foreword section above and as such is narrowed in scope accordingly.

Résumé

Le présent document passe en revue différents aspects du cycle, de la biologie et de la dynamique des populations de saumon atlantique de l'est du Canada. On y trouve des données sur les éléments suivants : cycle biologique et variations, ainsi que plasticité des caractéristiques du cycle biologique, taille et croissance en eau douce, caractéristiques biologiques des saumoneaux, taille et croissance en eau de mer, survie en eau douce et en mer et fécondité. Le document contient également une liste exhaustive de documents de référence, notamment des examens importants de divers sujets. Le présent rapport vise à fournir des données pertinentes aux fins mentionnées dans l'avant-propos qui précède, et sa portée a été limitée en conséquence.

Introduction

This paper presents a review of aspects of the life history, biology, and population dynamics of the Atlantic salmon of eastern Canada. Though the literature on these topics for Atlantic salmon in general is quite voluminous and comprehensive, information provided in this report is selective and tailored mainly to requirements specified in the Foreword section. Pertaining to the process of developing a Conservation Status Report for Atlantic salmon, those who wish to pursue various topics in greater detail than dealt with here can avail of the major reviews and works cited throughout the document.

Reference is made in this document to rivers within the provinces of eastern Canada, Salmon Fishing Areas (SFAs), and fishing zones (Qs) for the Province of Quebéc (Fig. 1).

Life History

Anadromous Populations

Anadromous Atlantic salmon display considerable phenotypic plasticity and variability in life history characters (Riddell and Leggett 1981; Saunders and Schom 1985; Thorpe 1986, 1989, 1994, 1998; Thorpe et al. 1998; Fleming 1996; Hutchings and Jones 1998; Klemetsen et al. 2003). It is an iteroparous species, one that can spawn repeatedly, as opposed to most species of Pacific salmon (*Oncorhynchus*), which are semelparous and die after a single spawning (Schaffer 1974; Fleming and Reynolds 2004). A defining characteristic of anadromous Atlantic salmon is the ability to return with a high degree of fidelity to the natal river or tributary for spawning (homing) (see reviews by Hasler and Scholz 1983; Stabell 1982, 1984; Hansen and Quinn 1998). Such precision in homing has led to the formation and maintenance of river-specific or local adaptations, resulting in much of the variability in genetic, life-history, behavioral, and other traits observed throughout the range of the species (Saunders and Schom 1985; Taylor 1991).

Figure 2 is a generalized depiction of the salient features of the life cycle of Atlantic salmon. This illustration will be the focus of an up-front broad-scale description of life history, to be followed by more detailed treatments of various aspects in the ensuing sections.

Depending on the stock, spawners returning to rivers are comprised of varying proportions maiden fish (those spawning for the first time) and repeat spawners. Most maiden salmon in turn consist of varying proportions of smaller fish that return to spawn after one winter at sea (1-sea-winter or 1SW) also known as grilse and larger fish that return after two or more winters at sea (2, 3-sea-winter, also designated as multi-sea-winter or MSW). Some rivers possess a component that returns to spawn after only a few months at sea (0-sea-winter or 0SW).

Collectively over its entire range in North America, adult Atlantic salmon return to rivers from feeding and staging areas in the sea mainly between May and November, but some runs can begin as early as March and April. In general, run timing varies by river, sea age, year, and hydrographic conditions. Run timing metrics pertain to where salmon are counted within a river system, whether it be an enumeration facility in the lower section of the river close to the estuary/ocean, or at a fishway located well upstream from the river mouth. As such, direct comparisons among rivers can be problematic although variability within a stock over time (years) is consistent for each individual system. Occasionally there can be some element of predictability in run timing of individual stocks; however, variation among years within rivers can still be substantive with median dates differing by five to six weeks or more in some populations. Large salmon enter earlier, on average, than small salmon in some rivers (e.g. LaHave River, Humber River, Western Arm Brook, Causapscal River). In other stocks the reverse is often true (e.g. Margaree River, Nashwaak River, Campbellton River, Highlands River, Mistassinin River) or there is little or no apparent difference (e.g. South River, Big Salmon River, Middle Brook, Terra Nova River, Bec-Scie River).

Run timing in Maritime rivers is frequently later, with return migrations extending over a greater interval of time than those of Quebec, Newfoundland, and Labrador salmon rivers. In the Miramichi, there are two distinct runs of salmon, an early run with peak migrations in early July and a late run with a peak in late Sept. to early Oct. (Chaput et al. 2001). Conne River and Humber River, Newfoundland, are characterized by median run timing dates of June 28, and are among the earliest in all of Atlantic Canada. In contrast, Nepisiguit, Big Salmon, and Margaree rivers have late migrations with median run dates occurring in late August and early September. Run timing is believed to be a heritable trait (Hansen and Jonsson 1991a) that is also influenced by environmental conditions. An example of two adjacent stocks influenced by similar environmental conditions but with very different run timing characteristics are Northeast Brook, Trepassey, and Biscay Bay River, Newfoundland. Here, median dates differ by more than three weeks between the two stocks with the former more similar to run timing of salmon returning to rivers in northern Labrador.

Spawning usually occurs in October and November in gravel-bottomed riffle areas of streams. Fertilization of eggs can involve both adult males and precocious male parr. Spawned-out or spent fish (kelts) either return to sea immediately after spawning or remain in fresh water until the following spring. Eggs incubate in the spawning nests or redds over the winter months and hatching usually begins in April. The hatchlings or alevins remain in the gravel for several weeks living off large yolk sacs. Upon emergence from the gravel in late May – early June, the yolk sac is absorbed and the free-swimming young fish, now referred to as fry or under-yearling parr, begin active feeding. Parr rear in fluvial (riverine) and lacustrine (standing water) habitats for two to eight years (Klemetsen et al. 2003) after which time they enter the smolt stage and migrate to sea.

Relative proportions of the various maiden sea-age and repeat spawning age groups and associated biological characteristics vary widely among stocks and with geographic location in North America (Porter et al. 1986). For example, stock composition can vary from being comprised of three sea ages, such as those on the Gaspé Peninsula, to consisting of a single sea age, which is characteristic of most of Newfoundland (Fig. 3). Even within populations with a simple sea-age structure like many of those of Newfoundland, there can be a multiplicity of individuals with different spawning histories contributing to egg deposition in a given year. In addition to virgin fish corresponding to the various smolt-age groups, which constitute the bulk of spawning escapements, there can be significant numbers of consecutive and alternate spawners present. All sea-age groups possess repeat spawners and this obviously greatly increases the potential for additional spawning types depending on the population. All these adult spawning types plus precociously maturing male parr may occur in the same population, constituting a "bet hedging" strategy (Stearns 1976; Lacey et al. 1983; Orzack and Tuljapurkar 1989; Roff 1992; Ellner and Hairston 1994; Einum and Fleming 2004), maximizing survival and population stability.

In Ungava Bay, at the northern extremity of the North American distribution, a form referred to as "estuarine" salmon occurs in addition to 1SW and MSW salmon (Robitaille et al. 1986). Unlike 1SW and older salmon, which undergo extensive oceanic migrations (Hansen and Quinn 1998), these fish can reach maturity and return to freshwater after only a few months in the estuary and are referred to as 0-sea-winter (0SW) salmon in Fig. 2. This form has also been encountered sporadically in low numbers over the years in some Newfoundland rivers (e.g. Campbellton River), but has become more prevalent in recent years (e.g. Downton et al. 2001). In eastern Hudson Bay (Nastapoka River), there is also a northern form that migrates to the estuary for a brief time, but this one differs from the estuarine salmon of Ungava Bay in that it does not undergo smoltification and growth rates are lower (Morin 1991). There are also populations in the inner Bay of Fundy that do not undertake long, distant migrations but rather tend to stay more localized (Amiro 1998, 2003). Unlike the estuarine or 0SW type however, inner Bay of Fundy populations are characteristically 1SW with a significant repeat spawner component (Amiro 1990).

The sexual maturation of wild anadromous male parr is widespread and highly variable throughout the distribution of the species (Dalley et al. 1983; Myers et al. 1986; Heinimaa and Erkinaro 2004) and they successfully mate with adult females both in the presence and absence of adult males (Myers and Hutchings 1987). Different mechanisms have been proposed to explain the co-existence of precocious and adult males within a single population of Atlantic salmon (see reviews by Fleming (1996) and Fleming and Reynolds (2004)). There is some evidence from breeding studies for a heritable basis for early maturity, or the existence of genetically distinct strategies. Other studies indicate a significant environmental influence, acting on genetically determined thresholds related to growth or physiological (e.g., energetic) state. Coexistence has been explained in terms of game theory wherein the two phenotypes represent alternate reproductive tactics within a single population. In contrast, the incidence of the maturation of wild anadromous female parr in fresh water is rare (Power 1969; Prouzet 1981; Baglinière and Maisse 1985; Hindar and Nordland 1989; Moore and Riley 1992). There have been cases where anadromous females that were stocked into ponds as swim-up fry have reached sexual maturity in fresh water (Harris 1973; Morrison 1983; O'Connell and Gibson 1989). These fish were subject to rapid growth and outlet configurations of the ponds prevented them from going to sea.

Non-anadromous Populations

Non-anadromous or resident salmon, complete their life cycle entirely in freshwater (Power 1958; Berg 1985). Isolation of non-anadromous from anadromous salmon appears to have occurred during isostatic rebound of coastal regions following the last ice age, approximately 10,000 years ago (Power 1958; Sutterlin and MacLean 1984; Berg 1985). Non-anadromous salmon occur not only above impassable physical barriers (e.g. Andrews 1966), but are also found in sympatry with anadromous salmon in river systems that are fully accessible to the sea (Scott and Crossman 1964; Hutchings 1986; Verspoor and Cole 1989). For some sympatric occurrences, there is evidence to suggest the forms are reproductively isolated (Verspoor and Cole 1989; Birt et al. 1991a, 1991b). Hutchings (1985) however, also viewed the occurrence of both forms in sympatry as phenotypic polymorphisms within a single population, as alternative evolutionarily stable strategies in the context of game theory as proposed by Maynard Smith (1982).

Size and Growth in Fresh Water

Atlantic salmon inhabit cool temperate streams of eastern Canada and can tolerate fresh water temperatures ranging from 0 to 28 °C (Elliott 1991). Juvenile Atlantic salmon begin feeding in the spring at water temperatures of 6 to 7 °C, and grow optimally at 16 to 19 °C (Javaid and Anderson 1967; Gibson 1978; Dwyer and Piper 1987; Jensen et al. 1989; Peterson and Martin-Robichaud 1989; Elliott, 1991; Elliott and Hurley 1997). Feeding ceases in larger juveniles at temperatures above 23°C and at water temperatures ranging from 22 to 24 °C, juvenile salmon seek refuge from thermal stress (Cunjak et al. 1993). The factors with the strongest correlation to body size and growth of juvenile salmon in fresh water include temperature, food availability and density (Gibson 1993; Elliott and Hurley 1997; Grant et al. 1998). Variations in growth rate are expected to result in variations in size and age at smoltification (Mangel 1994; Marschall et al. 1998). Several studies have reported on the short growing season of wild Atlantic salmon such that the size at age is reached earlier in the year than would be expected based on temperature alone (Randall and Paim 1982; Metcalfe 1994; Elliott and Hurley 1997; Strothotte et al. 2005).

Variations in Juvenile Salmon Size-At-Age

Growth in length and weight in Atlantic salmon juveniles in fluvial fresh water habitats tends to be initially rapid in June and July, sometimes into August, but limited in September and October (Randall 1982; Randall and Paim 1982; Heggenes and Borgstrom 1991; Juanes et al. 2000; Strothotte et al. 2005). The growth trajectories may also differ among age groups with growth of fry occurring over a longer period of time than that of parr (Randall and Chadwick 1986; Heggenes and Borgstrom 1991; Strothotte et al. 2005). Repeated sampling of juveniles from May to November in three rivers in the southern Gulf of St. Lawrence has provided further evidence of this seasonal growth dynamic (Fig. 4). In samples collected in the Miramichi River over the past 35 years, there is a strong association between size of fry and sampling date but this is not evident for parr of ages 1 and 2, which indicates that most of the parr growth for the year had probably occurred by the time of sampling in July and August (Swansburg et al. 2002).

Within a river, there are important among site differences in fork length of juveniles attained at the end of the growing season. In the Margaree River, end of growing season sizes of fry ranged from 5.0 to 7.0 cm whereas in the Miramichi, length ranged from less than 5.0 to over 6.0 cm (Fig. 4). Age-1 parr end of season sizes ranged from 7.5 to 11.0 cm among four sites in the Margaree River whereas in the Miramichi River, sizes ranged from 7.3 to 9.4 cm (Fig. 4).

Over a larger number of sites sampled in the Miramichi in 2001, age-1 parr mean size attained 10.4 cm and end of season age-1 parr length ranged almost 4 cm among sites whereas fry mean length ranged 1.5 cm. The Miramichi River covers 14,000 km^2 of drainage area and there are cool and warm water tributaries in the Northwest and Southwest Miramichi rivers which result in contrasting rearing environments for juveniles.

Swansburg et al. (2002) reported that in the Miramichi River, the fork length of juvenile Atlantic salmon parr decreased significantly during 1971 to 2000 and the decreased sizes-at-age were associated with increases in spring air and water temperatures. Although there remained a large component of the variance in size-at-age which could not be explained by density, date of sampling, tributary effects, and annual temperature indices, there was a strong correlation in the mean annual size-at-age of juveniles between the Northwest Miramichi and Southwest Miramichi rivers. There was also a positive and significant association between size-at-age of age-1 parr and size of fry in the previous year and size of age-2 parr and age-1 parr the previous year indicating that size advantages can be maintained at later ages.

Juvenile anadromous salmon use lacustrine habitat for rearing purposes to a considerable degree in Newfoundland rivers and over the years there have been varied studies of this aspect of life history (Pepper 1976; Pepper et al. 1984, 1985; Chadwick and Green 1985; Hutchings 1986; Ryan 1986; O'Connell and Ash 1989, 1993; Ryan et al. 1993; Dempson et al. 1996; O'Connell and Dempson 1996; Erkinaro and Gibson 1997a, 1997b; Gibson 2002). Habitats other than fluvial, including lacustrine, have been considered as marginal or secondary for juvenile anadromous salmon, occupied by individuals displaced from preferred stream habitat (Pepper et al. 1985; Gibson 1993), which is consistent with the traditional view that they are stream dwellers (Keenleyside 1962; Gibson 1966, 1988, 1993; Marschall et al. 1998). The widespread use of lacustrine habitat by parr is believed to be due to the relative lack of predators and competitors (Hutchings 1986; Gibson 1993; Gibson et al. 1993).

