

# The complex interaction of ecology and hydrology in a small catchment: a salmon's perspective

R. A. Cunjak,<sup>1\*</sup> T. Linnansaari<sup>1</sup> and D. Caissie<sup>2</sup>

<sup>1</sup> Canadian Rivers Institute and Department of Biology, University of New Brunswick, Fredericton, NB, Canada

<sup>2</sup> Fisheries and Oceans Canada, P.O. Box 5030, Moncton, NB, Canada

## Abstract:

For the past 22 years, we have monitored hydro-meteorological conditions and fish population dynamics in Catamaran Brook, a 52 km<sup>2</sup> catchment in the Miramichi River system of New Brunswick, Canada. Given the long-term nature of the multidisciplinary dataset, we are able to provide an overview of the complex interaction between streamflow and fish population dynamics drawing on previously published material as well as new data analyses. For autumn-spawning fishes like the Atlantic salmon, access to headwater reaches was directly related to streamflow during late October (when they ascend spawning tributaries), as well as the propensity of beaver dams in the stream (also a function of streamflow). Winter streamflow was positively correlated with egg survival, except when rain-on-snow conditions induced severe ice break-up events that likely caused the highest mortalities on record for salmon and other fishes. Juvenile recruitment was significantly influenced by density-dependent processes of growth and competition but further mediated by density-independent factors like winter flow. In spring, fry emergence was largely temperature-driven, although peaks in fry drift were sometimes synchronized with secondary discharge peaks and temperature. Tributaries like Catamaran Brook provide thermal refugia for coolwater fishes like salmon and trout during the summer when wide, shallow main-stem Atlantic rivers experience low discharge and high water temperatures that induce physiological and behavioural stress (i.e. > 23 °C). These phenomena are discussed in detail, especially in terms of how they may be compromised by future changes in hydrologic conditions resulting from predicted climate change scenarios. Copyright © 2012 John Wiley & Sons, Ltd.

KEY WORDS Atlantic salmon; ecology; streamflow; climate change

Received 15 April 2012; Accepted 29 October 2012

## INTRODUCTION

Linkages between hydro-geomorphic characteristics and the biotic responses in rivers are well documented (Hynes 1970, 1975; Schlosser, 1991; Thorp and Delong, 1994; Bunn *et al.*, 2006; Tetzlaff *et al.*, 2007). This is the basis for some of river ecology's most tried and tested theories of how physical processes shape riverine communities (e.g. Vannote *et al.*, 1980; Junk *et al.*, 1989). Indeed, basin hydrology and streamflow are probably the main drivers of river ecosystem function (Poff *et al.*, 1997; Bunn *et al.*, 2006). Deviation from normal streamflow patterns, because of anthropogenic activity, has been linked to ecosystem instability and declines in animal abundance (Ligon *et al.*, 1995; Poff *et al.*, 1997; Beechie *et al.*, 2006).

Understanding this complex relationship between river hydrology and ecology is obviously important if we are to make good on society's lofty goals of managing and conserving ecosystem function and ecological integrity (Dodson *et al.*, 1998; Tockner *et al.*, 1998; Thorp *et al.*, 2006). To further complicate the issue, climate change and its inherent, if inexact, probability for altering future temperature and hydrologic regimes (Meehl *et al.*, 2007; Prowse *et al.*, 2009) will impose new dynamics for the relationship between physical processes and river biota

(e.g. Linnansaari and Cunjak, 2012). A major difficulty in quantifying these inter-relationships, especially the implications of climate change, is the relative lack of biological and physical data that are comparable over large and variable geographic space (i.e. continents) and over a long time series (e.g. decades). The North-Watch Project (Carey *et al.*, 2010) provides such an opportunity as a large-scale comparative project focused on small stream basins in North America and Europe and the inter-linkages between climate, hydrology and ecology.

In this paper, we use a 22-year inter-disciplinary data series from one of the North-Watch study rivers (Catamaran Brook, Miramichi, Canada) to investigate the inter-relationship of Atlantic salmon, *Salmo salar*, and hydrologic factors inherent to the Miramichi basin and the boreal-temperate Canadian climate. Specifically, we address two objectives. First, we focus on how natural hydrologic variability in different seasons can influence the population dynamics of wild Atlantic salmon by focusing on each of the life-stages inhabiting the sub-basin – from eggs to juveniles (parr, smolts) to adults. The different behaviours and sensitivities of each life-stage, at different seasons, underscore the complexity of the streamflow-organism relationship. Our second objective is to use regional projections of (air) temperature from climate change models to predict future changes in water temperature, stream hydrology and habitat suitability in terms of the potential effect on salmon population dynamics

\*Correspondence to: Richard Cunjak, Biology Department and Canadian Rivers Institute, University of New Brunswick.  
Email: cunjak@unb.ca

in the Miramichi basin. It is hoped that the results will contribute to a better understanding of physical stressors and biotic responses and will stimulate discussion about the implications of future stressors (e.g. climate change) that will invariably change the hydrologic regime in rivers.

## METHODS/STUDY AREA

Catamaran Brook is a third-order tributary stream of the Miramichi River in central New Brunswick (Figure 1), with a drainage basin of 52 km<sup>2</sup> and a mean slope of 1.3%. Catamaran Brook is approximately 15–20 m wide in the middle and lower reaches and has a mean water depth of 0.21 m during average flow conditions. Habitat in Catamaran Brook is predominately riffles (31%), followed by runs (53%), flats (12%) and pools (4%; Cunjak *et al.*, 1993). The substrate is mostly coarse gravel and cobbles with median particle diameters twice as large in riffles (6.3–14 cm) as in the flats (2.7–6 cm); bed stability as measured by the tractive force,  $\tau$ , in 12 sites throughout the stream length, ranged from 2.5 to 12.5 kg/m<sup>2</sup> during bankfull flows (Giberson and Caissie, 1998). Mean annual discharge is 1.13 m<sup>3</sup> s<sup>-1</sup> with peak annual flows typically occurring in April/May associated with snowmelt freshets. The brook is a well-buffered, soft-water stream with an average pH of 7.26. The catchment is located on the margin of the Miramichi highlands, originating at an altitude of 250 m above sea level. The basin's geology is characterized as Paleozoic volcanic and sedimentary basement overlain by glacio-fluvial deposits of loamy to sandy loam texture. Forest cover is predominantly second-growth, southern boreal species such as *Picea glauca*, *Abies balsamea*, *Betula papyrifera*, *Acer rubrum* and *Populus tremuloides*.

The Catamaran Brook Habitat Research Project was initiated in 1990 as a joint initiative by government,

university and industry partners. The long-term objectives were 1) to quantify the impacts of forestry on the hydrology and aquatic biota, especially the wild Atlantic salmon population; and 2) to determine the important processes that characterized ecosystem function within the basin.

Hydrologic monitoring within the Catamaran Brook basin was mainly accomplished at separate meteorological and hydrometric stations in mid-basin (Figure 1), as well as numerous water temperature monitoring sites within the study reaches. The meteorological station monitors commonly measured parameters at hourly intervals such as air temperature and relative humidity, wind speed and direction (at a height of 10 m), incoming short-wave radiation (solar radiation) and precipitation. Meteorological data within the region indicates that the Catamaran Brook basin receives approximately 1130 mm of precipitation annually, of which, 300 mm fall in the form of snow and 830 mm in the form of rain (Caissie and El-Jabi, 1995; Caissie *et al.*, 2002). A streamflow gauging station is located at the mid-basin (area of 28.7 km<sup>2</sup>), and the annual runoff was calculated at 696 mm. Water losses through evapotranspiration (ET) were estimated at 434 mm annually. As in most northern latitude rivers, most of the evapotranspiration occurs during the summer. The water temperature monitoring within Catamaran Brook and the nearby Little Southwest Miramichi River constitute one of the longest water temperature time series in New Brunswick (> 20 years). Both of these sites were modeled using a variety of water temperature models (e.g. Caissie *et al.*, 2001, 2007).

