



## Evidence for bottom–up trophic effects on return rates to a second spawning for Atlantic salmon (*Salmo salar*) from the Miramichi River, Canada

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Increased return rates of consecutive repeat-spawning Atlantic salmon (*Salmo salar*) have been noted in the Miramichi River during the past two decades, and the short period for their reconditioning at sea suggests that they occupy the southern Gulf of St Lawrence ecosystem. A 40-year time-series of observations was used to examine linkages between return rates to a second spawning for Atlantic salmon in the Miramichi River and changes in the small fish community of the southern Gulf of St Lawrence that is potential prey for adult salmon. The positive association between the variations in the return rates of repeat spawners and the variations in the small fish biomass index early in the reconditioning year at sea provides evidence that abundant food supplies after return to sea following first spawning may be beneficial for the survival of Atlantic salmon to a second consecutive spawning. In contrast, no association was found between prey availability and return rates of alternate repeat spawners that presumably recondition outside the Gulf of St Lawrence.

**Keywords:** Atlantic salmon, bottom–up effects, repeat spawners, *Salmo salar*.

### Introduction

Survival during the marine phase is a crucial, yet poorly understood, determinant of the population dynamics of Atlantic salmon (*Salmo salar*; Jonsson and Jonsson, 2004). It has been hypothesized that the marine survival of Atlantic salmon in their first year at sea is related to climatic factors that influence growth opportunities and predation pressures (Jonsson and Jonsson, 2004; Friedland *et al.*, 2009). There is currently no clear consensus on the extent to which the natural (non-fishing) mortality of Atlantic salmon is influenced by bottom–up effects of prey availability relative to the top–down effects of predation loss. However, the dynamics of temperate and boreal marine fish communities appear to be determined largely by the top–down effects of predation and fishing, especially at higher latitudes (e.g. Frank *et al.*, 2005, 2007; Benoît and Swain, 2008).

Atlantic salmon are iteroparous and return to spawn as maiden (first-time) spawners after feeding at sea for 1 (one-sea-winter, 1SW), 2 (2SW), or more (multi-sea-winter, MSW) years, and as repeat spawners. Furthermore, salmon returning to a second or subsequent spawning can do so as consecutive or alternate

repeat spawners (Moore *et al.*, 1995; Klemetsen *et al.*, 2003; Niemelä *et al.*, 2006). Consecutive repeat spawners are fish returning to spawn 1 year after their previous spawning and after only a few months of reconditioning at sea. Alternate repeat spawners probably undertake a more extensive feeding migration and return to spawn after spending more than 1 year at sea. Given such a diversity of life-history strategies, it might be expected that different factors will determine marine survival for different spawner types.

The Miramichi River (New Brunswick, Canada, 47°N 65°W) contains the largest Atlantic salmon population in eastern North America. This population has been characterized by an increase in the number of types of spawners consistent with changes in survival (Moore *et al.*, 1995; Chaput and Jones, 2006). Between 1971 and 1986, there were generally <5% repeat spawners in the population, and those fish had undertaken no more than two previous spawning migrations. Since 1995, adult salmon on their sixth and seventh spawning migrations have been sampled in catches in estuary trapnets, and repeat-spawning salmon have comprised 6–21% of the total returns of all age groups (Chaput and Jones,

2006). Post-spawned salmon (kelt) overwinter in the Miramichi River and return to the ocean early in spring, immediately following ice-out of the river. Distances travelled and the area occupied by consecutive repeat spawners from the Miramichi River during reconditioning at sea are not known, but they are probably limited in their distribution to the Gulf of St Lawrence, given calculated swimming rates and the timing of return to other rivers in eastern Canada (Reddin *et al.*, 2004, 2011; Hubley *et al.*, 2008). Marine survival of consecutive repeat spawners is, therefore, likely to be determined by factors in the Gulf of St Lawrence ecosystem. Alternate repeat spawners from the Miramichi River are believed to undertake more extensive oceanic migrations, as far as West Greenland (Chaput *et al.*, 2010), and survival is, therefore, likely to be influenced by factors occurring over a much broader geographic scale. Differential opportunities for growth in the Gulf of St Lawrence ecosystem and farther afield may also affect maturation rates, in turn determining the relative composition of spawning types in the spawning population.

There is arguably a better understanding of the nature and abundance of Atlantic salmon prey than of their predators (Cairns, 2006; Rikardsen and Dempson, 2011). Here, we focus on the possible influence of potential prey abundance on salmon returning to spawn after reconditioning at sea. Specifically, the role of the abundance of small marine fish known to be important prey of adult Atlantic salmon (Rikardsen and Dempson, 2011) is considered. Annual bottom-trawl monitoring suggests large changes in the abundance of these small marine fish in the southern Gulf of St Lawrence since 1971 (Benoît and Swain, 2008). We used 40-year time-series of abundance and of demographics to estimate return rates to a second spawning of Atlantic salmon and examine linkages between these return rates and indices of changes in the small fish community of the southern Gulf of St Lawrence. The analysis examined two hypotheses. First, if prey abundance in the southern Gulf of St Lawrence affects salmon returns, the correspondence between the time-series of the respective indices should be stronger for consecutive repeat spawners than for alternate repeat spawners because consecutive repeat spawners are expected to have spent a much greater proportion of their reconditioning time at sea in the southern Gulf of St Lawrence. Second, given positive relationships between predator and prey size (Scharf *et al.*, 2000), correlations between prey abundance and return rates should be strongest for indices of prey–fish abundance that are limited to prey of the preferred size for a particular spawning group.

## Material and methods

### Input data

Atlantic salmon were captured and sampled annually at an estuary trapnet in the main stem of the Miramichi River between 1971 and 1992. From 1992 to 2010, trapnets were relocated to each of the main branches of the river and sampled annually. The operations, catches, and run-timing at the trapnets are described by Claytor (1996) and Hayward (2001).

Returns of Atlantic salmon to the Miramichi River, by size group (small salmon <63 cm fork length, FL; large salmon ≥63 cm FL), were estimated from the catches at index estuary trapnets, and catch rates were estimated using mark and recapture experiments between 1985 and 2010 (Chaput *et al.*, 2001, 2010; Chaput, 2010). For the period 1971–1984, catches at the main stem estuary trapnet, and an estimated efficiency based on a

single experiment in 1973, were used to estimate the returns (Chaput *et al.*, 2010). Estimates of spawning escapement were derived by deducting estimates of harvests from the estimates of returns (Chaput *et al.*, 2010).

The abundance of maiden 1SW and 2SW salmon and of salmon that initially spawned as 1SW or 2SW fish returning for a second spawning as either consecutive (1SW-C and 2SW-C) or alternate (1SW-A and 2SW-A) repeat spawners were estimated from the returns to the river and the age structure derived from a sampling programme. Salmon captured at the trapnets were measured (FL), and scales were taken for age determination. Since the mid-1980s, scale samples have been taken from essentially all large salmon captured at the trapnets, but the catches of small salmon were subsampled when the daily catch exceeded 30 fish. Ages and spawning histories were interpreted from scale samples following the standard criteria for Atlantic salmon (ICES, 1992). Between 1971 and 2010, the annual number of scales interpreted for age ranged from a low of 288 in 1983 to a high of 3784 in 2006.

