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Biological Characteristics and Population Dynamics of Atlantic Salmon (*Salmo salar*) from the Miramichi River, New Brunswick, Canada

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems 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.

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ABSTRACT

This report summarizes the information on biological characteristics of Atlantic salmon (*Salmo salar*) from the Miramichi River (New Brunswick, Canada) over the period 1971 to 2014. Emphasis is placed on characteristics of salmon from the Northwest Miramichi in support of a review of the risks to long-term fitness of wild Atlantic salmon of a proposed supplementation program consisting of the captive-rearing in freshwater of wild salmon smolts to the adult stage and release back to the river to spawn. Freshwater dynamics of Atlantic salmon are examined to assist in the evaluation of the risks and /or benefits of the proposed supplementation activity in achieving one of the stated goals which is to increase abundance of adult Atlantic salmon to the river. The Atlantic salmon population from the Miramichi is characterized by complex phenotypic diversity. In any given year, there are typically 6 year classes of immature fish and as many as 9 year classes of mature fish in the combined freshwater and marine ecosystems. There are defined run timing components of the population to the river and headwater areas at higher elevations are primarily utilized by early-run fish. There is an important sex ratio bias between the maiden sea age groups of fish. Increased return rate to a second spawning is an example of phenotypic plasticity in this population responding to changes in the ecosystem. Indices of juvenile abundance for the past four decades indicate that freshwater production of Atlantic salmon increased from low values in the 1970s and peaked in the late 1990s and early 2000s. Abundance indices of fry and small parr are currently well above those of the 1970s to mid-1980s. Preliminary stock and recruitment analyses indicate that the most important density dependent control occurs between the egg and fry stage with modelled theoretical carrying capacity of fry almost realized in the late 1990s. If the egg to fry recruitment dynamic is as severely compensatory as suggested by these analyses, there may be very little gain to be realized in increased smolt production and subsequent adult returns by supplementing the current spawning escapement levels with large numbers of captive-reared adult spawners. Density dependent factors will rapidly adjust the abundances of juveniles to levels which can be sustained by the productive capacity of the freshwater habitat.

Caractéristiques biologiques et dynamique des populations de saumon de l’Atlantique (*Salmo salar*) de la rivière Miramichi, au Nouveau-Brunswick (Canada)

RÉSUMÉ

Ce rapport résume les renseignements sur les caractéristiques biologiques du saumon de l’Atlantique (*Salmo salar*) de la rivière Miramichi (Nouveau-Brunswick, Canada) au cours de la période de 1971 à 2014. On a placé l'accent sur les caractéristiques du saumon dans la rivière Miramichi Nord-Ouest pour appuyer un examen des risques pour la valeur adaptative à long terme du saumon sauvage de l'Atlantique d'un programme d'ensemencement proposé consistant à élever en captivité des saumoneaux sauvages en eau douce jusqu'à l'âge adulte et à les remettre en liberté dans la rivière pour qu'ils aillent frayer. La dynamique du saumon de l’Atlantique en eau douce est examinée afin de faciliter l'évaluation des risques et des avantages de l'activité d'ensemencement proposée pour atteindre l'un des objectifs énoncés, qui est d'accroître l'abondance des saumons de l'Atlantique adultes dans la rivière. La population de saumon de l'Atlantique de la rivière Miramichi est caractérisée par une diversité phénotypique complexe. Pendant une année donnée, on trouve habituellement six classes d'âge de poissons immatures et neuf classes d'âge de poissons matures dans les écosystèmes marins et d'eau douce combinés. La population de la rivière compte des stocks de montaison définis, et les eaux d'amont situées à des élévations supérieures sont principalement utilisées par les stocks de montaison hâtive. Il existe un important biais sex-ratio entre les groupes d'âge en mer de poissons vierges. L'augmentation du taux de montaison au cours d'une deuxième période de frai est un exemple de plasticité phénotypique dans cette population en réponse aux changements dans l'écosystème. Les indices d'abondance des juvéniles pour les quatre dernières décennies indiquent que la production de saumon de l’Atlantique en eau douce a augmenté, passant de valeurs faibles dans les années 1970 pour culminer à la fin des années 1990 et au début des années 2000. Les indices d'abondance des alevins et des petits tacons se situent actuellement bien au-dessus de ceux enregistrés entre les années 1970 et le milieu des années 1980. Les analyses préliminaires des stocks et du recrutement indiquent que le plus important contrôle de la densité a lieu entre l'étape de l'œuf et celle de l'alevin et que la capacité de charge théorique de l'alevin a presque été atteinte à la fin des années 1990. La dynamique de recrutement œufs-alevins est fortement compensatoire, comme le laissaient croire ces analyses. Il se peut que le fait de compléter les niveaux actuels d'échappée de géniteurs par de grands nombres de reproducteurs adultes élevés en captivité ne procure que très peu de gains pour ce qui est d'accroître la production de saumoneaux et les montaisons d'adultes subséquentes. Les facteurs dépendants de la densité ajusteront rapidement l'abondance des juvéniles à des niveaux qui peuvent être maintenus par la capacité de production de l'habitat d'eau douce.

INTRODUCTION

The Miramichi River, at a maximum axial length of 250 km and draining an area of about 14,000 km^2, had until recently, the largest Atlantic salmon run of eastern North America. There are two major branches: the Northwest Branch covers about 3,900 km^2 and the Southwest Branch about 7,700 km^2 of drainage area (Randall et al. 1989). The two branches drain into a common estuary and subsequently drain into the Gulf of St. Lawrence at latitude 47°N (Fig. 1).

The Atlantic salmon (*Salmo salar*) population from the Miramichi River has been one of the most intensively monitored stocks of Atlantic salmon in eastern Canada. Two size groups of Atlantic salmon return to the river to spawn. The small salmon category consists of fish less than 63 cm fork length, which are generally referred to as grilse. These fish have usually spent only one full year at sea (one-sea-winter; 1SW) prior to returning to the river but the size group may also contain some previously spawned salmon. The large salmon category consists of fish greater than or equal to 63 cm fork length. This size group is generally referred to as multi-sea-winter (MSW) or just salmon and contains varying proportions of 1SW, 2SW (two-sea-winter) and 3SW (three-sea-winter) maiden (first time) spawners as well as previous spawners (Moore et al. 1995). Salmon which have spawned and have not returned to sea in the spring of the year are referred to as kelts or black salmon in contrast to bright salmon which are mature adult salmon moving into freshwater from the ocean.

In addition to the different runs and size groups, the Miramichi River is also considered to contain several stocks of Atlantic salmon (Saunders 1981). Separate branch assessments were introduced to account for some of this diversity and for the differences in exploitation between the Northwest and Southwest branches. Aboriginal fisheries were historically conducted almost exclusively in the Northwest Miramichi (exploitation also occurs in the estuarial waters of the Miramichi River, downstream of the confluence of the two branches) and recreational fisheries exploitation also differs between the Northwest and Southwest branches.

Annual assessments of the Atlantic salmon stock of the Miramichi River have been prepared since 1982 (Randall and Chadwick 1983) and the most recent assessment document is to the 2014 return year (DFO 2015a; Douglas et al. 2015). Status of the river in terms of adult returns, estimated egg depositions, and juvenile indices of abundance to 2014 are summarized in DFO (2015a).

This report summarizes the information on biological characteristics (size and age structure, sex ratios, fecundities, run-timing, and migrations at sea) over the period 1971 to 2014. Emphasis is placed on characteristics of salmon from the Northwest Miramichi in support of a review of the risks to long-term fitness of wild Atlantic salmon of a proposed supplementation program consisting of the captive-rearing in freshwater of wild salmon smolts to the adult stage and release back to the river to spawn (DFO 2016). Freshwater dynamics of Atlantic salmon are examined to assist in the evaluation of the risks and /or benefits of the proposed supplementation activity in achieving one of the stated goals which is to increase abundance of adult Atlantic salmon to the river.

PHYSICAL AND ECOSYSTEM CHARACTERISTICS

Detailed geophysical information of the Miramichi River is provided by Blousfield (1955). The two main branches of the Miramichi River are each comprised of two main rivers which join near the head of tide; the Renous and Southwest Miramichi rivers join at the head of tide in the Southwest Branch of the Miramichi, the Little Southwest and Northwest Miramichi rivers join at the head of tide in the Northwest branch of the Miramichi (Fig. 1). The two branches of the

Northwest Miramichi and the Renous River within the Southwest branch are characterized by a steep profile, achieving maximum elevations of almost 450 m within the first 100 km of river length (Randall et al. 1989; Fig. 1). The Southwest Miramichi within the Southwest branch has a more shallow profile, attaining a maximum elevation of just under 400 m at 200 km upstream of the head of the tide.

Wetted area for juvenile salmon production in the Miramichi River was calculated by Amiro (1983). The estimates are total wetted area, unweighted by habitat type, gradient or other variable of productive capacity. Total wetted area in the Northwest Miramichi is estimated at 1,679 ha of habitat, with more than 50% of the estimated area in stream order 4 or less (Table 1). Within the Northwest Miramichi, the habitat areas are approximately equivalent between the Little Southwest Miramichi River and the Northwest Miramichi River.

Eleven diadromous and 19 freshwater fish have been reported from the Miramichi River (Randall et al. 1989). As for non-native species, brown trout, rainbow trout, tiger trout, chain pickerel, and smallmouth bass have been recorded in the Miramichi. The single known occurrence of chain pickerel was eradicated shortly after discovery from Depres Lake in 2001, a headwater lake of the Cains River in the Southwest Miramichi (Connell et al. 2002). Smallmouth bass were first reported from Miramichi Lake in 2008, a headwater tributary of the Southwest Miramichi River, and efforts have been ongoing since to control the spread, and reduce abundance with the objective of eradicating the species from the watershed (DFO 2013; Biron et al. 2014).

BIOLOGICAL CHARACTERISTICS

This section on biological characteristics includes information on river ages, juvenile salmon characteristics, smolt characteristics, and adult salmon characteristics. The adult salmon characteristics include information on lengths and weights by spawning history groups and within season of return, fecundity, sex ratio by sea age group, run timing and marine migrations.

Returning adult salmon have been systematically captured and sampled in the Miramichi River since 1971. Salmon are captured in tidal trapnets which are fished daily over the entire migration period from the middle of May to late October. Fork length, origin (hatchery released fish are identified based on the absence of the adipose fin which was clipped from appropriate life stages prior to release), sex by external characteristics, and a scale sample is collected from up to 30 small salmon per day and generally all large salmon (>= 63 cm fork length). Small salmon and large salmon are tagged and released with external individually numbered tags prior to release. Data on other fish captured are also recorded. Hayward (2001) provides an overview of all counting facilities in the Miramichi River and more details of sampling operations are in Hayward et al. (2014).

RIVER AGE DISTRIBUTIONS

Juvenile salmon from the Miramichi River spend between two and five years in freshwater before going to sea. For the Northwest Miramichi system, based on sampling and run size estimates for the smolt migration years 1999 to 2006, the percentage of a yearclass going to sea after two years in freshwater varied from 29% to 61% whereas river age 4 smolts were never more than 2% of a yearclass (Table 2).

Based on characteristics of returning adult Atlantic salmon and weighted by estimates of returns, the majority (> 95%) of a yearclass of salmon from the Northwest Miramichi spent 2 or 3 years in rivers with on average 47% of all maiden-aged returning salmon having a river age of 2 years. A similar percentage (average 47%: range 11% to 85%) of the 1SW maiden salmon were of river age 2. For the 2SW maiden salmon, a slightly higher percentage was of river age 2 (average 53%; range 24% to 82%) (Fig. 2). There is a large amount of variation in the percentages at river age in the returns as adults from a yearclass. This is due to the annual variations in sea survival to which a yearclass is exposed. In the case of the Northwest Miramichi, a yearclass of salmon is at sea over four consecutive years of maiden returns (see text table for yearclass 2000 below).

Years at sea for the example yearclass = 2000			
Maiden sea age	river age 2	river age 3	river age 4
1SW	2003/2004	2004/2005	2005/2006
2SW	2003/2004 2004/2005	2004/2005 2005/2006	2005/2006 2006/2007

JUVENILE SALMON CHARACTERISTICS

Growth rates of salmon juveniles are highly variable among sites and years. Average size of age-0 parr (fry) is annually variable, mean fork lengths ranging between 4.0 and 5.5 cm (Fig. 3; Swansburg et al. 2002). Age-1 parr also show important variations in mean size among sites and among years, ranging between 7.5 cm to just over 9.0 cm in the Northwest Miramichi (Fig. 3). Age-2+ parr, those juveniles not leaving the river as 2-year old smolts range in mean size between 10.5 and 12.4 cm fork length (Fig. 3). Precocious male maturation is common in juveniles in the Miramichi (Cunjak and Therrien 1998; Brodeur 2006).

Smolt characteristics

Information on size, age, sex ratio and timing of Atlantic salmon smolts was obtained during monitoring and assessment programs in the Northwest Miramichi system from tidal waters and from the Little Southwest Miramichi River using a rotary screw trap (see description in Chaput et al. 2002).

Atlantic salmon smolts migrate from the Northwest Miramichi primarily from mid-May to early June. Date of peak catches at the estuary trapnet ranged from 16 May to 8 June over sampling years 1999 to 2011(Table 2). The date of the 5th percentile of catches, as an indicator of the initiation of the smolt migration ranged from 13 May to 24 May for the same years sampled (Table 2). Peak catches occurred in most years when water temperatures attained / exceeded 15ºC (Figs. 4a and 4b). Run duration is generally short, occurring over a period of about three weeks.

Smolts from the Northwest Miramichi are of relatively consistent size distribution annually, ranging between 10.5 to 18.0 cm with mean lengths of 13 cm (Fig. 5; Table 2). Mean weight of smolts ranged between 18 and 22 g annually (Table 2).

There are usually more females than males in the smolt run, the percentage female ranging between 42% and 63% with greater than 50% female in most years (Table 2).

ADULT SALMON CHARACTERISTICS

Atlantic salmon returning to the Miramichi are assessed on the basis of abundance of two size groups: small salmon (less than 63 cm fork length) and large salmon (>= 63 cm fork length).

Over the period 1992 to 2014, small salmon have comprised more than 50% of the returns to the Northwest Miramichi, with the maximum percentage of 90% in 2002 and the lowest percentage (50%) in 2012 and 2014 (Fig. 6). On average, the returns of small salmon have a lower percentage in the Southwest Miramichi (58%) than in the Northwest Miramichi (68%) although the annual variation in the percentages of small salmon is just as important in the Southwest Miramichi system (range: 34% to 83%) (Fig. 6). The proportion of the total annual returns made up of small salmon has declined over the period 1992 to 2014, especially so in recent years. The same general pattern is noted for 1SW maiden salmon as a proportion of the annual returns of maiden 1SW and 2SW salmon, 3SW salmon are very rare in the Miramichi (Fig. 6).

Sea age composition

Fish in the small salmon category are predominantly (>95%) maiden 1SW salmon, the other age groups include 2SW salmon and repeat spawning 1SW salmon as consecutives. The large salmon category is comprised of a more diverse life history including 1SW maiden salmon, 2SW maiden, 3SW maiden, and a large number of categories of repeat spawning salmon. Repeat spawning salmon can be short duration migrants (consecutive) which spend a few months at sea to recondition and return to rivers to spawn in consecutive years, or long duration migrants (alternates) that spend more than one year at sea post-spawning to recondition before returning to rivers to spawn. A total of 52 unique spawning histories have been interpreted from scales of salmon in the Miramichi and repeat spawners up to a seventh spawning migration have been sampled since the mid-1990s (Table 3).

When considered by smolt class, the majority of returning maiden salmon are 1SW maiden sea age (Fig. 6). Notable exceptions to this pattern were the returns from the 2008 and 2011 smolt migration years when 40% or more of the smolt class returned to the Northwest Miramichi at 2SW maiden sea age (Fig. 6). For the 2011 smolt class of the Southwest Miramichi, almost 60% of the smolts returned at 2SW maiden sea age when usually the percentage of 2SW in the return of the smolt class is less than 30% (Fig. 6). When considered by yearclass, taking into account the variable river ages and the different years when the salmon are at sea, the percentage of all maiden sea age returns comprised of 1SW salmon has oscillated at around 80% for the Northwest Miramichi and about 75% for the Southwest Miramichi (Fig. 6). There is less variability in the proportion of the maiden salmon that are 1SW and there is no apparent change in the proportion over time in the Northwest Miramichi but there is a perceptible decline in the Southwest Miramichi (Fig. 6).

Lengths and weights

Fork lengths of adult Atlantic salmon increase with the number of years at sea (Fig. 7). Maiden salmon at 1SW age have a median fork length of about 58 cm, 2SW salmon have a median fork length of about 75 cm, and 3SW salmon although rare in the Miramichi have a median fork length of about 84 cm (Fig. 7). Post spawners can return to sea to feed and grow and return to spawn repeatedly. As mentioned previously, Atlantic salmon on a seventh spawning migration have been observed in the Miramichi (Table 3). Consecutive spawners put on less length at each return migration than alternate spawners. First time repeat 1SW salmon that return as consecutives (1SWC) are intermediate in length between 1SW and 2SW maiden salmon whereas first time repeat alternate 1SW spawners (1SWA) are intermediate in length between 2SW and 3SW salmon (Fig. 7). The longest salmon recorded in the Miramichi have been 2SW repeat alternate spawners (Fig. 7). Sizes at age are similar between the Northwest Miramichi and Southwest Miramichi systems (Fig.7).

Adult salmon return to the Miramichi River over an extended period from late May to late October. Fork lengths of 1SW maiden and 1SW consecutive salmon increase over the season of return; median lengths of 1SW maiden salmon increase from 56 cm to about 59 cm over the June to October migration period whereas 1SW consecutive spawners increase in length from 62 cm in June to about 68 cm in October (Fig. 8). There is no discernible change in fork lengths of 2SW maiden and repeat spawning salmon during the seasonal migration, with perhaps the exception of the June returning 2SW salmon which were slightly shorter than 2SW salmon in the other months (Fig. 8).

Fork length distributions over years 1992 to 2013 show important (> 5 cm at median values) annual variations in size particularly for 1SW maiden salmon returns in October (Fig. 9). Although there are important variations in size distribution of 1SW consecutive and 1SW alternate spawners, the sample sizes are much smaller for these size groups. Annual variations in fork lengths of 2SW maiden and repeat salmon are also noted (Fig. 10).

Weights are not collected systematically at the monitoring trapnets of the Miramichi. Systematic sacrificing of salmon from the index trapnet prior to 1992 was conducted and these samples combined with opportunistic sampling in recent years of incidental mortalities were used to describe the weights at sea age. Maiden 1SW salmon have a median weight of 1.57 kg, 2SW maiden have a median weight of 4.50 kg. First time alternate repeat spawning 1SW salmon have a median weight of 5.51 kg whereas first time alternate repeat spawning 2SW salmon have a median weight of 9.00 kg (Fig. 11).

Sex ratio, fecundity, egg size

There are important differences in the proportion of females among the size categories and sea age histories. Small salmon, comprising the majority of 1SW salmon, are the majority male whereas large salmon, comprised by a majority of 2SW salmon, are the majority female (Fig. 12). Small salmon in the Northwest Miramichi River have a higher proportion of females than in the Southwest Miramichi. The proportion of small salmon from the early run (prior to September 1) averages 0.38 female whereas small salmon from the late run averages 0.18 female salmon (Fig. 12). The same proportions are noted from sampling sites in the Little Southwest Miramichi. There is much less difference in the proportion of females of large salmon, averaging about 0.80 female in both the early and late runs in the Northwest Miramichi and the Southwest Miramichi (Fig. 12). There are noted annual variations in the proportions female (Fig. 13).

Fecundity to body size relationships for salmon from the Miramichi River were reported by Randall (1989). These relationships, one for small salmon and the other for large salmon, combined with the average fork lengths and the proportions female in the runs of each size group, are used to estimate the number of eggs per fish for the annual stock assessments (Fig. 13; Douglas et al. 2015).

Data from spawning of females in the hatchery at South Esk were collected during 1991 to 1995 and are presented in Figure 14 (J. Hayward, DFO, unpublished data). Reid and Chaput (2012) also estimated eggs per female, by size and spawning history (Fig. 15).

Fecundity (number of eggs) increases with both length and with weight (Figs. 14, 15). The fecundity length relationships from Reid and Chaput (2012) are essentially identical to those from the hatchery data of 1991 to 1995 (Figs. 14, 15). These two relationships differ from those derived by Randall (1989) in having a lower number of eggs for small salmon and differing slopes for the large salmon.

Female 1SW maiden salmon, of median fork length 58 cm, have a predicted fecundity of about 2,900 eggs. Maiden 2SW salmon of median fork length 75 cm have a predicted fecundity of 5,900 eggs whereas salmon measuring 84 cm fork length (median length of 3SW salmon) have a predicted fecundity of 8,000 eggs. The highest measured fecundity from the hatchery data was 14,600 eggs from a female salmon measuring 97 cm fork length. Reid and Chaput (2012) measured a maximum fecundity of 15,500 eggs from a female salmon measuring 104 cm fork length.

Egg size (diameter, mm) is smallest for 1SW maiden salmon but otherwise unrelated to body size in other spawning age groups (Fig. 16). The largest eggs are produced by 2SW maiden and alternate repeat spawning salmon (Fig. 16). The egg sizes of consecutive repeat spawners are intermediate in size from those of 1SW maiden salmon and 2SW maiden and repeat alternate spawners (Fig. 16).

Reid and Chaput (2012) measured egg survival rate from female salmon to placement of eggs into incubation boxes in the hatchery (Fig. 17). Egg survival was very high, ranging from a low of 67.0% for a 2SW maiden female to a maximum of 99.4%. The majority (95%) of the measured survival rates exceeded 81%, and half of the measured survival rates exceeded 95% (Fig. 17). Spawning history was a statistically significant explanatory variable, although accounting for a very small proportion of the variance. The survival rate of eggs of consecutive repeat spawners was significantly lower than for 2SW maiden and alternate repeat spawners (Fig. 17).