The hydrology of Catamaran Brook is characterized by two high flow (spring and autumn) and two low flow (summer and winter) periods (Figure 2). Whereas Catamaran Brook can experience high flow events throughout the year, peak flows typically occur in the spring associated with the snowmelt freshet. The maximum recorded discharge (13 m<sup>3</sup>/s) in the 20+ year data series was measured twice (3 May 1991 and 14

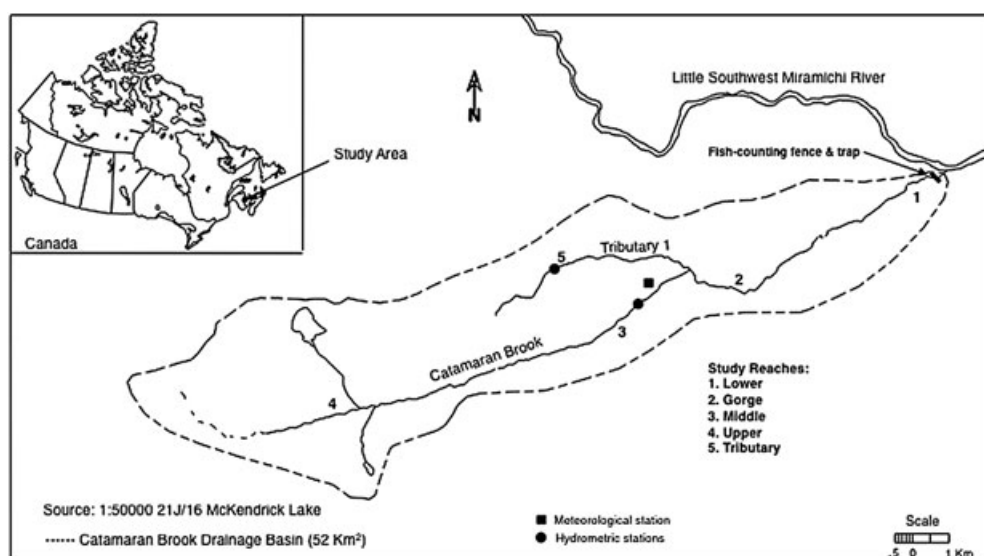


Figure 1. Map of the Catamaran Brook basin in central New Brunswick showing locations of hydrometric and meteorological stations and study reaches where annual fish sampling (electrofishing) took place. The fish-counting fence and trap located at the stream mouth is represented by the black bar

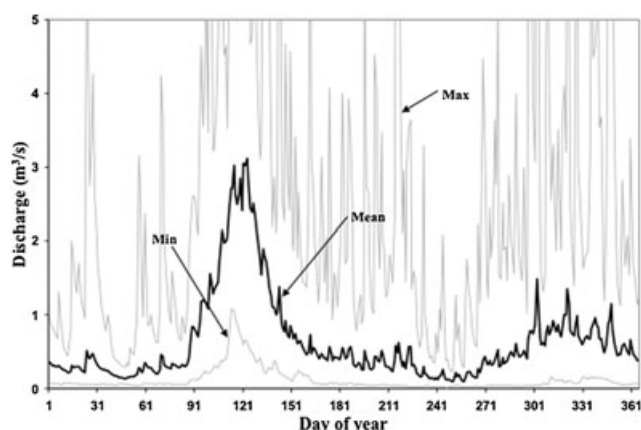


Figure 2. Streamflow characteristics of Catamaran Brook (1990–2010) showing high and low flow periods. The dark line shows mean discharge whereas the light lines show both minimum and maximum values

December 2010). Using a 30-day discharge running mean to define high and low flow periods, the winter low flow occurs around February 21 (day 52) and the spring flood occurs around 28 April (day 118; Figure 2). The summer low flow occurs around August 30 (day 242), whereas the autumn high flow period occurs around November 11 (day 315). Both the winter and summer low flow periods are of similar magnitude ( $0.21 \text{ m}^3/\text{s}$  vs  $0.17 \text{ m}^3/\text{s}$ , respectively).

Biological research, mainly focused on fish populations, has been ongoing since 1990. A full description of the various activities was outlined in Cunjak *et al.* (1993). Briefly, the major annual monitoring activities involving Atlantic salmon include the following:

- 1) a fish-counting fence near the stream mouth (Figure 1) operated from May to November each year (1990–2008) to enumerate and measure all fishes entering and leaving Catamaran Brook (Hardie *et al.*, 1998). Atlantic salmon smolts are typically age 3 when emigrating. On average, the annual estimated number of smolts emigrating from Catamaran Brook was 972. An estimated 110 adult salmon (ratio of 3 grilse: 1 multi-sea-winter salmon) entered Catamaran Brook each autumn to spawn (Cunjak, unpubl. data).
- 2) annual electrofishing surveys in 26–32 study sites from headwaters to the lower reaches have been conducted in the summer and autumn from 1990–2010 using a multiple-sweep depletion method to estimate fish abundance (Zippin 1958), distribution, species diversity and density (Mitchell *et al.*, 2004; Mitchell and Cunjak 2007b). The same sites were electrofished each year, with each site's area dictated by the entire habitat type it represented (i.e. pool, riffle, run, flat); consequently, wetted area of a site varied amongst years depending on discharge conditions at the time of sampling. In total, 17 fish species have been captured in Catamaran Brook. Atlantic salmon is the most abundant as well as being the species with the highest biomass. Approximately 100 000 wild juvenile salmon (all ages pooled) rear in Catamaran Brook each year (Cunjak and Therrien 1998).

- 3) daily estimates of emigrating salmon fry were determined from counts in 2–4 drift-traps set in the stream mouth from late May until early July, 1994–2002 (Johnston, 1997). Between 7000 and 33 000 salmon fry are estimated to emigrate from the brook every spring (Cunjak and Therrien, 1998).

## RESULTS AND DISCUSSION

### Adult spawning migration and autumn flows

In eastern Canada, Atlantic salmon spawn during the autumn. In small-order, tributary streams like Catamaran Brook, mature salmon typically ascend, from the main river, between late September (day 270) and early November (day 310) coincident with increasing autumn flows (Figure 2). A comprehensive analysis of the influence of autumn streamflows on adult salmon entering Catamaran Brook by Mitchell and Cunjak (2007a) demonstrated that adult abundance showed a strong positive relationship ( $r^2 = 0.65$ ) with maximum discharge during the period of upstream (spawning) migration (Figure 3). Moreover, regression analysis showed that the number of adults entering the stream in any year was better predicted by maximum discharge than by overall salmon abundance in the larger Miramichi River system (as estimated annually by federal biologists, Mitchell and Cunjak, 2007a). Similar correlations between streamflow and spawning salmon entry to a small tributary stream in Scotland were noted by Tetzlaff *et al.* (2007).