Growth of parr occupying lakes and ponds has been shown to be higher than for those of fluvial habitat (Pepper et al. 1985; Hutchings 1986; O'Connell and Ash 1993; Dempson et al. 1996). O'Connell and Ash (1993) demonstrated that juvenile growth rate in rivers in Newfoundland dominated by lacustrine habitat was higher than in those comprised mainly of fluvial habitat; Fig. 5a shows results for several rivers combined in each category. The lacustrine systems in this analysis were widespread geographically while the fluvial systems were mainly those of southwestern Newfoundland. Dempson et al. (1996) obtained similar results for lacustrine versus fluvial habitats within a single river system, Conne River (Fig. 5b). In another study for Conne River, Dempson et al. (2004a) reported higher lipid, protein, and energy levels for lacustrine parr than for fluvial parr. Hutchings (1986) considered the use of lacustrine habitat to be non-random and resultant enhanced growth and survival relative to fluvial habitat to be of adaptive significance.

Smolts

Variations in growth rate of juveniles are expected to result in variations in size and age at smoltification (Mangel 1994; Marschall et al. 1998). There is a negative association between an index of growth potential (combination of degree-days and day length) and mean age at smoltification for Atlantic salmon throughout its range (Metcalfe and Thorpe 1990). The age at smoltification has been shown to be in part associated with the growth rate or size achieved at several points in the life cycle and there is an increased probability of smoltification if a threshold size or growth rate is achieved by a critical time (Thorpe et al. 1998). As a consequence, small changes in initial growth rates of a cohort can affect the mean age at smoltification. In the Margaree River population, Strothotte et al. (2005) described a positive association between the age at smoltification (2 or 3 years) and size achieved at the end of the first freshwater year. In Newfoundland stocks, there are general and positive associations between marine survival, smolt size, and smolt condition (Dempson et al. 2003).

Smolt Size

During the last ten years, smolt monitoring programs in the Maritime provinces have provided information on wild Atlantic salmon smolt characteristics to complement the index river times series of the province of Québec. Wild smolts in the Nashwaak River and Big Salmon River in the Bay of Fundy are large relative to other MSW stocks, averaging between 14 and 16 cm fork length (Fig. 6). The lengths of smolts from the Gulf of St. Lawrence rivers extending from the western side of Cape Breton Island (SFA 18) to the north shore of the St. Lawrence (Q7) have ranged between 12 and 14 cm with the smallest overall sizes in the St-Jean River on the Gaspe peninsula (Q2) (Fig. 6). Smolts are also longer at age in the southern stocks of SFA 23, ranging from 14 to 16 cm for 2-year-old smolts and 15.5 to over 18 cm for 3- year-old smolts. The highest mean smolt lengths are recorded from Ungava Bay at 215 mm (Power 1969).

In Newfoundland, length varies from approximately 12 to 15 cm in the fluvial systems on the southwestern portion of the island; data for Highlands River as representative the MSW stocks of this area are shown in Fig. 6. For the remainder of Newfoundland (1SW stocks), mean smolt length ranges from around 15 to 18 cm. Lengths for two systems possessing substantive lacustrine habitat (Campbellton River and Western Arm Brook) exceeded all others presented in Fig. 6. Hutchings and Jones (1998) misquoted mean smolt length for two southeastern Newfoundland systems dominated by lacustrine habitat presented in O'Connell and Ash (1993). Values for the lacustrine systems Beaver River and Northeast River, Placentia should be much higher, namely 16.9 and 17.5 cm. O'Connell and Ash (1993) showed smolt size for lacustrine dominated systems to be higher than for fluvial systems. The importance of lacustrine habitat in determining smolt size is further illustrated in Figure 5c. An analysis of available data for 16 river systems, with watershed areas varying in size from < 100 to 6,400 km^2, shows a significant positive relationship between mean empirical smolt length and the ratio of lacustrine to fluvial (L/F) habitat (expressed as m^2) (Klemetsen et al. 2003).

With the exception of Newfoundland, there is a tendency for smolt length to increase with latitude (data summarized in Hutchings and Jones (1998)). Some rivers referred to above, ranging geographically from the south to the north coasts of Newfoundland, have mean smolt lengths overlapping those reported for Sand Hill River in southern Labrador (generally around 16 cm) by Anderson (1985). The departure from the clinal tendency exhibited by Newfoundland populations is an example of the modifying effects of local environmental conditions on growth, in this case most likely the utilization of lacustrine habitat for rearing.

Weight of salmon smolts is generally well described by length but mean weight at a standardized length can vary annually. Wild smolts at a fork length of 13.0 cm had annual predicted weights ranging from 20.5 to 21.5 for the Margaree River, 20.7 to 22.4 g for the Miramichi River, and 19.4 to 22.4 for the Restigouche River. Fulton's K condition factor, expressed as the ratio of the weight to the length cubed, provides an index of the relative weight at length. In the seven MSW salmon stocks of the mainland of eastern Canada, K was the lowest in the Saint-Jean River and highest in the southern Gulf stocks (Fig. 7). Smolts from the Margaree River were of similar K to de la Trinité stock and the Bay of Fundy rivers. Condition of smolts in the three Newfoundland systems (Campbellton, Highlands, Western Arm) was comparable to that of de la Trinité and St.-Jean. Smolts of higher condition factor have generally been shown to have better sea survival (Dempson et al. 2003).

Smolt Age

There are relatively few smolt monitoring programs in eastern Canada with which to describe smolt age distributions but there is much wider coverage in adult sampling programs. The proportion at smolt age from adult returns has been used to describe the smolt age characteristics of rivers in eastern Canada. While exceptions occur, there is a general tendency for smolt (river) age to increase with latitude in wild North American populations (Power 1981) (Fig. 8). Much of the variability has been explained by opportunities for growth that are influenced by local environmental characteristics (Power 1986). Maritime populations often have mean smolt ages between 2 and 3 years (see summary by Hutchings and Jones 1998); a similar situation applies to populations in southwest Newfoundland. In contrast, the rest of Newfoundland has salmon populations characterized by mean smolt ages between 3 and 4 years, similar to many Quebec stocks. Populations with mean smolt age of 4 or more years occur along the northwest coast of Newfoundland and into southern Labrador while mean smolt in some north Labrador stocks exceeds 5 years. Populations in Ungava Bay, northern Quebec also have mean smolt ages that exceed 5 years (Power 1969).

The fresh water age of returning adults to eastern Canada ranges between 1 and 7 years. Smolts of river age 8 have been reported from the rivers of Ungava Bay (Power 1969; Robitaille et al. 1986). There are few records of one year smolts in the large scale sample collections dating back to the 1970s and these are mostly from the southern portions of the range (the one-year old smolt records from Bonaventure (Q1), Grande rivière (Q2), and de la Trinité (Q7) are suspect). Maximum smolt ages were highest in the northern areas of eastern Canada and smolt ages 6 to 7 years were only observed in salmon from the northeast coast of Newfoundland, eastern north shore of Québec (Q9) and Labrador. Age 3-year-old smolts are found throughout the range of Atlantic salmon but at very low abundance in the most northern populations in Labrador (SFA 1) and Ungava Bay.

After adjusting for the year of smolt migration, two-sea-winter maiden salmon are comprised of higher proportions of younger smolt ages relative to the one-sea-winter maiden salmon, notably in the multi-sea-winter salmon stocks in the southern portion of the range. This is consistent with other observations that larger smolts frequently mature at younger sea ages than smaller smolts. In the two most northern rivers examined (St. Jean, Q2; de la Trinité, Q7), however, the proportion of age 3-year-old smolts in the returns of 1SW and 2SW from the same smolt cohort were not statistically different. The preponderance of 1SW salmon in many Newfoundland rivers could be related to the growth, size, and survival advantages of smolts conferred by lacustrine habitat (O'Connell and Ash 1993; Klemetsen et al. 2003).

Sex Ratios of Smolts

The incidence of male precocity in a population has been shown to be a function of growth rate, i.e. faster growth favors early maturity (Dalley et al. 1983; Myers et al. 1986; Randall et al. 1986; Thorpe 1986, 1987; Hutchings and Myers 1994). Precocious maturation however comes at a cost, with mature parr incurring greater mortality than non-maturing individuals (Saunders et al. 1982; Dalley et al. 1983; Myers 1984) and maturation can also inhibit smolting (Thorpe 1987; Saunders et al. 1994; Whalen et al. 2000; Dustin et al. 2005). Losses of males from both these processes can result in smolt runs dominated by females (Forsythe 1967; Saunders et al. 1982; Dalley et al. 1983) and there can be high correspondence between the proportions of females in smolt runs and subsequent 1SW adults (e.g. Dempson et al. 2004b). O'Connell and Ash (1993) reported female:male ratios for smolts and 1SW adults subject to enhanced growth in the lacustrine systems referred to above to be substantially higher than for counterparts in fluvial systems.

As already alluded to, the sex ratios in the smolt runs of eastern Canada show differences which are consistent with the sea age structure of the returning adults. In the rivers of insular Newfoundland which are comprised primarily of 1SW maiden salmon, the smolt migrations are strongly skewed toward females, generally in excess of 70% and as high as 90% depending on the river and year. In the MSW stocks of the mainland portion of eastern Canada, the percentage female is variable and determines in large part the proportion of the sea-age structure of the returning adults. There are limited data for sex ratios in the southern stocks of the Bay of Fundy and the Atlantic coast of Nova Scotia but Jessop (1975) reported smolt runs comprised of 60 and 66% female in 1971 and 1972 for Big Salmon River. In the southern Gulf of St. Lawrence, the percentage female in the Margaree has been the highest of the southern Gulf of St. Lawrence rivers, ranging between 70 and 79 for the years 2001 to 2005. In the Miramichi and Restigouche rivers, the sex ratios are nearly balanced with ranges of 52-61% and 44-60%, respectively. The percentage female in the smolts of Québec monitored rivers ranges from 56 to 72 for the Saint-Jean River and 53 to 70 for de la Trinité River.

Size and Growth of Non-Anadromous Salmon

In North America, there have been reports of non-anadromous Atlantic salmon measuring up to 56 cm in length for Labrador (Bruce 1974) and weighing as much as 3.9 kg for Newfoundland (Scott and Crossman 1964), 20.4 kg for Lake Ontario (Scott and Crossman 1998), and in excess of 12.2 kg for Maine, USA (Warner and Havey 1985), comparable in size to anadromous fish of various sea ages. At the opposite end of the size spectrum, populations of dwarf non-anadromous salmon occur in both fluvial (Gibson et al. 1996) and lacustrine (Bruce 1976; Barbour et al. 1979; Sutterlin and MacLean 1984) habitats. In the fluvial situation, dwarf mature females ranged in length from 8.4 to 12.3 cm (mean = 10.2) (Gibson et al. 1996) while lacustrine mature females ranged from around 11.0 to 14.9 cm (Bruce 1976). A variation of the above noted earlier is a transplantation experiment where anadromous salmon fry were stocked into a small landlocked urban pond in Newfoundland. The resulting growth rate of young salmon in this pond was two to five times as fast as in other Newfoundland ponds with age 2+ fish approximately 28.0 cm in length (O'Connell and Gibson 1989) illustrating the capacity for growth in certain situations.

Size and Growth in Marine Waters

Atlantic salmon management in eastern Canada is based on two size groups defined by fork length; small salmon < 63 cm in fork length, large salmon are of length ≥ 63 cm. Salmon return to rivers of eastern Canada to spawn predominantly after one, two, and in some areas three years at sea. A handful of scale samples from salmon from rivers in SFA 15 (Restigouche and Nepisiguit) have been interpreted as possessing four maiden years. In most regions, 1SW salmon are the most abundant maiden age group, representing almost 100% of maiden spawners in rivers of insular Newfoundland, with the exception of fish on the southwest coast (SFA 13). Two-sea-winter salmon are abundant in most rivers of the mainland of eastern Canada, especially in the southern Gulf of St. Lawrence, and are found rivers on the southwest coast of Newfoundland (but virtually absent for the remainder of Newfoundland) and in Labrador. Three-sea-winter salmon are infrequent other than in the rivers of the southwestern Gulf of St. Lawrence (Baie des Chaleurs – SFA 15, Q1, Q2), in southwestern Newfoundland (SFA 13) (Blair 1965) and in some rivers of the north shore of the St. Lawrence (Q8); they have occurred historically in the Saint John River (SFA 23) and St. Mary's River (SFA 20). With few exceptions, small salmon are comprised of 1SW maiden fish whereas the large salmon category is comprised of multiple maiden age groups and repeat spawners.

The observed differences in the proportions at age at maturity in the anadromous salmon of eastern Canada suggest that this trait reflects an adaptation of the populations to spatially variable conditions (Hutchings and Jones 1998). The factors which are considered to be important determinants of age at maturity include growth rates (in fresh water and at sea), survival in fresh water and at sea, fecundity, and heritability (Meerburg 1986; Chadwick et al. 1987; Friedland and Hass 1997; Hutchings and Jones 1998). Age at maturity of parents remains an important factor in determining age at maturity of progeny (see papers in Meerburg 1986).

Repeat spawning salmon are present in all rivers of eastern Canada and they contribute both biologically and economically to the value of the salmon resource (Atkinson and Moore 1999). As a result of changes in fisheries, repeat spawner abundances have increased in numerous rivers of eastern Canada, most notably in the MSW stock of the Miramichi River (Fig. 9). Repeat spawners, historically particularly prominent in some of the inner Bay of Fundy rivers in SFA 22 and have now become so in other areas since the reduction of exploitation in fisheries (Ducharme 1969; Moore et al. 1995). The percentage of large salmon comprised of repeat spawners over the past 35 years has increased from < 5 to between 30 and 55 in the last decade (Chaput et al. 2001). In contrast, the repeat spawner proportions have not changed in the Saint John River and the Saint Jean River (Fig. 9).

Small salmon are greater than 90% maiden salmon with repeat spawners in that size group most abundant in the rivers of the south and northeast coasts of Newfoundland. Repeat spawners constitute between 70 and 98% of the large salmon category in the south and northeast coasts of Newfoundland compared to only 5 to 30% in most other rivers of eastern Canada. Dempson et al. (2004c), noted an increase in the contribution of consecutive spawners during the Atlantic salmon commercial fishery moratorium years (post-1991) although in some stocks (e.g. Gander and Conne) the increase was only observed after several years into the moratorium. In MSW stocks, repeat spawners are derived from all age groups of maiden salmon. In the Miramichi River, repeat spawners were predominantly derived from 1SW maiden salmon in the 1970s but 2SW maidens are now proportionally as abundant as 1SW maidens attributable to the reduction on harvest of 2SW salmon resulting from the closure of the Maritime commercial fisheries and the mandatory release of all large salmon in the recreational fisheries since 1984.