Run timing

Temporal stock distinctiveness has also been highlighted as an important component of the Atlantic salmon resource (Saunders 1967). The run timing of Atlantic salmon to the Miramichi River has been previously characterized as bimodal, with the first mode occurring in the summer (prior to August 31) and the second in the fall (after August 31) (Fig. 18). Early runs and late runs have different composition in terms of small and large salmon proportions and sex ratios. The early runs in both branches are also exploited more heavily than the late runs.

Early and late runs of salmon to the Miramichi were obvious from DFO index trapnet catches in the early and mid-1990s but appears to have changed over time to a dominant summer mode (Douglas et al. 2015). These changes in run timing have been consistent for both large and small salmon and on both major branches of the Miramichi River (Fig. 19). The proportion of salmon captured at DFO index trapnets by August 31 has increased on the SW Miramichi River since 1994, attaining levels of 75-90% in recent years. A similar pattern was observed for salmon on the NW Miramichi River but the trend was less pronounced (Fig. 19). Decreases in the late run component have generally corresponded with increases in single-day peak catches in the early run portion (Douglas et al. 2015). The reduced late run of salmon to the Miramichi River is not believed to be related to fish abundance but rather to a shift in behavior where the fish enter the river during the summer and no longer stage in Miramichi Bay until autumn.

Movements of salmon at monitoring facilities in freshwater are characterized by a gradation of summer (prior to September 1) to fall (after August 31) movement dominance (Fig. 20). There was a dominant summer movement of salmon at the Northwest Miramichi and the Dungarvon River barriers; on average, 74% of the fish movements at the Northwest Miramichi barrier and 68% of fish movements at the Dungarvon River barrier occurred prior to September 1 (Fig. 20). The movement of fish was predominantly in the fall at the two mid-location facilities in the Southwest Miramichi; 82% fall movements at Clearwater Brook and 81% fall movements at Burnthill Brook (Fig. 20). Almost exclusively fall movements were recorded at Catamaran Brook, a small tributary in the lower portion of the Little Southwest Miramichi (Fig. 20).

There is a positive association between the proportion of the run which ascends to the counting facility early and the elevation of the facility, with fewer fish ascending the higher elevation sites in the fall.

Although early running salmon at the upstream facilities must correspond to early running salmon in the estuary, the fish which migrate to the upstream facilities in the fall are a mixture of early and late run salmon at the estuary. The fish tagged early in the estuary represent a higher proportion of all tag recoveries at the higher elevation sites and there is a strong linear positive association with elevation but not with distance of the facility (Fig. 21). Not all early tagged salmon ascend rapidly to the headwater sites. There was no statistically significant association between the proportion of the early tagged salmon which ascended to the facilities prior to September 1 and neither the elevation nor the distance of the facility from the head of tide (Fig. 21). However, there was a positive and significant association between the proportion of the tagged salmon recovered at the facilities which had been tagged from the early run in the tidal trapnets and the elevation of the facility, although not the distance of the facilities from the head of tide (Fig. 22). This suggests that salmon at the higher elevation areas of the Miramichi are mostly from the early run component; early and late run components return to intermediate and lower elevation sites.

An unpublished study by Dodson and Colombani (1997. The genetic identity of the Clearwater Brook population of Atlantic salmon (*Salmo salar*) ; a temporal and spatial study of Atlantic salmon population genetic structure in the Miramichi, St. John and Margaree, Atlantic Salmon Federation, Final Report) concluded that despite differences in the timing of runs, early and late-run fish mingle on the spawning grounds and that the timing of the spawning run is not genetically determined, but that development at sea and/or differences in marine migratory routes may determine run timing in these stocks of Atlantic salmon.

That being said, there is an important heritable component to run-timing. Salmon from Rocky Brook, a tributary of the Southwest Miramichi, are known to have an important proportion of fish which return to the Miramichi early and consequently have been extensively used to stock salmon in a number of rivers including the Margaree River (NS) and the Morell River (PEI) with the expressed objective of increasing early run returns to these rivers (Claytor et al. 1987; Cairns et al. 1996).

MARINE MIGRATIONS

Atlantic salmon from the Miramichi River undergo long oceanic migrations (Reddin 1985; Reddin and Lear 1990) and were historically harvested in a number of marine commercial fisheries including those of the Gulf of St. Lawrence, Newfoundland, Labrador, St. Pierre & Miquelon, and Greenland (see Saunders 1969; Kerswill 1971; Paloheimo and Elson 1974). Tags applied to smolts from the Miramichi River continue to be captured at West Greenland as non-maturing 1SW salmon in their second summer feeding at sea and recaptures of previously spawned adult salmon from the Miramichi River have also been consistently returned from the West Greenland fishery. Four Atlantic salmon tagged in their second winter at sea north of the Faroes Islands were recovered in southern Gulf of St. Lawrence rivers in the summer following tagging, three of these from the Miramichi River (Hansen and Jacobsen 2000).

The migrations of 1SW salmon at sea are less well known. They were captured as post-smolts (first year at sea) in a number of fisheries in eastern Canada (Ritter 1989) but are not available for capture (due to size, timing) in the Greenland fisheries.

GENETICS AND POPULATION STRUCTURING IN ATLANTIC SALMON FROM MIRAMICHI

Despite the long history of monitoring the Atlantic salmon population of the Miramichi, there is a paucity of information on their genetics and extent of local adaptation.

Møller (1970) indicated that based on transferrin polymorphisms, that there were genetically distinct populations of salmon between the Northwest Miramichi and the Southwest Miramichi systems and based on more homozygotes than expected in samples from the Miramichi River, he concluded that the samples were likely to have been mixtures of different populations. In a follow-up paper, Møller (2005) reported on differences in frequencies among samples collected during the smolt run and of adults returning to the Northwest Miramichi and concluded that these differences reflected population structuring within the river.

Riddell et al. (1981) reported on heritable quantitative genetic differences in body morphology of juvenile salmon from two tributaries of the Southwest Miramichi River, and suggested that these differences were adaptive and associated with differences in geomorphology of the streams.

Recently, salmon from the Miramichi River were sampled from four freshwater locations and two estuary points and genotyped at 15 microsatellite markers and 5568 loci using single nucleotide polymorphisms (SNPs) (Moore et al. 2014). The samples were collected from:

- Northwest Miramichi at barrier (headwaters)
- Little Southwest Miramichi seining samples (headwaters)
- Northwest Miramichi system sampled at tidal trapnet near head of tide
- Southwest Miramichi system sampled at tidal trapnet near head of tide
- Southwest Miramichi at Clearwater Brook (headwaters)
- Southwest Miramichi at Dungarvon Barrier (headwaters)

This work was part of a continent initiative to characterize the population structure of Atlantic salmon in eastern North America. Moore et al. (2014) confirmed the earlier work of Bradbury et al. (2014) that found 12 regional groups of salmon populations with the Miramichi River samples clustering with other populations of the southern Gulf of St. Lawrence (NB, NS, PEI) and the Saint John River system of NB into one group.

HATCHERY SUPPLEMENTATION

One of the earliest supplementation activities for Atlantic salmon in eastern Canada began in 1873 with the establishment of the Atlantic salmon hatchery on the Miramichi River at South Esk. The South Esk hatchery has been in continuous operation since 1873 stocking a variety of juvenile Atlantic salmon life stages annually into the Miramichi watershed (Table 4). Between 1959 and 1970 experimental plantings of Restigouche origin stock (Salmon Fishing Area 15) were distributed to the Southwest Miramichi, Northwest Miramichi, and Little Southwest Miramichi rivers as well as to Rocky Brook (upper tributary of the Southwest Miramichi River). Within the past 30 years, Miramichi origin stock were distributed in the Tabusintac and Buctouche rivers and Rocky Brook (Southwest Miramichi) stock was outplanted to rivers in Prince Edward Island as well as the Margaree River in Nova Scotia. All recent enhancement activities have involved targeted supplementation activities placing juvenile progeny back to tributaries from which the parents were collected.

The Miramichi River remains reliant on natural production with on average, 99% of returning adults coming from wild production (Chaput et al. 2001).

POPULATION DYNAMICS

The benefits to long-term stock abundance of supplementation activities must take into account the factors that regulate population abundances at different stages. Density dependent compensatory mortality in the freshwater phase is well established for Atlantic salmon (Elliott 2001; Jonsson et al. 1998; Gibson 2006). On the other hand, survival at sea is considered to be density independent (Hansen and Quinn 1998; Gibson 2006).

Cunjak and Therrien (1998) provided estimates of egg to 0+ parr and 0+parr to 1+ parr survival rates from Catamaran Brook, a small tributary of the Little Southwest Miramichi. Unadjusted for abundance of the preceding age group, egg to 0+ survival varied between 9% to 61% while survival rates from 0+ to 1+ parr ranged from 14% to 75%. The annual variations were explained in terms of both density dependence and environmental variability (density independent) effects. Interstage survival rates can therefore only be discussed relative to the abundance of the preceding age group. As there are multiple yearclasses of juveniles in the river at the same time, the density dependent mortality resulting from competition for limited resources (food, refuge) occurs within and among yearclasses.

POPULATION DYNAMICS IN FRESHWATER

Juvenile freshwater stages

Data and Methods

Since 1993, the number of sites sampled for juvenile abundance in the Miramichi has varied from a low of three sites in 1991 to a high of 77 sites in 1994 (Moore and Chaput 2007). Different numbers of sites were annually sampled in each river, and the number of sites was not proportional to river size.

Juvenile abundance at a site is expressed in terms of density (fish per 100 m^2), for fry, small parr, and large parr size groups. The method for converting single sweep catch per unit effort data to density is described by Chaput et al. (2005). Annual calibration data, or combinations of several years, were used to derive the regression relationships.

Biomass of Atlantic salmon juveniles is derived from the mean density at size and the mean weight at size for each site. Percent Habitat Saturation (PHS), proposed as a relative measure of habitat use and potential interaction between juveniles within the stream, was calculated for each site (Grant and Kramer 1990). It considers both the densities of fish and body lengths. A PHS value of 28 is used as a reference value; it represents the value at which density dependent effects have a 50% probability of being expressed (Grant and Kramer 1990).

Douglas et al. (2015) provided indices of abundance for the four main rivers of the Miramichi: the Northwest Miramichi and the Little Southwest Miramichi for the Northwest Miramichi system, the Southwest Miramichi and the Renous River for the Southwest Miramichi system. Spawning escapements are estimated for the Northwest Miramichi system and the Southwest Miramichi system since 1992. To derive an index of juvenile abundance for each system corresponding to the years with corresponding egg deposition estimates, the river specific mean juvenile indices from Douglas et al. (2015) were weighted by the respective habitat areas in each river (8.21 million m^2 for the Little Southwest Miramichi and 8.38 million m^2 for the Northwest Miramichi River; 5.83 million m^2 for the Renous River and 29.54 million m^2 for the Southwest Miramichi River). For the years 1992 to 2014, there were a total of 22 stock and recruitment observations for the Northwest Miramichi River and 21 for the Southwest Miramichi River.

Relationships between fry and small parr were examined over the longer time series of observations, from 1971 to 2014. Annual indices were calculated when there were at least four sites in a main river sampled. Over the period 1971 to 2014, there were 37 observations for the Northwest Miramichi system and 36 for the Southwest Miramichi system.

Two stock recruitment models were examined for the relationships between eggs and fry, and for fry to small parr. All data were expressed in units of abundance per 100 m² of habitat. A linear proportional model was used as the default model against which the compensatory Beverton-Holt model was compared.

The linear proportional model was of the form:

$$R_{t+1} = \alpha \, S_t \, e^{\varepsilon_t} \;\; with \; \varepsilon \sim N(0, \sigma^2) \tag{1}$$

with R_{t+1} the abundance of fry, or small parr,

S_t the abundance of eggs, or fry

α the mean survival rate, distributed a priori [0,1], and

e^{ε} the residual error with lognormal distribution.

The Beverton-Holt model was of the form:

$$R_{t+1} = \frac{\alpha \, S_t}{\left(1+\frac{\alpha}{Rmax} S_t\right)} \; e^{\varepsilon_t} \;\; with \; \varepsilon \sim N(0, \sigma^2) \tag{2}$$

with R_{t+1}, S_t, α, and e^{ε} as above and

Rmax the maximum abundance of the recruiting life stage (carrying capacity).

For the Beverton-Holt model, the mean egg deposition (eggs per 100 m²) that results in 50% of carrying capacity (half saturation) is calculated directly as Rmax/α. This value has been proposed as a potential limit reference point for conservation of fish populations (DFO 2015b).

The models were fitted in a Bayesian framework with uninformative priors for α, Rmax, and σ^2:

- α ~ Beta(1,1)
- Rmax ~ Uniform(0, 500)
- σ^2 ~ Inv-gamma(0.01, 0.01)

The parameters were estimated using Monte Carlo Markov Chain (MCMC) in Gibbs sampling with OpenBUGS (Lunn et al. 2013). Convergence was interpreted based on visualization of MCMC draw sequences and of quantile distributions of variance. Posterior distributions of the parameters were summarized from 10,000 MCMC draws after burn-in of 50,000 draws. Model fits were assessed using the DIC values in OpenBUGS, a synonymous index to AIC of model sufficiency.

The consequence of inter-yearclass competition on survival rates was examined by plotting the residuals of the abundances of the recruiting stages against the annual mean biomass of the juvenile size groups which potentially would have competed with the recruitment stage. For the fry recruitment stage, small and large parr present during the year of sampling at the fry stage would have competed for resources with fry; for the small parr recruitment stage, it would be fry and large parr of the same year that would have competed. Biomass (g per 100 m²) rather than numerical abundance of the competing life stages was used, as resource requirements for the life stages were assumed to be more closely related to mass than number of animals.

Results

Trends in egg depositions (eggs per 100 m²) and juvenile abundance by age/size groups (fry or age 0+ parr, small parr or age 1, large parr or age 2+) are shown in Figure 23. Over the period of assessment 1971 to 2014 for the Miramichi, the egg depositions were estimated to have exceeded the conservation egg deposition rate of 240 eggs per 100 m² in the mid-1970s and again from 1986 to 1997 (Fig. 23). Estimated egg depositions in both the Northwest and Southwest Miramichi systems were highest at the beginning of the assessment series in 1992 and declined and remained at lower levels into the 2000s. Egg depositions in the Southwest Miramichi exceeded the conservation requirement in most years and have been higher than in the Northwest Miramichi. Estimated egg depositions were high in both systems in 2011 (Fig. 23).

Juvenile densities over the longer time series from 1971 to 2014 showed relatively low levels until the late 1980s when indices of abundance increased, in response to increased egg depositions estimated for the Miramichi River overall (Douglas et al. 2015). Indices of fry abundance peaked in the late 1990s and have generally declined since, with the exception of the indices of abundance noted in 2012 following on the high egg depositions of 2011 (Fig. 23). The trends in abundance indices of small parr follow those of fry, with abundances peaking in the late 1990s to early 2000s and declining since (Fig. 23). Only the Northwest Miramichi River and the Renous River were sampled at a sufficient number of sites (> 4 per river) in 2013 but at least in the Northwest Miramichi, the small parr abundance index was high, following on the high fry index of the previous year (Fig. 23). Trends in large parr abundance indices differ somewhat from trends of fry and small parr; large parr indices have generally been increasing over the period 1971 to 2014 in both the Northwest and Southwest systems with large parr abundances being higher in the Northwest versus the Southwest (Fig. 23).

Trends in indices of standing stock biomass of salmon mirror the trends in abundances at age; biomass values have been highest in the late 1990s and 2000s, declining recently from peak values of over 400 g of salmon biomass per 100 m² in both systems (Fig. 24). Percent habitat saturation also increased from low values in the 1970s and 1980s to high mean values that exceeded the reference value of 28 in the late 1990s and 2000s, but has declined in recent years (Fig. 24).

Of interest in the context of the supplementation question is how much additional juvenile production, and ultimately adult returns can be expected from increasing egg depositions. Abundance indices, as number of fish per size group, standing stock biomass of all salmon, and percent habitat saturation were at maximum values in the late 1990s and have declined in recent years. The indices remain above the lower values estimated in the 1970s and 1980s.

The associations between the estimated egg deposition rates (total eggs divided by total freshwater rearing area) and indices of fry abundance, small parr abundance lagged to the year of egg deposition are shown in Figure 25. The maximum mean fry density in any of the four rivers over the time series has been 143 fry per 100 m² in the Southwest Miramichi River in 1999 (Fig. 25). The maximum mean annual value for the Northwest or Southwest system, or the Miramichi River has been 134 fry per 100 m².

The estimated egg depositions for the Miramichi during the 1970s are not consistent with juvenile indices with mean fry indices being substantially too low compared to contemporary values since 1992 (Figs. 23, 25). This suggests that the egg depositions for that time period were overestimated.

The fry to small parr associations and the small parr to large parr associations show cohort consistency through the time series (Fig. 25).

Egg to fry dynamic

The subsequent stock and recruitment dynamic was modelled using the Northwest and Southwest system time series which extends from the 1998 to 2013 egg deposition years. The estimated egg deposition data from 1992 to 2013 and corresponding fry abundance indices from 1993 to 2014 suggest a strong compensatory relationship (Figs. 26, 27). There was stronger statistical support for the Beverton-Holt (BH) SR relationship than the linear proportional relationship for the Southwest Miramichi system (Fig. 26) and the Northwest Miramichi system (Fig. 27) and the individual main rivers in each of the systems (Figs. 26, 27). The median value of α, the slope at the origin, of the BH relationship is about 0.69 for the Southwest Miramichi and 0.93 for the Northwest Miramichi. This indicates that egg to fry survival is very high at very low egg densities however the values should be interpreted with caution:

- The α parameter was constrained in the model to be between 0 and 1 which is biologically realistic however the posterior distribution of α is highly uncertain (95% Bayesian Credibility Interval 0.39 – 0.98 for the Southwest system, 0.70-1.00 for the Northwest system).
- The total egg deposition is divided by total rearing area but the fry indices are derived from sampling at a limited number of sites which are not randomly or proportionally distributed among habitat types, tributaries, and stream orders of the rivers (Moore and Chaput 2007). As such, the fry indices from these selected sites are likely higher than the average density of fry over all habitats in the river. As a result the α parameter would be biased upward.
- There is no accounting of the uncertainties in either the egg deposition estimates nor of the indices of fry. If these uncertainties were included, the average relationships would be different and the parameter estimates even more uncertain.

The maximum carrying capacities of fry, as derived using the monitored sites in the river, are greater than 158 fry per 100 m^2 (95% BCI 114-409 fry per 100 m^2) for the Southwest Miramichi system and 105 fry per 100 m^2 (95% BCI 84 – 144 fry per 100 m^2) for the Northwest Miramichi system (Figs. 26, 27). Within each of the systems, the Southwest Miramichi River (exclusive of the Renous River) has a carrying capacity for fry of 173 fish per 100 m^2 and the Northwest Miramichi River is at 148 fry per 100 m^2 (Figs. 26, 27), values higher in each case than the system values because of the lower abundances of fry sampled from the Renous River in the Southwest system and in the Little Southwest in the Northwest system (Fig. 23).

The same caveats regarding the interpretation of the carrying capacity values as absolute levels discussed for the α parameter apply here as well.

In terms of fits, there is a pattern of temporal blocking of the residuals in the Southwest Miramichi data, with positive residuals for approximately the first half of the analysed time series (1993 to 2001 year classes) followed by negative residuals in the second half (Fig. 26). The consequence of inter yearclass competition on the residuals was not consistent with the hypothesis of fry survival being reduced when there is a high abundance of parr; the opposite dynamic was suggested in the Southwest with the abundance of fry higher in years when parr biomass was also high (Fig. 26).

In contrast, there was no pattern of temporal blocking of residuals for the Northwest Miramichi data series. There was no evident effect of biomass of parr size groups on predicted fry abundance (Fig. 27).

The predicted egg density that results in 50% of carrying capacity (half saturation) is estimated to be 221 eggs per 100 m^2 (median; 95% BCI 122 – 1,033 eggs per 100 m^2) for the Southwest Miramichi system. For the Northwest Miramichi system, the egg density for half saturation is estimated at 113 eggs per 100 m^2 (95% BCI 87 – 191 eggs per 100 m^2). For the Northwest

Miramichi River (excluding the Little Southwest Miramichi), the half saturation value is 159 eggs per 100 m² (95% BCI 118-278 eggs per 100 m²).

Fry to small parr dynamic

The fry to small parr dynamics did not suggest a strong compensatory relationship; the abundance of small parr is a linearly proportional function of fry the previous year in the Southwest Miramichi but there is a weak compensatory relationship for the Northwest Miramichi (Fig. 28). The proportionality parameter for the Southwest Miramichi was estimated at 0.29 (95% BCI 0.25 – 0.37) and a very high carrying capacity (median = 227 small parr per 100 m²; 95% BCI 60-483). For the Northwest Miramichi, the proportionality value was estimated at 0.81 (95% BCI 0.56-0.99) and a carrying capacity value of 51 small parr per 100 m² (95% BCI 35 – 148) (Fig. 28). There is no pattern of temporal blocking of residuals for either river system and the biomass of competing yearclasses (estimated as the average of the biomass of combined small parr and large parr in the fry year and the combined biomass of fry and large parr in the small parr year) was not associated with variations in small parr abundance corrected for fry abundance (Fig. 28).