The proportion of adults composed of grilse (1 sea-winter, small salmon), as well as female body size, was also log-related to stream discharge (Mitchell and Cunjak, 2007a). This provides further evidence of the importance of streamflow as higher autumn flows resulted in more, large multi-sea-winter female salmon but fewer grilse entering the stream. This finding has significant conservation implications because the larger the female, the more eggs are available for deposition. The number of eggs is typically

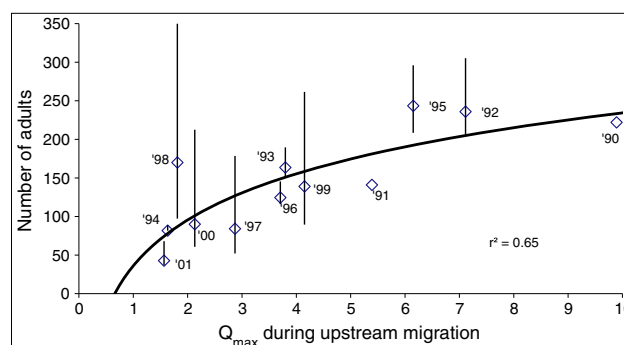


Figure 3. Annual estimates of adult Atlantic salmon entering Catamaran Brook as a function of maximum stream discharge ( $Q_{\max}$ ) during the period of upstream migration, September–November. Estimates were derived using the Peterson method based on marking upstream migrants and recapturing post-spawned adults at the counting-fence during the same autumn. Vertical lines represent 95% confidence intervals for adult estimates (constructed from graph of binomial confidence limits, Krebs 1989). (modified from Mitchell & Cunjak 2007a)

the key variable used by salmon biologists when assessing the potential for a population to be self-sustaining; by contrast, grilse are predominantly male and of relatively less 'value' from a conservation perspective.

Spawning activity in Catamaran Brook typically takes place between late October and the first two weeks in November (Cunjak, unpubl. data). Immediately following spawning, spent adults (kelts) descend the stream, while stream discharge is still relatively high (Figure 2), to overwinter in the larger, deeper Miramichi River system. There has likely been strong selection pressure for this winter strategy in the ice-covered rivers of eastern Canada. Small tributary streams, like Catamaran Brook, experience significant ice accumulation in early winter (Stickler *et al.*, 2010). Subsequent low winter flows (Figure 2), in combination with ice build-up, would greatly reduce habitat availability (Cunjak *et al.*, 1998), particularly for large-bodied fishes such as salmon kelts. In many rivers, postspawning mortality of Atlantic salmon is considered to be high (e.g. Klemetsen *et al.*, 2003). However, in some Canadian rivers, kelt survival and multiple spawning can be significant. For example, in the Miramichi River system, repeat spawners now contribute between 25% and 35% of annual egg deposition (Chaput and Jones 2006). Therefore, a strategy wherein salmon kelts emigrate from spawning tributaries while stream discharge is still relatively high is adaptive and probably important to maintaining population stability.

Autumn flows in streams like Catamaran Brook can have other important ecological consequences. Beaver dams are common, natural barriers in many Canadian streams. Their potential impact as a barrier to migrating fishes is a direct function of streamflow, especially maximum daily discharges of sufficient magnitude to breach dams and stimulate fish movement. In 1994, autumn flows were among the lowest on record (Figure 3). That year, a beaver dam was constructed in the lower reach of the brook, < 1 km upstream of the mouth. Spawning salmon, concentrated in the lower reaches, were unable to pass upstream. The result was an unusually high density of spawning and redds, below average egg survival (17%) and high egg predation (Cunjak and Therrien, 1998) – evidence of density-dependent consequences for salmon population dynamics. Such complicated salmon-beaver-streamflow inter-relationships in Catamaran Brook has also been shown to affect fish community structure, especially the abundance of cohabiting slimy sculpin (Mitchell and Cunjak, 2007b).

#### Winter streamflow and survival of eggs and juveniles (parr, smolts)

Winter conditions can have significant impacts on stream fishes at the individual, population and community levels (Cunjak *et al.*, 1998; Huusko *et al.*, 2007; Linnansaari and Cunjak 2010; Linnansaari *et al.*, 2008). The eggs of fall-spawning salmonids are especially dependent on the physical conditions of winter as eggs (and developing alevins) represent a non-mobile stage that exists entirely during the cold season. Based on linear regression analysis

of the first six years of data collected in Catamaran Brook, results suggested that the survival of Atlantic salmon eggs (to the summer fry stage) was positively dependent on winter streamflow (calculated as the discharge following autumn spawning and until the start of the snowmelt freshet; Cunjak *et al.*, 1998). Extending this research by including 11 years for which egg survival data were available continues to show a significant positive relationship ( $r^2=0.41$ ;  $p < 0.05$ ) between egg survival and winter streamflow (Figure 4a), which may be related to some of the complex inter-relationships of stream hydraulics and inter-gravel water chemistry (Malcolm *et al.*, 2012). It should be noted, however, that extreme high winter flows associated with an ice-break-up event can also be a major physical disturbance in rivers (Prowse 2000) with the potential for causing significant mortality for stream fishes. For example, during the winter of 1995/1996 in Catamaran Brook, a mid-winter rain-on-snow event precipitated a rare mechanical ice break-up and bed scour that probably caused very high egg and parr mortalities (Cunjak *et al.*, 1998).

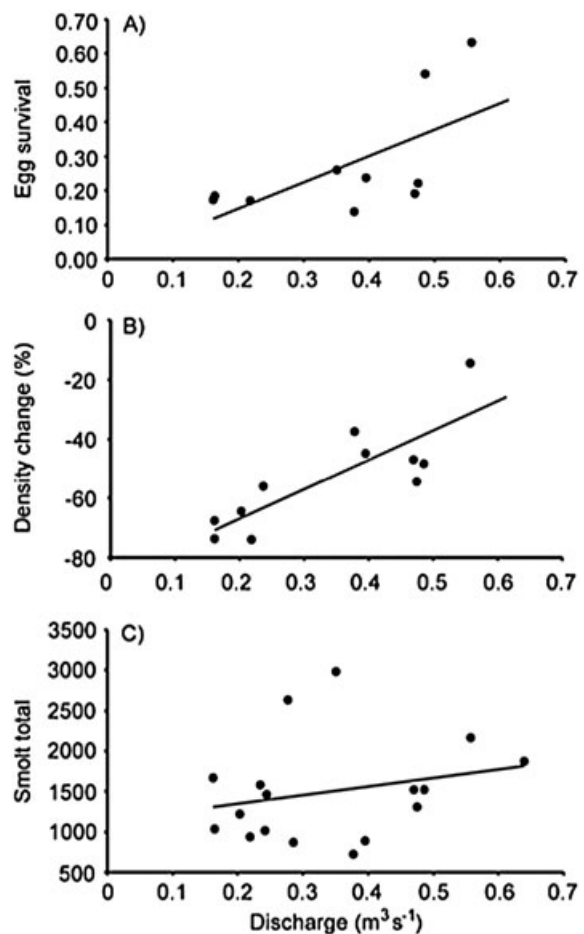


Figure 4. Relationship between winter discharge (1 December to 31 March) and A) salmon egg survival, 1990–2000, B) % change in autumn-to-summer density of juvenile Atlantic salmon (composite of all age classes), 1990–2002, in the Lower Reach of Catamaran Brook, and C) estimated smolt totals, 1990–2008, in Catamaran Brook. Note that the winter 95/96 data point was removed from all three plots because it was an ice-affected anomaly (see Cunjak *et al.*, 1998)

The influence of winter streamflow on the juvenile (parr) stage of Atlantic salmon has been suggested in previous studies (Frenette *et al.*, 1984; Gibson and Myers, 1988). In winter, juvenile salmon display photonegative behavior and shelter beneath coarse substrates during the daytime (Rimmer *et al.*, 1983). Because shelters are rarely shared between individuals (Cunjak, 1988), the amount of suitable daytime sheltering locations may become a limiting resource that is controlled by stream discharge and its direct effect on total wetted streambed and habitat availability. This hypothesis seems to be supported based on seasonal electrofishing data available for 13 years (1990–2002) from 8 to 10 sites in the Lower Reach of Catamaran Brook (where sample sizes for different age-classes are sufficient for analysis). As shown in Figure 4b, the percent reduction in average density of salmon parr from autumn to the following summer was least when winter streamflow was high, but the density change declined markedly as average winter flow decreased ( $r^2 = 0.69$ ,  $p = 0.001$ ).