Repeat spawners were less abundant during the first two decades of the time-series and, as a result, were less frequently observed in the samples collected from the monitoring trapnets, likely leading to sampling stochasticity in the determination of the size-dependent frequency of life-history types. To address the issue of sampling stochasticity before 1990, the following smoothing algorithm was applied to the annual age samples:

$$\overline{n}_{k,j,y} = \frac{\sum_{i=0}^I n_{k,j,y+i}}{I+1}, \quad (1)$$

where  $\overline{n}_{k,j,y}$  is the smoothed number of scale samples by the size group of salmon  $k$  (small salmon <63 cm FL; large salmon ≥63 cm FL), for life-history type  $j$  (1SW, 1SW-C, 1SW-A, 2SW, 2SW-C, 2SW-A, OTHER) in sampling year  $y$ ,  $n_{k,j,y+i}$  the number of samples with interpreted ages and the life-history type by the size group of salmon  $k$  and life-history type  $j$  for sampling year  $y+i$ , and  $I=3$  for sampling years 1971–1984,  $I=2$  for 1985–1987,  $I=1$  for 1988/1989, and  $I=0$  for 1990–2010. This approach effectively applies a degree of interannual smoothing that is inverse to the amount of data available for a given year, thereby minimizing, to a reasonable level the extent to which interannual changes in demographic composition are averaged over years.

Changes in the size and species composition of the fish community in the southern Gulf of St Lawrence were described based on catch rates (stratified mean kg per standard tow and associated standard error) in a bottom-trawl survey conducted annually each September since 1971. The survey methodology is described by Hurlbut and Clay (1990). That survey provides indices of abundance, biomass, and size composition for >50 fish species and a number of large invertebrates (e.g. crabs, lobster, squid), as well as biomass indices for many smaller invertebrates such as shrimps (Benoît and Swain, 2008; Benoît *et al.*, 2009). A 19-mm trawl codend liner was used in all years to retain small fish. Where necessary, catch rates were adjusted for changes in gear, vessel, or survey protocol, as described by Benoît and Swain (2003) and Benoît (2006). To calculate the indices of small fish biomass, catchability adjustments were applied to survey catch rates based on length-dependent catchability models developed for a number of species (Harley and Myers,

2001) and applied to species with generally similar body shapes and behaviour (Benoît and Swain, 2008).

Atlantic salmon are opportunistic (generalist) predators in the ocean (Lear, 1980; Jacobsen and Hansen, 2000; Cairns, 2006; Renkawitz and Sheehan, 2011; Rikardsen and Dempson, 2011). Salmon ranging in length from 40 to >100 cm FL feed on a variety of fish species, including capelin (*Mallotus villosus*), herring (*Clupea harengus*), sandlance (*Ammodytes* spp.), barracudina (family Paralepididae), and various invertebrate prey including squid, euphausiids, and amphipods (Lear, 1980). In coastal areas of eastern Canada, salmon consume capelin, sandlance, rainbow smelt (*Osmerus mordax*), cod (*Gadus* sp.), herring, and brook trout (*Salvelinus fontinalis*; Blair, 1965). Less is known about the diet of repeat-spawning salmon during reconditioning at sea, but there is ample evidence from reconditioning programmes of post-spawners in hatcheries that they readily consume small fish, including rainbow smelt, capelin, and Atlantic silverside (*Menidia menidia*; Johnston *et al.*, 1990). Except brook trout, all the fish species above are sampled by the trawl survey.

Relationships between predator and prey length during their marine phase are unavailable for Atlantic salmon. Based on the observation that the diets of many marine fish are dominated by fish prey that are 10–20% of the predator’s length (e.g. Scharf *et al.*, 2000) and the observed sizes of salmon in this study (50–100 cm), the annual biomass of marine fish was calculated as the sum over species for two size groups,  $\leq 10$  and  $\leq 20$  cm total length. The taxonomic composition of these two groups was divided into functional groups based on the feeding characteristics of adults: planktivores (e.g. herring, capelin, barracudina, and sandlance), fish- and shrimp-eaters (e.g. redfish, *Sebastes* spp.), piscivores (e.g. Atlantic cod, *Gadus morhua*, and white hake, *Urophycis tenuis*), small benthivores (e.g. daubed shanny, *Leptoclinius maculatus*, and mailed sculpin, *Triglops murrayi*), medium benthivores (e.g. winter flounder, *Pseudopleuronectes americanus*, and sea raven, *Hemitripterus americanus*), and large benthivores (e.g. American plaice, *Hippoglossoides platessoides*, and thorny skate, *Amblyraja radiata*).

**Analyses**

Return rates to a second consecutive or alternate spawning were calculated separately for 1SW and 2SW maiden salmon. These return rates were calculated as the ratio of the estimated return of fish for a second spawning to the estimated spawning escape-ment of salmon at the corresponding maiden age:

$$RR_{k,j,y} = \frac{N_{k,j,y}}{N_{j,y}}, \tag{2}$$

where  $RR_{k,j,y}$ , distributed [0,1], is the return rate to a second spawning of either consecutive ( $k = C$ ) or alternate ( $k = A$ ) repeat-spawning salmon for maiden sea-age group  $j$  (1SW and 2SW) corresponding to the year of kelt migration  $y$  (maiden spawning year + 1),  $N_{k,j,y}$  the estimated abundance of salmon at a second spawning by spawning history type, and  $N_{j,y}$  the maiden-spawning salmon abundance for kelt migration year  $y$ . The abundance of maiden-spawning salmon is corrected for removals in the in-river fisheries in the maiden spawning year.

Uncertainties in the return rate estimates were quantified using parametric bootstraps (Efron and Tibshirani, 1993) for  $N_{k,j,y}$  and  $N_{j,y}$ , based on a lognormal distribution with the mean and

standard deviation parameters derived from the assessments (Chaput *et al.*, 2010). Uncertainties in the proportions at age were also derived using a parametric bootstrap, assuming a multinomial distribution by size group and resampling with a sequential beta-distribution, whose parameters were the sample size of the age group of interest and the sample size of the remaining age groups. In all, 10 000 independent bootstrap iterations were performed always.

Point estimates (means by life stage and year of observation) were used as input data. The annual estimated abundance estimates of consecutive or alternate repeat spawners were modelled separately. For each, combinations of two explanatory variables in the following Bayesian inference model were examined:

$$N_{k,j,y} \sim \text{Lognormal}(\bar{N}_{k,j,y}, \sigma_{k,j}^2), \tag{3}$$

with  $N_{k,j,y}$  as defined previously and assumed lognormally distributed, and

$$\bar{N}_{k,j,y} = \log(N_{j,y} \times RR_{k,j,y}). \tag{4}$$

Our analyses were based on one of four assumptions regarding the return rates to a second spawning for salmon in spawner group  $k$  of age  $j$  and in kelt return year  $y$ :

$$RR_{k,j,y} = \begin{cases} \alpha_k & \text{i.e. age- and time- invariant} \\ \alpha_{k,j} & \text{i.e. age- dependent, time- invariant} \\ \alpha_k Bio_{m,y}^\beta & \text{i.e. age- invariant, prey- dependent} \\ \alpha_{k,j} Bio_{m,y}^\beta & \text{i.e. age- and prey- dependent,} \end{cases} \tag{5}$$

where  $\alpha$  is a time-invariant component of the return rate,  $Bio_{m,y}$  the index of small marine fish biomass in size category  $m$  (either  $m \leq 10$  cm or  $m \leq 20$  cm) corresponding to the year of kelt migration  $y$ , and  $\beta$  an exponent allowing for a possible non-proportional relationship between prey abundance and return rate, which is expected *a priori* given that, *inter alia*, survival is bounded [0,1].

From these basic assumptions for the return rate, several competing models were formulated (Table 1). In the model, the logit ( $RR_{k,j,y}$ ) transform, distributed  $(-\infty, +\infty)$ , is used as well as non-informative priors for  $\alpha_{k,j}$  [ $N(0,100)$ ],  $\beta_{k,j}$  [ $N(0, 100)$ ] and  $\sigma_{k,j}^{-2}$  [ $\text{gamma}(0.01, 0.01)$ ].