Smolt production

The contemporary estimates of annual smolt abundance from the Northwest Miramichi and the Southwest Miramichi are highly variable and generally low relative to values expected from rivers in this area (Elson 1975; Symons 1979). Smolt abundance estimates from the Northwest Miramichi system varied from 1.0 to 4.6 smolts per 100 m² of total riverine habitat with more than half the estimates being less than 2 smolts per 100 m² (Table 2). Estimated abundances of migrating smolts from the Little Southwest Miramichi have consistently been less than 1.6 smolts per 100 m² (Table 2). Smolt production from the Southwest Miramichi system has generally been much higher than the Northwest Miramichi, ranging from 1.0 to 6.1 smolts per 100 m², with annual estimates greater than 2.5 smolts per 100 m² since 2004 (Table 2).

Compared to the parr abundances at the monitored sites, that ranged from greater than 30 per 100 m² small parr and large parr combined, it seems that there is a low smoltification rate (product of survival rate and smolt emigration probability) for juveniles in both branches of the Miramichi.

MARINE RETURN RATES

Smolt return rates

Estimated return rates of Northwest Miramichi system smolts to maiden spawners (sum of 1SW and 2SW returns from a smolt class) were estimated to be as low as 0.6% to as high of 7.6% for the smolt migration years 1999 to 2006 and 2011 (Table 2). Estimated return rates for the Southwest Miramichi system were also variable, ranging from 1.7% to 11.9%, the high values for each branch being estimated from returns of the 2001 smolt class (Table 2).

These return rate values are in the range of values estimated from monitored multi-sea-winter salmon populations of the Maritime provinces and Quebec (ICES 2015).

Repeat spawner return rates

The Atlantic salmon population of the Miramichi River is characterized by an expanding spawning history structure (Table 3). Between 1971 and 1986, there were few repeat spawners in the river with at most two previous spawning migrations. Since 1992 and 1995, adult salmon on their sixth and seventh spawning migrations, respectively, have been sampled in the catches at the estuary trapnets and repeat spawning salmon have comprised 6% to 21% of the total returns of all age groups (Chaput and Jones 2006). Post-spawned salmon (kelt) over-winter in the Miramichi River and return to the ocean early in the spring, immediately following ice-out of the river. The area occupied at sea by consecutive spawners from the Miramichi River during reconditioning is not known, though it is likely limited to the Gulf of St. Lawrence given the timing of their return back to the Miramichi. Alternate spawners from the Miramichi River undertake long oceanic migrations, as far as West Greenland, as evidenced from recaptures in marine fisheries.

The proportion of maiden salmon in the total returns to the Miramichi has declined from over 95% prior to 1986 to about 85% since 1996 while the relative abundance of salmon on a second spawning migration has increased from less than 5% of total returns prior to 1995 to over 10% in most years since (Fig. 29). Repeat spawners have become most important in the large salmon category as these fish grow when they return to the sea post-spawning (Fig. 29).

Estimated return rates to a second spawning of both 1SW and 2SW salmon increased between1972 and 2010 (Chaput and Benoît 2012). Since the late 1990s, return rates to a second spawning have ranged from 8% to 25% for 1SW salmon, and 10% to 40% for 2SW salmon. Increased return rates to consecutive spawning have contributed the most to the increased return rates for both the 1SW and 2SW maiden life histories (Fig. 30). A higher proportion of the returns to a second spawning were of the alternate spawning history in both 1SW and 2SW salmon prior to the 1990s but since then, the proportions of the second consecutive spawning returns have exceeded those of the alternate spawning history in both 1SW and 2SW salmon (Fig. 30). Chaput and Benoît (2012) reported on a positive association between the variations in the return rates of repeat spawners and the variations in a small fish biomass index from the southern Gulf of St. Lawrence, an area which could be used by kelts early in the reconditioning year at sea, which provides evidence that abundant food supplies at sea may be beneficial for the survival of Atlantic salmon to a second consecutive spawning. This contrasted with the absence of an association between prey availability and return rates of alternate repeat spawners, suggesting that return rates of the alternate strategy are conditioned by high seas factors.

CONCLUSIONS

The Atlantic salmon population from the Miramichi is characterized by complex phenotypic diversity that is moderately variable over the medium term (about two generations or 10 years). Juveniles rear in freshwater for two to five years, with most migrating to sea after two and three years of freshwater residency and return to rivers as 1SW maiden and 2SW maiden salmon. In any given year, there are six year classes of immature fish in the combined freshwater and marine ecosystem (four years in river including eggs, two years at sea). Chaput and Jones (2006) estimated that for the Miramichi River, the number of year classes present in the annual spawning migration has increased from four to five in the 1970s to as many as nine year classes in the returns of the 1990s. This large number of immature age groups and the increased number of contributing year classes provides population resilience to stochastic and demographic perturbations.

Although there is a paucity of empirical evidence to inform on sub-basin population structuring in the Miramichi, a number of phenotype characteristics are consistent with such structure. Salmon in headwater areas of the river at higher elevations are predominantly fish which returned to tidal waters prior to September 1 and the proportions of late run salmon increase in lower elevation areas in the river. There is an important sex ratio bias between the maiden sea age groups with males being more abundant in the 1SW salmon than in 2SW salmon. This is consistent with life history theory: fitness of males can be optimized at smaller body sizes (i.e. precocious male parr, small salmon) whereas reproductive fitness of female salmon is enhanced by increased body size which is associated with increased egg size, increased egg number per female, and more diverse spawning habitat resulting in increased survival of offspring (Fleming 1996).

Although presently subjected to seemingly lower return rates from sea for maiden age groups, the contemporary return rates of maiden salmon estimated for the Miramichi are in the same range of return rates for other stocks in the Maritime provinces and Quebec. Empirical evidence from monitored stocks indicates that sea survival of maiden salmon was substantially higher historically than at present and that it is low marine survival that is constraining abundance of Atlantic salmon throughout the North Atlantic (ICES 2015).

Increased return rates to a second spawning, particularly for the consecutive life history component, is interpreted to be a response to improved feeding opportunities in the southern Gulf of St. Lawrence, an example of phenotypic plasticity in this population in response to changes in the ecosystem.

Separate branch estimates of returning adult salmon were initiated in 1992. Although the methods used to estimate the returns of 1992 to 1997 warrant revisiting, the model used to estimate the returns for the period 1998 to 2014 has been peer reviewed and is considered to provide accurate estimates of branch specific returns.

For the Miramichi River and its branches, the question remains whether freshwater productivity is at a level expected from a “normal” multi-sea-winter Atlantic salmon population of the Maritime provinces. Indices of juvenile abundance, dating more than four decades, obtained using consistent procedures and using models to estimate site specific abundances, indicate that freshwater production of Atlantic salmon increased to peak values in the late 1990s and early 2000s. Although abundance indices of fry and small parr have declined somewhat since, the abundance indices are at levels well above those of the 1970s to mid-1980s. Increased abundances of large parr over the four decades of monitoring points to changes in the freshwater dynamics which may be contributing to increased density dependent regulation in freshwater (through increased competition for resources) and reduced smolt production. Smolt production from the Northwest Miramichi was at low to medium rates (less than three smolts per 100 m^2) despite the high indices of abundance of small parr (potential contributors of 2-year old smolts) and large parr (potential contributors of 3-year old and older smolts).

Preliminary stock and recruitment analyses presented here indicate that the most important density dependent control occurs between the egg and fry stage with modelled theoretical carrying capacity of fry almost realized in the late 1990s. Fry densities, although highly variable annually, remain at moderate levels in all rivers despite the decline in egg depositions to values below the conservation requirement (management reference point synonymous with a limit reference point) in the past decade.

If the egg to fry recruitment dynamic is as severely compensatory as suggested by these analyses, there may be very little gain to be realized in smolt production and subsequent adult returns by supplementing the spawning escapement with large numbers of captive-reared adult spawners. Density dependent factors will rapidly adjust the abundances of juveniles to levels which can be sustained by the productive capacity of the freshwater habitat, carrying capacity constraints which are inferred to be at play in the Miramichi at the present time.

Due to the strong density dependent survival that is realized in freshwater, the addition of a large number of captive-reared adult progeny to the river will result in increased density-dependent mortality of natural/wild progeny. While an immediate increase in the number of juveniles may appear to be beneficial overall, any reduced fitness of the captive-reared progeny with phenotypic differences (body size, growth rates, maturation rates) will result in reduced abundance of wild Atlantic salmon (DFO 2016; Fraser 2016).

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TABLES

Table 1. Physical and environmental characteristics of the Miramichi River and the two main branches, the Southwest Miramichi and the Northwest Miramichi (Figure 1).

Characteristics	Miramichi	Southwest Miramichi	Northwest Miramichi
Latitude (range)		46º10' to 47º20'	
General direction of flow		west to east into Gulf of St. Lawrence	
Max. elevation		470 m	
Longest distance from the sea		250 km	
Number of days with ice cover		December to April; 100 to 170 days (1961 – 2002)	
Mean air temperature		-11ºC in January; +19ºC in July	
River order	7	7	6
Basin area (million ha)	1.36	0.77	0.39
Wetted rearing area (ha) for salmon production by stream order			
Stream Order			
1	15	6	8
2	222	125	97
3	666	338	314
4	1,493	885	507
5	1,250	617	633
6	1,478	1,358	120
7	336	336	0
Total	5,461	3,666	1,679

Table 2. Summary of smolt migration characteristics from monitoring programs in the Northwest Miramichi system, the Little Southwest Miramichi River, and the Southwest Miramichi system, 1998 to 2011. Values in grey shading are uncertain and considered to be underestimates.

River	Smolt year	Run size estimate: Median	Run size estimate: 95% confidence interval		Smolts per 100 m²: Median	Smolts per 100 m²: 95% C.I.	Size (mean): mm	Size (mean): g	Prop. female	Prop. at freshwater age: 2	Prop. at freshwater age: 3	Prop. at freshwater age: 4	Run timing: Peak	Run timing: 5th perc.	Return rates at maiden age: 1SW	Return rates at maiden age: 2SW	Return rates at maiden age: Combined
Northwest	1998	na	na	na	na	na	129	21.8	0.49	0.28	0.71	0.01	16-May	15-May	na	na	na
Miramichi	1999	390,500	315,500	506,000	2.3	1.9 - 3.0	132	22.4	0.63	0.36	0.62	0.02	19-May	15-May	3.1%	1.3%	4.3%
	2000	162,000	118,000	256,000	1.0	0.7 - 1.5	131	21.2	0.58	0.34	0.63	0.03	02-Jun	18-May	5.2%	0.5%	5.7%
	2001	220,000	169,000	310,000	1.3	1.0 - 1.8	130	21.1	0.53	0.38	0.60	0.01	29-May	21-May	6.8%	0.8%	7.6%
	2002	241,000	198,000	306,000	1.4	1.2 - 1.8	128	20.7	0.57	0.52	0.48	0.00	02-Jun	24-May	2.5%	0.8%	3.3%
	2003	286,000	224,500	388,000	1.7	1.3 - 2.3	128	21.2	0.53	0.50	0.49	0.01	28-May	24-May	4.2%	1.0%	5.1%
	2004	368,000	290,000	496,000	2.2	1.7 - 3.0	131	22.1	0.57	0.41	0.58	0.01	19-May	16-May	2.6%	0.5%	3.1%
	2005	*151,200*	*86,000*	*216,000*	0.9	na	130	21.4	0.52	0.40	0.60	0.01	08-Jun	19-May	na	na	na
	2006	*435,000*	*255,000*	*1,230,000*	2.6	na	130	23.3	0.56	0.44	0.56	0.01	16-May	13-May	na	na	na
	2011	768,000	576,000	1,137,000	4.6	3.4 - 6.8	133	18.1	0.42	0.61	0.38	0.00	21-May	21-May	0.3%	0.2%	0.6%
Little	2005	*46,330*	*32,710*	*68,050*	na	na	130	na	0.58	0.22	0.76	0.02	14-May	13-May	na	na	na
Southwest	2006	87,520	41,760	665,300	1.0	0.5 - 7.6	130	na	0.51	0.51	0.49	0.00	18-May	10-May	na	na	na
Miramichi	2007	138,200	106,000	185,500	1.6	1.2 - 2.1	125	na	0.57	0.34	0.66	0.00	22-May	12-May	na	na	na
	2008	124,100	96,320	164,900	1.4	1.1 - 1.9	130	21.6	0.50	0.38	0.61	0.01	21-May	16-May	na	na	na
	2009	85,000	66,000	112,000	1.0	0.8 - 1.3	129	na	0.52	0.38	0.62	0.00	18-May	13-May	na	na	na
	2010	46,500	28,500	82,500	0.5	0.3 - 0.9	140	na	na	0.35	0.64	0.01	12-May	07-May	na	na	na
	2011	67,900	49,900	104,500	0.7	na	131	22.8	0.47	0.44	0.56	0.00	26-May	21-May	na	na	na
Southwest	2001	306,300	290,000	464,000	1.0	0.8 - 1.3	127	19.2	0.47	0.64	0.35	0.00	31-May	22-May	8.6%	3.3%	11.9%
Miramichi	2002	711,400	498,000	798,000	1.7	1.4 - 2.3	126	18.8	0.54	0.55	0.44	0.01	01-Jun	19-May	3.1%	1.4%	4.5%
	2003	485,000	393,000	615,000	1.3	1.1 - 1.7	128	19.6	0.58	0.59	0.41	0.00	22-May	22-May	6.8%	2.0%	8.8%
	2004	1,167,000	969,000	1,470,000	3.2	2.6 - 3.5	130	21.1	0.54	0.60	0.40	0.00	17-May	16-May	1.8%	0.8%	2.5%
	2006	1,332,000	983,000	1,809,000	3.8	2.8 - 5.1	131	23.1	0.55	0.54	0.46	0.00	17-May	09-May	1.5%	0.5%	2.0%
	2007	1,344,000	1,120,000	1,668,000	3.8	3.2 - 4.7	132	20.7	0.49	0.59	0.41	0.00	27-May	21-May	1.6%	0.8%	2.4%
	2008	901,500	698,000	1,262,000	2.5	2.0 - 3.6	126	19.7	0.60	0.67	0.33	0.00	28-May	22-May	1.0%	0.7%	1.7%
	2009	1,035,000	807,000	1,441,000	2.9	2.3 - 4.1	128	22.1	0.53	0.69	0.31	0.00	18-May	15-May	3.3%	2.2%	5.5%
	2010	2,165,000	1,745,000	2,725,000	6.1	4.9 - 7.7	137	23.9	0.51	0.57	0.43	0.00	21-May	07-May	1.5%	0.4%	1.8%

Table 3. Number of samples by spawning histories of Atlantic salmon aged from the Southwest Miramichi system and the Northwest Miramichi system, 1992 to 2013. Spawning histories are interpreted as: XSW is the maiden sea winter age at first spawning, the sequence of C (consecutive) and A (alternate) represent the at sea reconditioning history for each successive spawning event. The maximum total sea age of salmon interpreted to date is nine years (2SWAAAC, 2SWACCCCC).

Spawning History	Southwest Miramichi	Northwest Miramichi
1SW	17,792	9,791
1SWA	631	331
1SWAA	26	16
1SWAAA	2	2
1SWAAAC	1	na
1SWAAC	6	6
1SWAACC	2	na
1SWAC	66	46
1SWACA	1	na
1SWACC	22	24
1SWACCC	11	2
1SWACCCC	1	na
1SWACCCCC	na	1
1SWC	869	393
1SWCA	10	na
1SWCAC	1	na
1SWCC	151	63
1SWCCA	1	na
1SWCCC	38	10
1SWCCCC	8	4
1SWCCCCC	3	1
1SWCCCCCC	3	na
2SW	9,043	4,479
2SWA	705	366
2SWAA	89	48
2SWAAA	8	4
2SWAAAC	1	na
2SWAAC	18	7
2SWAACC	3	na
2SWAACCC	1	na
2SWAC	314	139
2SWACA	3	na
2SWACC	121	63
2SWACCC	23	10
2SWACCCC	5	1
2SWACCCCC	1	na
2SWC	910	431
2SWCA	12	5
2SWCAC	7	1
2SWCACC	1	na
2SWCC	334	145
2SWCCA	1	1
2SWCCC	174	69
2SWCCCC	65	25
2SWCCCCA	na	1
2SWCCCCC	17	7
2SWCCCCCC	3	1
3SW	14	7
3SWA	1	2
3SWAC	na	1
3SWC	4	1
3SWCC	1	1

Table 4. Enhancement activities conducted in the Miramichi River, 1978 to 2008 (Chaput et al. 2010). Stage of stocking is represented by: UF = unfed fry, FF = feeding fry, FG = fall fingerlings, P = 1+ parr, Sm = smolts.

River	Longitude (degree decimal W)	Latitude (degree decimal N)	Origin of fish stocked	Life stages of fish stocked	Range in annual numbers of fish stocked	Range of years when stocking occurred
Northwest Miramichi	-65.8333	46.9500	NW Miramichi	F, FG, P, Sm	13,000 - 133,000	1978 - 2007
Little Southwest Miramichi	-65.8333	46.9500	LSW Miramichi	F, FG, Sm	800 - 106,400	1978 - 2008
Renous and Tributaries	-65.7833	46.8167	SW Mir., Dungarvon	F, FG, P, Sm	2,200 - 118,000	1987 - 2007
Southwest Miramichi	-65.5833	46.9667	Tributary specific	F, FG, P, Sm	9,000 - 469,400	1978 - 2008

FIGURES

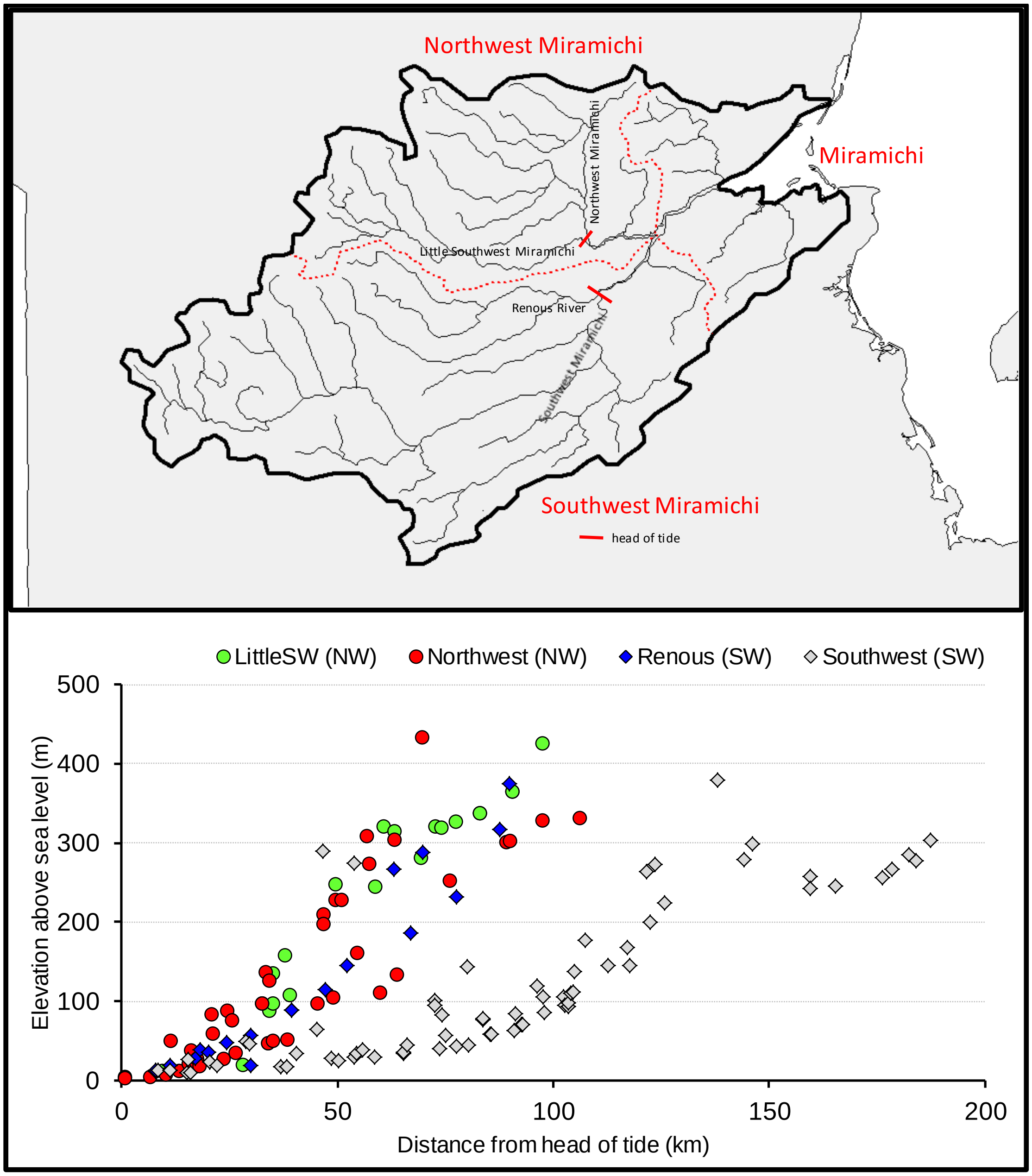


Figure 1. The Miramichi River drainage area and location of main rivers within the Miramichi referred to in text (upper panel) and approximate relief profile (elevation in m above sea level versus distance in km from the head of tide) of the four main rivers based on locations of electrofishing sites within the river (lower panel).