Could seasonal streamflow also influence the numbers of smolts emigrating in the spring? In coastal Washington streams where summer is the critical low-flow season, Seiler *et al.* (2001) found that coho salmon smolt production in spring increased when the previous summer's flows increased. Hvidsten (1993) provided some evidence that Atlantic smolt production could be enhanced by increasing winter discharge in a regulated river in Norway. In Catamaran Brook, between 1990 and 2008, the relationship between winter streamflow and smolt abundance the following spring was weak (Figure 4c) even when accounting for variable capture efficiencies at the fence (Cunjak and Therrien, 1998). The lack of a significant relationship between salmon smolts and winter discharge indicates there are probably a number of factors affecting smolt production, not just the pre-smolt winter streamflow (e.g. Hvidsten, 1993; Beecher *et al.*, 2010). In Catamaran Brook, juvenile salmon spend an average of three years in the stream before emigrating as smolts. Also, unlike eggs, juvenile (pre-smolt) salmon in Catamaran Brook are able to move in response to changing flow and temperature conditions, in all seasons (Hardie *et al.*, 1998) including immigration to, and emigration from, the brook prior to smolt enumeration (Cunjak and Therrien, 1998).

#### Spring flow pulses in synchrony with salmon fry drift (1994–2002)

In the Miramichi River system, Atlantic salmon fry emerge from the substrate in early June. Randall (1982) noted that salmon fry emergence in Catamaran Brook peaked during the second and third weeks of June, similar to what was subsequently found by Johnston (1997). Emergence timing by salmonid fishes has generally been attributed to temperature-driven development rates (Gustafson-Marjanen and Dowse 1983; Crisp 1988), although egg size and dissolved oxygen concentrations in redds also have an influence (Malcolm *et al.*, 2012). Once the appropriate degree-days have been accumulated, and yolk sac absorption has occurred coincident with the

initiation of exogenous feeding (Dill, 1977), alevins initiate emergence from the gravel and drift downstream immediately thereafter (Johnston, 1997).

In Catamaran Brook, where fry drift has been monitored every spring between 1994 and 2002, we found that emergence generally occurred during mid-June (Figure 5). The exception to this timing was 1999 when fry drift was concentrated during the first few days of June (Figure 5). The relatively early drift timing is attributed to the atypically low flows and warm water temperatures experienced in the spring of 1999. For instance, daily discharge measurements in Catamaran Brook during May and June of 1999 were the lowest measured for the years when fry drift was monitored (1994–2002). The mean discharge for this period in 1999 was  $0.34 \text{ m}^3 \text{ s}^{-1}$  compared with an average discharge of  $0.84 \text{ m}^3 \text{ s}^{-1}$  (May–June, 1994–2002). Water temperatures in Catamaran Brook during May and June were also higher than normal in 1999; water temperature in May was  $+2.1^\circ \text{C}$  higher than the average for May from 1994–2002, and June water temperature in 1999 was  $+3.4^\circ \text{C}$  higher than the long-term average. Differences in Atlantic salmon drift timing associated with water temperature regimes have also been shown found by Johnston (1997) and Bujold *et al.* (2004) in New Brunswick and Newfoundland rivers, respectively.

Fry drift in Catamaran Brook seemed to occur largely independent of the stream discharge regime. However, closer examination of emergence timing and secondary

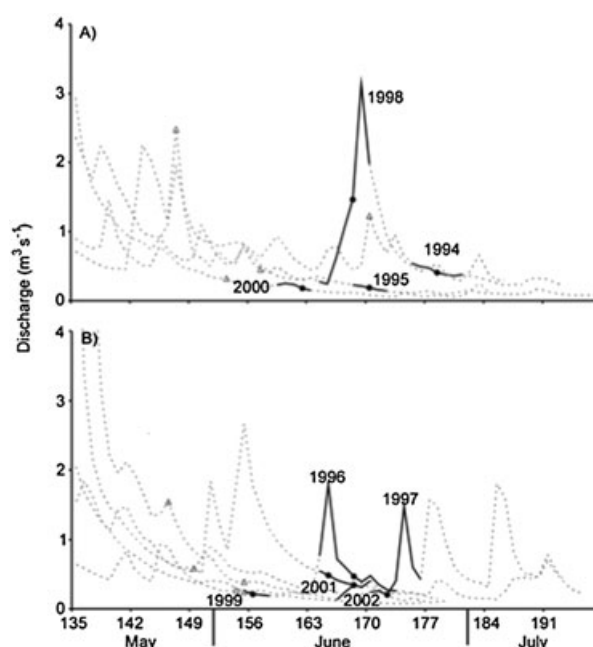


Figure 5. The relationship between stream discharge and the drift timing of Atlantic salmon fry in Catamaran Brook, 1994–2002. A) Hydrographs of individual years when the measured spring discharge (April–May) was higher than the spring median discharge of the study period (i.e. high spring flow years). B) Hydrographs of individual years when the spring discharge (April–May) was lower than the spring median discharge of the study period (i.e. low spring flow years). The thick black line emphasizes of each discharge curve highlights the inter-quartile range when 25–75% of all captured fry drifted in a given year; the filled circle highlights the date when 50% of all drifting fry of each year had been captured (i.e. median). Triangles represent the start date of fry drift sampling for a given year. The x-axis indicates the ordinal date of each calendar month

discharge peaks in the hydrographs indicates that timing coincided with secondary discharge peaks in the month of June in most years (Figure 5). Johnston (1997) noted a similar synchrony with small increases in stream discharge in Catamaran Brook and the nearby Little Southwest Miramichi River, and similar observations were made by Bujold *et al.* (2004) in a Newfoundland river system. Synchronization with small discharge events may be used as a trigger to facilitate dispersal of salmon fry downstream, as with other riverine fishes (e.g. coregonids, Naesje *et al.*, 1995). Such a relation may be adaptive for dispersal once development has been completed, especially following the larger snowmelt freshet which may be too large, and associated with temperatures too cool, to optimize swimming performance and settling after dispersal.