Spawning age structure has become more complex in many rivers with salmon in the Miramichi River on their seventh spawning migrations observed almost annually since 1995 (Chaput and Jones 2006). Salmon repeat as either consecutive or alternate spawners and in all combinations of these in subsequent spawning migrations. Switching between consecutive and alternate life histories also occurs frequently. Collectively over the years, with smolt-age combinations included, as many as 20 spawning types have been encountered for Conne River (Dempson et al. 2001) and 26 for Gander River (O'Connell et al. 2001), both of which are 1SW stocks, whereas in the Miramichi River with its significant MSW component, 49 sea age types have been interpreted, excluding the freshwater age combinations. The broad spawning age structure has resulted in 8 or 9 year classes present on the spawning grounds in the recent decade, an increase from the 4 to 5 year classes in the earlier years when there were fewer repeat spawners (Chaput and Jones 2006).

Growth

Growth in the marine environment is rapid relative to that in fresh water. Whereas after two to four years of growth in fresh water, smolts attain average fork lengths of 12 to 18 cm, after one year of growth at sea, length can range from 45 to as much as 65 cm. After two years at sea, salmon measure in the range of 70 to 80 cm. At relatively similar age, there is a large variation in fork length (Cairns 2003). Weights increase about 75-fold between the smolt stage and 1SW salmon stage, and over 200 fold from smolts to 2SW salmon (Cairns 2003). Weight is strongly associated with length and salmon measuring 60 cm weigh about 2 kg, 80 cm salmon weigh about 5 kg, and a 100 cm salmon weighs upwards of 11 kg.

Growth of adults at sea, like juveniles in fresh water, is seasonal and described by the cyclic patterns of circuli spacings on the scales, from observations of non-maturing 1SW salmon at West Greenland, from post-smolt surveys at sea, and from monitoring of wild smolts reared in sea cages (see Cairns 2003; Dempson et al. 1999). Atlantic salmon which are destined to spawn reduce or cease their feeding activities on their return migrations, as much as several months prior to entering the rivers (see summary in Cairns 2003). In the Miramichi River where salmon return to fresh water over a five month period from late May to late October, there is a very modest increase in length during the season of return, by about 3 to 4 cm (+6%) for 1SW salmon and 3 cm (+4%) for 2SW salmon (Moore et al. 1995). Differences in length between male and female salmon are small, with male salmon in the Miramichi River longer by about 1.5 cm in both 1SW and 2SW salmon (Moore et al. 1995).

Size at maiden age varies among rivers. One-sea-winter maiden salmon mean lengths range between 48 and 59 cm. There does not seem to be any consistent pattern regarding size of 1SW salmon and latitude. Indeed larger 1SW salmon, say ≥ 55 cm, can be found among populations from the Maritimes, Québec, and Newfoundland and Labrador with 1SW salmon averaging greater than 60 cm occurring in some Ungava Bay rivers (Power 1969; Hutchings and Jones 1998). Two-sea-winter salmon mean lengths range from just over 60 cm in some rivers of the south coast of Newfoundland to between 75 and 80 cm in most of the other rivers. 3SW salmon mean lengths vary between 75 cm to over 100 cm.

The lengths of salmon at maiden age of return as measured at several river monitoring facilities have increased over time (Fig. 10). Some of the changes correspond to the closures of commercial fisheries instituted over the period 1970 to 2004. Mean sizes of 1SW maiden salmon are greater post-1991 in 11 of 14 rivers, the exceptions being Restigouche River, Saint Jean River and Conne River (Scheffe a posteriori test, $P < 0.05$; Fig. 11). Generally, the mean sizes during 1970 to 1983 and 1984 to 1991 did not change with the exception of the Miramichi River in which size increased over the three management periods. 1SW maiden salmon mean length in the recent management period ranges between 54 and 59 cm in contrast to the 1970-1983 period when mean length ranged from just under 52 to almost 57 cm (Fig. 11). Mean lengths of 2SW maiden salmon have increased in some rivers but are unchanged in others. Some of the changes in mean lengths of 2SW maiden salmon observed in the Miramichi have been attributed to closures of size-selective commercial fisheries (Moore et al. 1995). Mean sizes of 2SW maiden salmon are greater post-1991 in only 2 of 8 rivers, the Miramichi River and de la Trinité River (Scheffe a posteriori test, $P < 0.05$; Fig. 12).

Size of repeat spawners varies in relation to the spawning history of individual fish and whether spawning occurred as consecutive or alternate year events. For example, whereas maiden 1SW salmon at Conne River, Newfoundland, average 51.1 cm in fork length, first-time consecutive spawners averaged 55.9 cm while salmon with two consecutive spawning marks had a mean length of 62.0 cm. In contrast, alternate spawners that typically spend another entire year at sea averaged 69.6 cm in length. In two MSW salmon stocks of the Gulf, first time consecutive 1SW maiden salmon had an average length of 67.2 in the Miramichi compared to 63.2 cm in the Restigouche (Fig. 13). First time 1SW alternate spawners had mean lengths of 83.5 and 81.7 cm. 2SW repeat spawners had mean lengths of 81.9 to 86.8 as first time consecutives, and 91.5 to 98.0 cm as first time alternates. Growth of salmon between spawning events results in repeat spawner lengths overlapping onto and eventually exceeding maiden salmon lengths.

Sex Ratios

There are important regional differences in the proportion female in the 1SW maiden salmon components in eastern Canada. 1SW maiden salmon in the Bay of Fundy and Atlantic coast of Nova Scotia are generally comprised of between 20 and 70% female, the exceptions being some stocks from eastern Cape Breton and the salmon stock in the Saint John River above Mactaquac which are generally ≤ 10%. The stocks from the Gulf of St. Lawrence and Québec

(SFA 15-18, Q1-Q7, Q10) are characterized by a low percentage of female in the 1SW maiden salmon (1 to 20%), with very few females (< 5%) in many rivers of Chaleur Bay (SFA 15, Q1-Q2). In Newfoundland, maiden 1SW salmon are predominantly female, ranging from 45 to almost 100% in some rivers. The Labrador and north shore Quebec stocks (Q8, Q9) are more similar to the Bay of Fundy/Atlantic coast of Nova Scotia rivers, percentages female ranging from 13 to 71% for the seventeen rivers with information.

Large salmon are characterized by percentages female which are generally greater than 50% whereas 2SW maiden salmon have variable but high proportions female which can exceed 90% in some stocks.

For stocks in which large salmon represent greater than 50% of the total returns to the river, the small salmon (1SW maiden) are predominantly males, greater than 80% (Fig. 14). In other stocks where small salmon are greater than 50% of the returns, the proportion female in the small salmon will generally be biased to females, with exceptions to this for some Labrador stocks and a few Gulf of St. Lawrence stocks.

Percentage female within a river varies annually, for some within a fairly narrow range (for example 1SW salmon in Saint-Jean) while in other stocks, the annual variation is quite large (for example 1SW salmon in Middle Brook SFA 5) (Fig. 15). For 1SW maiden salmon, there was no statistically significant (linear regression, P>0.05) change in the proportion female over time in 7 of 13 rivers examined. There were significant increases in the proportion female in 4 of the 13 rivers (Saint John, de la Trinité, Northeast Trepassey, Sand Hill) whereas in the Miramichi River and the Exploits River, there were significant decreases. For 2SW salmon there were statistically significant increases in the proportion female in 4 of 6 rivers whereas there was no change in the Saint John River and the Nashwaak River.

Survival

The anadromous life history of Atlantic salmon provides opportunities to monitor survival in the two distinct environments occupied by salmon at the different stages of its life cycle. In a large number of rivers, total counts (or estimates) of returning adults can be obtained. From these and by accounting for removals in fisheries, egg depositions can be derived. All ages of juvenile salmon can be readily monitored up to the smolt stage at which point the total production of a cohort going to sea can be quantified. From these, fresh water survival from the egg to the smolt stage can be studied. Marine survival or in some cases return rates can also be quantified on those rivers where the total smolt production and subsequent adult returns are monitored.

In Freshwater

The abundance of Atlantic salmon in fresh water is regulated by density dependent and density independent factors (Elliott 2001). In fresh water, survival is at least compensatory such that relative survival decreases as abundance increases, and vice versa. Compensatory survival in fresh water results from competition for limited resources including food and space, with its multidimensional components (Marschall et al. 1998; Cunjak et al. 1998). Self thinning principles have been proposed as the mechanism for regulation of population abundance (Grant et al. 1998). The major density dependent regulatory factors are assumed to occur generally in the early life stages but can also act at later stages as individuals compete for limited resources (Elliott 2001; Jonsson et al. 1998).

Overall survival in freshwater can be approximated from estimates of numbers of eggs deposited and subsequent production of migrating smolts. Indices of inter-stage survivals in freshwater, as for example, fry to age-1 parr, can be obtained from indices of juvenile abundances at age. The translation of these indices into absolute measures of survival are difficult because these life stages were frequently sampled in classic rearing habitat (Elson 1957) which represents different proportions of all habitat within rivers. As a result, the juvenile survival indices derived may differ from those integrated over all habitat types.

Symons (1979) provided an earlier review of interstage survival rates in fresh water and summarized ranges of survival rates for egg to fry of 9 to 20%, annual rates for parr of 28 to 57% and parr to smolt survival rates of 35 to 65%. Locke (1998) summarized a number of interstage survival rates from the literature and illustrates the wide range of estimated survival rates at all stages among the studies. Symons (1979) suggested that based on interstage survival rates, egg-to-smolt survival would be higher for populations with younger smolt ages but the observations from eastern Canada as reported by Chaput et al. (1998) do not support that view; egg-to-smolt survival is actually higher in the more northern rivers with older mean smolt age.

Egg-to-smolt or freshwater survival can vary substantially both among rivers as well as within rivers over time to the extent that the variability often exceeds that observed among estimates of marine survival. Egg-to-smolt survival rates from monitored rivers in eastern Canada range from a low of 0.1% to a high of 6.5% (Fig. 16). Based on the data available, Chaput et al. (1998) reported that egg to smolt survival was higher in Newfoundland rivers where juveniles have the potential to rear in lacustrine habitat, rather than exclusively fluvial habitat. Within Newfoundland, Klemetsen et al. (2003) reported that salmon rearing in lacustrine habitat may have somewhat higher freshwater survival rates than corresponding stocks rearing predominately in fluvial environments. Indeed, egg-to-smolt survival averaged 0.52% (minimum = 0.36; maximum = 1.09%) for Northeast Brook, Trepassey, with an L/F value of 5.2 over 12 year-classes. In contrast, freshwater survival for Conne River (N = 14 year classes), with an L/F value of 24.1, averaged 1.24%, varying from 0.45 to 2.55% among individual year-classes. For Western Arm Brook, freshwater survival averaged 1.39% over 29 year-classes where the L/F value is 69.6. Klemetsen et al. (2003) showed some evidence that smolt-to-adult survival increases with L/F ratio, suggesting that smolt survival increases with smolt size (see also below).

The overall compensatory function of survival is expressed in the decrease in egg-to-smolt survival with increasing egg deposition observed in numerous monitored stocks of eastern Canada (Fig. 17).

At Sea

For salmon, there are numerous estimates of M for the freshwater stages because they can be readily monitored and are not subjected to fisheries. Estimates of M during the marine phase are much more difficult to obtain because the adults enumerated back to the river have until recently been exposed to both natural and fishing mortality factors at sea. Ritter (1989) reviewed the literature on survival of salmon at sea and concluded that sea survivals were stock dependent with average sea survivals (return rates) for North American populations to the first sea winter of 10 to 20% per year. The sea survivals of European stocks are generally higher with return rates to the coast of River Bush smolts in the order of 35% (Crozier and Kennedy 1994) and those to other rivers generally being greater than 10% (Ó Maoiléidigh et al. 2003).

Doubleday et al. (1979) suggested that the greatest mortality occurred in the initial stages at sea when the fish were small compared with later in life (after one year at sea) when the fish were much larger, consistent with the inverse-weight hypothesis. Since smolts are about 1% the weight of salmon after one year at sea (20-40 g versus 2000-4000 g), then variations in integrated mortality would be expected to be defined by smolt size.

Many factors act to influence the survival and production of Atlantic salmon (Saunders 1981; Dempson et al. 1998; McCormick et al. 1998; Parrish et al. 1998; Armstrong et al. 1998). Consequently, survival, and hence adult salmon abundance, is often highly variable, both in Atlantic (Chadwick 1988; Dempson et al. 1998) as well as in Pacific salmon populations (Noakes et al. 1990; Hargreaves 1994). Some factors, such as run timing and smolt size, can have a consistent influence on the subsequent survival to the adult life stage (e.g. Ward and Slaney 1988; Hansen and Jonsson 1989, 1991b; Ritter 1989; McCormick et al. 1998; Salminen et al. 1995; Finstad and Jonsson 2001). In contrast, Hargreaves (1994) stated that many attempts have been made to relate marine survival rates to environmental parameters, and while observed patterns have often assisted in forecasting subsequent salmon abundance, frequently the resulting relationships showed little consistency among stocks, and among years within a stock.

A review of marine mortality of Atlantic salmon and its measurement concluded that contributory factors are complex and attempts to identify a single, dominant factor have been unfounded (Potter et al. 2003). Survival was found to vary substantially both among stocks and regions as well as within a stock over time. In populations for which multiple sea-age classes exist, estimates of return rates are underestimates of survival because some of the fish are destined to remain at sea and either die or return as MSW fish (Hutchings and Jones 1998; Chaput 2003). No attempt has been made to adjust for this in the current synopsis.

Counts of Atlantic salmon smolts and adults enable estimates of marine survival to be derived. Examination of survival trends over time can provide insight into the effects of management measures designed to reduce marine exploitation, or, in the absence of fisheries allow estimates of natural survival to be calculated. Alternate methods including inverse weight and maturity schedules have also been applied to determine estimates of natural survival (see review by Chaput 2003).

Survival of smolts to 1SW, or in the case of Newfoundland salmon < 63 cm in length, is generally low. Since the Newfoundland commercial salmon fishery moratorium began in 1992, and hence the opportunity to obtain 'natural' survival in the absence of directed marine fisheries, survival has exceeded 10% in less than 3% of all individual estimates available (N = 76) (Fig. 18). The majority of survival values for monitored Newfoundland stocks fall within the range of 2 to 7%, averaging around 5% and thus similar to the return rates reported for 1SW Miramichi salmon, while return rates to 1SW salmon in Québec rivers are generally less than 1% (Fig. 18). Indeed, for Newfoundland small salmon there is no difference in the distribution of survival values between the pre-moratorium and moratorium periods (G = 4.090, P = 0.665). In some populations (e.g. St. Jean, de la Trinité, Conne, and Northeast Brook, Trepassey) survival is lower since the Newfoundland commercial salmon fishery closed than it was prior to the moratorium in 1992 even in the absence of adjustments to account for marine exploitation prior to fishery closures. This was largely unexpected given that estimates of the median marine exploitation rates during the period 1984 to 1991 were 45.3% (29.6 – 57.1%) on small salmon and 74.2% (57.7 – 83.7%) on large salmon (Dempson et al. 2001a). Survival to the 2SW stage is also quite low averaging less than 1% in most monitored rivers and again with several stocks experiencing lower survival in recent years by comparison with those years affected by directed commercial fisheries (Fig. 19).