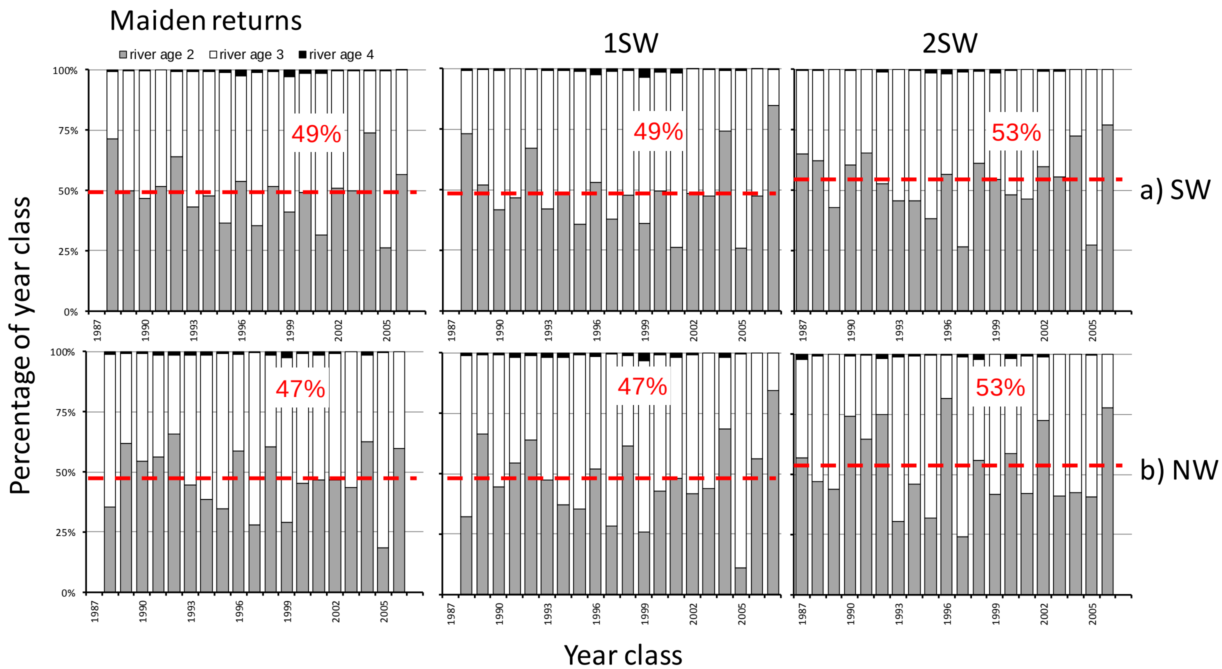


Figure 2. Percent at river age (2, 3, 4 years) by year class for the sum of maiden returns (1SW, 2SW) (left panel), for 1SW maiden (middle panels), and 2SW maiden (right panels) for the Southwest Miramichi River (a; top row) and the Northwest Miramichi River (b; lower row). The values in each cell are the average percentage by year class which were river age 2. The year class values are derived based on scale sampling of adult salmon returning to the estuary trapnets in each branch weighted by the returns of salmon to each branch (median value) for 1998 to 2013. Year class refers to the year of spawning (fall) and is calculated as the year of return minus maiden sea age (1 or 2), minus river age (2, 3, 4) minus one.

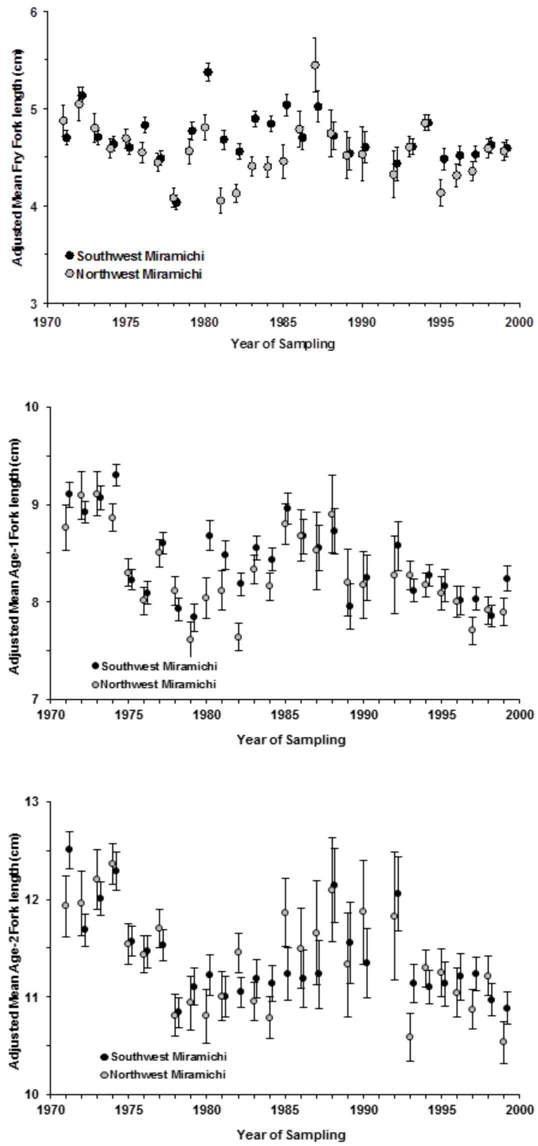


Figure 3. Annual adjusted mean fork length of fry (top), age-1 parr (middle), and age-2 parr (lower) from the Northwest Miramichi and Southwest Miramichi rivers, 1971 to 1999 (Swansburg et al. 2002). Mean fork lengths (cm +/- 1 standard error) were adjusted for date of sampling, density of the age group, tributary, and year separately for each branch. Data from 1991 are omitted because an inadequate number of sites were sampled.

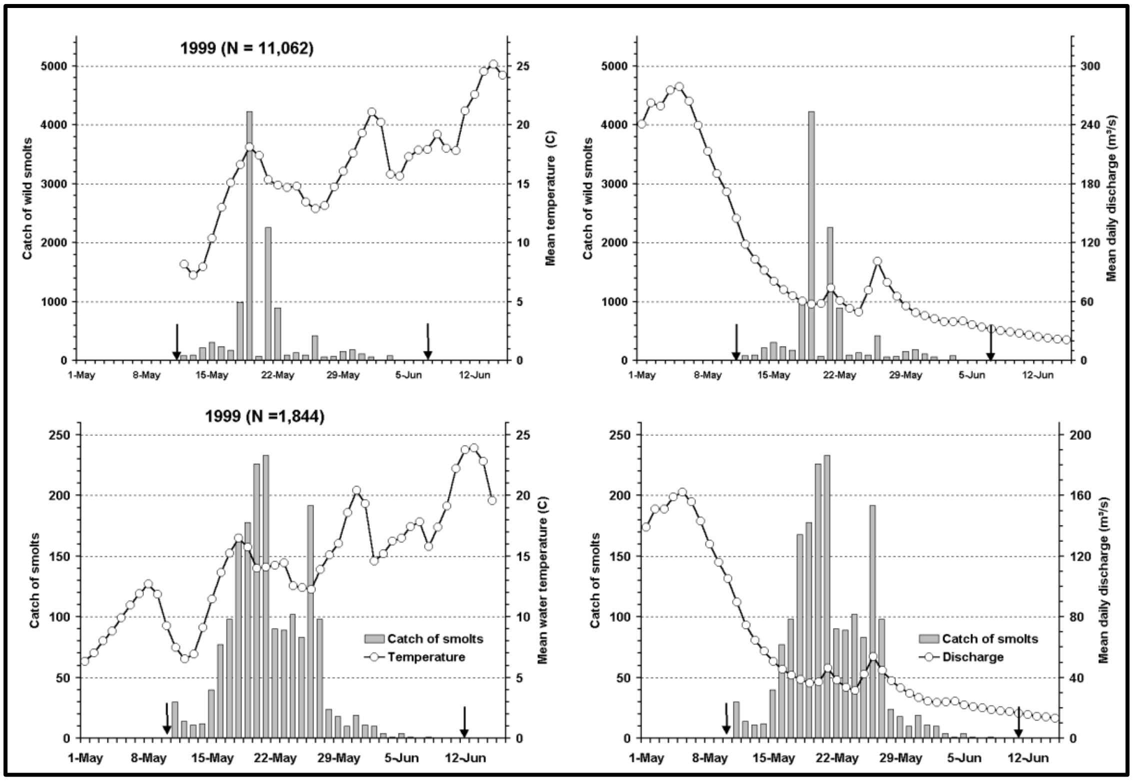


Figure 4a. Timing of catches of wild smolts in 1999 from the estuary tidal trapnet of the Northwest Miramichi system (top row) and at the rotary screw trap in the Little Southwest Miramichi (near Catamaran Brook, about 29 km above the head of tide; bottom row) relative to the mean daily water temperature (left column) and mean daily discharge (right column) (from Chaput et al. 2002). Arrows represent the total smolt migration period.

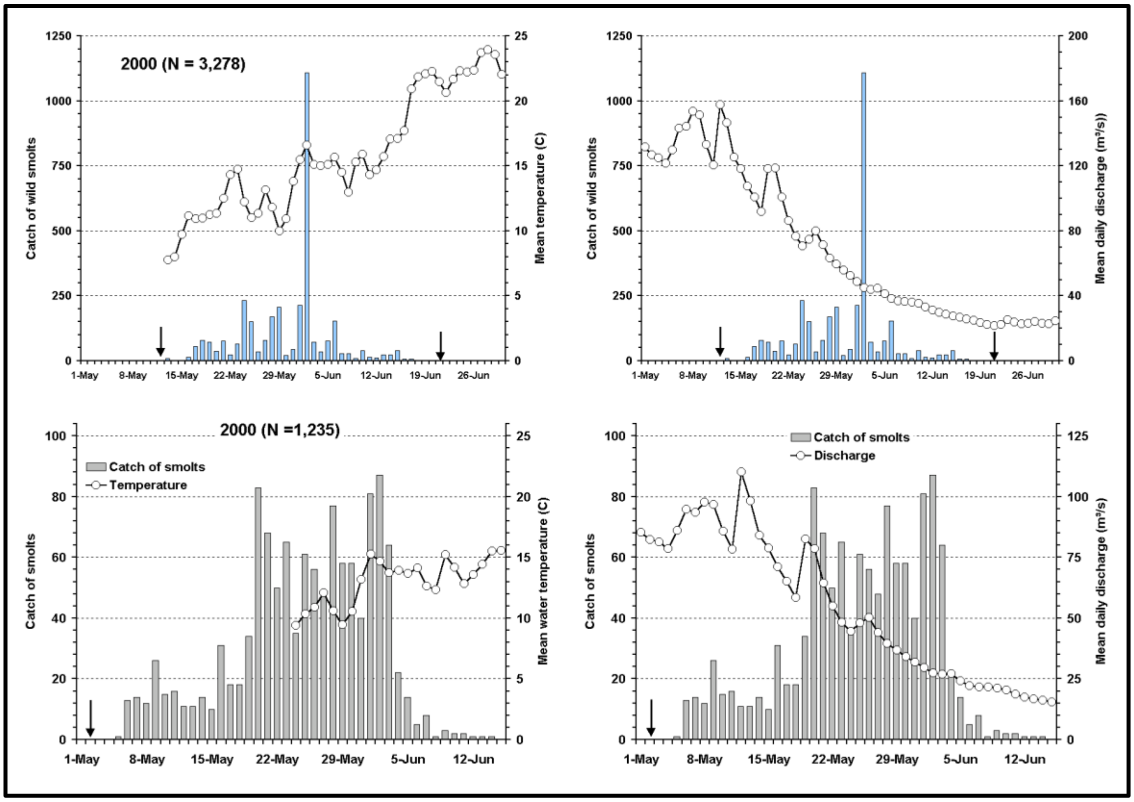


Figure 4b. Timing of catches of wild smolts in 2000 from the estuary tidal trapnet of the Northwest Miramichi system (top row) and at the rotary screw trap in the Little Southwest Miramichi (near Catamaran Brook, about 29 km above the head of tide; bottom row) relative to mean daily water temperature (left column) and mean daily discharge (right column) (from Chaput et al. 2002). Arrows represent the total smolt migration period.

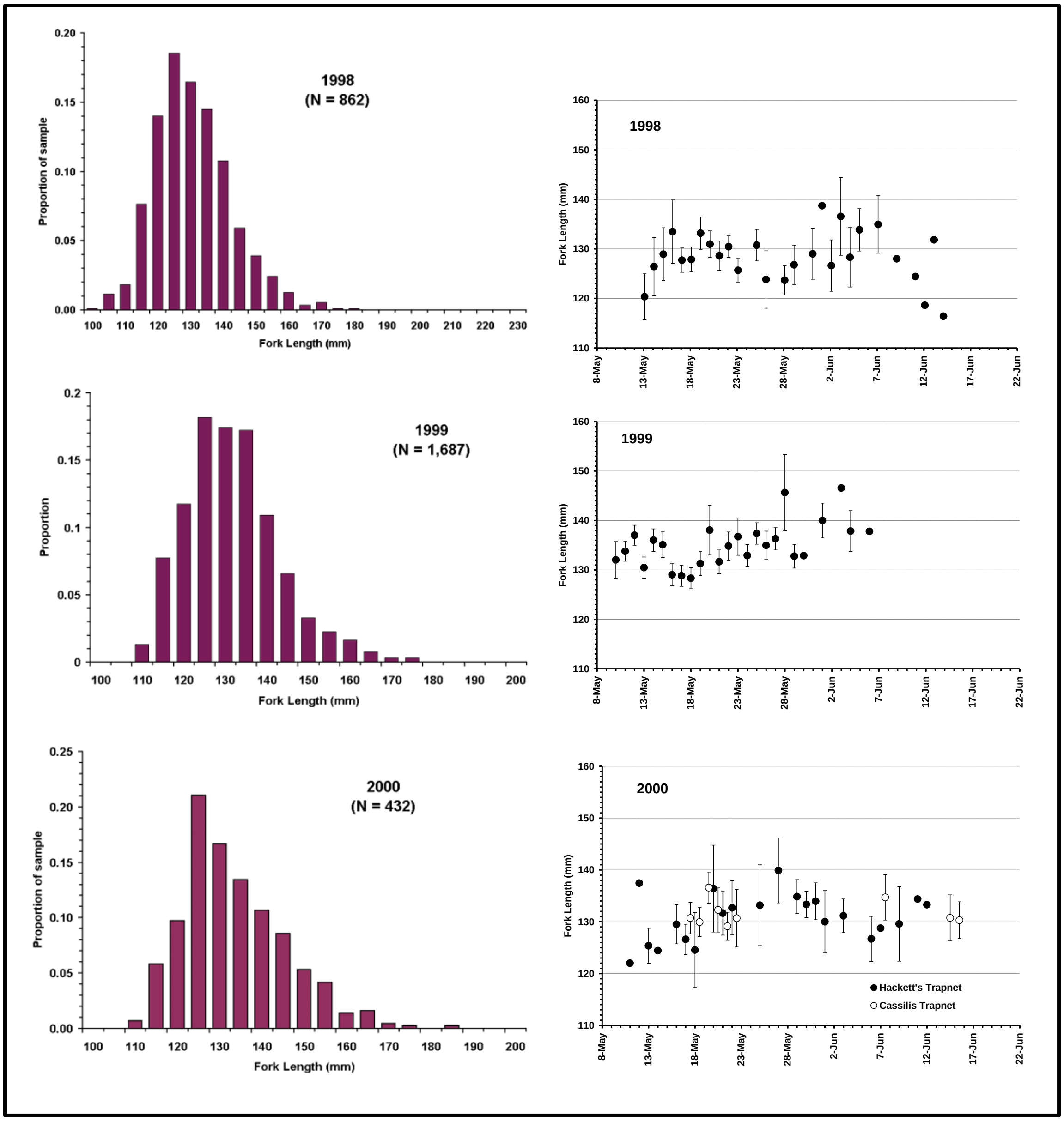


Figure 5. Fork length (mm) distribution of wild smolts (daily samples weighted by daily total catch) (left panel) and mean size (with 2 standard error bars) by date within year from the Northwest Miramichi from 1998 to 2000 (from Chaput et al. 2002).

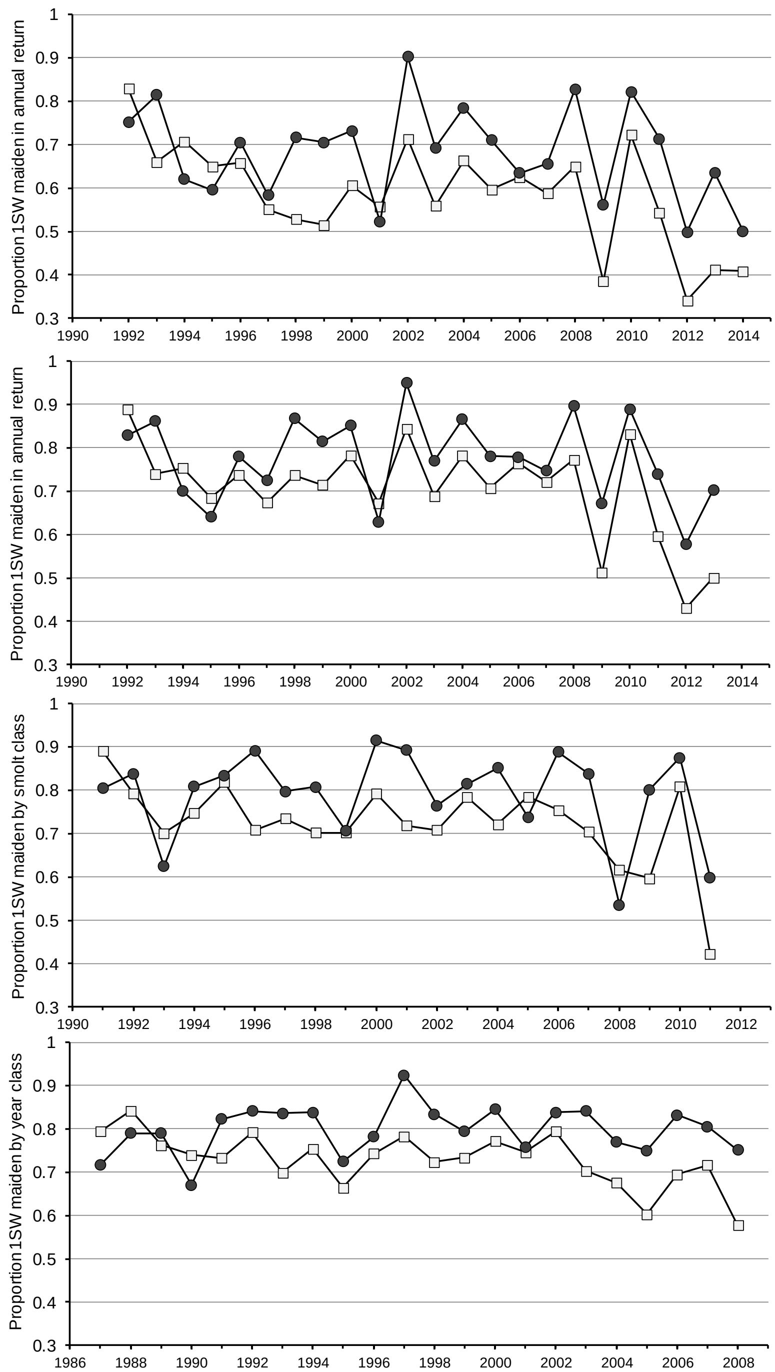


Figure 6. Proportion small salmon in the annual return of all salmon (upper panel), proportion 1SW maiden in the annual return of maiden sea age salmon (second row), proportion 1SW maiden in the returns of maiden sea age salmon by smolt class (year of smolt migration, third row), and proportion 1SW maiden of total maiden return by yearclass (bottom panel), for the Northwest Miramichi (black symbols) and the Southwest Miramichi (open square symbols) systems (Douglas et al. 2015; DFO 2015a).

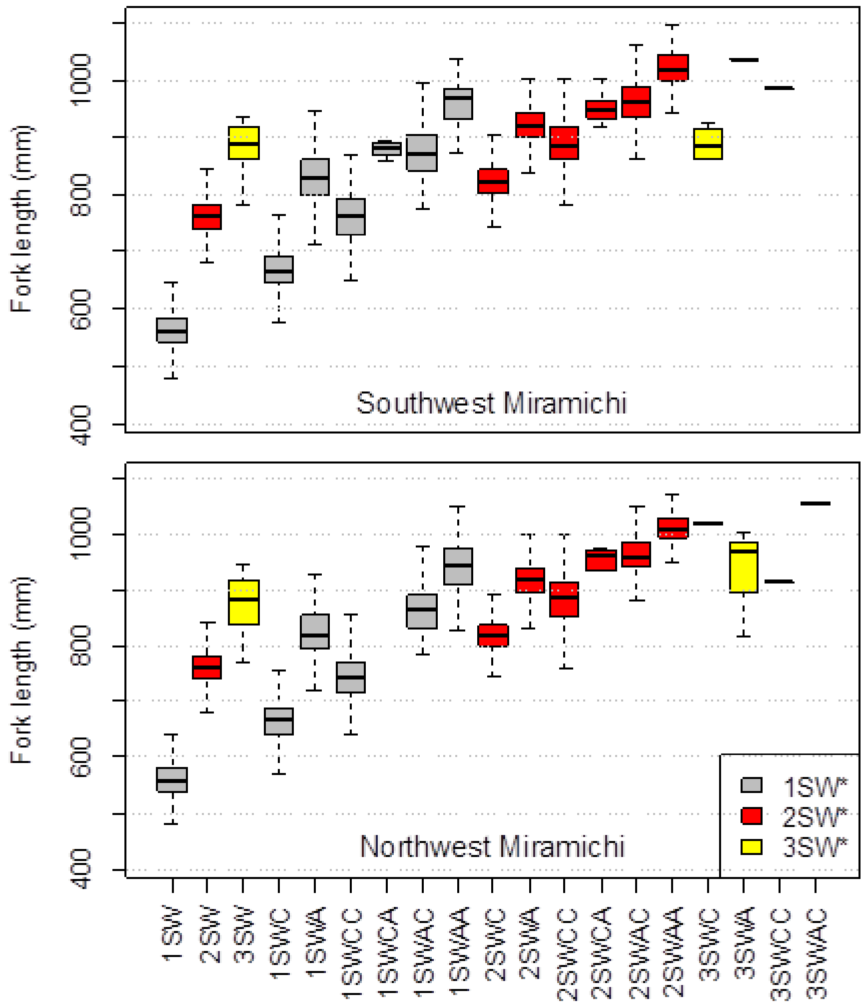


Figure 7. Boxplots of fork length (mm) distributions of wild Atlantic salmon from the Southwest Miramichi system (top panel) and the Northwest Miramichi system (bottom panel) by spawning history type from 1992 to 2013. The 1SW, 2SW and 3SW labels are maiden first time spawners. The other categories are repeat spawners according to sea age at first spawning followed by a sequence of repeat spawner types, with C representing consecutive spawning life history and A representing alternate spawning life history. Single letters (C, A) are categories of fish on a second spawning. CC, CA, AC, and AA represent categories of fish with three or more spawning events with the first two repeat spawning histories indicated by the letter codes.