#### *Summer flow-water temperature relationship and potential constraints to growth and density*

The Miramichi River system is known to be a system where the water temperature gets quite warm during the summer and many days can exceed 23 °C. This water temperature (i.e. 23 °C) has been shown to be of significance for juvenile Atlantic salmon, wherein feeding and growth ceases when instantaneous temperatures exceed this threshold (Elliott, 1991; Elliott & Hurley 1997) and salmon parr exhibit a physiological stress response that may lead to behavioural thermoregulation (Breau *et al.*, 2007; Breau *et al.*, 2011; Mather *et al.*, 2008). In the case of Catamaran Brook, the mean water temperature (July and August) was calculated at 17.4 °C, whereas the Little Southwest Miramichi River showed a mean value of 19.6 °C (1992–2011). The mean number of days when the maximum daily water temperature ( $T_{\max}$ ) exceeded 23 °C in Catamaran Brook was 11 days per year compared with 28 days for the Little Southwest Miramichi River. The number of high temperature events recorded annually in the Little Southwest Miramichi River is presented in Figure 6 for 1992 to 2011 (1994 missing). During some years (1999, 2001 and 2002), the number of days with high water temperature ( $T_{\max} > 23$  °C) exceeded 50 days. Catamaran Brook also

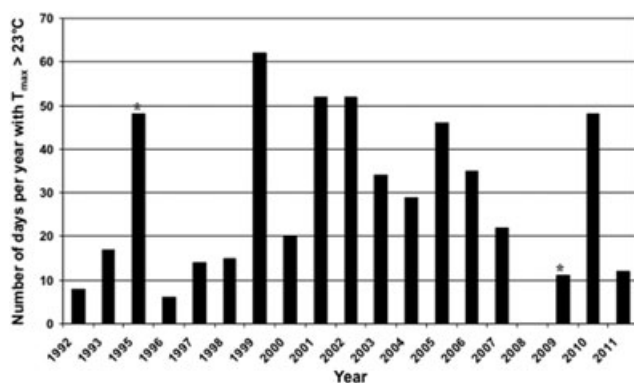


Figure 6. Number of days per year where maximum daily water temperature ( $T_{\max}$ ) exceeded 23 °C in the Little Southwest Miramichi River (1992–2011). The \* indicates a year with incomplete summer data. No data were collected in the summer of 1994

showed a large number of high temperature days during these years but less than in the Little Southwest Miramichi River (e.g. Catamaran Brook: 41 days (1999), 25 (2001) and 24 (2002)). During these high temperature events, coolwater fishes like salmonids show evidence of heat stress and seek thermal refugia to cope with such high temperatures (Gibson 1966; Lund *et al.*, 2002; Breau *et al.*, 2007). Moreover, these events typically coincide with low streamflow conditions (Figure 7) during hot summers. When summer flows were greater than 0.6 m<sup>3</sup> s<sup>-1</sup> (Catamaran Brook) or 40 m<sup>3</sup> s<sup>-1</sup> (Little Southwest Miramichi River), the number of days experiencing high water temperature events were few. However, when summer discharge in Catamaran Brook was lower than 0.2 m<sup>3</sup> s<sup>-1</sup>,  $T_{\max}$  exceeded 23 °C for approximately 10 days (Figure 7a); at the same river stage in the Little Southwest Miramichi River, a summer discharge of 15 m<sup>3</sup> s<sup>-1</sup> resulted in 32 days per year when  $T_{\max}$  exceeded 23 °C (Figure 7b).

Although summer water temperature in Catamaran Brook can reach levels causing physiological stress in juvenile Atlantic salmon (Breau *et al.*, 2011), maximum water temperatures rarely rise above a threshold causing acute mortality (i.e. > 28 °C; Elliot, 1991). The coincident low stream discharges (Figure 7) at high summer temperatures mean that less space is available in the brook for territorial juvenile Atlantic salmon. This situation may lead to a production bottleneck if space becomes limiting, particularly for the age-class that is most numerous (i.e. 0+ salmon).

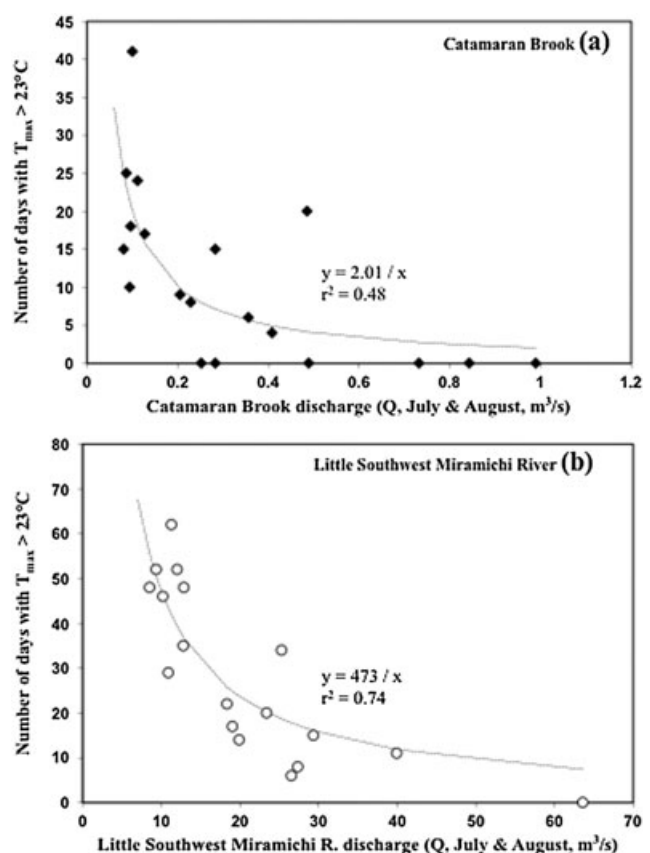


Figure 7. Number of days when maximum daily water temperature ( $T_{\max}$ ) exceeded 23 °C for Catamaran Brook (a) and Little Southwest Miramichi River (b) as a function of river discharge (m<sup>3</sup> s<sup>-1</sup>). Data cover the period of July and August from 1992 to 2010



The possible effects of the lowest summer flows on 0+ salmon were examined using the density data reported in Mitchell *et al.* (2004) for the Lower and Gorge reaches of Catamaran Brook (Figure 1). We examined the proportional change in densities of the different age classes (0+, 1+ and 2+) from summer to autumn for each year from 1990 to 2002 using simple linear regression. For young-of-the-year salmon (0+), there was a positive relationship between the summer low flow and the percent change in summer-to-autumn density that was common to both reaches (Figure 8; no differences in slope,  $p=0.87$ , or intercept,  $p=0.58$ , between the linear regressions of the two reaches; combined regression for the two reaches  $r^2=0.31$ ;  $p=0.01$ ). It appears that years with the lowest summer flows experienced a proportionately greater reduction in 0+ density by the autumn of the same year.

For 1+ and 2+ salmon parr, very little of the variability in the summer-to-autumn density change was explained by the summer low flows and the relationships were statistically non-significant in both reaches ( $r^2=0.02$ – $0.10$ ;  $p>0.05$ ). The lack of relationship for salmon parr is likely explained by the propensity for movement by these older life-stages in response to potential low-flows and/or high temperature conditions (see Cunjak *et al.*, 1993; Breau *et al.*, 2007) and the fact that absolute densities of the 1+ and 2+ parr are much lower in comparison to the 0+ age class (Mitchell *et al.*, 2004). Therefore, a lower level of density-dependent response can be expected unless the reduction in flow, and thus, available space, is extreme. Indeed, although overall density patterns were not observed for older parr with regard to low-flow summers, it is notable that the greatest decline in summer-to-autumn densities in the Gorge reach (where a density increase due to immigration was not likely) occurred in 1999, the year of the lowest average summer flow (decline of 84 %, 77 %, and 83 % for 0+, 1+ and 2+, respectively, in 1999 *versus* average decline of 26 % during other years in the dataset).