Model fit and parsimony were evaluated using the deviance information criterion (DIC); the model with the smallest DIC, with a difference of at least 5, is estimated to be the one that would best predict a replicate dataset of the same structure as that currently observed (Spiegelhalter *et al.*, 2010).

We examined the assumption that the residuals of the observed and predicted returns of repeat spawners were independent and identically distributed (i.e. not autocorrelated) by calculating the first-order autocorrelation values of the residuals (Hilborn and Walters, 1992). For the models with the lowest DIC values and for which there was significant autocorrelation (95% Bayesian credibility interval, BCI, of the autocorrelation coefficient  $\phi$  excluded zero), a first-order autoregressive model of the following form was examined:

$$\bar{N}_{k,j,y} = \begin{cases} \log(N_{j,y} \times RR_{k,j,y}) & \text{for } y = 1972 \\ \log(N_{j,y} \times RR_{k,j,y}) + \omega_{k,j,y} & \text{for } y = 1973 \text{ to } Y, \end{cases} \tag{6}$$

**Table 1.** DIC and median of the posterior distributions of the first-order autocorrelation parameter of the residuals by maiden sea age ( $j$ ; 1SW and 2SW) for the models of the return rates to predict the abundance of consecutive ( $k$ ) repeat-spawning salmon.

Model	Covariate ( $m$ )	DIC	First-order autocorrelation ( $\phi_j$ )	
			Maiden sea age ( $j$ )	
			1SW	2SW
$\alpha_k; \sigma_k^2$		1 266	0.81	0.67
$\alpha_{k,j}; \sigma_{k,j}^2$		1 256	0.78	0.61
$\alpha_{k,j}; \sigma_k^2$		1 255	0.77	0.61
$\alpha_k + \beta_k \log(\text{Bio}_{y,m}); \sigma_k^2$	Bio $\leq$ 10	1 221	0.52	0.27
	Bio $\leq$ 20	1 258	0.73	0.59
$\alpha_{k,j} + \beta_k \log(\text{Bio}_{y,m}); \sigma_k^2$	Bio $\leq$ 10	1 196	0.33	-0.04*
	Bio $\leq$ 20	1 244	0.68	0.49
$\alpha_k + \beta_{k,j} \log(\text{Bio}_{y,m}); \sigma_k^2$	Bio $\leq$ 10	1 203	0.44	-0.04*
	Bio $\leq$ 20	1 245	0.70	0.48
$\alpha_{k,j} + \beta_{k,j} \log(\text{Bio}_{y,m}); \sigma_k^2$	Bio $\leq$ 10	1 197	0.29	0.01*
	Bio $\leq$ 20	1 244	0.63	0.53
$\alpha_{k,j} + \beta_{k,j} \log(\text{Bio}_{y,m}); \sigma_{k,j}^2$	Bio $\leq$ 10	1 199	0.29	0.02*
	Bio $\leq$ 20	1 246	0.63	0.53
First-order autoregressive models				
$\alpha_{k,j} + \beta_{k,j} \log(\text{Bio}_{y,m}); \phi_{k,j}; \sigma_k^2$	Bio $\leq$ 10	1 192	0.04*	0.01*
	Bio $\leq$ 20	1 220	0.23*	0.14*
$\alpha_{k,j} + \beta_{k,j} \log(\text{Bio}_{y,m}); \phi_{k,j}; \sigma_{k,j}^2$	Bio $\leq$ 10	1 193	0.03*	0.01*
	Bio $\leq$ 20	1 222	0.23*	0.15*

For first-order autocorrelation values, an asterisk indicates that the 95% BCI of the posterior distribution included zero.

where  $Y = 2010$  for  $k = C$  and  $Y = 2009$  for  $k = A$ , and where

$$\omega_{k,j,y} = \omega_{k,j,y-1}\phi_{k,j} + \varepsilon_{k,j,y} \quad (7)$$

$$\varepsilon_{k,j,y} = (1 - (\phi_{k,j})^2)\sigma_{k,j}^2, \quad (8)$$

where  $\omega_{k,j,y}$  is the residual ( $\log(N_{k,j,y}) - \bar{N}_{k,j,y}$ ) for year  $y$ ,  $\phi_{k,j}$  the autocorrelation parameter bounded by  $|\phi| < 1$ , and  $\sigma_{k,j}^2$  the process error variance, as in Equation (3).

The posterior distributions of the model parameters were derived using the Markov Chain Monte Carlo (MCMC) with Gibbs sampling in OpenBUGS (Spiegelhalter *et al.*, 2010). Convergence, assessed using the tools in OpenBUGS based on three chains of initial values, was achieved after 250 000 MCMC samples. A further 250 000 MCMC samples were drawn, and the posterior distributions were described based on every 100th sample, to reduce the MCMC autocorrelation.

### Results

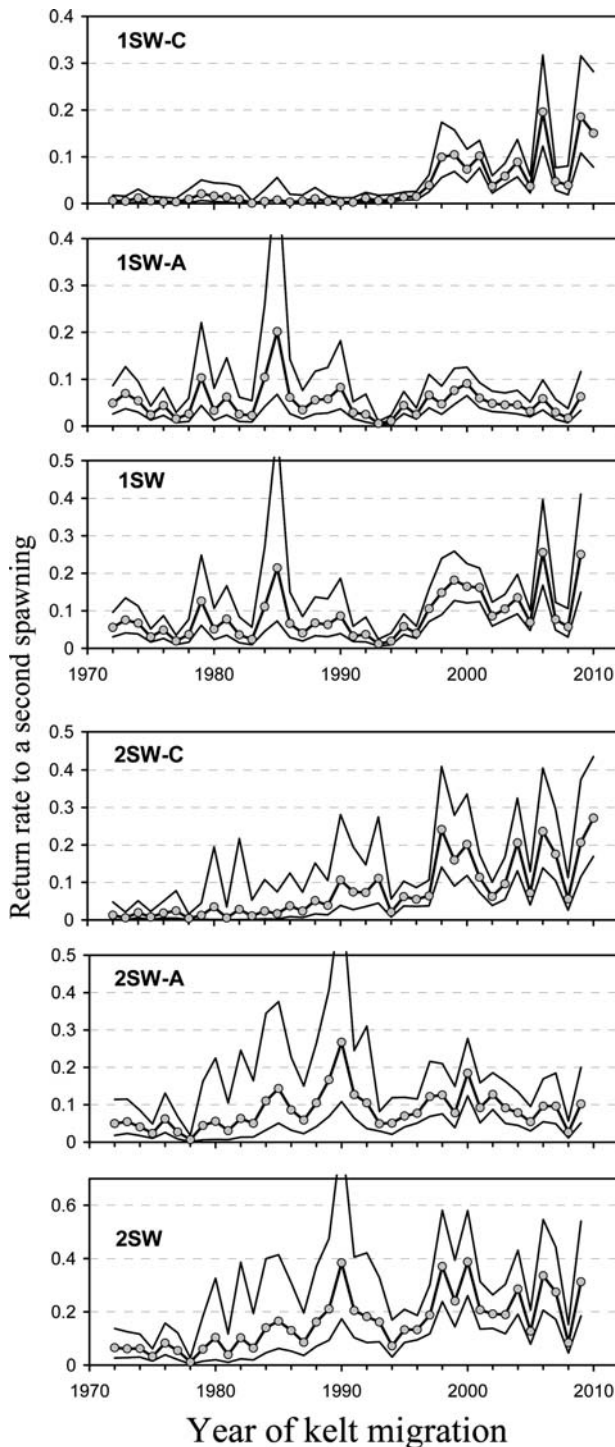
The proportion of maiden salmon in the total returns to the Miramichi declined from >95% before 1986 to ~85% since 1996, whereas the relative abundance of salmon on a second spawning migration increased from <5% of total returns before 1995 to >10% in most years since 1995 (Chaput *et al.*, 2010). Repeat spawners have become more abundant in the large-salmon category ( $\geq 63$  cm FL), because those fish grow when they return to the sea post-spawning. Upon their return to rivers to spawn, maiden 1SW salmon measure between 50 and 65 cm FL and maiden 2SW salmon measure from just under 70 to ~85 cm FL (Moore *et al.*, 1995). The average difference in size between maiden and returning consecutive repeat-spawning salmon is >10 cm for 1SW salmon (19% of maiden length) and 6 cm for 2SW salmon (8% of maiden length). The average size difference