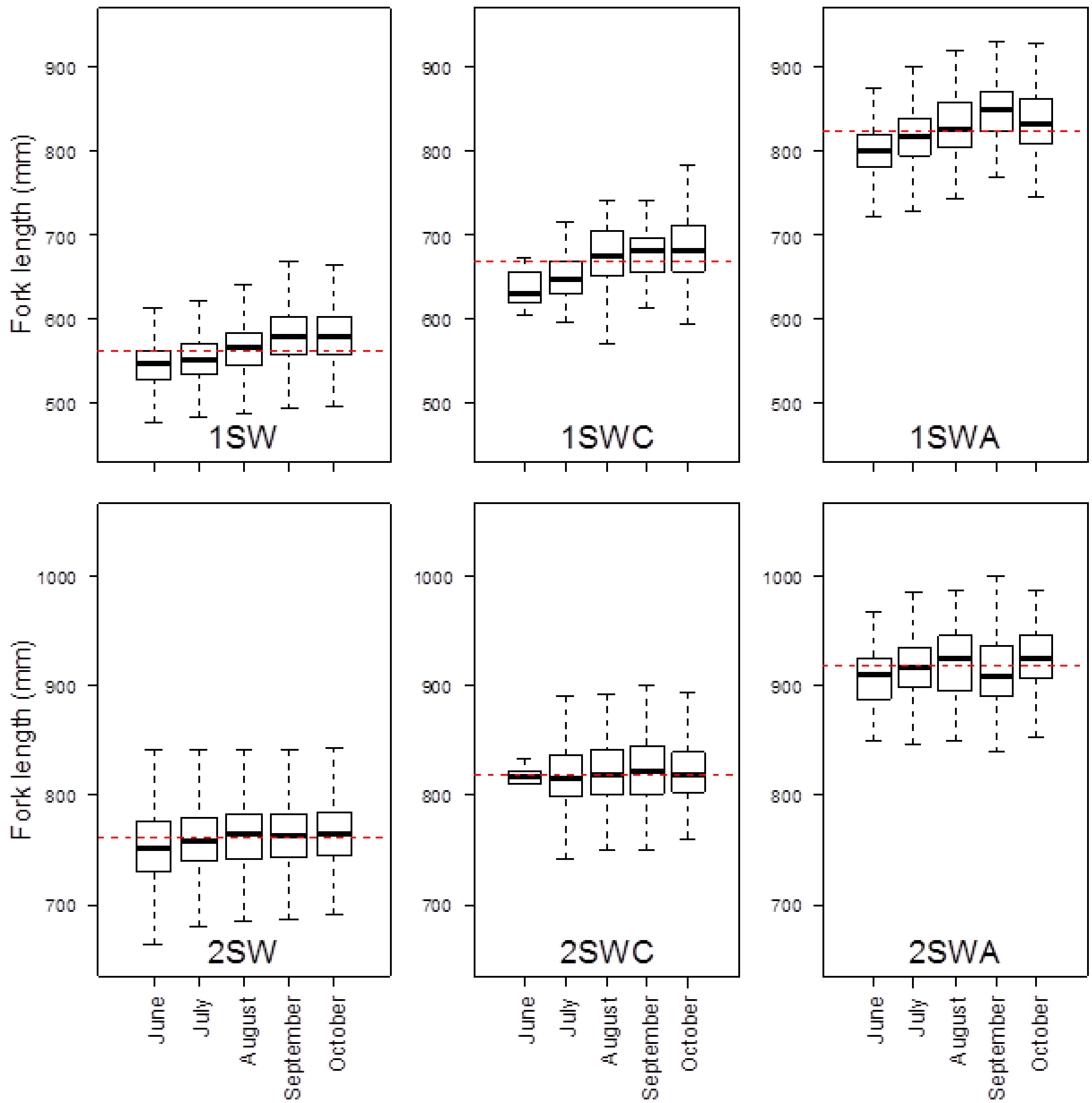


Figure 8. Fork length (mm) distributions by month (June to October) of 1SW (top row) and 2SW (bottom row) life histories as maiden return (left column), consecutive first time repeat spawners (middle column) and alternate first time repeat spawners (right column) based on catches at tidal trapnets in the Northwest Miramichi, 1992 to 2013. The horizontal dashed line in each plot is the mean over all years for the corresponding age group.

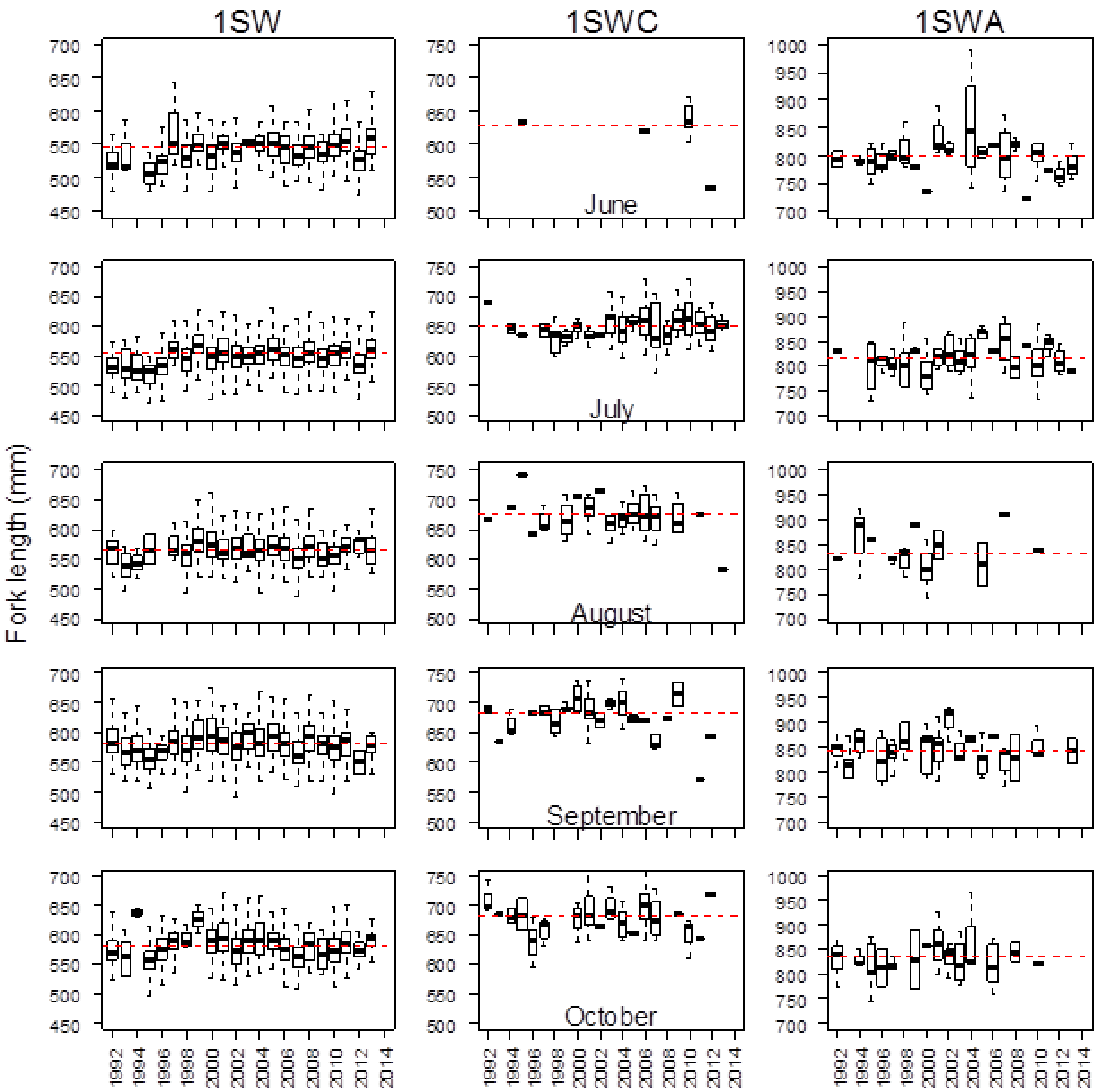


Figure 9. Fork length (mm) distributions by month (June to October) of 1SW maiden (left column), 1SW consecutive first time repeat spawner (middle column) and 1SW alternate first time repeat spawner (right column) based on catches at tidal trapnets in the Northwest Miramichi, 1992 to 2013. Horizontal dashed line in each plot is the mean over all years for the corresponding age group and month.

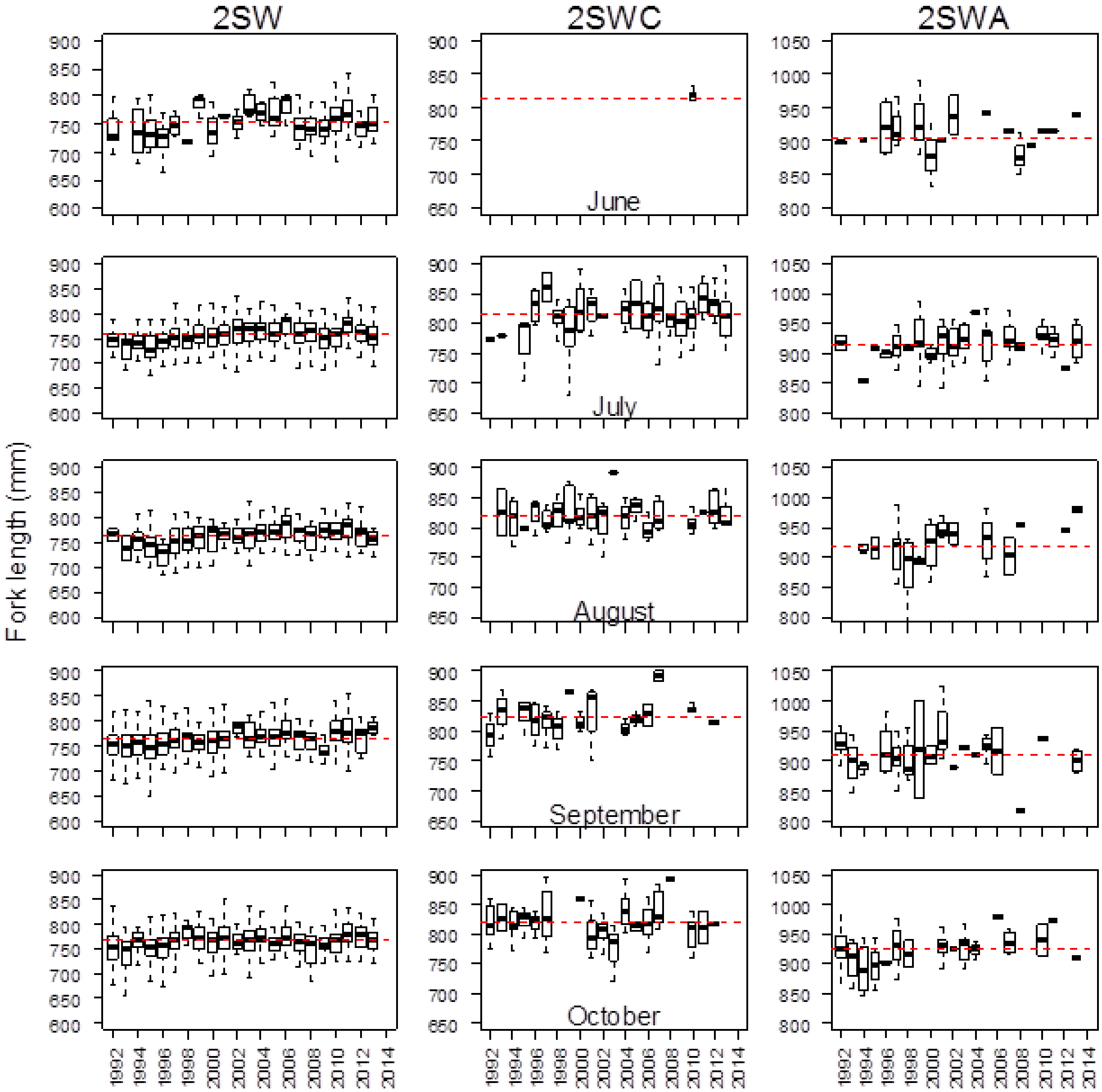


Figure 10. Fork length (mm) distributions by month (June to October) of 2SW maiden (left column), 2SW consecutive first time repeat spawner (middle column) and 2SW alternate first time repeat spawner (right column) based on catches at tidal trapnets in the Northwest Miramichi, 1992 to 2013. Horizontal dashed line in each plot is the mean over all years for the corresponding age group and month.

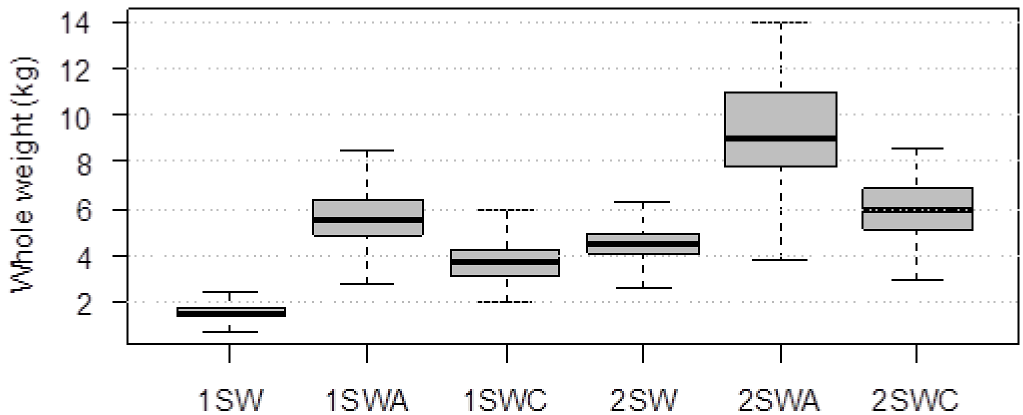


Figure 11. Whole weight (kg) of Atlantic salmon from the Miramichi River by spawning history type. Spawning history types are limited to maiden sea ages (1SW, 2SW), first time consecutive repeat spawners (1SWC, 2SWC), and first time alternate repeat spawners (1SWA, 2SWA), over all years (1971 to 2013) and months.

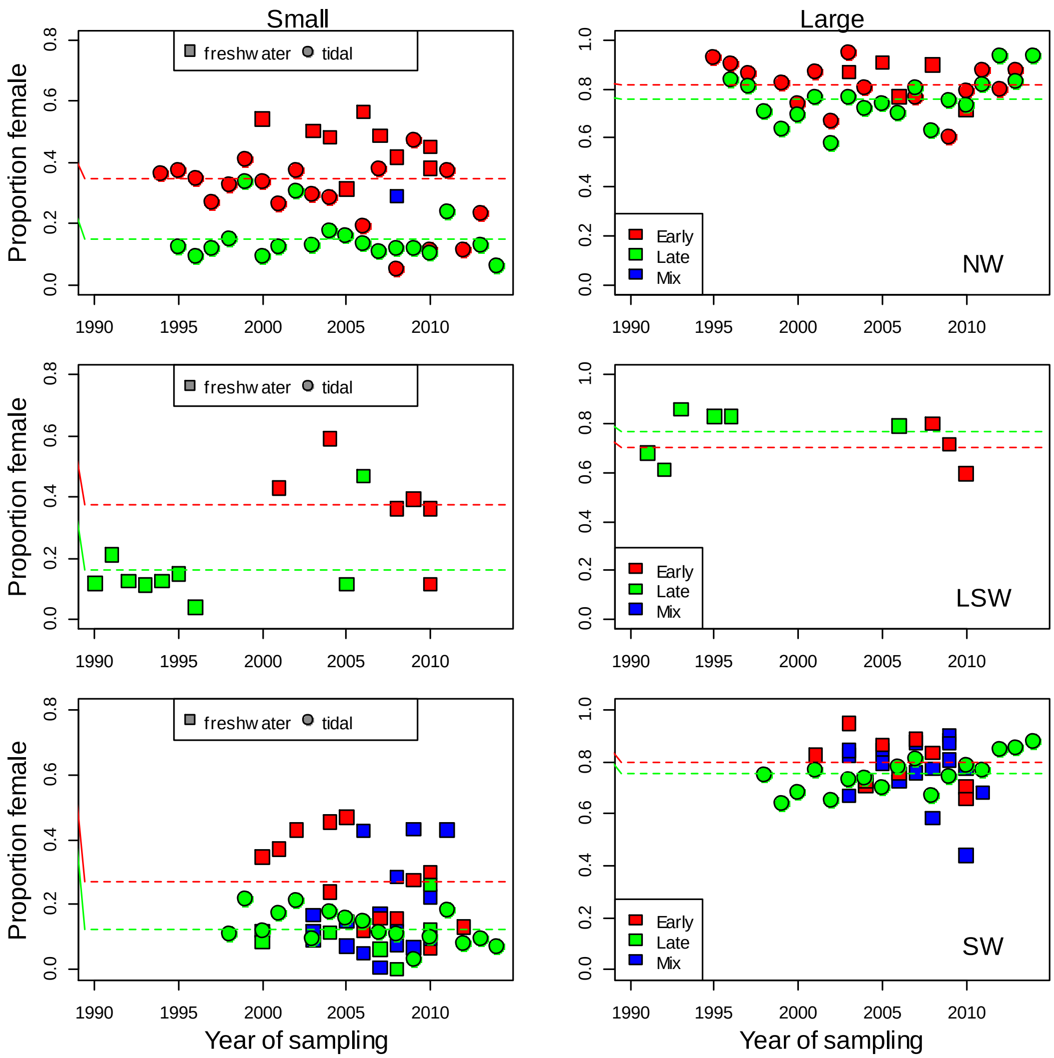


Figure 12. Proportion of females in small salmon (left column) and large salmon (right column) by season of return group (early, late, mixed) from samples in the Northwest Miramichi system (top row), the Little Southwest Miramichi River (middle row), and the Southwest Miramichi system (bottom row). Only samples for which sex was determined for 30 or more fish are shown. Square symbols represent samples obtained at freshwater locations (counting fences, seining) whereas circles are samples from estuary trapnets. Horizontal dashed lines and corresponding colours are the means of the samples in each panel. The early run trapnet samples from the Northwest are from the FSC trapnet catches of June and July. The late run trapnet samples from the Northwest are from the Cassilis trapnet for the months of September and October whereas for the Southwest Miramichi the samples are from the Millerton trapnet. Early run freshwater samples are from the Northwest Barrier for the Northwest Miramichi or from the Dungarvon Barrier and Rocky Brook for the Southwest Miramichi. Samples from the Little Southwest are either from the Catamaran Brook counting fence for the late run or broodstock sampling at Moose Landing and Smiths Forks considered to be from the early run component. Mixed run timing samples from the Northwest are from the Sevogle River. Mixed run timing samples from the Southwest Miramichi include Clearwater, Burnthill, Juniper, and Big Hole samples.

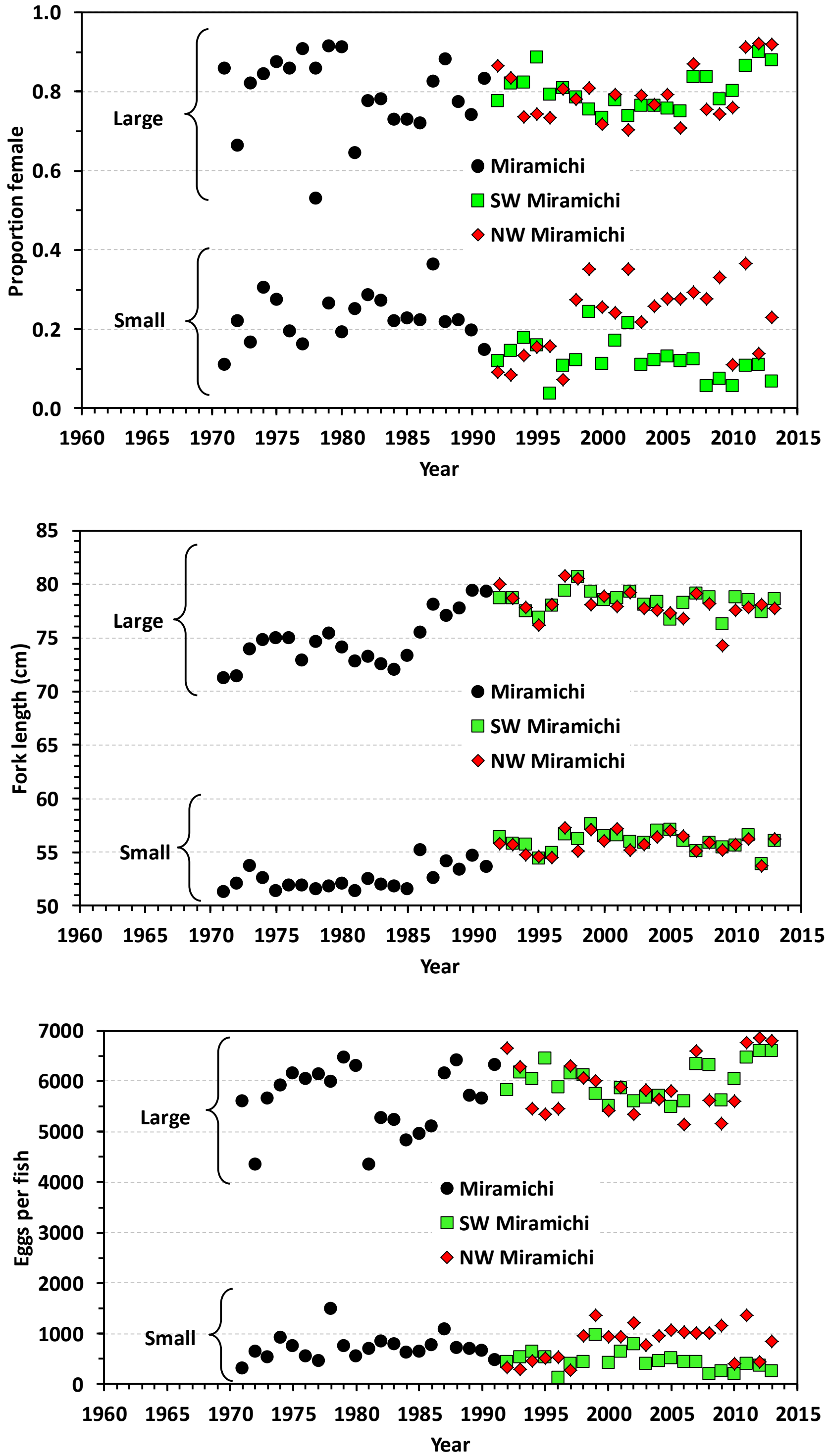


Figure 13. Plots of proportion of females (upper panel), mean length (cm, middle panel), and eggs per fish (lower panel) of wild Atlantic salmon by size group (small salmon, large salmon) from the Miramichi River overall (1971 to 1991) and in the Northwest Miramichi and the Southwest Miramichi branches, 1992 to 2013 (Douglas et al. 2015).