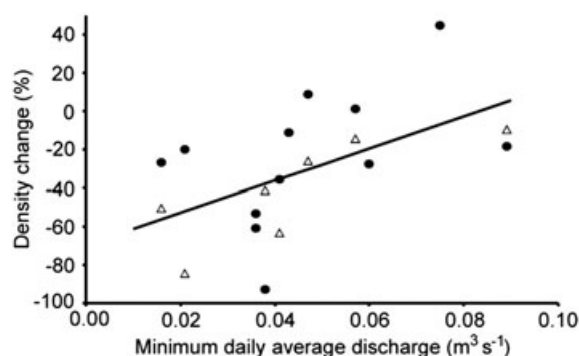


Figure 8. The linear relationship between lowest daily mean summer flow ( $Q_{\min}$ , 1 June to 30 September) and % reduction in densities of 0+ Atlantic salmon from summer to autumn in the Lower (filled circles) and Gorge (open triangles) reaches of Catamaran Brook. The linear relationship ( $y=834.72x - 69.58$ ,  $r^2=0.31$ ;  $p=0.01$ ) is fitted to the combined data from both reaches. Data points represent the composite densities pooled over all electrofished study sites within both reaches (i.e. 5 and 3 sites in Lower and Gorge reaches, respectively). The 0+ densities in 2001 were excluded from the analysis because of the apparent year-class failure and consequent extremely low densities recorded both in the summer and autumn electrofishing surveys

### Climate change relations and implications

To put the present study into a climate change context, the mean annual air temperature recorded at the Miramichi Airport (station 8100989) for the last 110 years (1900–2010) was analysed (Figure 9). During that period, the air temperature increased by  $2.28^\circ\text{C}$  (slope =  $0.0208$ ). Over the next 100 years, the climate within the Miramichi River basin is expected to change significantly. Results from the Canadian coupled global climate model CGCM3.1/T63 under two Emission Scenarios (B1 and A2) show a significant increase in air temperature, in the range of  $3$ – $5^\circ\text{C}$  (Turkkan *et al.*, 2011). The B1 scenario is considered a more optimistic scenario (with low population growth). By contrast, the A2 scenario (high population growth) is considered a ‘business as usual’ scenario and will result in a significant increase in  $\text{CO}_2$  by 2100. Under these different scenarios, the air temperature within the Miramichi is expected to increase by  $1.2^\circ\text{C}$ ,  $2.2^\circ\text{C}$  and  $2.9^\circ\text{C}$  (for the period 2010–2039, 2040–2069, 2070–2099 under scenario B1) or  $1.4^\circ\text{C}$ ,  $3.2^\circ\text{C}$ , and  $5.2^\circ\text{C}$  (2010–2039, 2040–2069, 2070–2099 under scenario A2 (Turkkan *et al.*, 2011). These projected increases are consistent with currently observed trends within the Miramichi River. Because water temperature is strongly correlated with air temperature (Caissie *et al.*, 2001), any future change in air temperature will ultimately affect the thermal regime of river. Under a warmer climate, it is expected that both Catamaran Brook and the Little Southwest Miramichi River will experience more frequent high water temperature events than what is currently observed.

Similar to water, snow and ice conditions are largely controlled by air temperature, and climate models show that both conditions are decreasing with corresponding increases in air temperatures (Zhang *et al.*, 2011). These changes are expected to have an impact on winter discharge (i.e. higher winter flows) and earlier ice break-up and spring freshets (Zhang *et al.*, 2001). The recent review of Linnansaari and Cunjak (2012) focused on how climate change might alter freshwater environments in winter and how fishes may respond. Most global climate models predict increases in air temperature, and precipitation will be greatest during the

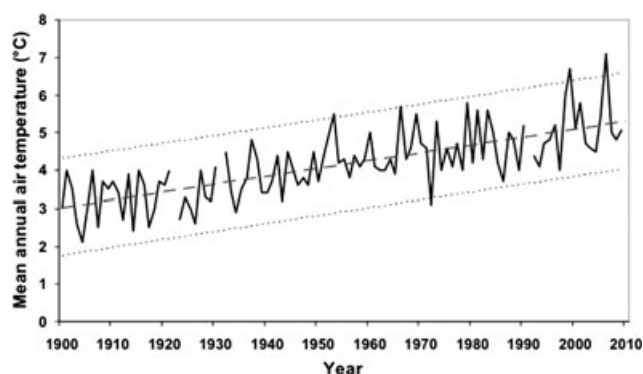


Figure 9. Mean annual air temperature in the Miramichi region of New Brunswick, Canada, between 1900 and 2010. Data are from Environment Canada, Miramichi Airport, station 8100989. The coarse dashed line represents the best fit from the linear regression model, and the upper and lower (fine dashed) lines represent the 95% confidence intervals

winter in northeastern North America (where Atlantic salmon occur). For coldwater fishes, like salmon, in temperate latitudes (like New Brunswick), increased winter growth opportunities are possible as long as food availability can meet increased metabolic demands. Similarly, warmer winter temperatures and higher winter flows could improve egg survival and accelerate alevin development and so reduce the time that this life-stage is immobile in the gravel. However, earlier emergence is only beneficial if food (invertebrate prey) is available earlier, when fry emerge to initiate exogenous feeding. The predicted changes in ice and flow dynamics in winter will be complex. Although warmer, wetter winters may reduce the likelihood of severe mechanical ice-break-ups, a variable winter hydrologic regime (rather than a stable, ice-covered state) may prove energetically demanding as fishes like salmon adapt to fluctuating flow conditions involving increased swimming activity and increased metabolic demands at water temperatures that, while warmer, are still outside the range of physiological and metabolic efficiency. Finally, the reduction in ice cover will increase access to rivers by fish predators, including homeotherms like mink and otter, for whom activity and swimming performance are less affected by temperature (as they are for poikilotherms).

## CONCLUSIONS/SUMMARY

That Atlantic salmon should display ample evidence of relationships with streamflow is not surprising. The very nature of rivers – flowing water – is the principle characteristic of rivers, the consequence of water running down a slope. Therefore, selective forces would naturally act on riverine species, like Atlantic salmon, to exploit flow characteristics. How spawning adults are stimulated to ascend small streams in response to high autumn flows, or the density-dependent relationship of salmon parr and winter streamflows, are suggestive of evolutionarily adaptive traits. What is surprising, however, is the evidence for markedly negative impacts of atypical, extreme flow events. The destructive consequences of mid-winter mechanical ice break-ups on the survival of juvenile salmon (Cunjak *et al.*, 1998) and other fish species (e.g. slimy sculpin, Edwards and Cunjak 2007) is highly unpredictable but has significant implications on fish community dynamics. Similarly, the summer low flows that directly increase the probability of high water temperature stress events has major implications for growth and survival of coolwater fishes like salmonids. Even more disconcerting is the fact that these 'rare', or extreme, flow events may increase in frequency in the future as predicted under various climate-warming scenarios. Despite the complicated nature of such relationships, our responsibility as scientists will be to promptly respond to the hydro-ecological changes that will characterize river ecosystems in the coming decades to provide appropriate information to resource managers to protect and conserve ecosystem process and function.