between maiden and returning alternate repeat-spawning salmon was 27 cm (47% of maiden length) for 1SW salmon and 16 cm (21% of maiden length) for 2SW salmon after more than 12 months feeding at sea.

Estimated return rates to a second spawning for both 1SW and 2SW salmon increased between 1972 and 2010 (Figure 1). Since the late 1990s, return rates to a second spawning have been between 8 and 25% for 1SW salmon and between 10 and 40% for 2SW salmon. Increased return rates to consecutive repeat spawning have contributed most to the increased return rates for both 1SW and 2SW maiden life histories. The return rates to consecutive spawning were less than a few percentage points for 1SW and 2SW salmon before 1984, but have increased since the late 1990s to between 5 and 20% annually for 1SW salmon and from just under 10 to >25% for 2SW salmon. Before the 1990s, second spawning alternate spawners for both 1SW and 2SW salmon dominated the returns, whereas since then, the proportions of second consecutive spawners exceeded those of the alternate spawners for both 1SW and 2SW salmon returns.

There is a positive association between the return rates of 1SW and 2SW salmon as consecutive repeat spawners for the corresponding year of kelt migration (Figure 2). In contrast, there is considerably less evidence for such an association for 1SW and 2SW salmon as alternate repeat spawners.

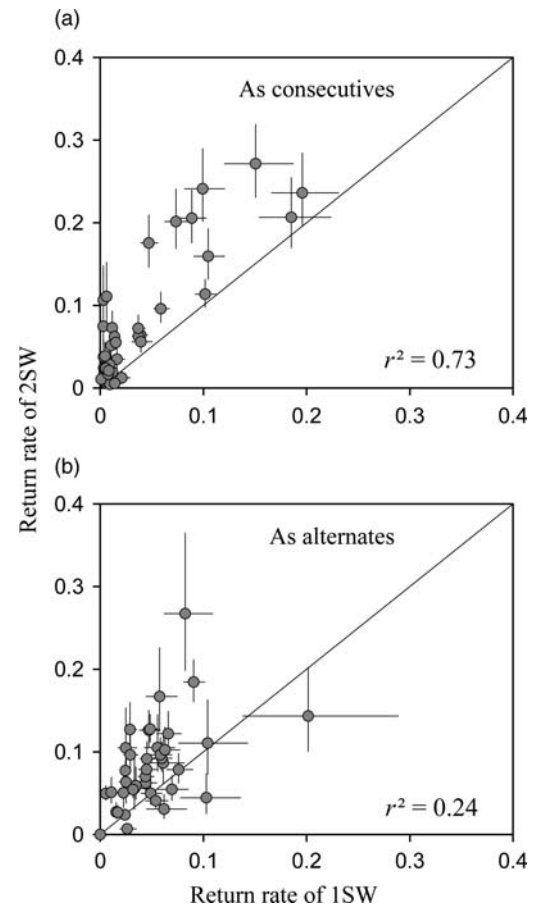
The abundance estimates of maiden salmon in the 1SW and 2SW spawner groups were high in the early 1970s and from 1985 to 1994 (Figure 3). Consecutive repeat-spawning 1SW salmon increased in abundance from the early 1990s, associated with an increased return rate (Figures 1 and 3). Similarly, the abundance of consecutive 2SW spawners increased markedly from the mid-1980s to the early 1990s and has since fluctuated around a higher level. In contrast, the abundance of alternate 1SW spawners was highest in the first two decades of the time-series, peaking in 1990 and rapidly decreasing to a stable and



**Figure 1.** Return rates (median and 95% confidence interval based on bootstrap percentiles) to a second spawning as consecutive (1SW-C and 2SW-C) and alternate (1SW-A and 2SW-A) repeat spawners and combined (1SW and 2SW) by the year of kelt migration to sea in spring.

lower level since then. Alternate 2SW spawner abundance also peaked around 1990, with comparable lesser abundance before and following the peak.

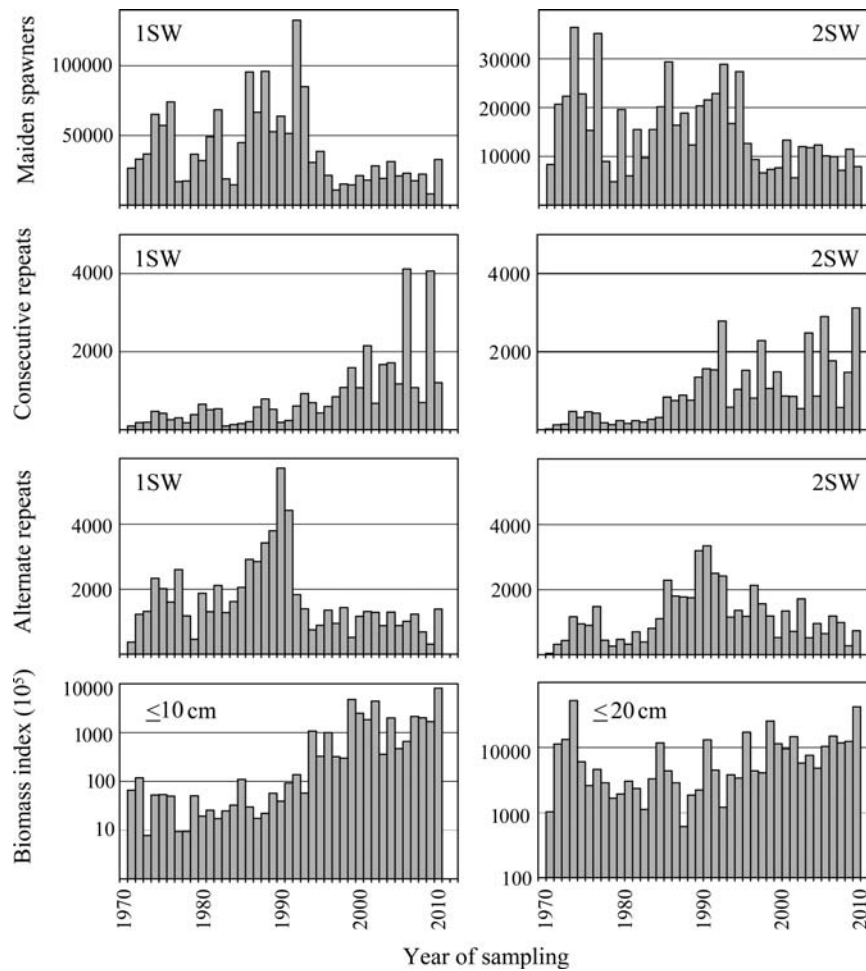
The small fish biomass index from the southern Gulf of St Lawrence increased from 1971 to 2010 for both the  $\leq 10$  and



**Figure 2.** Associations between annual return rates to a second spawning of 1SW and 2SW salmon (a) as consecutives and (b) as alternates for common kelt migration years. The diagonal line is the 1:1 line. The symbols are the medians and the error bars the interquartile ranges, and  $r^2$  is the coefficient of determination for the linear association.