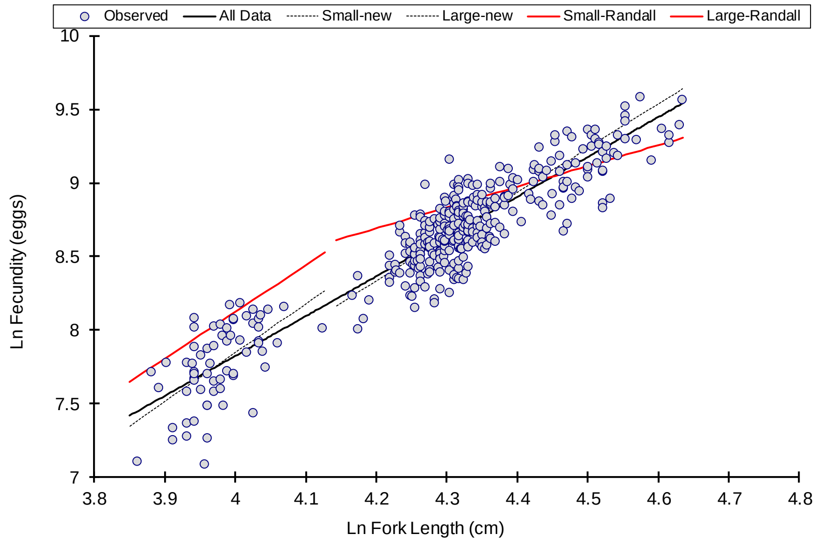


Figure 14. Length (cm) to fecundity relationships for Atlantic salmon from the Miramichi River. The data are from egg estimations in the hatchery collected during 1991 to 1995 (J. Hayward, DFO, unpublished data). The eggs per fish were estimated by volume displacement. The red lines are the relationships from Randall (1989) based on immature eggs from salmon sampled on entry to the river. The Randall (1989) relationships by size group are the ones used to estimate eggs in estimated returns and spawners to the Miramichi River. The parameters of the natural log of the regression of fecundity on length are: slope = 2.7075, intercept = -3.0065.

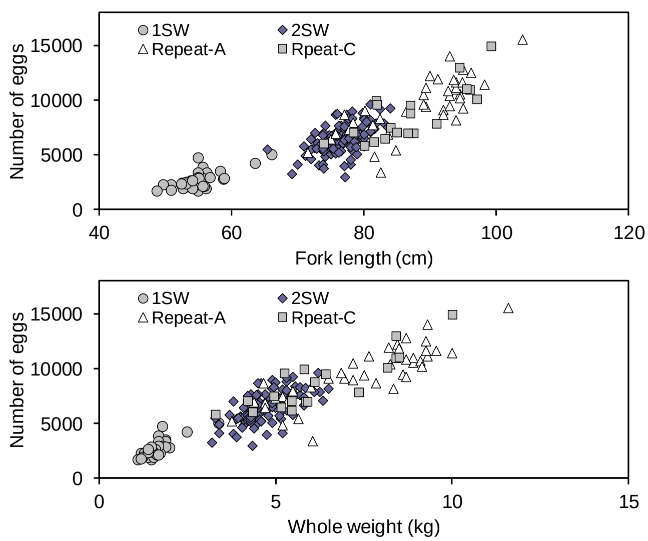


Figure 15. Fecundity (number of eggs) at fork length (cm) (top panel), and at whole weight (kg) (bottom panel) for Atlantic salmon from the Miramichi River. Data and analyses are from Reid and Chaput (2012). The parameters of the natural log of the regression of fecundity on length are very similar to those from J. Hayward (DFO, unpublished data) (slope = 2.7005, intercept = -2.9768).

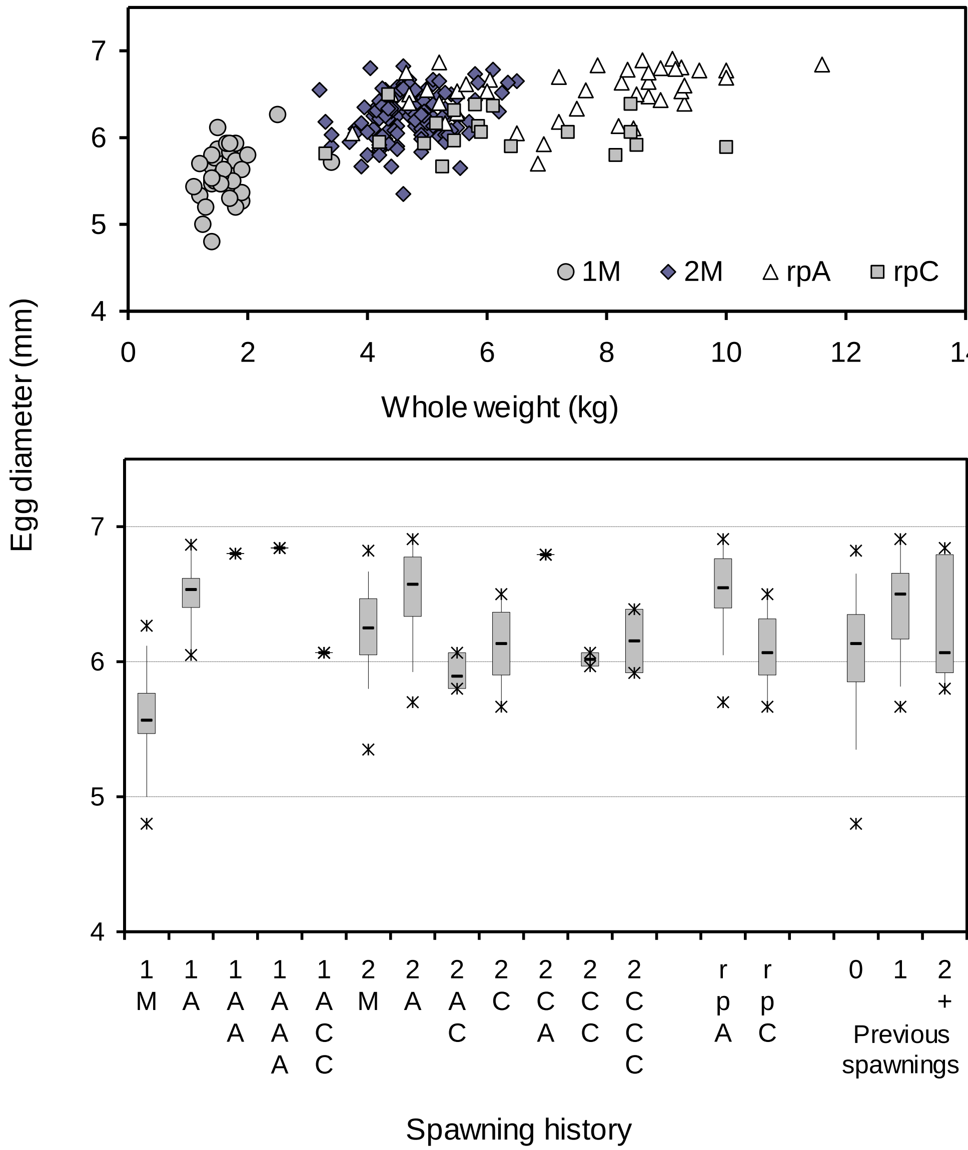


Figure 16. Estimated diameter (mm) of Atlantic salmon eggs from the Miramichi River relative to the spawning history of the female salmon (Reid and Chaput 2012). Maiden spawners are 1M and 2M. The number in each spawning history group refers to the maiden sea age. First time repeat consecutive spawners are 1C and 2C whereas first time repeat alternate spawners are 1A and 2A and so on. rpA represents all salmon that returned to second spawning as alternate, regardless of maiden sea age or the number of spawning events. Similarly, rpC represents all salmon that returned to a second spawning as consecutive regardless of maiden sea age or number of spawning events.

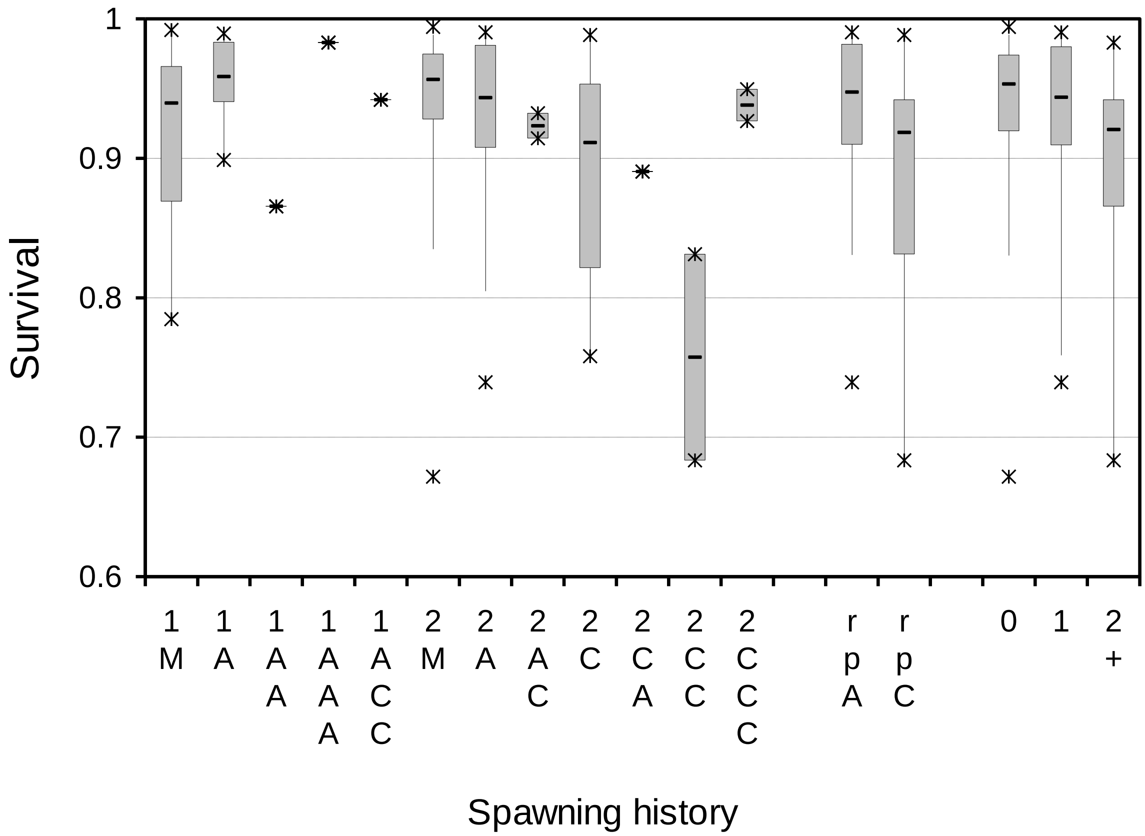
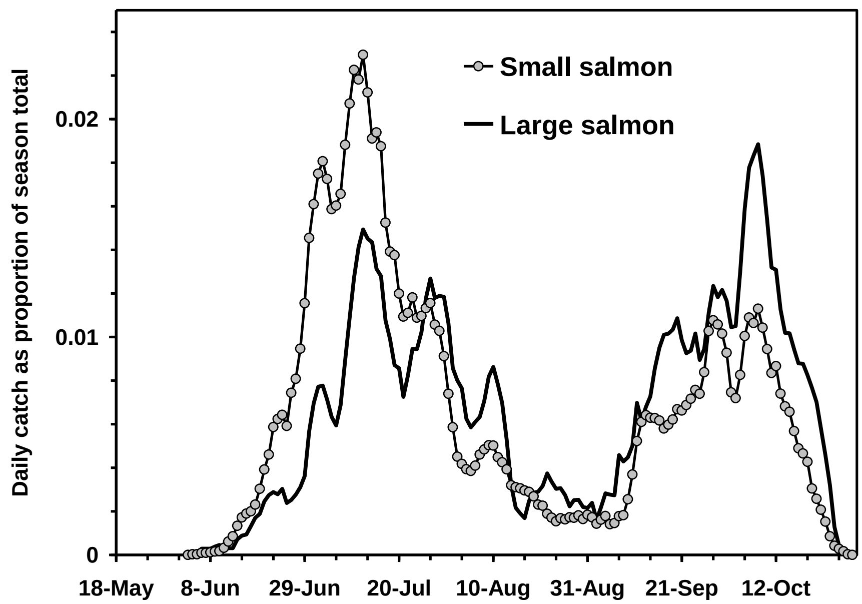


Figure 17. Estimated survival (proportion) to placement in incubation boxes in the hatchery of Atlantic salmon eggs from the Miramichi River relative to the spawning history of the female salmon (from Reid and Chaput 2012). Spawning history refers to those in Figure 15.



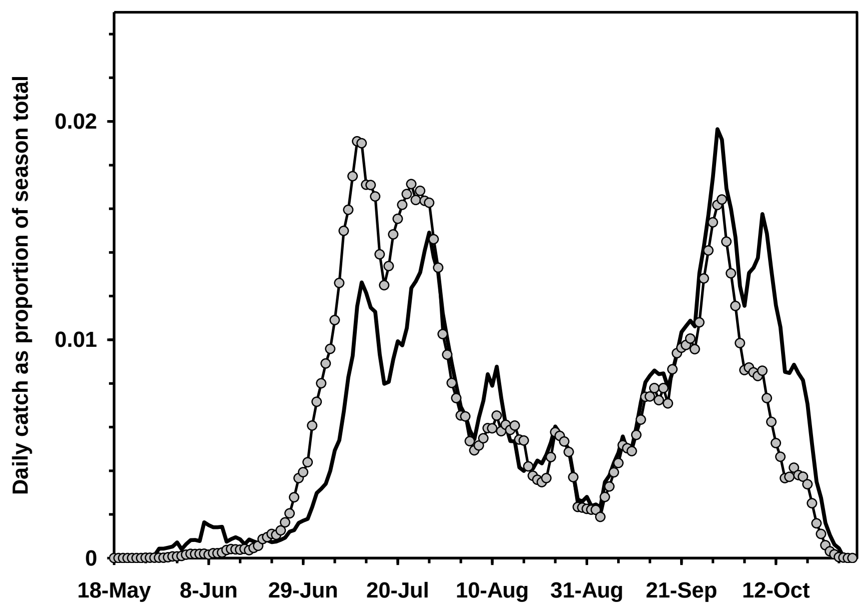


Figure 18. Timing of catches at estuarine trapnets in the Northwest Miramichi (upper) and the Southwest Miramichi (lower). Plots are mean proportions of the total annual catch for the years 1998 to 2004 (from Chaput et al. 2010).

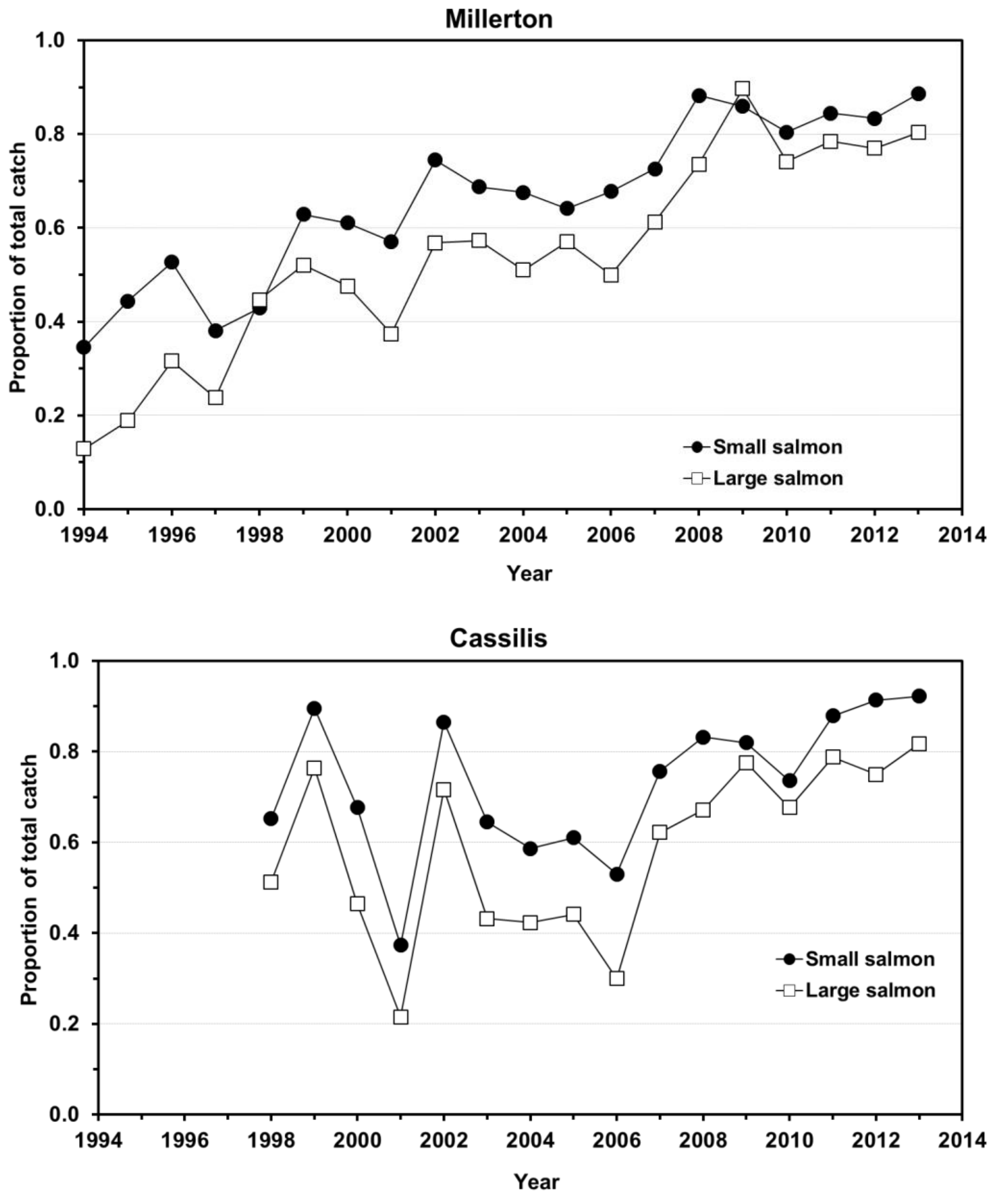


Figure 19. Proportion of annual catches of large salmon and small salmon which were captured by August 31 at DFO Index trapnets at Millerton on the Southwest Miramichi River (upper panel) and at Cassilis on the Northwest Miramichi River (lower panel) for 1998 to 2013. (from Douglas et al. 2015).

