STABLE ISOTOPES ISSUE

R. A. Cunjak · J.-M. Roussel · M. A. Gray J. P. Dietrich · D. F. Cartwright · K. R. Munkittrick T. D. Jardine

Using stable isotope analysis with telemetry or mark-recapture data to identify fish movement and foraging

Received: 14 September 2004 / Accepted: 11 March 2005 / Published online: 16 June 2005 © Springer-Verlag 2005

Abstract Information about animal movements has often been inferred from stable isotope analysis (SIA), but is dependent on animals assimilating site-specific isotopic signatures via diet. This potential weakness in ecological interpretation can be overcome by using other investigative tools that provide precise information about individual movement patterns. In this paper, we demonstrate the value of combining SIA with telemetry or mark-recapture data from trapping, electrofishing and remote detection of individuals to study the movement and feeding ecology of fishes in different habitats. In a fjord lake system in Newfoundland, Canada, juvenile Atlantic salmon delayed downstream migration (smolts) or actively moved into a large lake (parr) where they foraged for periods reflecting different life history strategies. In the Miramichi River (New Brunswick, Canada), SIA provided evidence of distinct foraging habitats (tributary versus large river). By tracking fish implanted with passive integrated transponder (PIT) tags, we distinguished between movements related to

Communicated by Jim Ehleringer

R. A. Cunjak (⊠) · M. A. Gray · D. F. Cartwright T. D. Jardine Canadian Rivers Institute and Department of Biology, University of New Brunswick, P.O. Box 4400, Fredericton, NB, Canada, E3B 5A3 E-mail: cunjak@unb.ca

J.-M. Roussel

Institut National de la Recherche Agronomique, Laboratoire d'Ecologie Aquatique, UMR 985, 65 rue de St Brieuc, 35042 Rennes, France

J. P. Dietrich

Ontario Ministry of Natural Resources, Glenora Fisheries Station, K0K 2T0 41 Hatchery Lane, RR#4, Picton, ON, Canada

K. R. Munkittrick Canadian Rivers Institute and Department of Biology, University of New Brunswick, Saint John, NB, Canada, E2L 4L5 foraging versus seeking cool water refugia during high temperature events. Finally, site fidelity and limited mobility of slimy sculpin, a small benthic fish, was established where $\delta^{13}C$ in muscle tissue showed a progressive enrichment downstream and where a median displacement of < 10 m was estimated for sculpin tagged with PIT tags. Technological improvements have permitted non-destructive tissue sampling of wild fishes for SIA, and the tagging and remote detection of animals smaller than was previously possible. These advancements and the combination of investigative tools promise new insights into animal ecology.

Keywords River habitat · Slimy sculpin · Atlantic salmon · Passive integrated transponders

Introduction

Stable isotope analysis (SIA) has been used in the past 15 years to study movements of various animals including mayflies, butterflies, birds, and fishes (Doucett et al. 1999; Hershey et al. 1993; Hobson and Wassenaar 1997; Hobson et al. 1999). Conclusions about movement patterns are dependent on animals foraging and assimilating isotopically distinct foods (Hobson 1999). For fishes, based on strong freshwater-marine gradients in stable carbon (13 C/ 12 C), nitrogen (15 N/ 14 N), and sulphur (³⁴S/³²S) isotope ratios, Doucett et al. (1999) identified spawning locations of freshwater resident and anadromous brook trout (Salvelinus fontinalis), and Hesslein et al. (1991) determined that lake whitefish (Coregonus clupeaformis) captured in an Arctic creek were feeding on marine prey and subsequently migrated upstream. However, much of the research on movement involving SIA relates to populations of organisms with little or no information on individual movement patterns or specialization (e.g., Matthews and Mazumder 2004) that could help us better understand the underlying reasons (mechanisms) for the observed behaviour.

Remote data collection relating an animal's spatial position (i.e. telemetry sensu Cooke et al. 2004) presents technological challenges for studying small organisms, size of transmitters being a major constraint. Radiotelemetry batteries for small-bodied animals exhaust very quickly, and tagged animals can be encumbered by trailing an emitting antenna such that physiological and behavioral effects may be significant (Bridger and Booth 2003). Passive integrated transponder (PIT) tags are radio frequency identification products that have been used by fish and wildlife researchers where individual identification is desired. Commercially available glass encapsulated tags range in size from 11 mm to 50 mm, and can relay a unique signal code after induction by an electro-magnetic field sent from the detector, with no need for a battery (within the tag) or an external antenna. PIT tags have been used extensively in fish culture to evaluate individual performance (Baras et al. 2000), and to monitor movements through fishways (Castros-Santos et al. 1996) and in the wild (Roussel et al. 2000; Barbin Zydlewski et al. 2001). PIT technology has also been applied to behavioural studies of activity patterns and habitat use (Metcalfe et al. 1999; Martin-Smith and Armstrong 2002). Similarly, mark-recapture techniques such as tagging and tattooing (Carlin 1955; Cunjak 1992; Dussault and Rodríguez 1997) have proven successful in tracking individual fishes in freshwater and marine environments, albeit the scarcity of recapturing marked individuals can limit interpretation of the data (Hobson 1999).