## ACKNOWLEDGEMENTS

The authors thank the many individuals who have worked at Catamaran Brook over the years and who have contributed to the data collection and analysis; Aaron Fraser and Peter Hardie deserve special mention for their dedication to the project. This paper represents Contribution Number 121 to the Catamaran Brook Habitat Research Project.

## REFERENCES

- Beecher, HA, Caldwell BA, DeMond SB, Seiler D, Boessow SN. 2010. An Empirical Assessment of PHABSIM Using Long-Term Monitoring of Coho Salmon Smolt Production in Bingham Creek. *Washington, North American Journal of Fisheries Management* **30**: 1529–1543.
- Beechie T, Buhle E, Ruckelshaus M, Fullerton A, Holsinger L. 2006. Hydrologic regime and the conservation of salmon life history diversity. *Biological Conservation* **130**: 560–572.
- Breau, C, Cunjak, RA, Bremset, GG. 2007. Age-specific aggregation of wild juvenile Atlantic salmon (*Salmo salar*) at cool water sources during high temperature events. *Journal of Fish Biology* **71**: 1179–1191.
- Breau C, Cunjak RA, Peake SJ. 2011. Behaviour during elevated water temperatures: can physiology explain movement of juvenile Atlantic salmon to cool water? *Journal of Animal Ecology* **80**: 844–853.
- Bujold V, Cunjak RA, Dietrich JP, Courtemanche DA. 2004. Drifters versus residents: assessing size and age differences in Atlantic salmon fry. *Canadian Journal of Fisheries and Aquatic Sciences* **61**: 1–10.
- Bunn SE, Thoms MC, Hamilton SK, Capon SJ. 2006. Flow variability in dryland rivers: boom, bust and the bits in between. *River Research and Applications* **22**: 179–186.
- Caissie D, El-Jabi N. 1995. Hydrology of the Miramichi River drainage basin. In *Water, science, and the public: the Miramichi ecosystem*, Chadwick EMP (eds). Canadian Special Publication of Fisheries and Aquatic Sciences: Ottawa, Canada, 123 pp. 83–93.
- Caissie D, El-Jabi N, Satish MG. 2001. Modelling of maximum daily water temperatures in a small stream using air temperatures. *Journal of Hydrology* **251**(1–2): 14–28.
- Caissie D, Jolicoeur S, Bouchard M, Poncet E. 2002. Comparison of streamflow between pre and post timber harvesting in Catamaran Brook (Canada). *Journal of Hydrology* **258**: 232–248.
- Caissie D, Satish MG, El-Jabi N. 2007. Predicting water temperatures using a deterministic model: Application on Miramichi River catchments (New Brunswick, Canada). *Journal of Hydrology* **336**: 303–315.
- Carey SK, Tetzlaff D, Seibert J, Soulsby C, Buttle J, Laudon H, McDonnell J, McGuire K, Caissie D, Shanley J, Kennedy M, Devito K, Pomeroy JW. 2010. Inter-comparison of hydro-climatic regimes across northern catchments: synchronicity, resistance and resilience. *Hydrological Processes* **24**: 3591–3602.
- Chaput G, Jones R. 2006. Reproductive rates and rebuilding potential for two multi-sea-winter Atlantic salmon (*Salmo salar* L.) stocks of the Maritime provinces Fisheries and Oceans Canada CSAS Res. Doc. 2006/027: 31p.
- Crisp DT. 1988. Prediction, from temperature, of eyeing, hatching and "swim-up" times for salmonid embryos. *Freshwater Biology* **19**: 41–48.
- Cunjak RA. 1988. The behaviour and microhabitat of young Atlantic salmon (*Salmo salar*) during winter. *Canadian Journal of Fisheries and Aquatic Sciences* **45**(2156): 2160.
- Cunjak RA, Therrien J. 1998. Inter-stage survival of wild juvenile Atlantic salmon, *Salmo salar* L. *Journal of Fisheries Management and Ecology* **5**: 209–224.
- Cunjak RA, Caissie D, El-Jabi N, Hardie P, Conlon JH, Pollock L, Giberson DJ, Komadina-Douthwright S. 1993. The Catamaran Brook (New Brunswick) habitat research project: biological, physical, and chemical conditions (1990–1992). Canadian Technical Report of Fisheries and Aquatic Sciences 1914: 81 p.
- Cunjak RA, Prowse TD, Parrish DL. 1998. Atlantic salmon in winter: "the season of parr discontent"? *Canadian Journal of Fisheries and Aquatic Sciences* **55**(Suppl. 1): 161–180.
- Dill PA. 1977. Development of behaviour in alevins of Atlantic salmon, *Salmo salar*, and rainbow trout, *S. gairdneri*. *Animal Behavior* **25**: 116–121.
- Dodson J, Gibson RJ, Cunjak RA, Friedland K, de Leaniz CG, Gross M, Newbury R, Nielsen J, Power M, Roy S. 1998. Elements in the development of a conservation plan for Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **55**(Suppl. 1): 312–323.