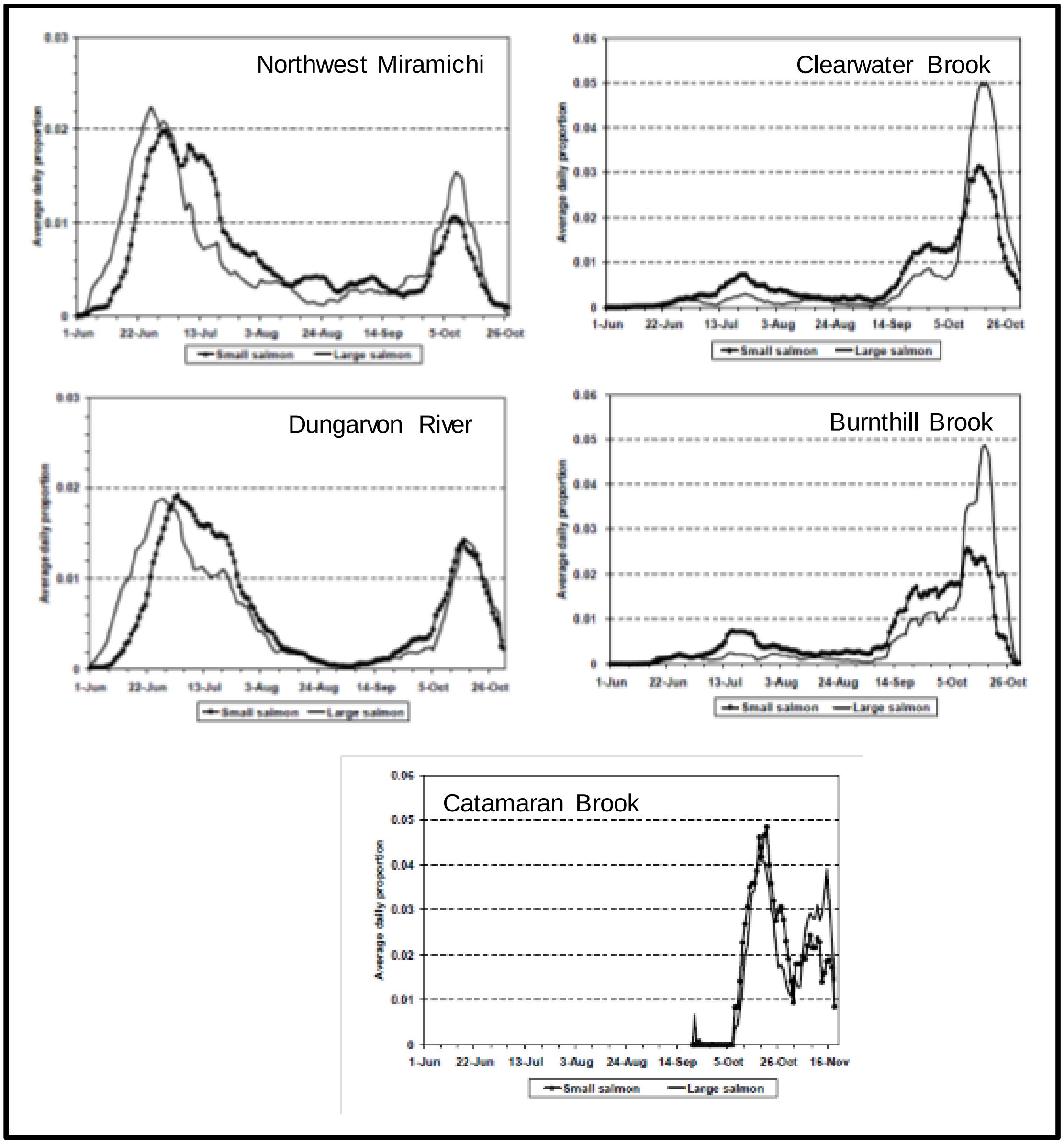


Figure 20. Run-timing of small salmon and large salmon at the Northwest Miramichi barrier (left upper panel), the Dungarvon River barrier (Southwest Miramichi; left lower panel), the Clearwater Brook counting fence (Southwest Miramichi; right upper panel) and the Burnthill Brook counting fence (Southwest Miramichi; right lower panel), and the Catamaran Brook counting fence (Little Southwest Miramichi; bottom row) (from El-Jabi et al. 2004). Daily proportions are the average of 1995-2003 for Northwest Miramichi, of 1995-2002 for Dungarvon River, of 1999-2003 for Clearwater Brook, of 2000 - 2003 for Burnthill Brook, and 1999-2002 for Catamaran Brook.

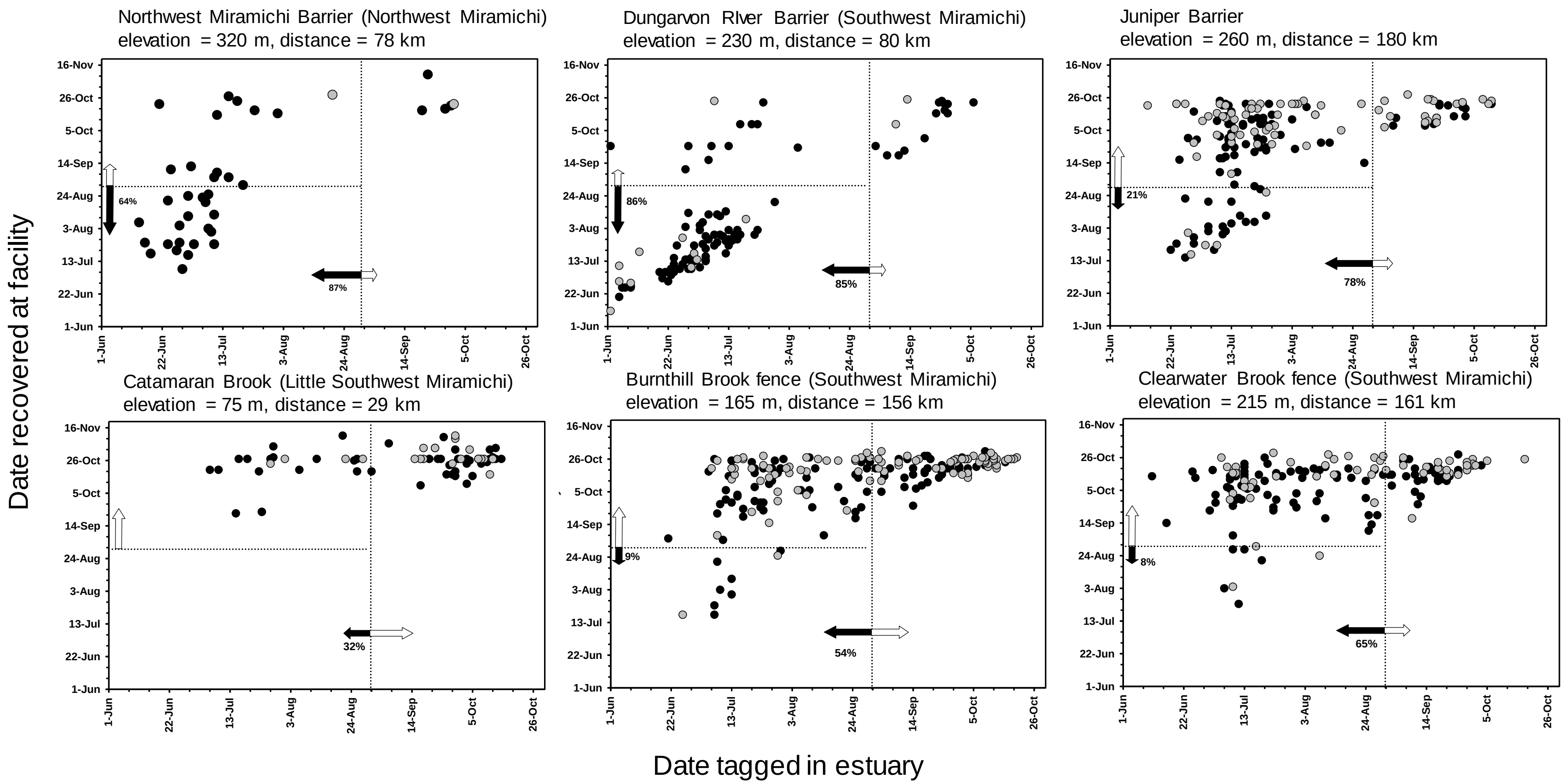


Figure 21. Date of recovery of salmon at upriver counting fences relative to the date when fish were originally tagged in the estuary for two facilities in the Northwest Miramichi system (left column) and four counting facilities in the Southwest Miramichi system (middle and right columns). Grey symbols are large salmon (fork length >= 63 cm) and black symbols are small salmon (fork length < 63 cm). The distance from head of tide and the elevation (m) of each facility are indicated above each panel. The vertical arrow with black shading in each panel and the corresponding value indicates the percentage of the tagged fish which were recovered at the facility in the early portion (prior to September 1) of the season. The horizontal arrow in black shading and the corresponding value in each panel is the percentage of all tags recovered at the facility which had been placed on salmon captured in the estuary prior to September 1 (i.e. early run salmon) (from El-Jabi et al. 2004).

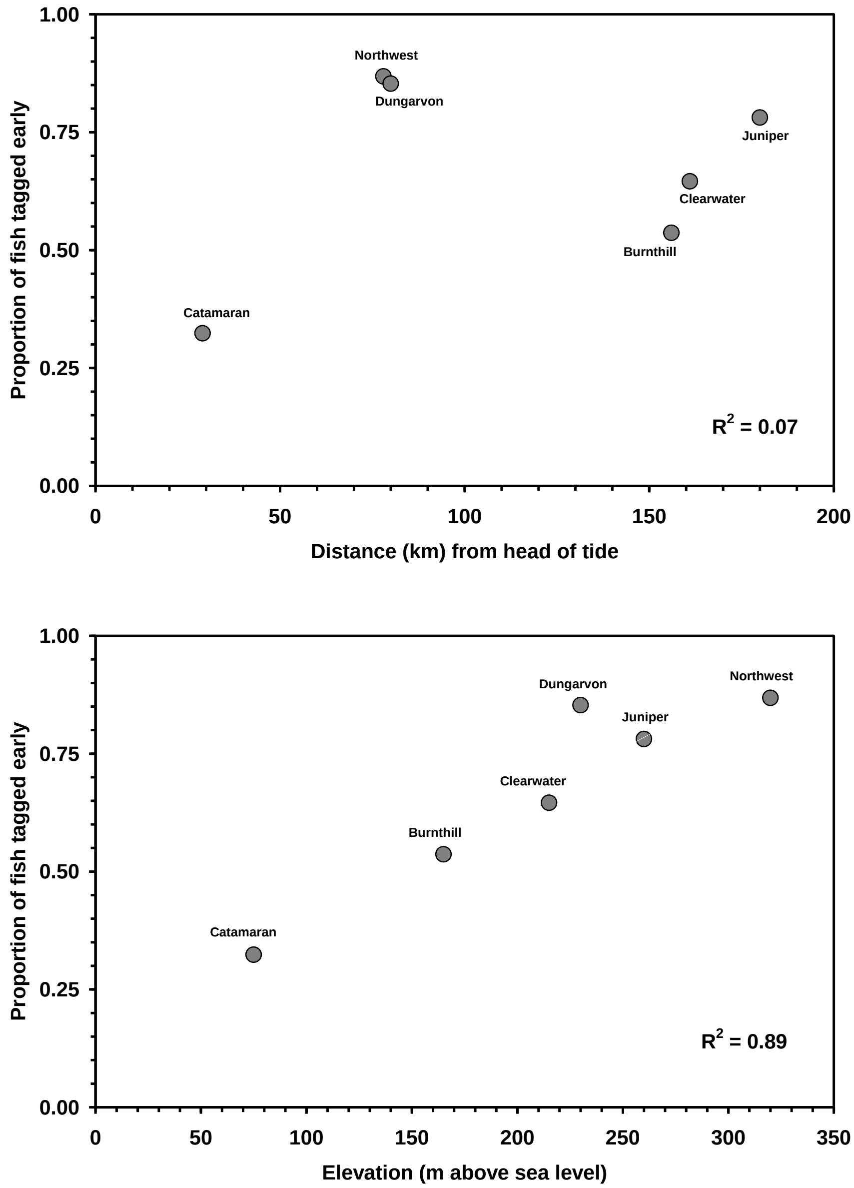


Figure 22. Association between the proportion of all tagged fish recovered at the counting facilities which had been tagged before September 1 relative to the distance (km) from the head of tide (upper panel) or the elevation (m above sea level) (lower panel) of the counting facility (from El-Jabi et al. 2004).

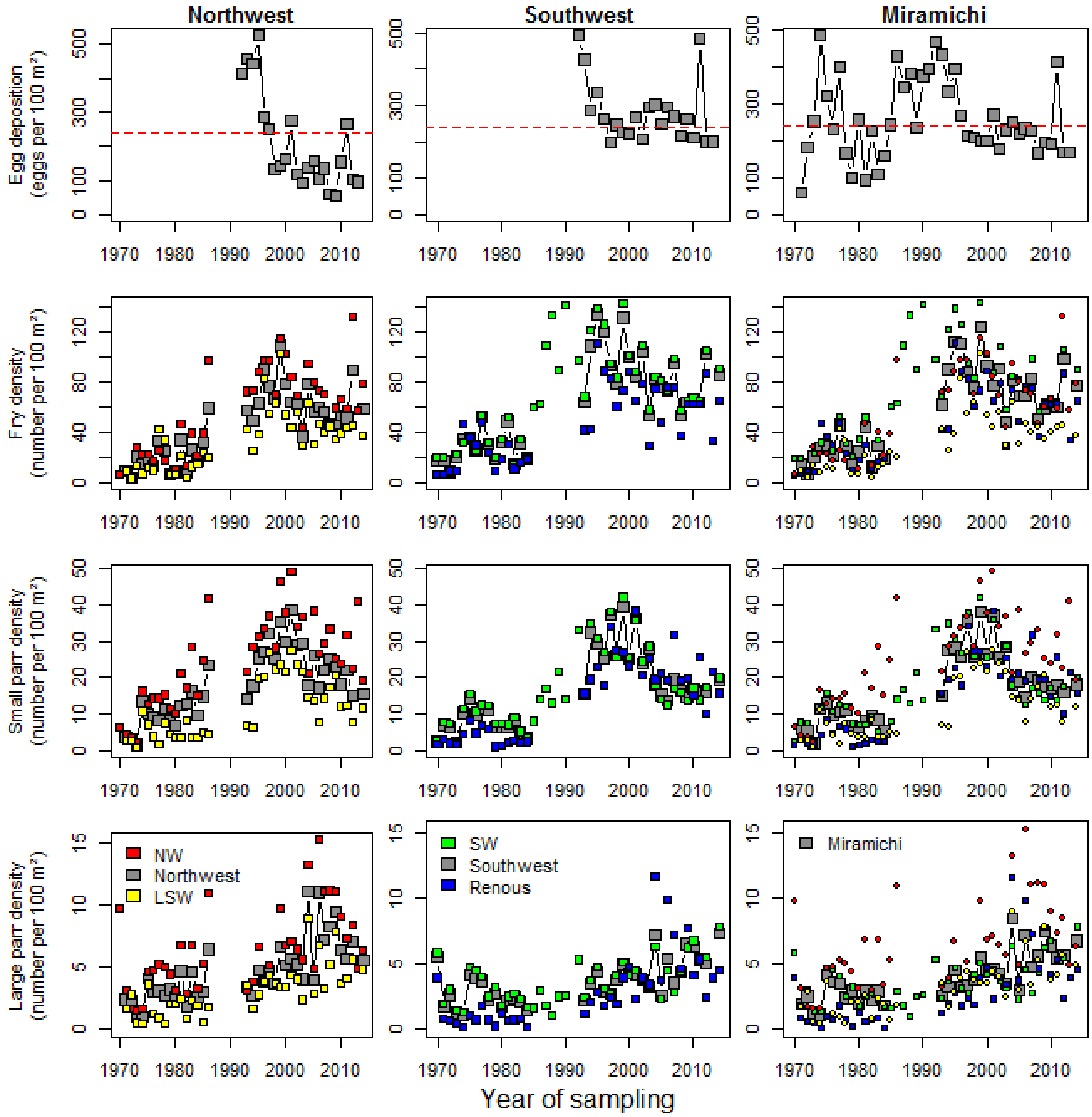


Figure 23. Annual estimates of egg depositions (eggs per 100 m²; upper row), age 0+ parr densities (fish per 100 m²; second row), small parr densities (third row), and large parr densities (bottom row), from the Northwest Miramichi system (left column) and the Southwest Miramichi system (middle column), and the Miramichi River (right column), 1971 to 2014. Average values are shown for years where four or more sites were sampled in each river. The horizontal dashed red line in the upper panel is the conservation egg deposition rate of 240 eggs per 100 m². The symbols in grey for juvenile indices are the weighted (by habitat area) average values of the river indices.

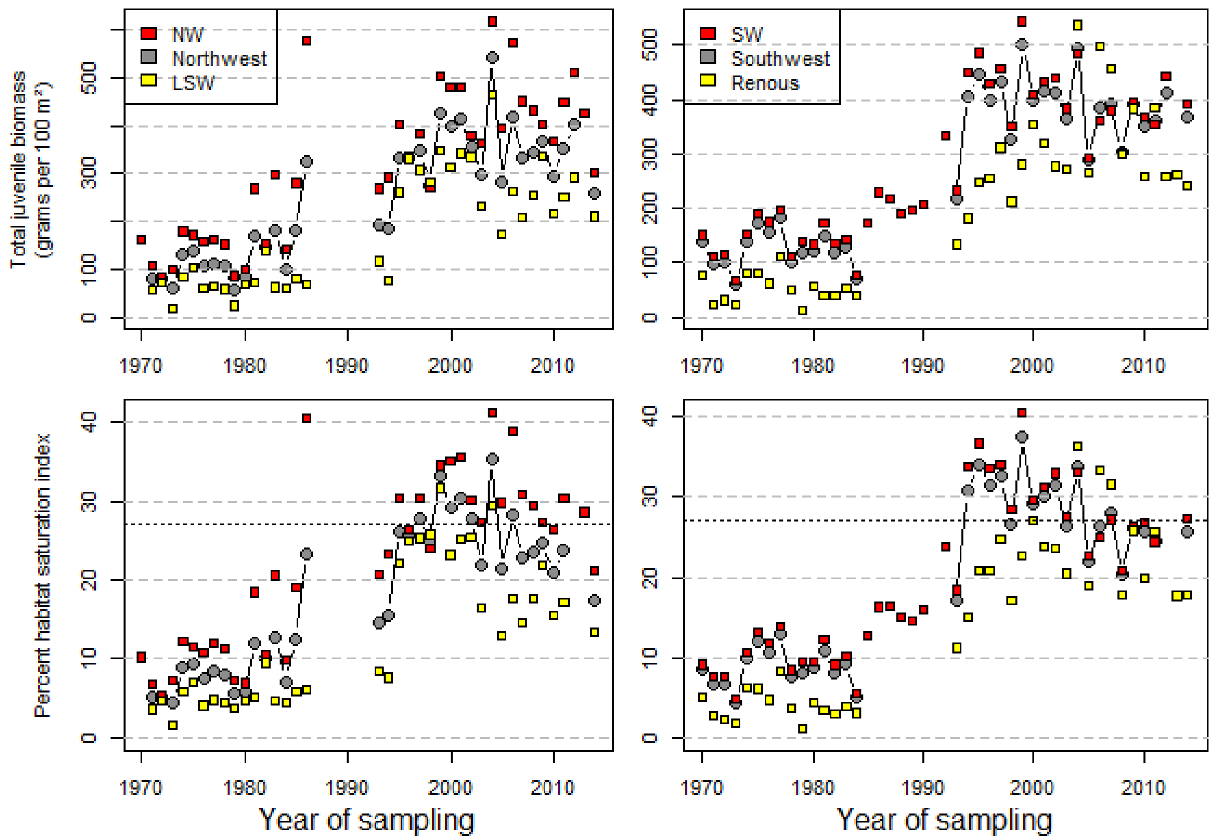


Figure 24. Annual estimates of total salmon juvenile biomass (grams per 100 m²; upper row) and Percent Habitat Saturation Index (PHS, Grant and Kramer 1990) (bottom row) for the Northwest Miramichi system (left column) and the Southwest Miramichi system (right column) 1971 to 2014. Average values are shown for years where four or more sites were sampled in each river. The dotted black line in the panels of the lower row refers to the PHS reference value of 28. The symbols in grey for juvenile indices are the weighted (by habitat area) average values of the river indices.

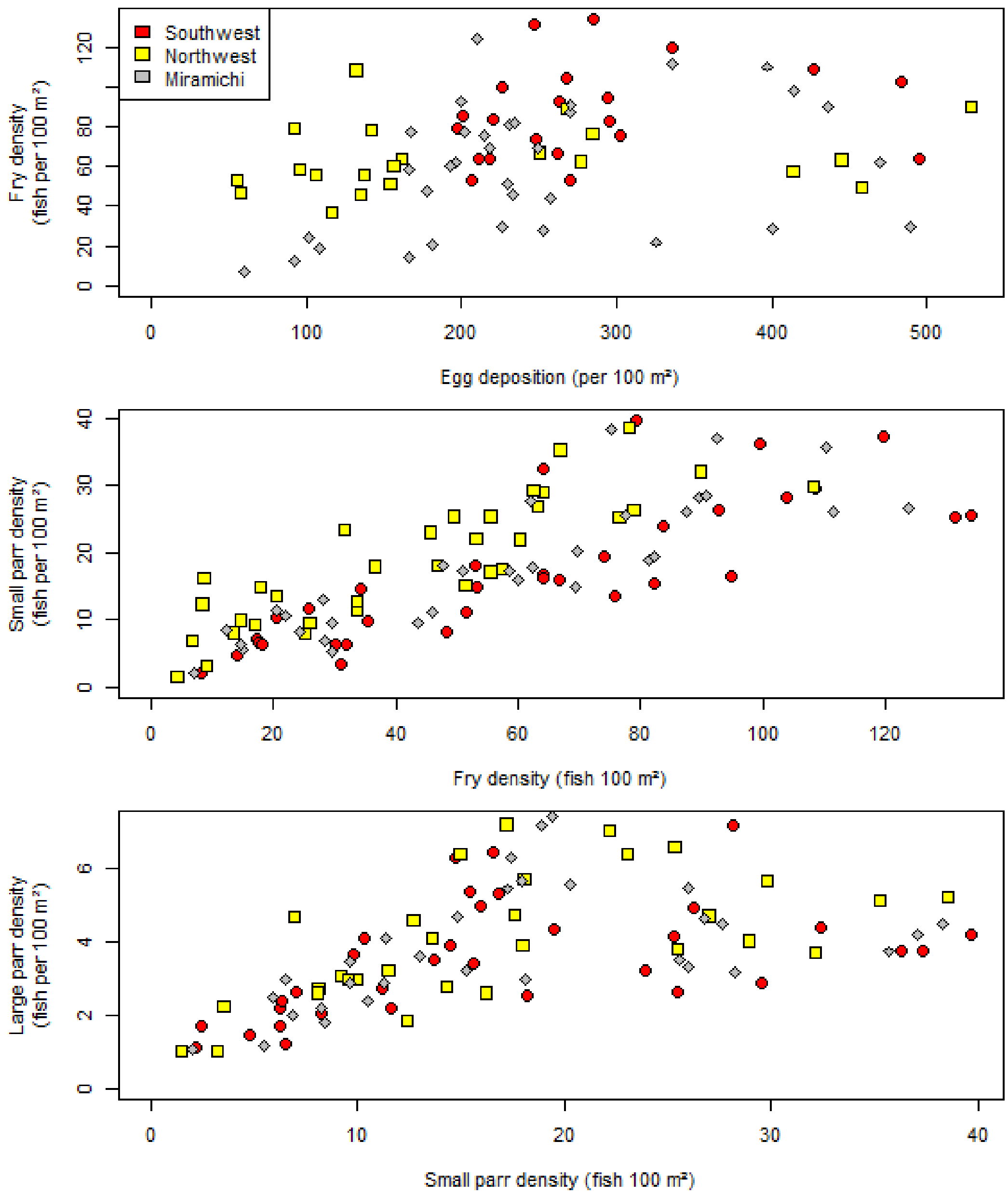


Figure 25. Stock and recruitment associations between estimated egg deposition density in year i and subsequent indices of fry densities in year i+1 (upper row), fry densities in year i and subsequent indices of small parr in year i+1 (middle row), and small parr densities in year i and subsequent large parr densities in year i+1 (bottom row) for the Northwest Miramichi system, the Southwest Miramichi system, and the Miramichi River overall.