Doubleday et al. (1979) used the inverse weight hypothesis to estimate natural survival of non-maturing 1SW salmon during the second year at sea. Assuming an exponential growth function, they obtained natural mortality rate estimates between Greenland and home waters (approx. 12 months) from 3% to 12%, or less than 1% per month. Based on recent size at age data from several North American rivers and assuming a linear growth function, monthly mortality rates of about 3% were estimated (Chaput 2003).

In addition to marine survival estimates of maiden salmon, survival of repeat spawners can also be determined for some stocks. Dempson et al. (2004c) used scale pattern analysis to identify first time consecutive spawners for six Newfoundland rivers. Survival was estimated by comparing the numbers of salmon returning to spawn a second time in year $i + 1$ with the corresponding number of maiden 1SW fish that spawned previously in year i. Similar to the situation in freshwater and that observed among maiden salmon, survival of repeat spawners also varied considerably among years within stocks. While survival of first time repeat spawners was commonly less than 20%, estimates of over 30% or greater occurred in some rivers in some years. Mean survival of repeat spawners was highest for Terra Nova River, Northeast River, Placentia and Middle Brook (mean > 18%), and lowest for Exploits River, Gander River, and Conne River (mean < 10%). This contrasts with repeat spawner survivals to a second spawning for the Miramchi which were about 5% for 1SW and between 5% and over 30% for 2SW salmon in the late 1980s (Moore et al. 1995). More recent analysis of the Miramichi stock shows an increase in the return rate as consecutive spawners in both the 1SW and 2SW salmon components with the overall return to a second spawning of 2SW salmon at about 20% over the recent five years. 1SW repeat spawner return rates remain at less than 10%.

Fecundity

Fecundity varies considerably both within and among salmon stocks. Egg number and size increase with body size (Thorpe et al. 1984; Jonsson et al. 1996). In a dwarf or stunted freshwater resident population from Newfoundland, mean fecundity was 33.0 eggs (Gibson et al. 1996). In contrast, Randall (1989) reported mean fecundities of 12606 and 16585 eggs for 3SW and previous spawning salmon in Restigouche River. Although absolute fecundity varies greatly among individuals, as expected owing to high variability in adult body size, relative fecundity (eggs per kilogram) as a measure of reproductive effort, varies much less but is inversely related to fish size. For Miramichi River, New Brunswick, relative fecundity ranged from 1331 eggs kg^{-1} in previous spawning salmon (mean length 82.1 cm) to 2035 eggs kg^{-1} in 1SW fish (Randall 1989). Rouleau and Tremblay (1990) reported values of 1628 eggs kg^{-1} for 2SW salmon, 1256 eggs kg^{-1} for 3SW salmon, and 1244 eggs kg^{-1} for repeat spawners. In a survey of 2440 specimens from 10 Newfoundland rivers, mean relative fecundity varied from 1278 to 2500 (O'Connell et al. 1997). The variability in relative fecundity that can occur within a stock is rarely, if ever, taken into consideration when estimates of egg deposition are determined. Consequences related to conservation spawning levels achieved and studies on population dynamics are obvious.

There can be a trade-off between egg size and fecundity (Fleming 1996; Jonsson et al. 1996). Fish either may spawn large and few eggs or small and many eggs. Fast growth of parr in fresh water before smolting has been associated with smaller relative egg size at maturity, a phenotypic response that has been explained as an adaptation to the potential growth opportunities in the nursery river. This assumes that feeding opportunities that parents experience as juveniles in rivers is a good predictor of what their offspring will experience. Thorpe et al. (1984) cited instances of both negative and positive correlations between egg size and egg number and also one study showing no correlation.

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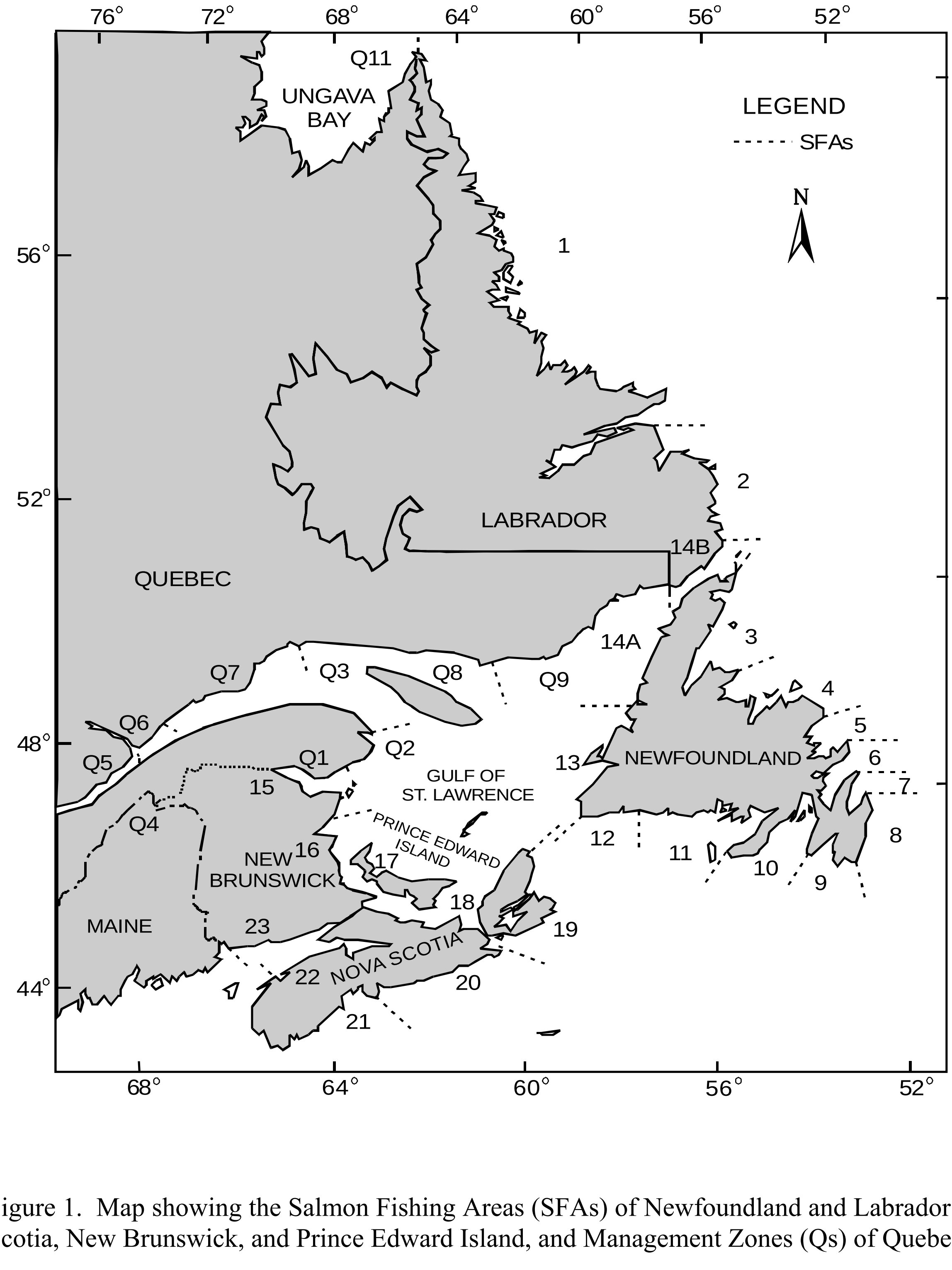


Figure 1. Map showing the Salmon Fishing Areas (SFAs) of Newfoundland and Labrador, Nova Scotia, New Brunswick, and Prince Edward Island, and Management Zones (Qs) of Quebec.

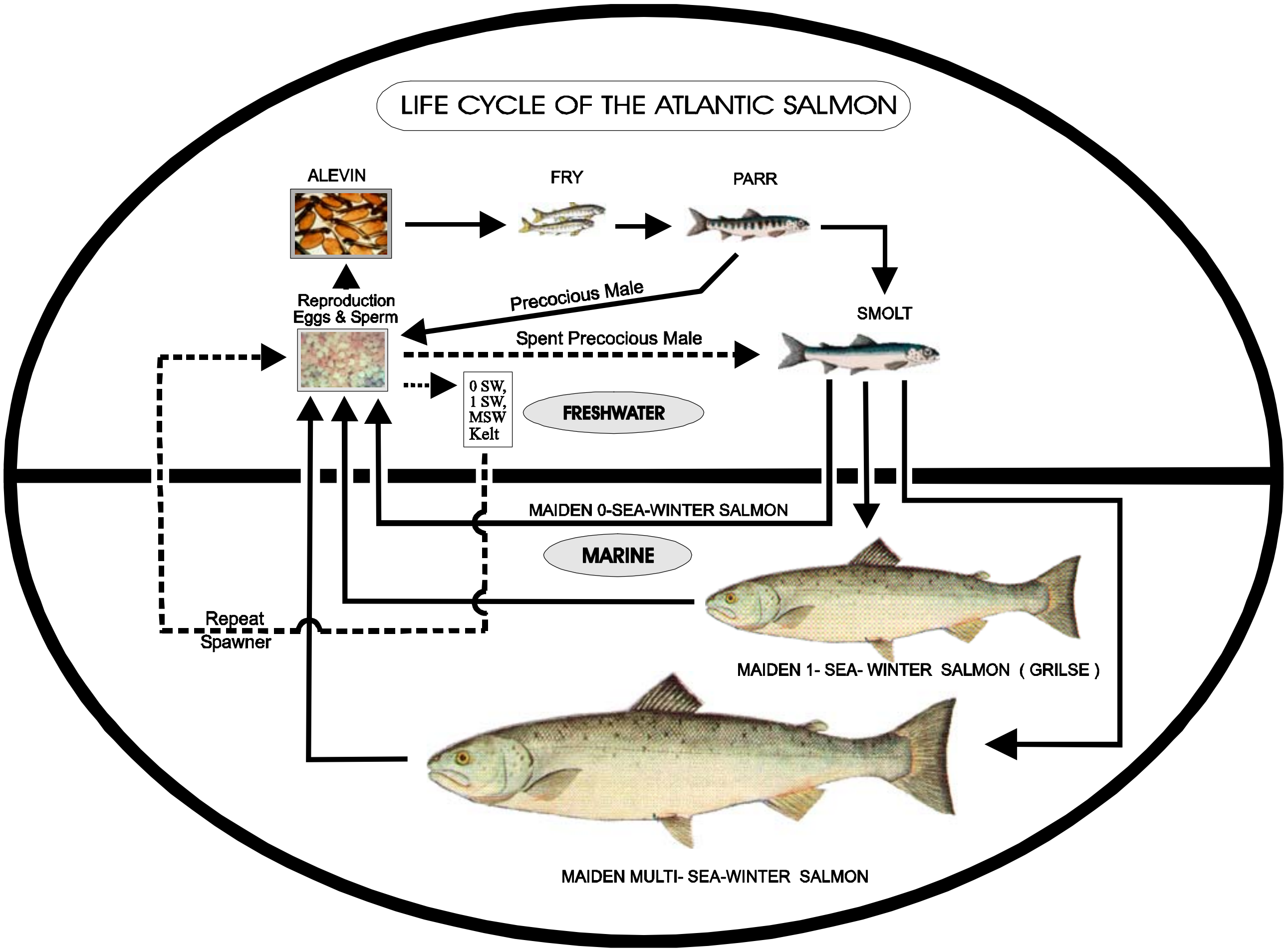


Figure 2. Generalized life cycle of the Atlantic salmon.

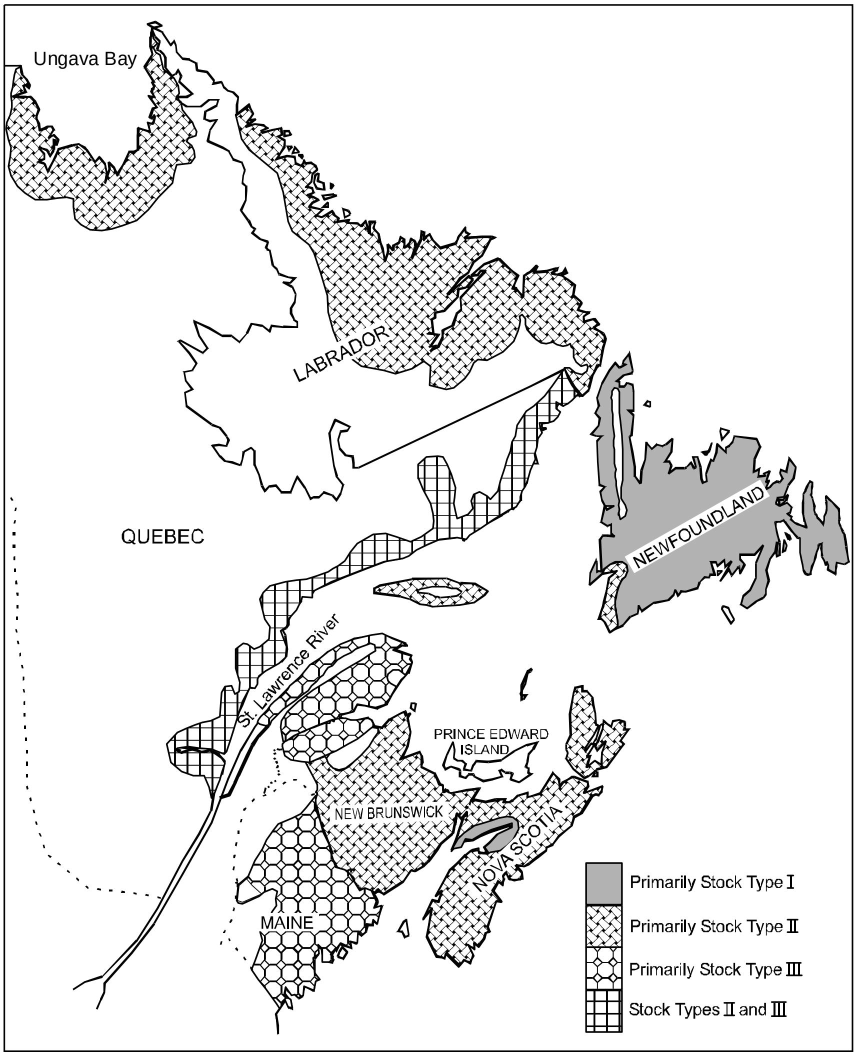


Figure 3. Distribution of generalized groupings of stock types of self-sustaining populations of Atlantic salmon in North America. Stock Type I consists mainly of 1SW spawners, Type II has 1SW and 2SW spawners, and Type III is comprised of 1SW, 2SW, and 3SW spawners. Within each stock type area there may be a few stocks which belong to another stock type. Adapted from Porter et al. (1986).