$\leq 20$  cm length groups (Figure 4). The increase was particularly evident in the plankton-feeding species group, which includes capelin, rainbow smelt, herring, and barracudina. The increase in the biomass index of small fish  $\leq 10$  cm was greatest since the late 1990s, whereas the increase in the biomass index for fish  $\leq 20$  cm long was less marked and began in the early 1990s. The high value of the index for fish  $\leq 20$  cm long in the period 1972–1974 was attributable primarily to large catches of rainbow smelt. The distribution of capelin and of most small-bodied species expanded during the period of abundance increase (Benoît *et al.*, 2003; Grégoire *et al.*, 2008). The increase in the small fish ( $\leq 10$  cm) biomass index matches most strikingly the increase in 1SW and 2SW consecutive repeat-spawner abundance estimates, but not alternate repeat-spawner abundance estimates (Figure 3).

There were significant (95% BCI excludes zero) first-order autocorrelations of the residuals of predicted annual abundance estimates of consecutive and alternate repeat spawners (Tables 1 and 2). After incorporating the first-order autocorrelation, there was relatively strong support, based on the DIC, for the model of consecutive repeat-spawner abundance estimates that included maiden abundance and small fish ( $\leq 10$  cm) biomass as



**Figure 3.** Input data used to explore the associations between small fish biomass index and returns of 1SW and 2SW salmon to a second spawning as consecutives or alternates. The point estimates of the annual values are shown.

explanatory variables (Tables 1 and 3; Figure 5). The predicted abundance estimates of 1SW consecutive repeat spawners increased, though at a decreasing rate, i.e. in Equation (5),  $0 < \beta_j < 1$ , as the small fish index increased (Table 3). There was no support for a model that included the  $\leq 20$  cm small fish index (Table 3, Figure 5).

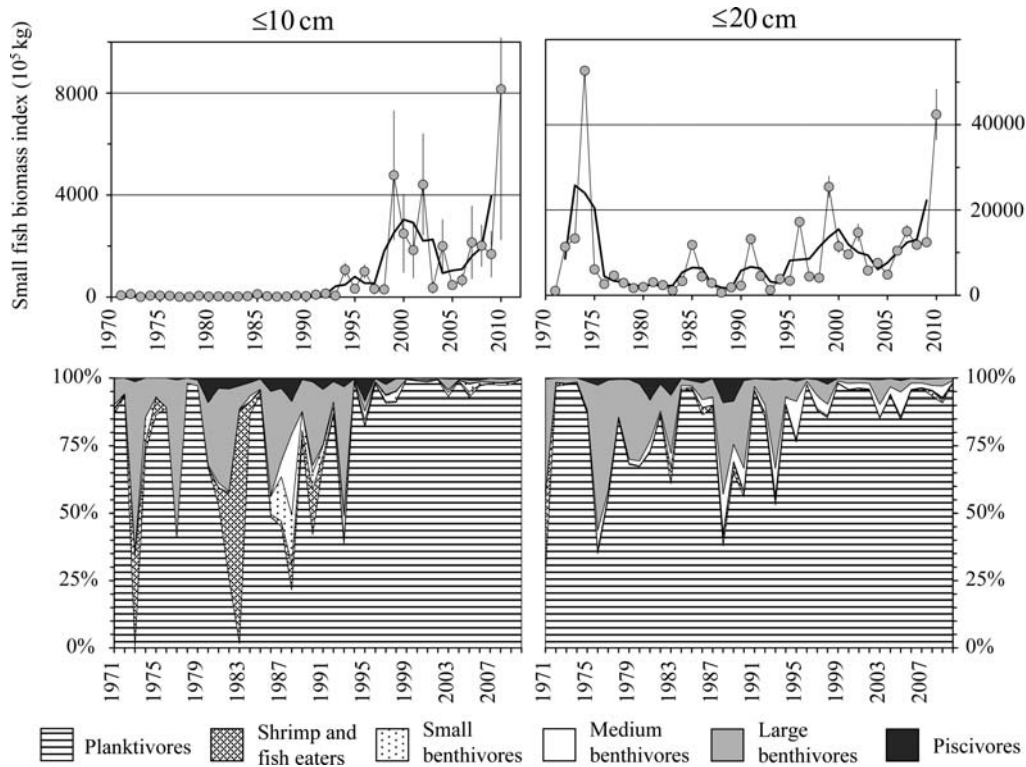
For alternate repeat spawners after incorporating autocorrelation, the maiden abundance was a sufficient explanatory variable for the abundance of repeat spawners, and there was no support, based on the DIC, for including either of the small fish biomass indices as explanatory variables (Tables 2 and 3; Figure 6).

## Discussion

The associations described between the abundance of repeat spawners and the small fish biomass index from the southern Gulf of St Lawrence provide support for one of the two hypotheses proposed regarding bottom-up effects on return rates to a second spawning for Atlantic salmon from the Miramichi River. Consistent with the predictions, the correspondence of prey abundance in the southern Gulf of St Lawrence was strongest for consecutive repeat spawners. These fish are likely to have spent a much greater proportion of their reconditioning time at sea in the southern Gulf of St Lawrence. However, the support for our second hypothesis

that the association between prey abundance and return rates is strongest for indices of prey-fish abundance that correspond to the preferred prey sizes is less clear. Based on the observed sizes of maiden spawners and assumed predator-prey size relationships of 10–20% (Scharf *et al.*, 2000), it was expected that returns of the smaller 1SW-C and 1SW-A spawners would relate best to the biomass index of fish  $\leq 10$  cm long (which was observed most strongly for the 1SW-C), and returns of the larger 2SW-C and 2SW-A spawners would relate best to the  $\leq 20$ -cm index. Failure to characterize the predator size-dependent preferences of salmon properly and an inability to limit reliably the calculation of the biomass index to only those species and survey locations that were available to, and selected by, salmon may explain this finding. Nonetheless, the overall positive influence of prey abundance on the Atlantic salmon return rate to second spawning is noteworthy.

There was a significant autocorrelation in the residuals of the models for predicting the abundance estimates of 1SW and 2SW consecutive and alternate repeat spawners. The presence of autocorrelation can lead to inappropriate rejection of the null hypothesis of no association between two time-series because of a biased and generally underestimated process variance (Pyper and Peterman, 1998). There are some methods for addressing



**Figure 4.** Time-series of catchability-adjusted biomass (mean, one standard deviation error bars;  $\times 10^5$  kg) indices and species group composition (% by weight) for small-bodied fish  $\leq 10$  cm (left panels) and  $\leq 20$  cm (right panels), from the southern Gulf of St Lawrence, 1971–2010. The thick lines in the index plots are 3-year running averages.

**Table 2.** DIC and median of the posterior distributions of the first-order autocorrelation parameter of the residuals by maiden sea age ( $j$ ; 1SW and 2SW) for the models of the return rates to predict the abundance of alternate ( $k$ ) repeat-spawning salmon.