- Edwards, PA, RA Cunjak. 2007. Influence of water temperature and streambed stability on abundance and distribution of slimy sculpin (*Cottus cognatus*). *Environmental Biology of Fishes* **80**: 9–22.
- Elliott JM. 1991. Tolerance and resistance to thermal stress in juvenile Atlantic salmon, *Salmo salar*. *Freshwater Biology* **25**: 61–70.
- Elliot JM, Hurley MA. 1997. A functional model for maximum growth of Atlantic salmon parr, *Salmo salar*, from two populations in northwest England. *Functional Ecology* **11**: 592–603.
- Frenette M, Caron M, Julien P, Gibson RJ. 1984. Interaction entre le débit et les populations de tacons (*Salmo salar*) de la rivière Matamec, Québec. *Canadian Journal of Fisheries and Aquatic Sciences* **41**: 954–963.
- Giberson D, Caissie D. 1998. Inter-annual variability in hydraulic habitat characteristics in three reaches of Catamaran Brook. *Canadian Journal of Fisheries and Aquatic Sciences* **55**: 485–494.
- Gibson RJ. 1966. Some factors influencing the distributions of brook trout and young Atlantic salmon. *Journal of the Fisheries Research Board of Canada* **23**: 1977–1980.
- Gibson RJ, Myers RA. 1988. Influence of seasonal river discharge on survival of juvenile Atlantic salmon, *Salmo salar*. *Canadian Journal of Fisheries and Aquatic Sciences* **45**: 344–348.
- Gustafson-Marjanen KI, Dowse HB. 1983. Seasonal and diel patterns of emergence from the redds of Atlantic salmon (*Salmo salar*) fry. *Canadian Journal of Fisheries and Aquatic Sciences* **40**: 813–817.
- Hardie P, Cunjak RA, Komadina-Douthwright S. 1998. Fish movement in Catamaran Brook, NB (1990–1996). Canadian Data Report of Fisheries and Aquatic Sciences 1038: 64p.
- Huusko A, Greenberg L, Stickler M, Linnansaari T, Nykänen M, Vehanen T, Koljonen S, Louhi P, Alfredsen K. 2007. Life in the ice lane: the winter ecology of stream salmonids. *River Research and Applications* **23**: 469–491.
- Hvidsten NA. 1993. High winter discharge after regulation increases production of Atlantic salmon (*Salmo salar*) smolts in the River Orkla, Norway. In: Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. *Canadian Special Publication of Fisheries and Aquatic Sciences* **118**: 175–177.
- Hynes HBN. 1970. *The ecology of running waters*. University of Toronto Press: Toronto, Ontario.
- Hynes HBN. 1975. The stream and its valley. *Verhandlungen des Internationalen Verein Limnologie* **19**: 1–15.
- Johnston TA. 1997. Downstream movements of young-of-the-year fishes in Catamaran Brook and the Little Southwest Miramichi River, New Brunswick. *Journal of Fish Biology* **51**: 1047–1062.
- Junk WJ, Bayley PB, Sparks RE. 1989. The flood-pulse concept in river-floodplain systems. In *Proceedings of the international large river symposium (LARS)*, Dodge DP (ed). Canadian Special Publication in Fisheries and Aquatic Sciences: Ottawa, 106.
- Klemetsen A, Amundsen PA, Dempson JB, Jonsson B, Jonsson N, O'Connell MF, Mortensen E. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish* **12**: 1–59.
- Krebs CJ. 1989. *Ecological methodology*. Harper Collins Publishers: New York.
- Ligon FK, Dietrich WE, Trush WJ. 1995. Downstream ecological effects of dams. *Bioscience* **45**: 183–192.
- Linnansaari T, Cunjak RA. 2010. Patterns in apparent survival of Atlantic salmon (*Salmo salar*) parr in relation to variable ice conditions throughout winter. *Canadian Journal of Fisheries and Aquatic Sciences* **67**: 1744–1754.
- Linnansaari T, Cunjak RA. 2012. Fish: Freshwater Ecosystems (Chapter 6). In *Temperature Adaptation in a Changing Climate: Nature at Risk*, Climate Change Series, No.3, Storey KB, Tanino K (eds). CAB International Publishing: Wallingford, UK, 248p. pp 80–97.
- Linnansaari T, Cunjak RA, Newbury R. 2008. Winter behaviour of juvenile Atlantic salmon *Salmo salar* L. in experimental stream channels: effect of substratum size and full ice cover on spatial distribution and activity pattern. *Journal of Fish Biology*, **72**: 2518–2533.
- Lund SG, Caissie D, Cunjak RA, Vijayan MM, Tufts BL. 2002. The effects of environmental heat stress on heat-shock mRNA and protein expression in Miramichi Atlantic salmon (*Salmo salar*) parr. *Canadian Journal of Fisheries and Aquatic Sciences* **59**: 1553–1562.
- Malcolm IA, Gibbins CN, Soulsby C, Tetzlaff D, Moir HJ. 2012. The influence of hydrology and hydraulics on salmonids between spawning and emergence: implications for the management of flows in regulated rivers. *Fisheries Management and Ecology*. DOI: 10.1111/j.1365-2400.2011.00836.x.
- Mather ME, Parrish DL, Campbell CA, McMenemy JR, Smith JM. 2008. Summer temperature variation and implications for juvenile Atlantic salmon. *Hydrobiologia* **603**: 183–196.
- Meehl GA, Stocker TF, Collins WD, Friedlingstein P, Gaye AT, Gregory JM, Kitoh A, et al. 2007. Global climate projections. In *Climate Change 2007: The Physical Science Basis*, Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, et al. (eds). Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change Cambridge University Press: Cambridge, pp.747–845.
- Mitchell SC, Cunjak RA. 2007a. Relationship of upstream migrating Atlantic salmon (*Salmo salar*) and stream discharge within Catamaran Brook, New Brunswick. *Canadian Journal of Fisheries and Aquatic Sciences* **64**: 563–573.
- Mitchell SC, Cunjak RA. 2007b. Streamflow, salmon and beaver dams – Roles in the structuring of stream fish communities within anadromous salmon dominated streams. *Journal of Animal Ecology* **76**: 1062–1074.
- Mitchell S, Fraser A, Hardie P, Cunjak RA. 2004. Electrofishing data summaries for Catamaran Brook, New Brunswick, 1990–2002. Canadian Data Report of Fisheries and Aquatic Sciences 1130. Fisheries and Oceans Canada, Moncton, NB. 69 pp.
- Naesje T, Jonsson B, Skurdal J. 1995. Spring flood: a primary cue for hatching of river spawning Coregoninae. *Canadian Journal of Fisheries and Aquatic Sciences* **52**: 2190–2196.
- Poff NL, Allan JD, Bain MB, JR Karr, Prestegard KL, Richter BD, Sparks RE, et al. 1997. The natural flow regime. *BioScience* **47**: 769–784.
- Prowse TD. 2000. River-ice ecology. National Water Research Institute, Ottawa, Canada, Cat.En37-123/2000E, 64p.
- Prowse TD, Furgal C, Wrona FJ, Reist JD. 2009. Implications of climate change for northern Canada: Freshwater, marine, and terrestrial ecosystems. *Ambio* **38**: 282–289.
- Randall RG. 1982. Emergence, population densities, and growth of salmon and trout fry in two New Brunswick streams. *Canadian Journal of Zoology* **60**: 2239–2240.
- Rimmer DM, Paim U, Saunders RL. 1983. Autumnal habitat shift of juvenile Atlantic salmon (*Salmo salar*) in a small river. *Canadian Journal of Fisheries and Aquatic Sciences* **40**: 671–680.
- Schlösser IJ. 1991. Stream fish ecology: a landscape perspective. *BioScience* **41**: 704–712.
- Seiler D, Hanratty P, Neuhauser S, Topping P, Ackley M, Kishimoto LE, Peterson L, Hino M, Volkhardt G. 2001. Wild salmon production and survival evaluation –annual report October 1996–September 1997. Washington Department of Fish and Wildlife, Fish Program Science Division, Report FPA 01-16, Olympia.
- Stickler M, Alfredsen K, Linnansaari T, Fjeldstad H-P. 2010. The influence of dynamic ice formation on hydraulic heterogeneity in steep streams. *River Research and Applications* **26**: 1187–1197.
- Tetzlaff D, Soulsby C, Bacon PJ, Youngson AF, Gibbins C, Malcolm IA. 2007. Connectivity between landscapes and riverscapes—a unifying theme in integrating hydrology and ecology in catchment science? *Hydrological Processes* **21**: 1385–1389.
- Thorp JH, Delong MD. 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. *Oikos* **70**: 305–308.
- Thorp JH, Thoms MC, Delong MD. 2006. The riverine ecosystem synthesis: biocomplexity in river networks across space and time. *River Research and Applications* **22**: 123–147.
- Tockner K, Schiemer F, Ward JV. 1998. Conservation by restoration: the management concept for a river-floodplain system on the Danube River in Austria. *Aquatic Conservation: Marine and Freshwater Ecosystems* **8**: 71–86.
- Turkkan N, El-Jabi N, Caissie D. 2011. Floods and droughts under different climate change scenarios in New Brunswick. Canadian Technical Report of Fisheries and Aquatic Sciences 2928: 55p.
- Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**: 130–137.
- Zhang X, Harvey KD, Hogg WD, Yuzyk TR. 2001. Trends in Canadian streamflow. *Water Resources Research* **37**(4): 987–998.
- Zhang X, Brown R, Vincent L, Skinner W, Feng Y, Mekis E. 2011. Canadian climate trends, 1950–2007. Canadian Biodiversity: Ecosystem Status and Trends 2010, Technical Thematic Report No. 5. Canadian Councils of Resource Ministers. Ottawa, ON. iv + 21 p.
- Zippin C. 1958. The removal method of population estimation. *Journal of Wildlife Management* **22**: 82–90.