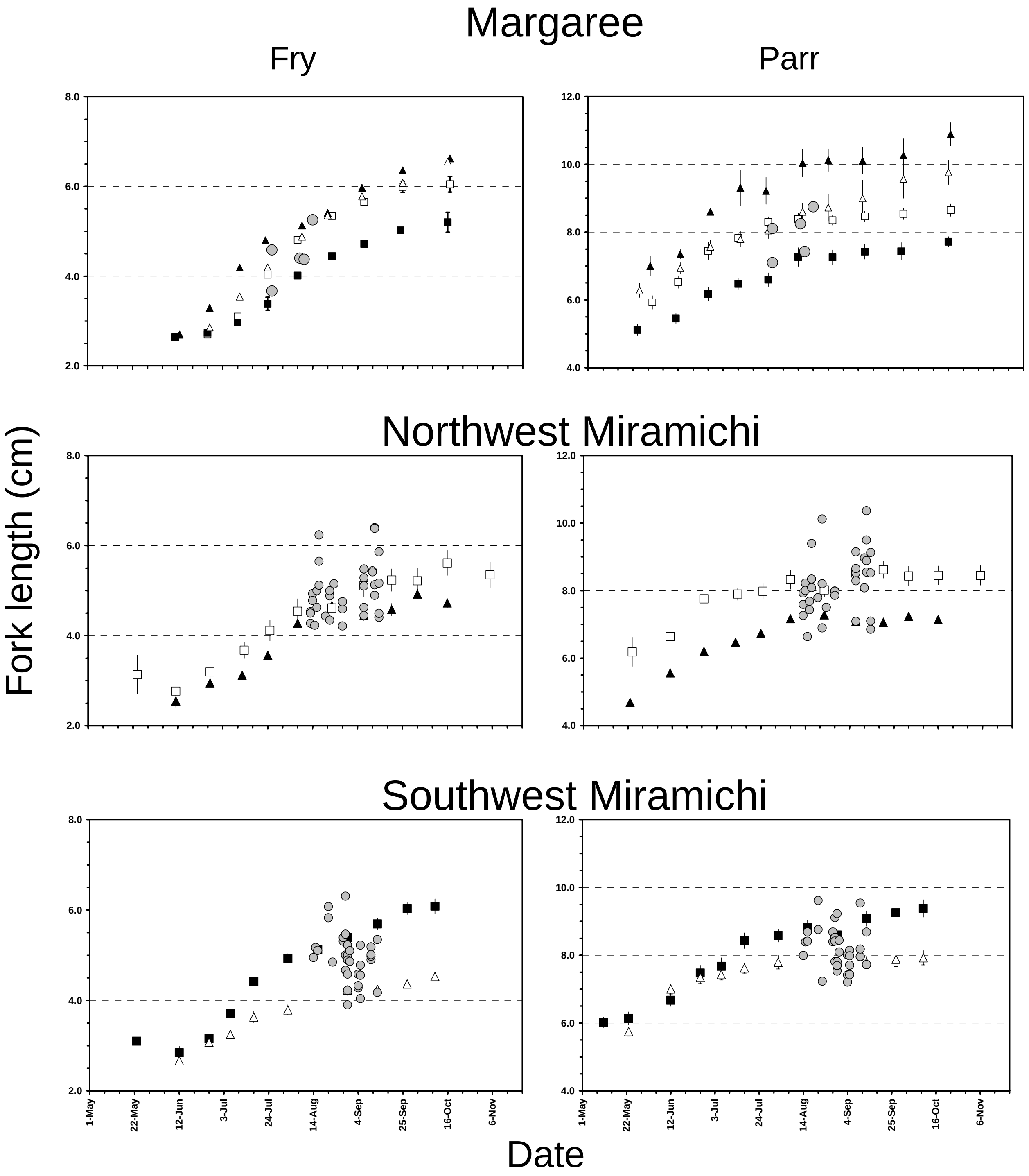


Figure 4. Seasonal fork length trajectories for 2001 by research sampling locations of fry (left panels) and parr age 1 (right panels) from the Margaree (SFA 18) (upper panels), Northwest Miramichi (middle panels) and Southwest Miramichi (SFA 16) (lower panels) rivers for 2001. Grey bullets are mean lengths at other sites sampled in 2001.

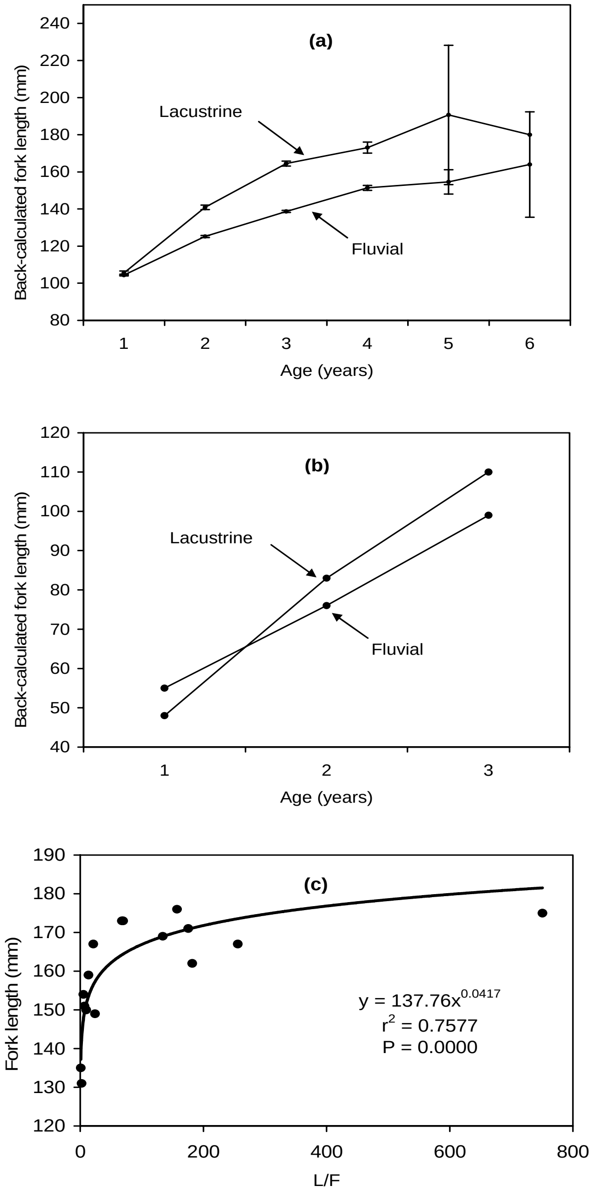


Figure 5. Combined back-calculated length-at-age for Atlantic salmon smolts from certain Newfoundland rivers dominated by lacustrine habitat versus systems comprised mainly of fluvial habitat (a) and for lacustrine versus fluvial habitat for Conne River (SFA 11) parr (b). Also shown (c) is the relationship between mean empirical smolt length and the ratio of lacustrine to fluvial (L/F) habitat (expressed as m^2) for 16 river systems in Newfoundland. Panel a is from O'Connell and Ash 1993), panel b is from Dempson et al. (1996), and panel c is from Klemetsen et al. (2003).

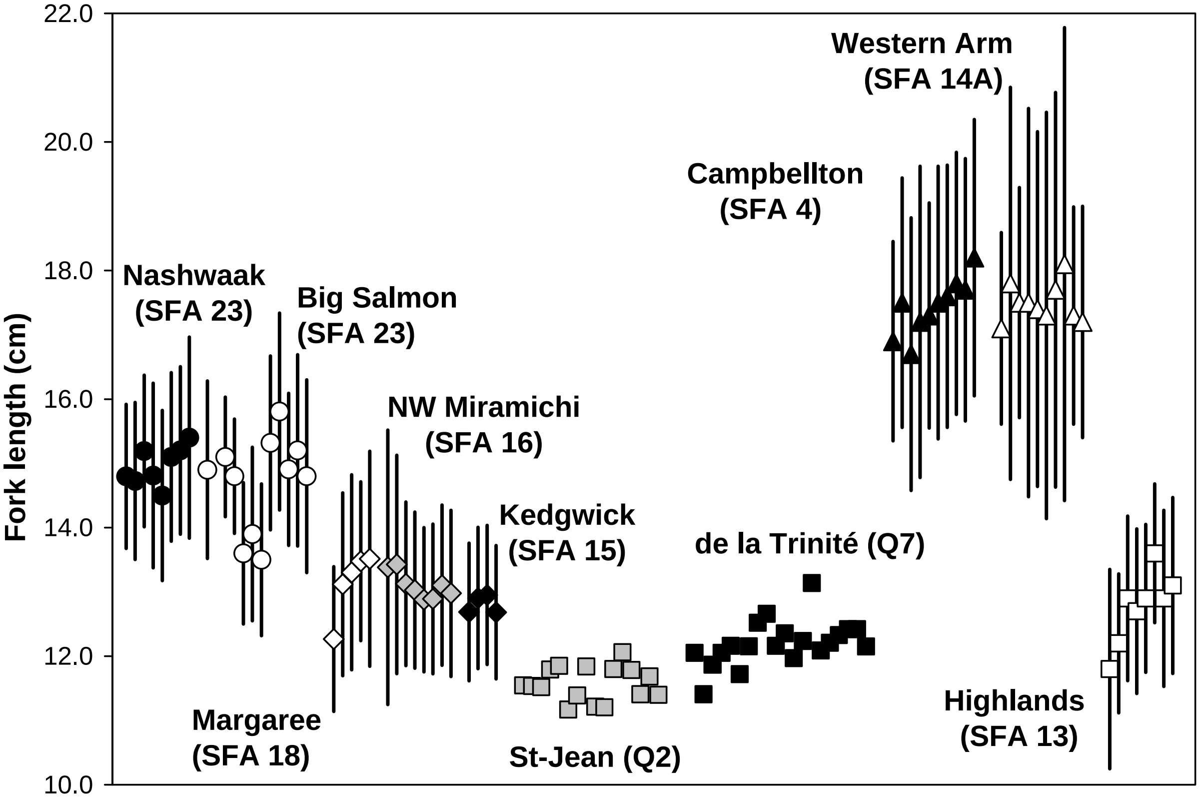


Figure 6. Fork length (mean ± 1 std. dev.) of Atlantic salmon smolts, all ages combined, from mainland eastern Canada MSW stocks and Newfoundland 1SW (Campbellton and Western Arm) and MSW (Highlands) stocks. Data are presented sequentially by year of smolt migration for each river: mainland stocks Nashwaak – 1998 to 2005, Big Salmon – 1966, 1968 to 1972, 2001 to 2005, Margaree – 2001 to 2005, Northwest Miramichi – 1998 to 2005, Kedgwick – 2002 to 2005, St-Jean – 1989 to 2004, de la Trinité – 1985 to 2004; Newfoundland stocks Campbellton – 1995 to 2004, Western Arm – 1994 to 2003, Highlands – 1993 to 2000.

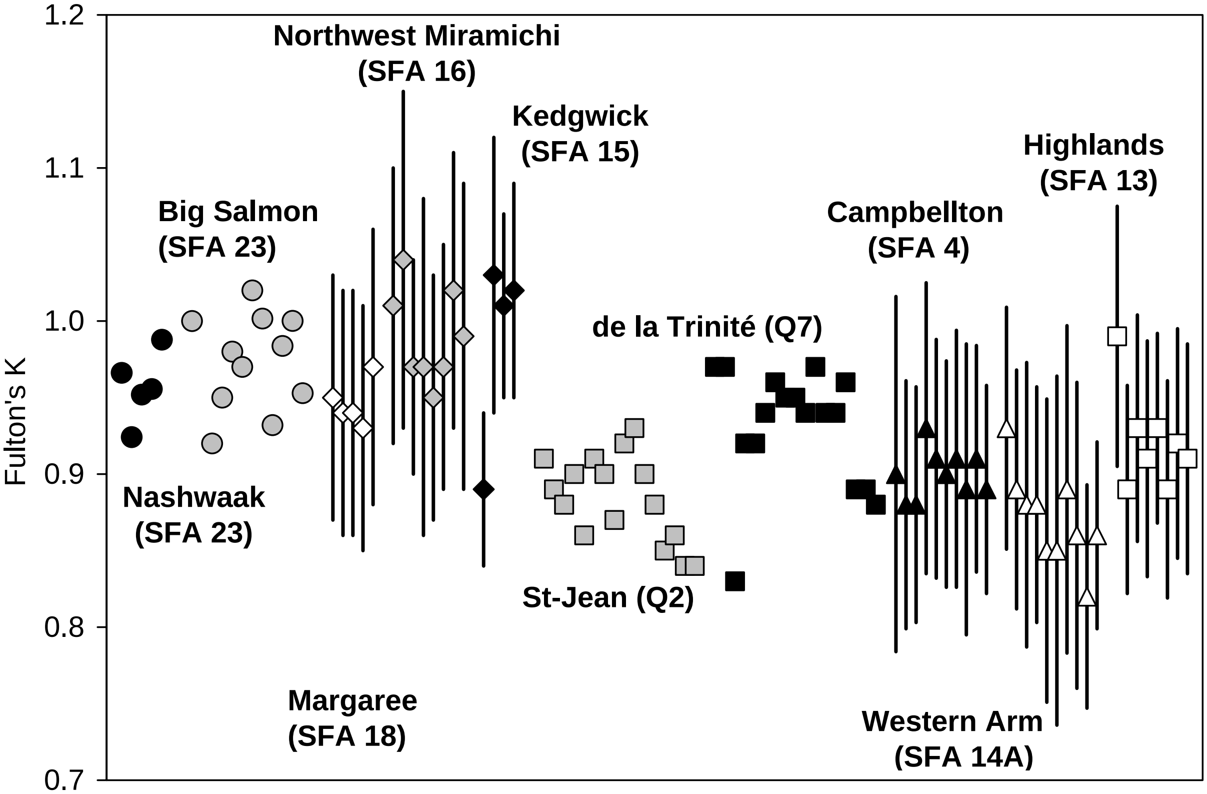


Figure 7. Condition factor (mean, ± 1 std. dev.) of wild Atlantic salmon smolts, expressed as Fulton's K in seven MSW salmon stocks of the mainland of eastern Canada and two 1SW (Campbellton and Western Arm) stocks and one MSW (Highlands) stock in Newfoundland (see caption for Figure 6 for further details on geographic location).