Model	Covariate	DIC	First order autocorrelation ( $\phi_j$ )	
			1SW	2SW
$\alpha_k; \sigma_k^2$		1 245	0.44	0.54
$\alpha_{k,j}; \sigma_{k,j}^2$		1 237	0.35	0.47
$\alpha_{k,j}; \sigma_k^2$		1 235	0.35	0.47
$\alpha_k + \beta_k \log(\text{Bio}_{y,m}); \sigma_k^2$	$\text{Bio} \leq 10$	1 245	0.47	0.51
	$\text{Bio} \leq 20$	1 246	0.43	0.53
$\alpha_{k,j} + \beta_k \log(\text{Bio}_{y,m}); \sigma_k^2$	$\text{Bio} \leq 10$	1 235	0.39	0.43
	$\text{Bio} \leq 20$	1 236	0.34	0.46
$\alpha_k + \beta_{k,j} \log(\text{Bio}_{y,m}); \sigma_k^2$	$\text{Bio} \leq 10$	1 233	0.36	0.42
	$\text{Bio} \leq 20$	1 237	0.35	0.46
$\alpha_{k,j} + \beta_{k,j} \log(\text{Bio}_{y,m}); \sigma_k^2$	$\text{Bio} \leq 10$	1 235	0.37	0.42
	$\text{Bio} \leq 20$	1 238	0.34	0.46
$\alpha_{k,j} + \beta_{k,j} \log(\text{Bio}_{y,m}); \sigma_{k,j}^2$	$\text{Bio} \leq 10$	1 237	0.37	0.42
	$\text{Bio} \leq 20$	1 240	0.34	0.46
First-order autoregressive models				
$\alpha_{k,j}; \phi_{k,j}; \sigma_k^2$		1 221	0.02*	0.07*
$\alpha_{k,j} + \beta_{k,j} \log(\text{Bio}_{y,m}); \phi_{k,j}; \sigma_k^2$	$\text{Bio} \leq 10$	1 221	0.05*	0.01*
	$\text{Bio} \leq 20$	1 223	0.05*	0.05*
$\alpha_{k,j} + \beta_{k,j} \log(\text{Bio}_{y,m}); \phi_{k,j}; \sigma_{k,j}^2$	$\text{Bio} \leq 10$	1 223	0.03*	0.03*
	$\text{Bio} \leq 20$	1 224	0.03*	0.02*

For first-order autocorrelation values, an asterisk indicates that the 95% BCI of the posterior distribution included zero.

autocorrelation of time-series data, including adjusting the test procedure to adequately control the type I error rate (rejection of the null hypothesis when it is not false), or various treatments of the dataseries before analyses, but all methods have

shortcomings (Pyper and Peterman, 1998). In the model analyses conducted, the autocorrelation was directly considered as an additional parameter in the model to estimate, and the resulting process errors, as expressed by the confidence interval ranges of

**Table 3.** Parameter estimates and DIC values from modelling the second-time spawning abundance by spawning history types (*k*) for the 1SW and 2SW maiden ages (*j*) relative to maiden abundance and the indices of small fish biomass (*m*) from the southern Gulf of St Lawrence.

Model	Parameter	Maiden age at maturity ( <i>j</i> )				DIC
		1SW		2SW		
		Median	95% BCI	Median	95% BCI	
Consecutive ( <i>k</i> ) repeat spawners (Table 1)						
(a) $\alpha_{k,j}; \sigma_{k,j}^2$	$\alpha_j$	-4.01	-4.39 to -3.63	-2.96	-3.35 to -2.56	1 255
	$\sigma_j$	1.27	1.04 to 1.64	1.09	0.88 to 1.4	
(b) $\alpha_{k,j} + \beta_{k,j} \log(\text{Bio}_{y,m}); \sigma_{k,j}^2; m \leq 10 \text{ cm}$	$\alpha_j$	-6.53	-7.28 to -5.76	-5.00	-5.74 to -4.26	1 199
	$\beta_j$	0.50	0.35 to 0.64	0.40	0.26 to 0.55	
	$\sigma_j$	0.83	0.67 to 1.06	0.79	0.64 to 1.02	
(c) $\alpha_{k,j} + \beta_{k,j} \log(\text{Bio}_{y,m}); \phi_{k,j}; \sigma_{k,j}^2; m \leq 10 \text{ cm}$	$\alpha_j$	-6.15	-7.12 to -5.02	-5.00	-5.77 to -4.07	1 193
	$\beta_j$	0.44	0.22 to 0.95	0.47	0.25 to 1.88	
	$\sigma_j$	0.61	0.48 to 0.81	0.58	0.47 to 0.75	
	$\phi_j$	0.59	-0.05 to 0.93	0.09	-0.43 to 0.61	
(d) $\alpha_{k,j} + \beta_{k,j} \log(\text{Bio}_{y,m}); \phi_{k,j}; \sigma_{k,j}^2; m \leq 20 \text{ cm}$	$\alpha_j$	-6.55	-9.60 to -3.63	-4.32	-7.63 to -0.93	1 222
	$\beta_j$	0.29	-0.04 to 0.64	0.16	-0.23 to 0.54	
	$\sigma_j$	0.76	0.62 to 0.98	0.74	0.59 to 0.96	
	$\phi_j$	0.88	0.59 to 0.97	0.65	0.23 to 0.88	
Alternate ( <i>k</i> ) repeat spawners (Table 2)						
(a) $\alpha_{k,j}; \sigma_{k,j}^2$	$\alpha_j$	-3.11	-3.33 to -2.88	-2.55	-2.78 to -2.32	1 235
	$\sigma_j$	0.68	0.55 to 0.87	0.66	0.53 to 0.85	
(b) $\alpha_{k,j}; \phi_{k,j}; \sigma_k^2$	$\alpha_j$	-3.10	-3.37 to -2.75	-2.57	-2.87 to -2.28	1 221
	$\sigma_j$	0.49	0.39 to 0.65			
	$\phi_j$	0.65	-0.02 to 0.94	0.70	0.14 to 0.92	
(c) $\alpha_{k,j} + \beta_{k,j} \log(\text{Bio}_{y,m}); \phi_{k,j}; \sigma_{k,j}^2; m \leq 10 \text{ cm}$	$\alpha_j$	-3.28	-4.03 to -2.53	-3.11	-3.81 to -2.40	1 223
	$\beta_j$	0.03	-0.10 to 0.18	0.11	-0.02 to 0.24	
	$\sigma_j$	0.50	0.39 to 0.66	0.45	0.36 to 0.60	
	$\phi_j$	0.63	0.08 to 0.94	0.67	0.13 to 0.93	
(d) $\alpha_{k,j} + \beta_{k,j} \log(\text{Bio}_{y,m}); \phi_{k,j}; \sigma_{k,j}^2; m \leq 20 \text{ cm}$	$\alpha_j$	-3.95	-6.22 to -1.61	-2.54	-4.76 to -0.28	1 224
	$\beta_j$	0.10	-0.17 to 0.37	0	-0.26 to 0.25	
	$\sigma_j$	0.49	0.39 to 0.64	0.47	0.37 to 0.62	
	$\phi_j$	0.57	0.02 to 0.90	0.71	0.20 to 0.93	

The posterior distributions are summarized with the median and the 95% BCI values.

the predicted values, were greater than when the autocorrelation was not modelled. Although the conclusions of these time-series analyses are not immune to the possibility of a spurious correlation, we can point to several reasons why the return rates could most likely be related to improved feeding conditions rather than to other factors that would also be acting on the abundance of small fish in the southern Gulf of St Lawrence.