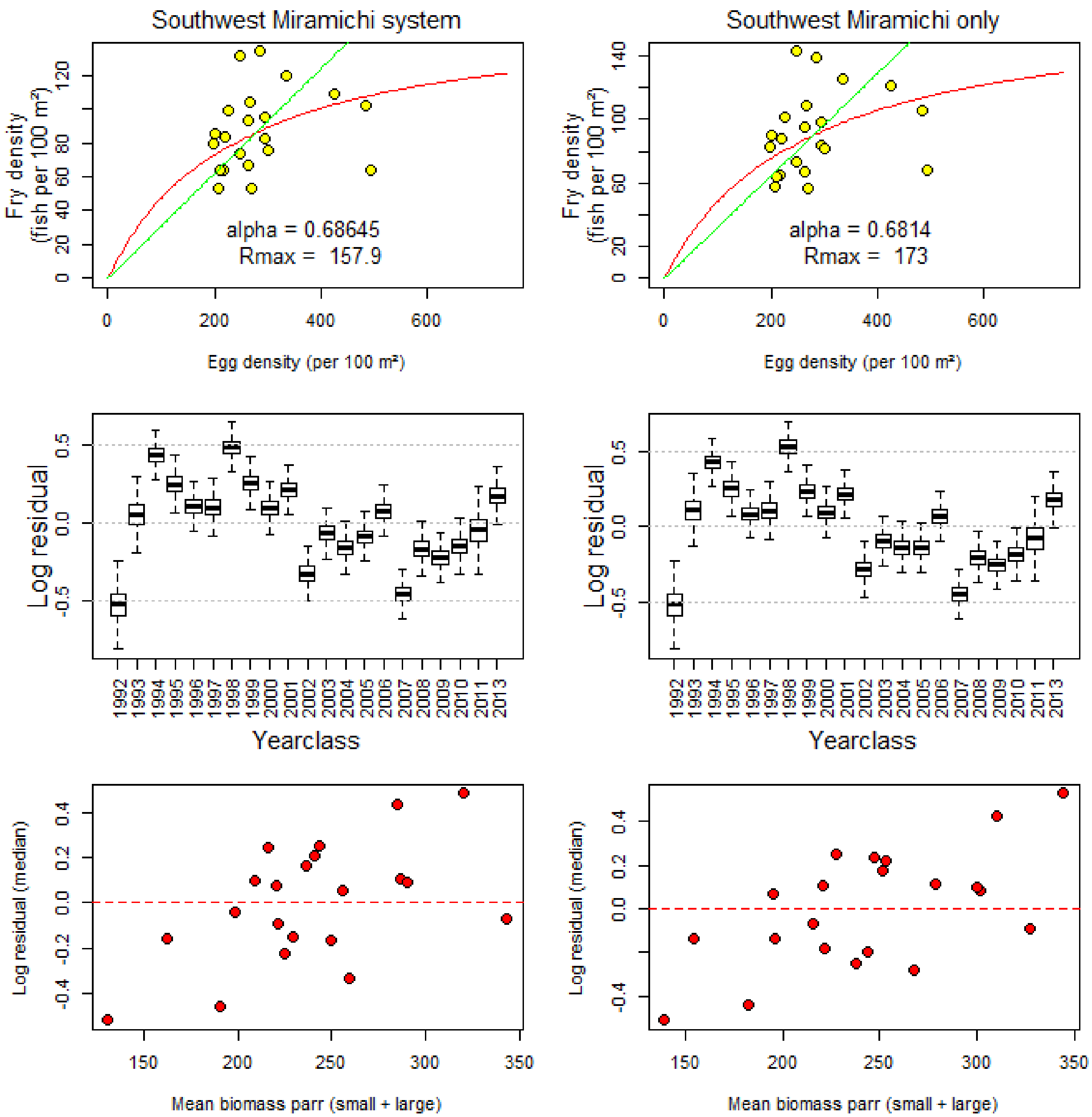


Figure 26. Stock and recruitment analysis (upper row) of egg deposition in year i to index of fry abundance in year i+1 for the Southwest Miramichi system (left column) and the Southwest Miramichi River only (right column). The red line in the upper row panels is the median Beverton-Holt stock and recruitment curve whereas the green line is the proportional linear fit (with multiplicative error) of the same data. The middle row is the residuals from the posterior distributions of the predicted abundance of fry by yearclass. The bottom row panels are the associations between the log residual (median) and the mean biomass of parr (small and large combined) as a potential explanatory variable of residual error in fry abundance after adjusting for egg deposition by yearclass. For the Southwest Miramichi system, the Beverton-Holt SR fit was statistically more likely than the linear proportion fit (DIC: 191.6, 202.4, respectively). For the Southwest Miramichi River, the Beverton-Holt SR fit was statistically more likely than the linear proportion fit (DIC: 193.9, 203.8, respectively).

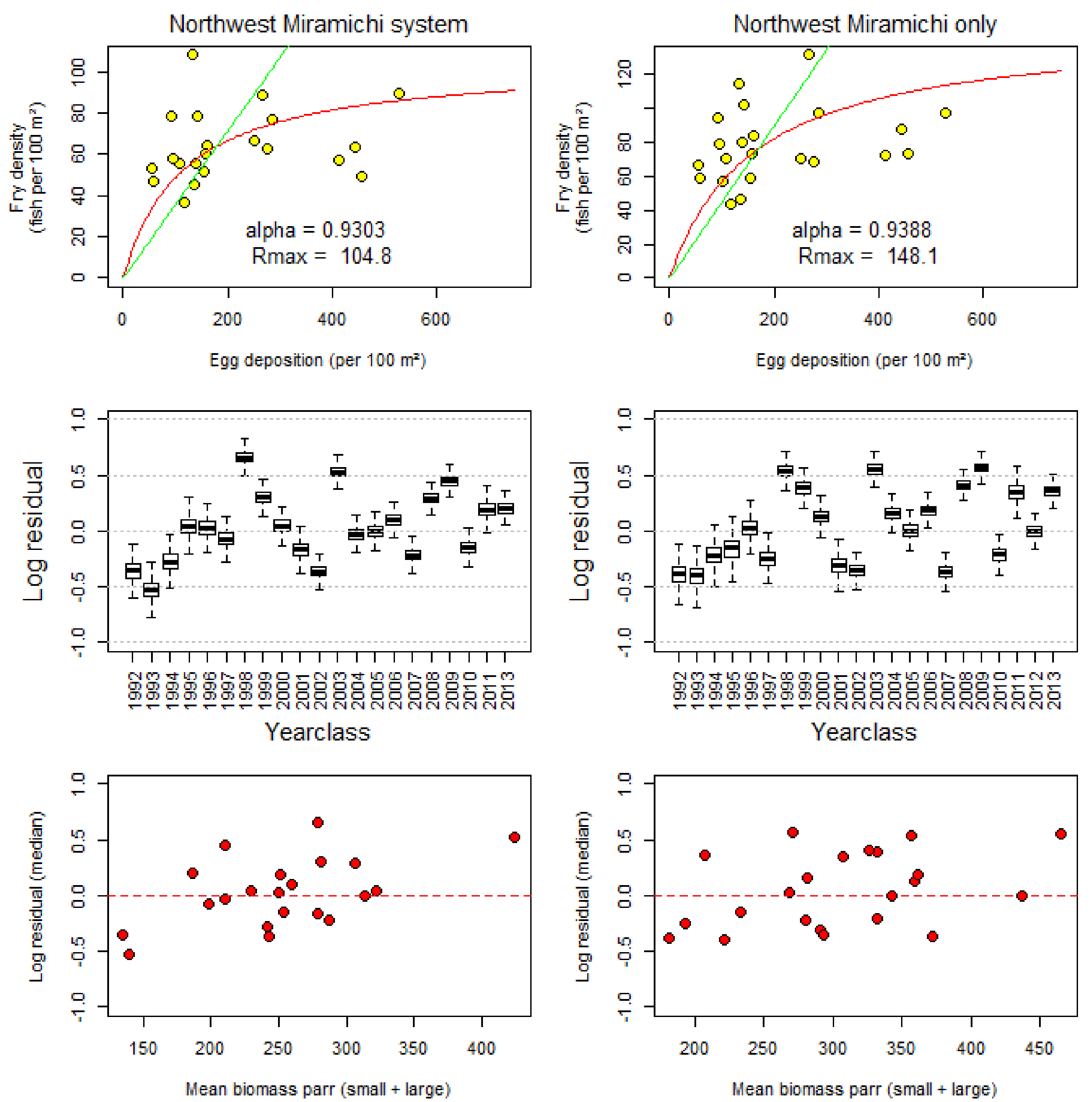


Figure 27. Stock and recruitment analysis (upper row) of egg deposition in year i to index of fry abundance in year i+1 for the Northwest Miramichi system (left column) and the Northwest Miramichi River only (right column). The red line in the upper row panels is the median Beverton-Holt stock and recruitment curve whereas the green line is the proportional linear fit (with multiplicative error) of the same data. The middle row is the residuals from the posterior distributions of the predicted abundance of fry by yearclass. The bottom row panels are the associations between the log residual (median) and the mean biomass of parr (small and large combined) as a potential explanatory variable of residual error in fry abundance after adjusting for egg deposition by yearclass. For the Northwest Miramichi system, the Beverton-Holt SR fit was statistically more likely than the linear proportion fit (DIC: 187.0, 216.5, respectively). For the Northwest Miramichi River, the Beverton-Holt SR fit was statistically more likely than the linear proportion fit (DIC: 208.7, 234.3, respectively).

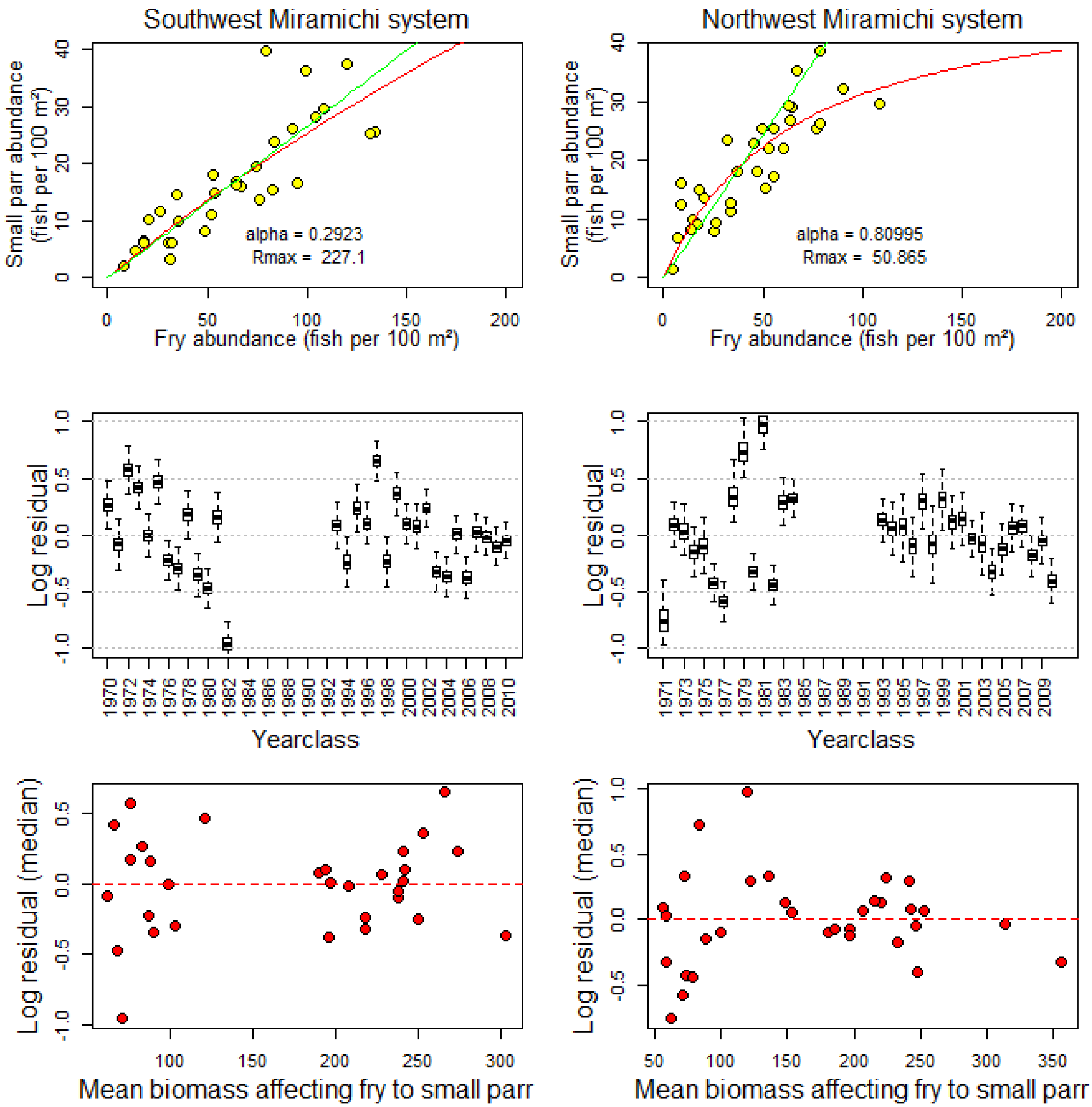


Figure 28. Stock and recruitment analysis (upper row) of fry abundance index in year i to index of small parr abundance in year i+1 for the Southwest Miramichi system (left column) and the Northwest Miramichi system (right column). The red line in the upper row panels is the median Beverton-Holt stock and recruitment curve whereas the green line is the proportional linear fit (with multiplicative error) of the same data. The middle row is the residuals from the posterior distributions of the predicted abundance of small parr by yearclass. The bottom row panels are the associations between the log residual (median) and the mean biomass of juveniles which would have interacted with the fry to small parr transition (average of the combined biomass of small parr and large parr in the fry year and the fry biomass and large parr biomass of the small parr sampling year) as a potential explanatory variable of residual error in small parr abundance after adjusting for fry abundance of the yearclass. For the Southwest Miramichi system, the linear proportional fit and the Beverton-Holt SR fits are indistinguishable (DIC: 187.2, 186, respectively). For the Northwest Miramichi system, the Beverton-Holt SR fit was statistically more likely than the linear proportion fit (DIC: 207.1, 222.2, respectively).

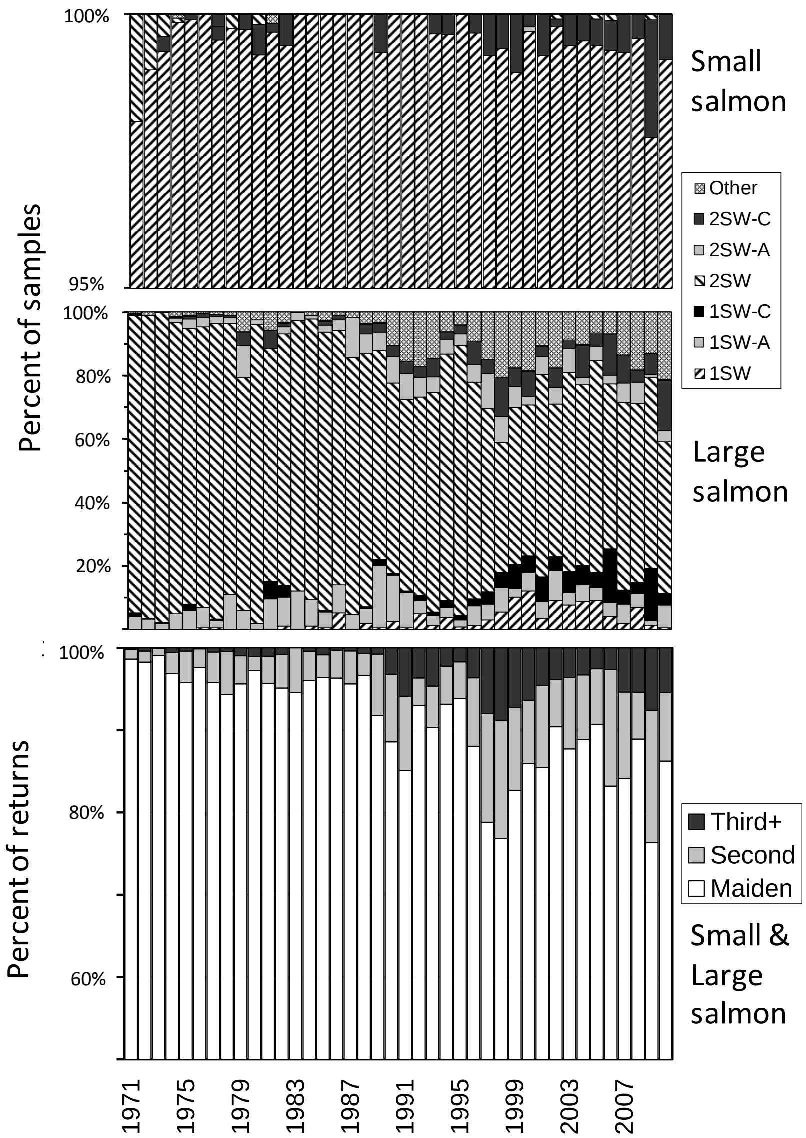


Figure 29. Percentage as maiden (1SW, 2SW), second time spawners (1SW-C, 1SW-A, 2SW-C, 2SW-A) and other spawning histories from small salmon (upper panel) and large salmon (middle panel) interpreted scale samples and percentage of estimated returns (size groups combined) which were maiden, second time spawners, and third plus time spawners (lower panel) in the Miramichi River, 1971 to 2010.

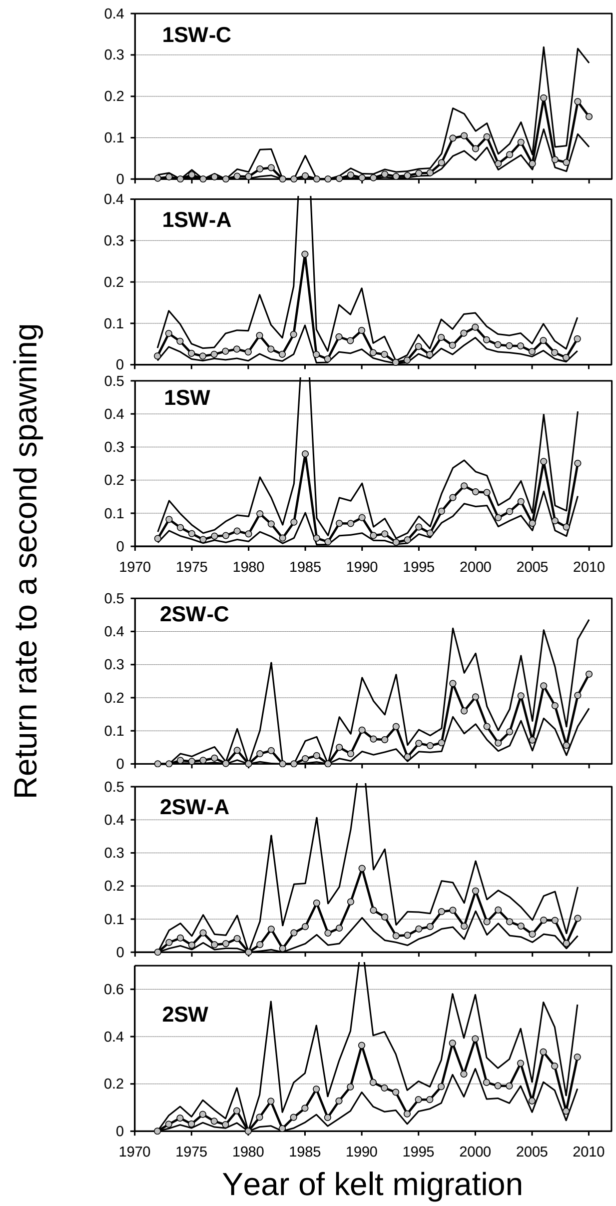


Figure 30. Return rates (median; 2.5 to 97.5 percentile range) to a second spawning as consecutives (1SW-C; 2SW-C), as alternates (1SW-A; 2SW-A) and combined (1SW; 2SW) by year of kelt migration (from Chaput and Benoit 2012). Kelt refers to the post-overwinter condition of salmon as they return to sea in the spring.