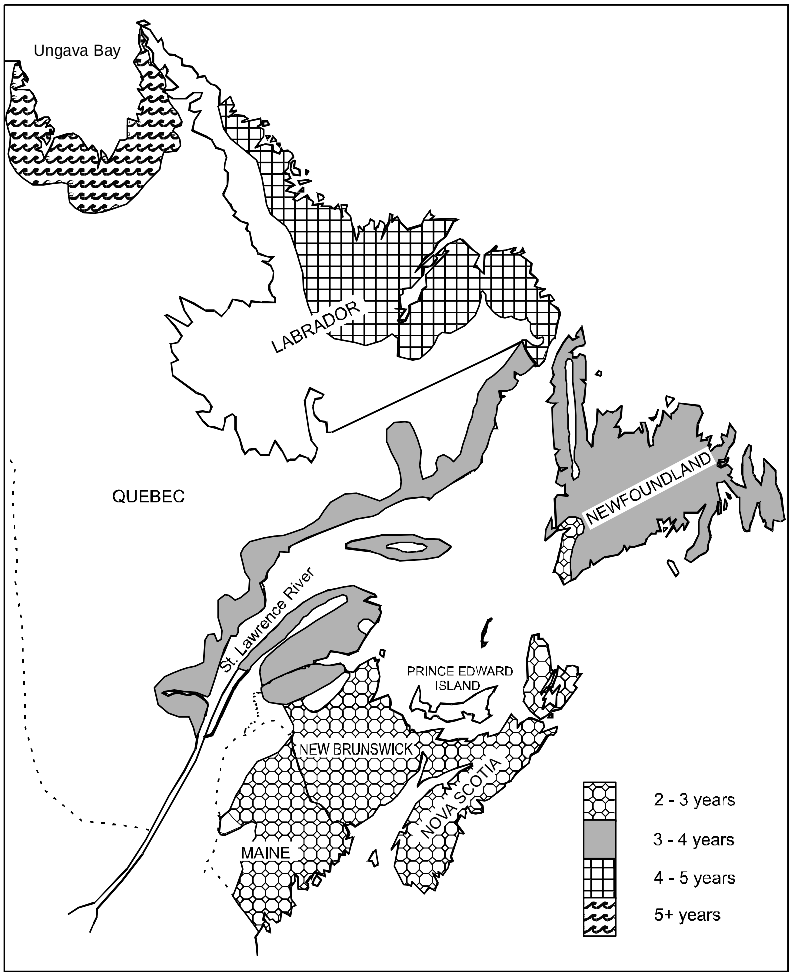
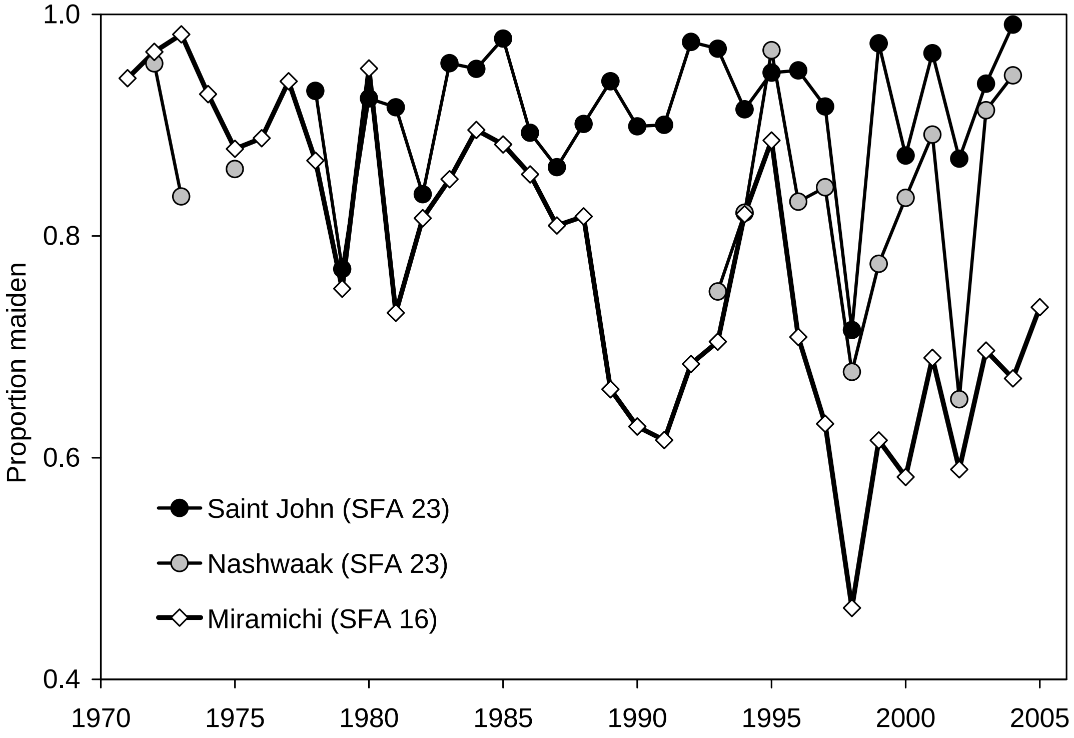


Figure 8. Distribution of generalized stock groupings by smolt (river) age of self-sustaining populations of Atlantic salmon in North America. Within each zone, exceptions to the generalization may occur.



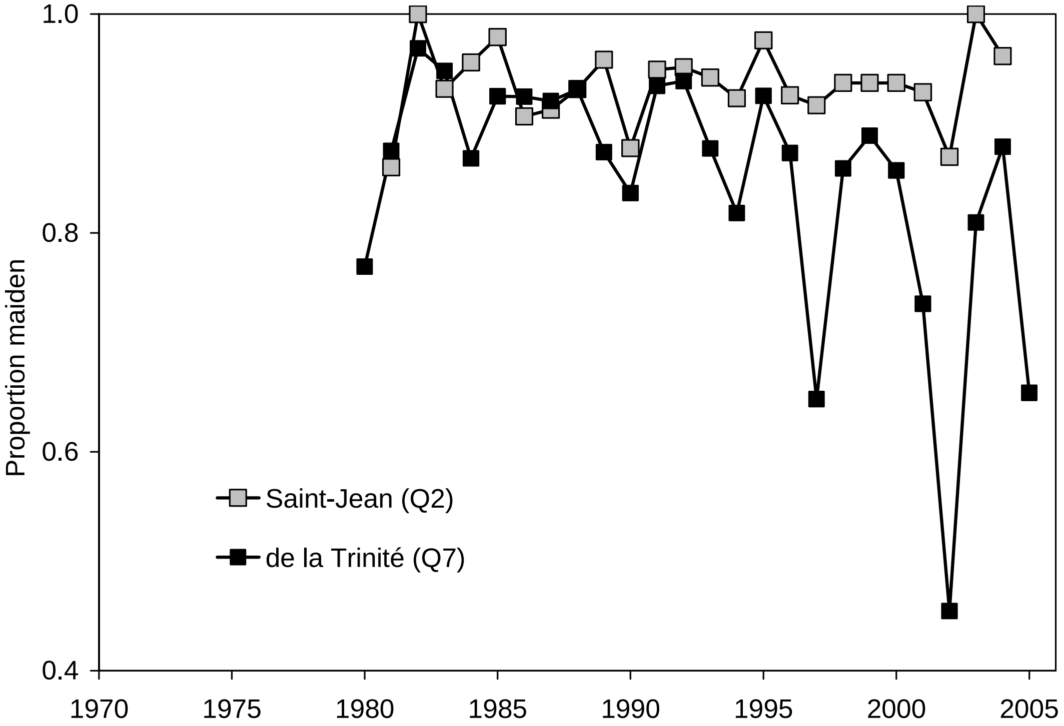


Figure 9. Changes in the annual proportion of repeat spawners in the large salmon category in five monitored rivers of mainland eastern Canada.

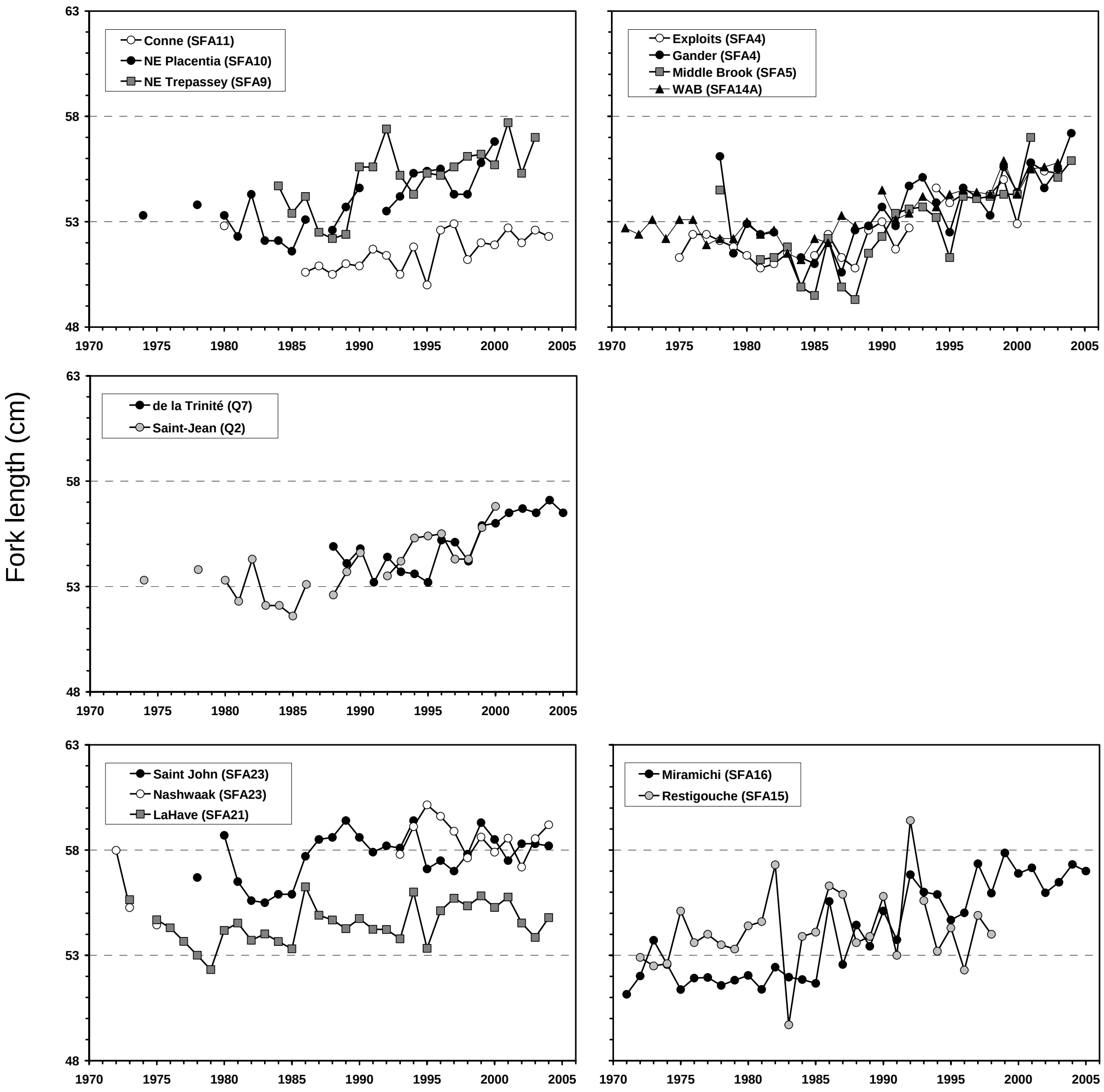


Figure 10. Annual variations in mean fork length of 1SW maiden salmon from selected rivers of eastern Canada.

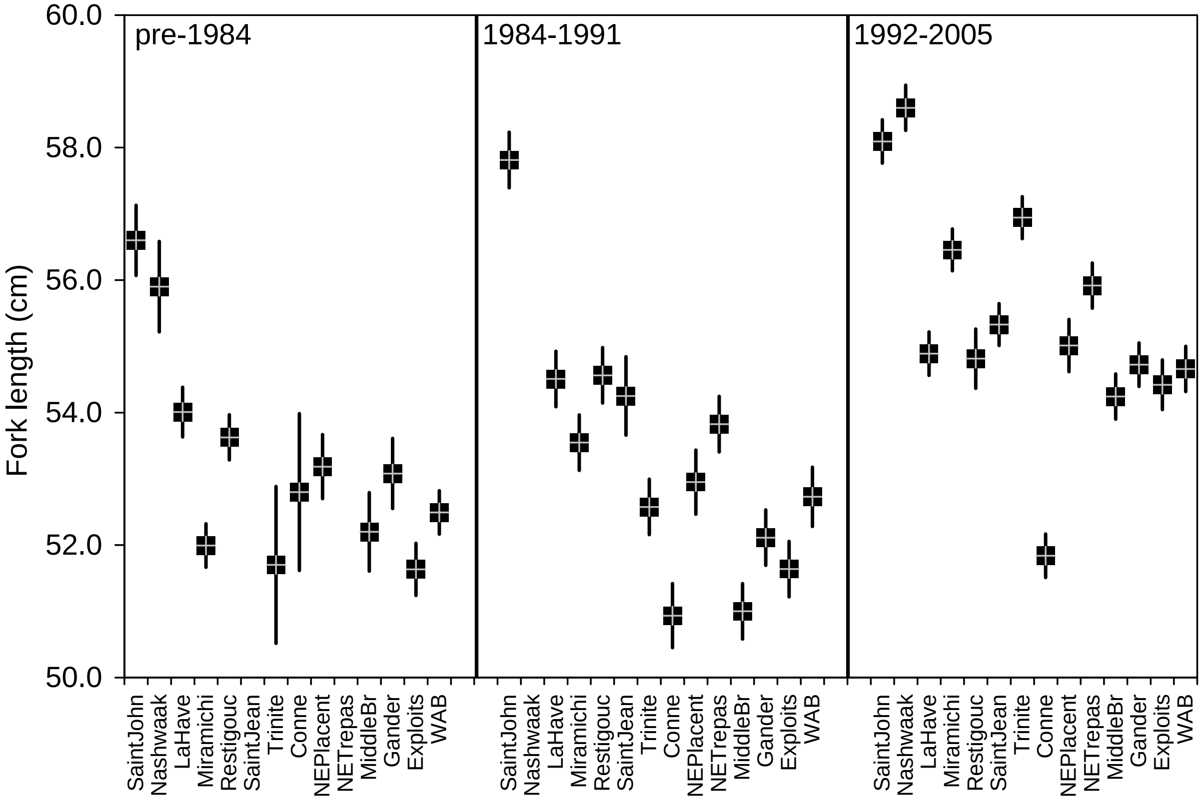


Figure 11. Mean fork length of 1SW maiden salmon from 14 selected rivers for three management periods. The management periods are: pre-1984 represents 1970 to 1983 when the commercial fisheries of the Maritime provinces and portions of Québec were closed or under quota management, 1984 to 1991 when the commercial fisheries of the Maritimes and portions of Québec were closed and Newfoundland commercial fisheries quotas were introduced, and post 1991 when the moratoria on salmon and cod commercial fisheries were introduced. Mean (± std. err.) of the annual values by river are shown.