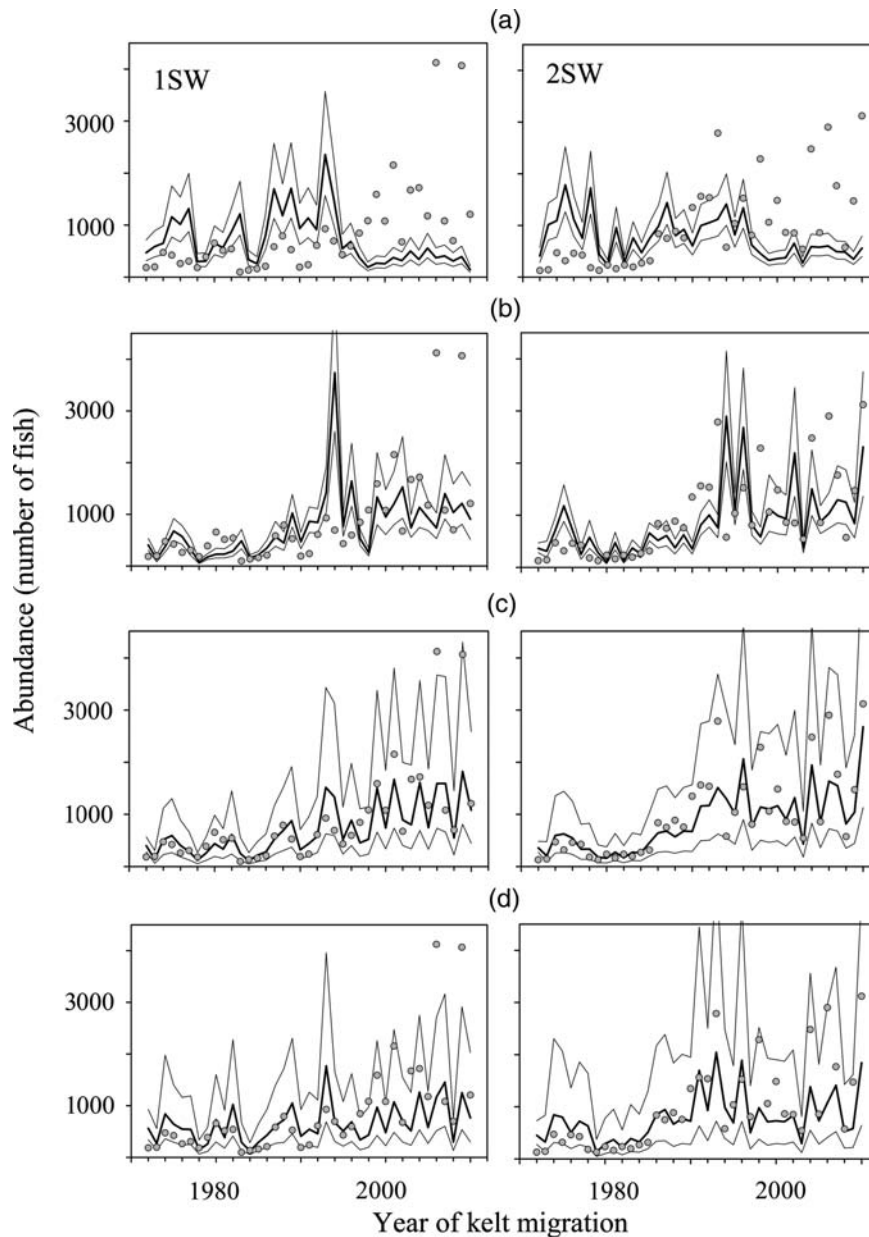
Benoit and Swain (2008) attribute, by weight of evidence, the increase in the small fish index to reduced predation pressure resulting from the collapse of the previously dominant groundfish stocks (e.g. cod, skate, flatfish species) in the area. Atlantic salmon post-spawners are too large to have been preyed upon by these dominant groundfish species, so the increased return rate is unlikely to be the result of reduced predation by these groundfish species on salmon. Post-spawned Atlantic salmon prey on many small fish species that are common in the southern Gulf of St Lawrence, and there is a large potential overlap in both space and time between short-migration, consecutive-returning salmon and the small marine fish of the southern Gulf of St Lawrence. The present analysis provides evidence that this increased biomass of small fish has benefited Atlantic salmon by providing an increased and abundant food source for reconditioning and return to a second spawning (bottom-up effect). However, with a total North Atlantic population of 3–10

million adult-sized individuals (Chaput, 2012), the abundance of Atlantic salmon in the southern Gulf of St Lawrence ecosystem is very unlikely to cause a change in small fish abundance. As a beneficiary, though not an agent, of small fish abundance change, Atlantic salmon in the Gulf of St Lawrence provide an ideal species in which to detect the bottom-up influences of prey abundance on a large fish in the marine environment.

Understanding the factors that influence the marine survival of post-spawning salmon is complicated by the confusion of maturation strategy choice (consecutive vs. alternate) and actual survival. Increased return rates of repeat spawners certainly represents improved survival rates to a second spawning, but the relative proportions of consecutive and alternate repeat spawners may also reflect the choice of reproductive tactic. An environmental effect on either survival or life history in the wild is, in itself, very interesting and noteworthy. We briefly discuss the evidence available to tease the effects apart.

Hubley and Gibson (2011) describe a model that uses abundance by sex and maiden sea age to separate return rates and maturation rates in a population of salmon for which return rates have declined over the past two decades, in contrast to the increased return rates noted in the Miramichi population. There has been a switch in the relative abundance of consecutive and alternate repeat spawners since 1998 for both 1SW and 2SW age groups;