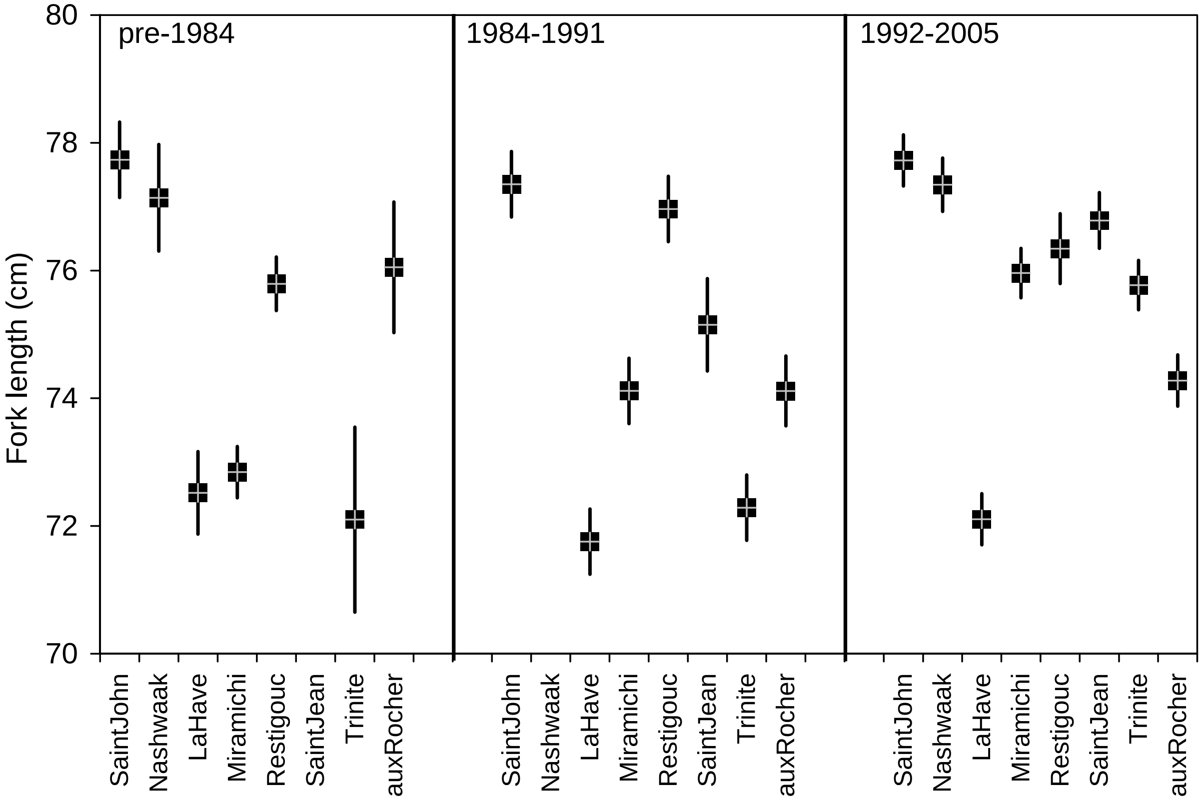


Figure 12. Mean fork length of 2SW maiden salmon from eight selected rivers for three management periods. The management periods are: pre-1984 represents 1970 to 1983 when the commercial fisheries of the Maritime provinces and portions of Québec were closed or under quota management, 1984 to 1991 when the commercial fisheries of the Maritimes and portions of Québec were closed and Newfoundland commercial fisheries quotas were introduced, and post 1991 when the moratoria on salmon and cod commercial fisheries were introduced. Mean (± std. err.) of the annual values by river are shown.

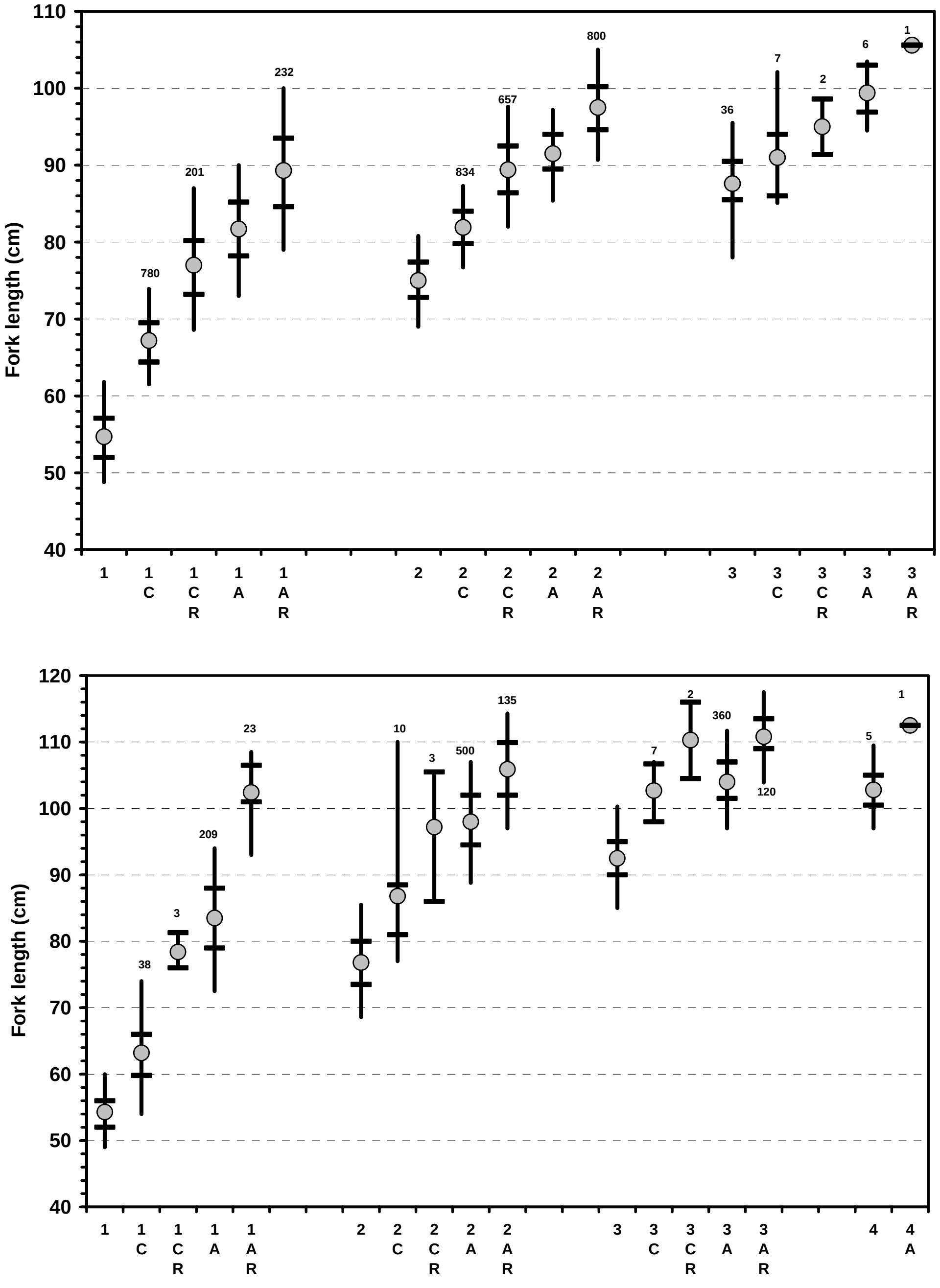


Figure 13. Length by spawning history from Miramichi (upper) and Restigouche (lower). Sample is indicated, otherwise N > 1,000. Mean, Q1, Q3 and P5 to P95 range. Numbers on x-axis refer to maiden sea age, C = consecutive spawners, A = alternate spawners, R = repeated consecutive or alternate spawnings.

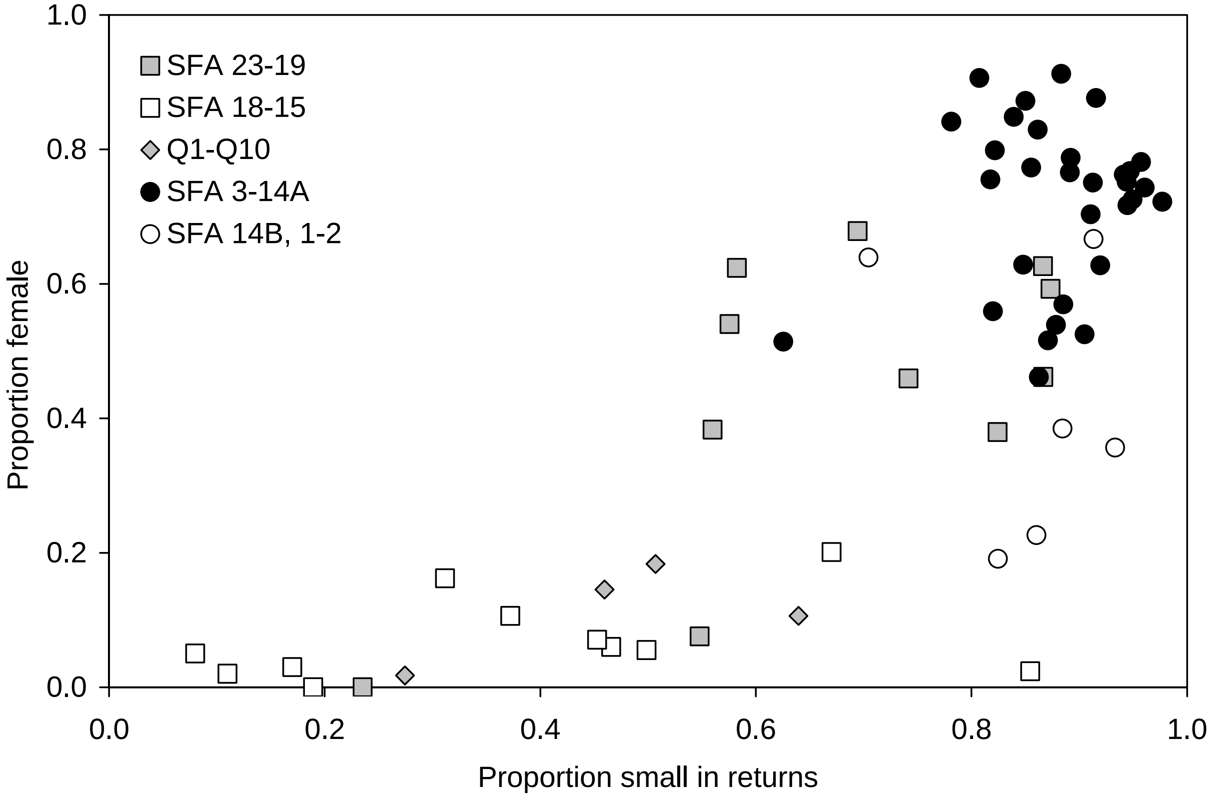


Figure 14. Association between the proportion female in the 1SW maiden salmon and the proportion of the returns which are small salmon, from eastern Canada.

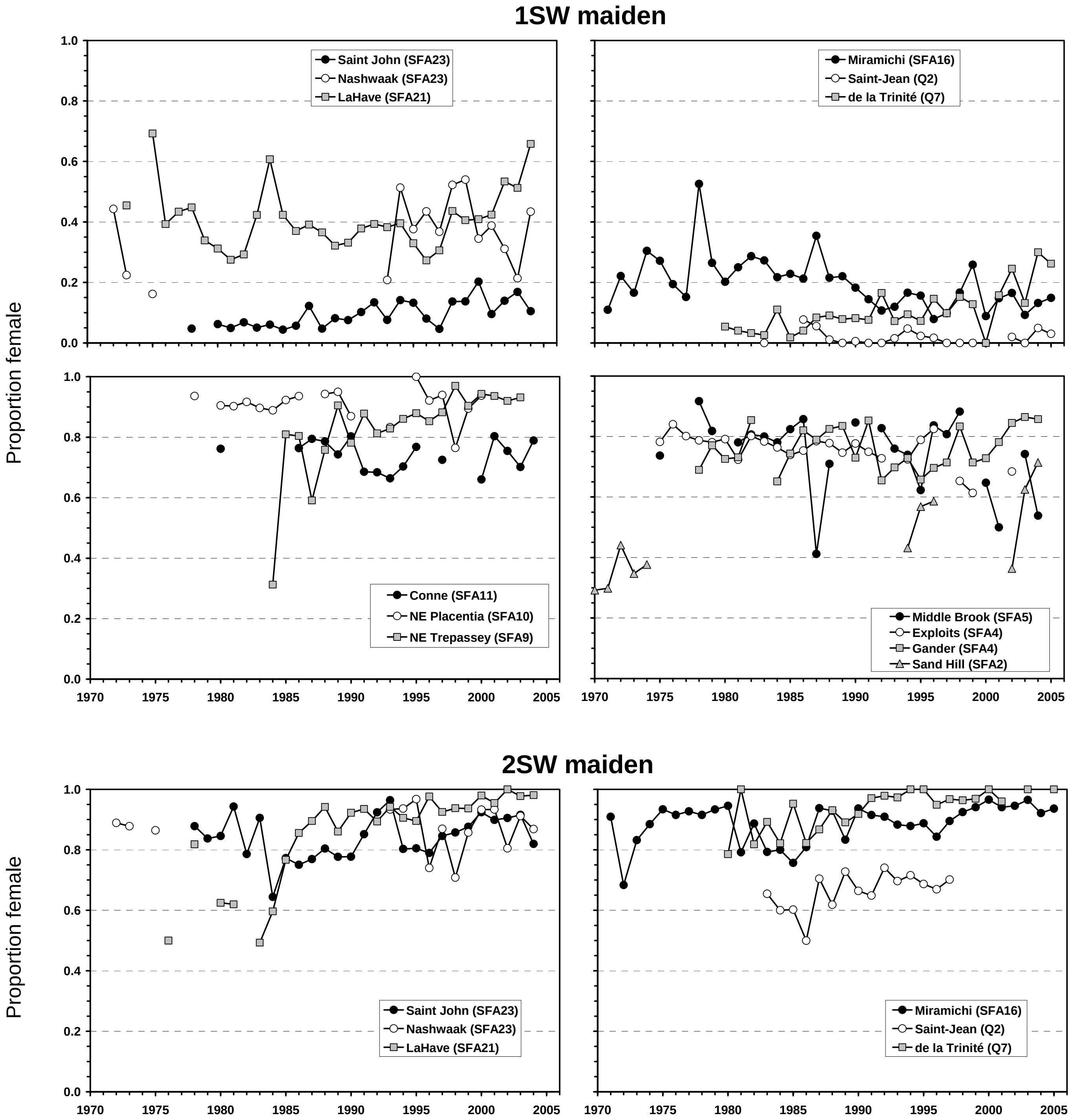


Figure 15. Annual variation in the proportion female in 1SW maiden (upper) and 2SW maiden (lower) salmon from selected rivers of eastern Canada.