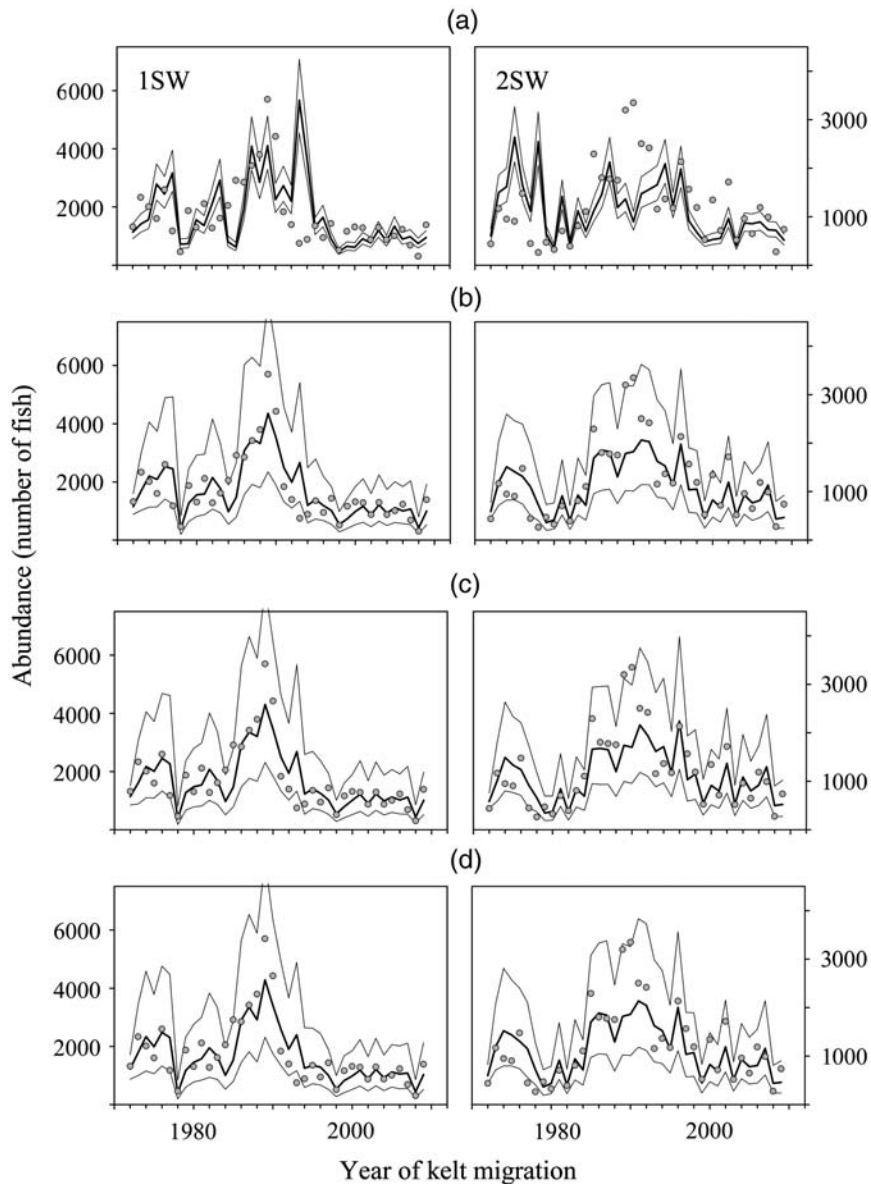


**Figure 5.** Predicted abundance (lines; median and 95% credibility interval) and observed abundance (circles) of consecutive second-time spawners of 1SW (left panels) and 2SW (right panels) salmon by year of kelt migration. (a)–(d) refer to the four models in the sequence shown and labelled as such in Table 3.

before 1998, alternate repeat spawners were more abundant, but since 1998, consecutive repeat spawners have become more abundant. Large variations in age at maturity and spawning histories are noted in Atlantic salmon (Moore *et al.*, 1995; Niemelä *et al.*, 2006), suggesting that the rematuration process may, to a large extent, be conditioned by the environment. Post-spawning salmon can be readily reconditioned in a hatchery by feeding with rainbow smelt, Atlantic silverside, and capelin, and post-spawned salmon can rapidly put on weight under manipulated light and temperature conditions (Crim *et al.*, 1992; Johnston *et al.*, 1992). Johnston *et al.* (1992) state that the level of reconditioning influences the rematuration process, such that kelts with high condition generally initiate gonadal development more frequently, which would be consistent with the association between

prey abundance and the increased return rates of consecutive repeat spawners described in this study.

A number of small-bodied fish species that are common marine prey of Atlantic salmon is present in the southern Gulf of St Lawrence, including capelin, herring, and barracudina. Rainbow smelt are estimated to be the most abundant anadromous fish in the Miramichi River, and the spawning migration of rainbow smelt corresponds spatially (lower portions of the Miramichi River) and temporally (April and May) with the downstream migration and reconditioning period of post-spawned Atlantic salmon (Chaput, 1995). Rainbow smelt are also found in the shallower and generally nearshore strata of the southern Gulf of St Lawrence, which would make them available to post-spawned salmon during their reconditioning migration at sea



**Figure 6.** Predicted abundance (lines; median and 95% credibility interval, lines) and observed abundance (circles) of alternate second-time spawners of 1SW (left panels) and 2SW salmon (right panels) by year of kelt migration. (a)–(d) refer to the four models in the sequence shown and labelled in Table 3.

(Benoît *et al.*, 2003). Niemelä *et al.* (2006) reported that repeat-spawner abundance could be described based on previous maiden-spawner abundance and sea temperatures in spring of the year of the kelt migration, the supposition being that warmer temperatures favoured survival and/or rematuration rates.

Combined return rates can be interpreted as survival rates to a second spawning, and for 2SW salmon, they are about twice the values estimated for 1SW salmon. This could be explained by differences in the overwinter post-spawning survival of male and female salmon. Overall, male and female salmon expend the same relative amount of energy during spawning, but the survival rate is less for males because of injuries and infections resulting from competition for mates (Fleming, 1996). Generally, >80% of 1SW salmon in the Miramichi River are male, in contrast to 2SW salmon, which are mostly

(>75%) female (Moore *et al.*, 1995; Chaput *et al.*, 2010). On the other hand, the pattern in overall survival is also consistent with a general macroecological trend for decreased mortality with body size in fish as a result of the lower risk of size-dependent predation (Gislason *et al.*, 2010).

The increased abundance of consecutive repeat spawners has contributed to the large increase in the abundance of salmon on a second spawning migration. The abundance of salmon on their third or more spawning migration has also increased at a time when 1SW and 2SW maiden abundance has declined, which suggests that the marine conditions favouring the survival of the large-bodied post-spawners have improved. Declines in maiden 2SW salmon have been most obvious since the 1989–1991 maiden sea years, when relative productivity, expressed as recruits per spawner, with recruits measured at the 1SW non-

maturing stage in the second summer at sea, decreased and remained low (Chaput *et al.*, 2005).

The expanding spawning age structure of the Atlantic salmon population in the Miramichi River has been associated with reductions in fisheries exploitation (Moore *et al.*, 1995). The most important changes in fisheries exploitation were in 1984 with the closure of the commercial fisheries in the southern Gulf of St Lawrence and in 1992 with the closure of the sea fisheries in Newfoundland and Labrador, and reductions in the West Greenland fishery (Moore *et al.*, 1995). Increased return rates of consecutive repeat spawners would be unrelated to reduced exploitation in the distant-water fishery at West Greenland because those fish do not migrate to those areas during the short period they are at sea between spawnings nor to the closure of the commercial fisheries of Newfoundland and Labrador after 1992. This short period at sea, as noted by the timing of returns of consecutive spawning salmon at the estuary monitoring traps (GC, pers. obs.), suggests that they probably feed within the Gulf of St Lawrence.

The fact that the small fish biomass index appears to have little or no influence on the return rates of alternate repeat spawners is consistent with these fish spending little time in the southern Gulf of St Lawrence, so the return rates would not be expected to respond directly to improved prey fields in the first months at sea. Alternate repeat spawners are presumed to migrate to the Labrador Sea and beyond, as evidenced by recaptures of tagged kelts from the Miramichi River at West Greenland in September and October of the year of kelt migration (Chaput *et al.*, 2010), and to spend less time than consecutive repeat spawners in the Gulf of St Lawrence after returning to sea in April and May. These alternate repeat spawners would be unable to return to the Miramichi River in time for spawning in the same year, and this longer duration at sea to feed results in greater growth in length than for consecutive repeat spawners. Alternatively, survival conditions in the later part of the marine migration of alternate repeat spawners may have deteriorated such that any improvement in early marine-phase survival associated with abundant prey is cancelled out by greater mortality offshore.

The most important new information derived from this study is that ecosystem changes in the Gulf of St Lawrence, expressed as increased biomass of small-bodied fish, appear to have resulted in an increased return rate to a second and consecutive spawning of Atlantic salmon in the Miramichi River. The increased abundance and return rates of these large-bodied fish have occurred at the same time as historically important large marine fish in the Gulf of St Lawrence are manifesting increased adult mortality, probably through predation by grey seals (*Halichoerus grypus*; Benoît and Swain, 2008; Benoît *et al.*, 2011; DFO, 2011). The lack of a top-down effect by grey seals on Miramichi salmon, despite evidence of this effect on large marine fish in the ecosystem, is consistent with the considerably greater swimming speed of salmon, likely conferring on them a greater ability to evade this predator, and less temporal and spatial overlap with seals than the groundfish species. The increase in the return rates of salmon provides an exception to the ecosystem dynamic described by Benoît and Swain (2008); specifically, the absence of evidence for the bottom-up effects of prey availability on adult marine fish. For Atlantic salmon, prey abundance in the southern Gulf of St Lawrence appears to be an important and direct driver of post-spawner survival and rematuration, particularly for consecutive repeat spawners that probably reside in the Gulf of St Lawrence before returning to spawn.

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