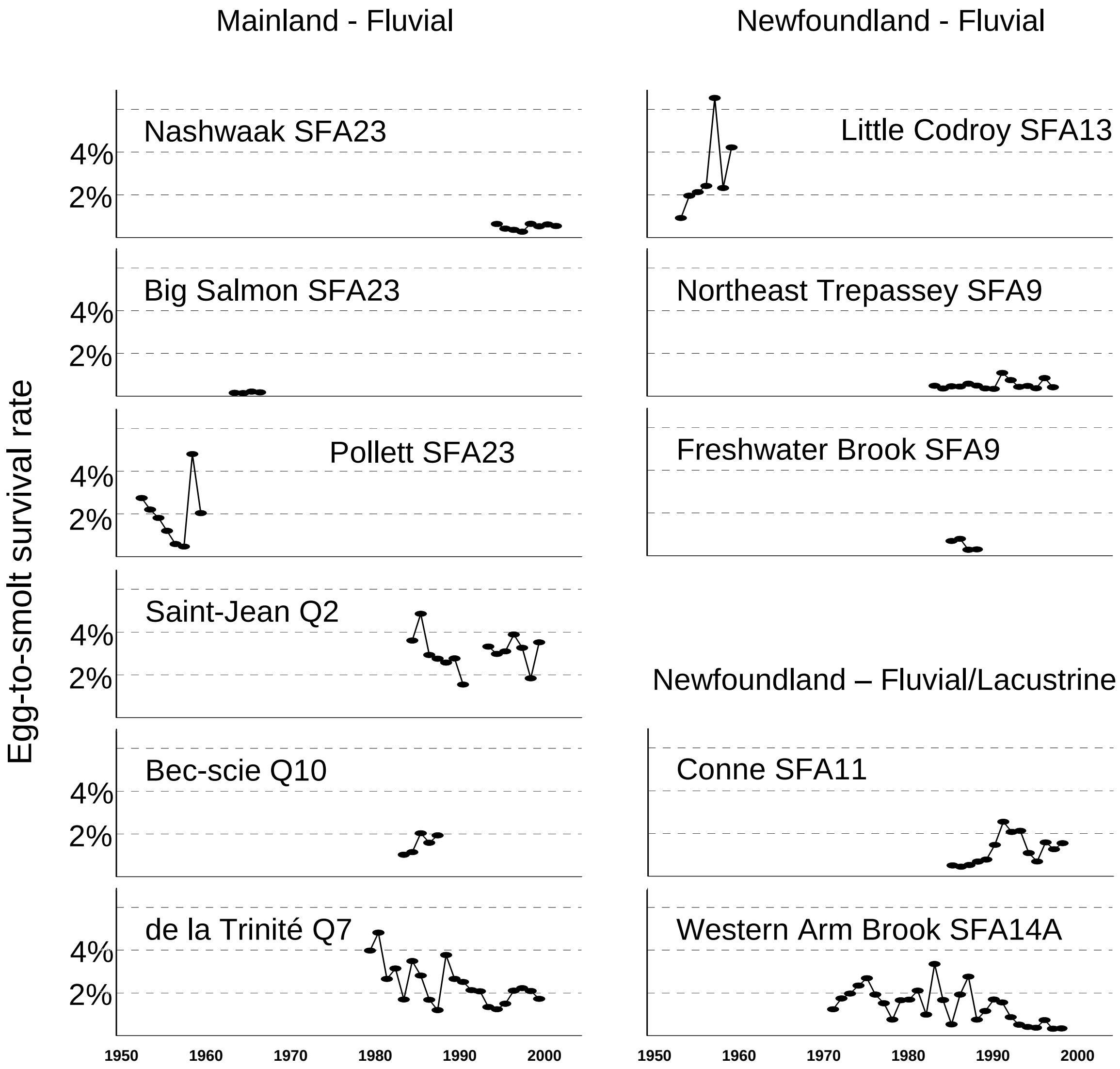
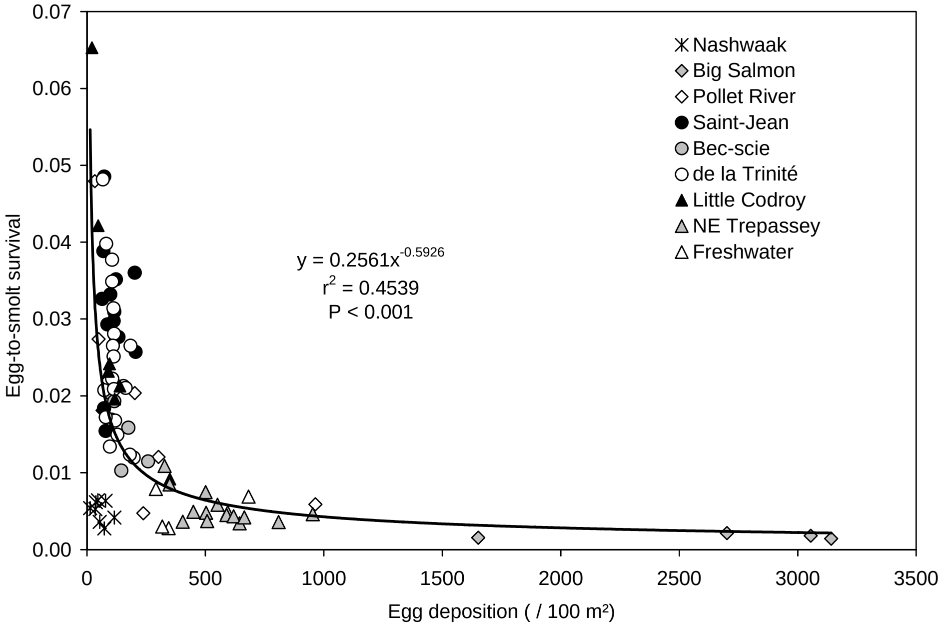


Figure 16. Annual variations in egg to smolt survival rates by year of egg deposition from rivers of eastern Canada.



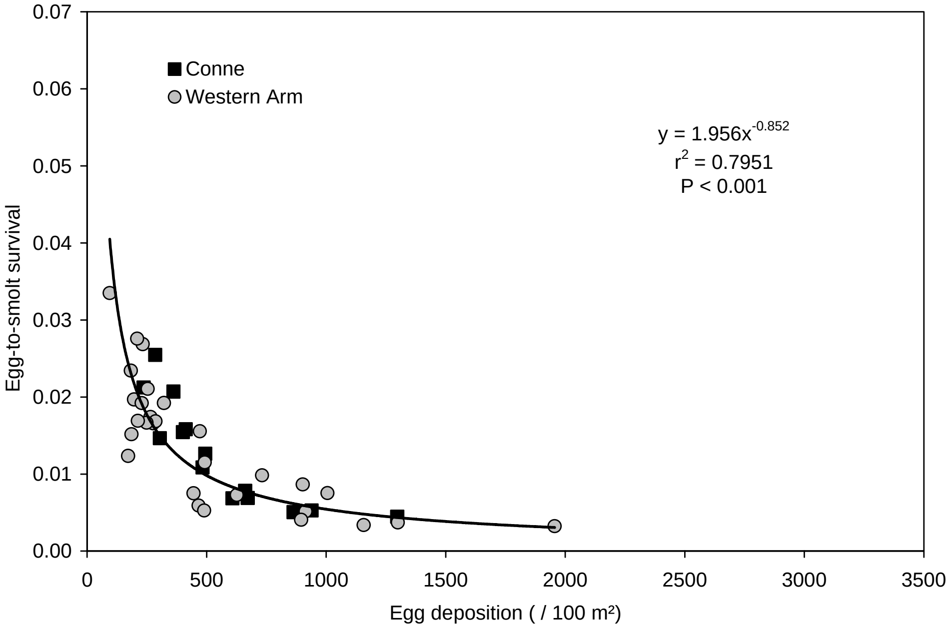


Figure 17. Measured egg to smolt survival rates as a function of egg deposition rates for rivers with fluvial habitat (upper) and rivers in which lacustrine habitat is utilized extensively by juveniles (lower). Egg deposition rates are based on wetted area of fluvial habitat.

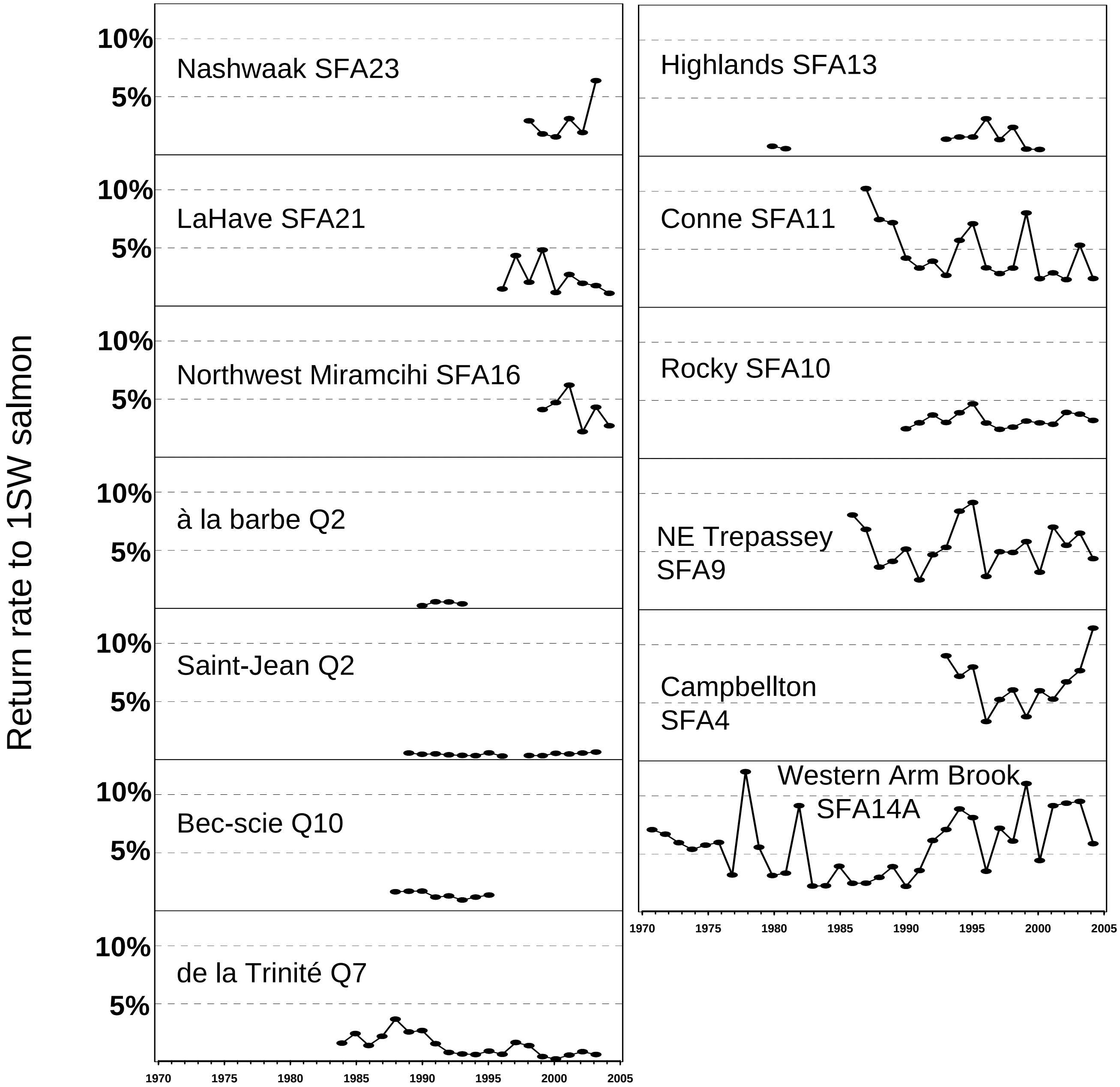


Figure 18. Summary of return rates to 1SW salmon for rivers of eastern Canada, 1970 to 2004 smolt migration years.

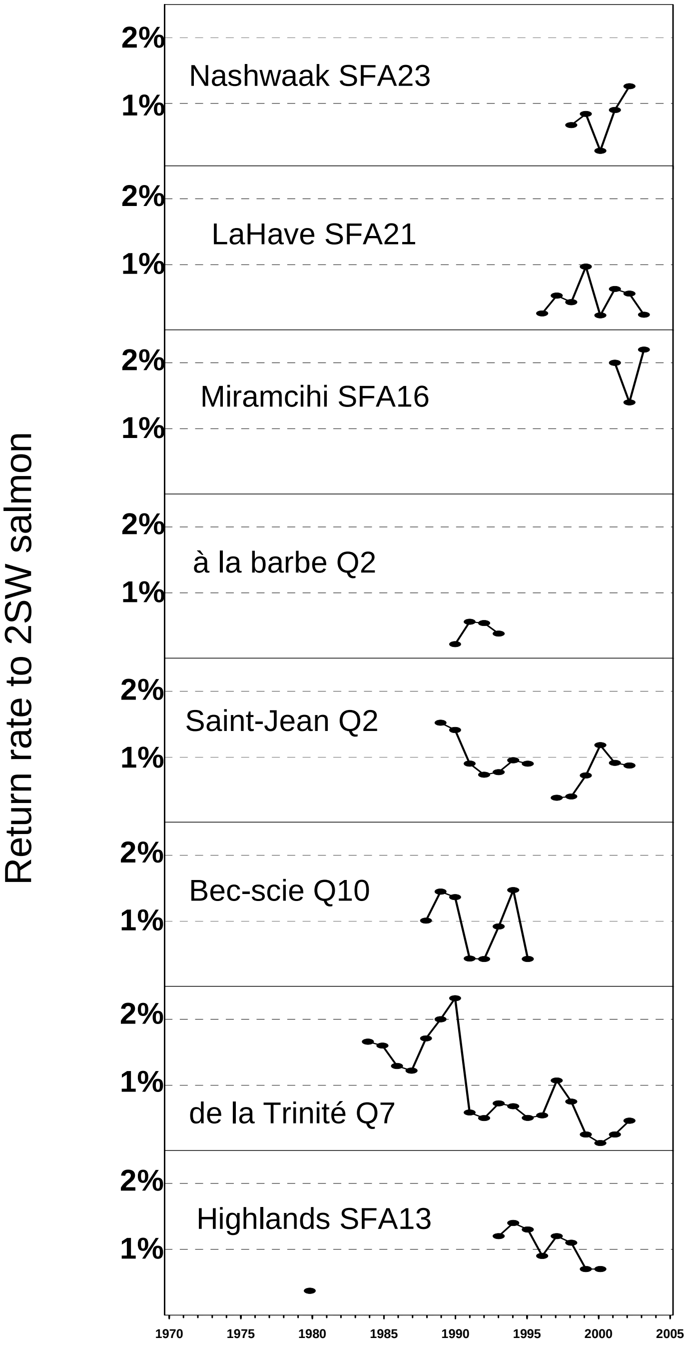


Figure 19. Summary of return rates to 2SW salmon for rivers of eastern Canada, 1970 to 2004 smolt migration years.