The objective of this paper is to demonstrate the value of combining SIA with telemetry or mark-recapture data to study the individual movement patterns and feeding ecology of stream fishes in diverse river systems. To meet this objective, three case studies will be presented that clearly demonstrate the value of combining technological tools for investigating ecological problems at different spatial scales. The studies also demonstrate the broad applicability of the techniques by involving ecologically distinct species from diverse riverine environments: (1) juvenile, freshwater-resident stage (parr) of Atlantic salmon (Salmo salar) that often occupy territories in shallow, fast-flowing streams such as those of the Miramichi River system in New Brunswick; (2) Atlantic salmon smolts (schooling stage of iuvenile salmon en route to the sea) and parr using lacustrine habitats in the Western Brook system of Newfoundland; and, (3) slimy sculpin (*Cottus cognatus*), a small-bodied, benthic fish common to eastern Canadian freshwater systems.

Case study 1—Atlantic salmon smolts and parr, Western Brook, Newfoundland

Previous research in Newfoundland and European river systems has demonstrated the increased growth opportunities for juvenile salmon from lacustrine foraging, and the potential for enhanced smolt production from lentic habitats of river systems (Chadwick and Green 1985; Halvorsen and Svenning 2000). Parr have been observed migrating both downstream and upstream to access lacustrine habitats (Hutchings 1986; Erkinaro and Gibson 1997) where they are likely to undergo parr-smolt transformation. Lacustrine production of Atlantic salmon smolts may account for 50–75% of total smolt production in Newfoundland systems (Chadwick and Green 1985; Dempson et al. 1996; Dietrich 2001). Previous studies have described both passive (Hansen et al. 1984; Thorpe et al. 1981) and active mechanisms (Johnson and Groot 1963; Bourgeois and O'Connell 1986) for smolt movement through lacustrine habitats during seaward migration. These movements may result in migratory delays (Hansen et al. 1984; Dietrich 2001).

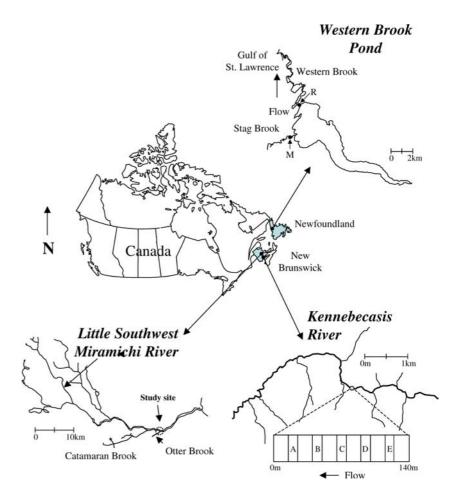
The Western Brook system in Newfoundland, Canada contains three distinct rearing environments: a small headwater tributary (Stag Brook, SBK), a large, oligotrophic lake (Western Brook Pond, WPD), and the lower reaches of the system that make an abrupt transition to the marine environment (Western Brook, WBK). Based on distinct carbon signatures of invertebrate food sources in SBK ($-28.13 \pm 0.55\%$ SE), WBK $(-23.02 \pm 0.77\%$ SE) and WPD $(-19.56 \pm 0.88\%$ SE), Jardine et al. (2005) used SIA to identify freshwater and marine food sources and nutrient assimilation in Atlantic salmon parr and smolts and brook trout in the three rearing environments. However, due to uncertainties in the temporal component of nutrient uptake, SIA alone was unable to explain data variability within the different habitats. Interpretation of mark-recapture data, meanwhile, was limited by low recapture numbers (Dietrich 2001). A combination of the two techniques allowed the following questions to be addressed:

- 1. Were smolts delaying in the lake during emigration, and if so, for how long, and were they feeding?
- 2. Were salmon parr moving into the lake, and were they using the lake to forage?

Method

The Western Brook system is located in Gros Morne National Park, Newfoundland (49°44′N, 57°46′W) and has a catchment area of 171.2 km². WPD is an ultraoligotrophic fjord lake with a surface area of 22.8 km², a mean depth of 72.5 m, and a maximum depth of 165 m (Kerekes 1994). WBK flows from WPD for approximately 9 km before emptying into the Gulf of St. Lawrence (Fig. 1). It has a mean width of 35 m, a substrate ranging from boulders to gravel and sand, and the estimated discharge during average summer flow was 7.48 m³/s (Dietrich 2001). SBK, a third-order stream, is the largest tributary entering the lake (Fig. 1), and the only one accessible to diadromous fishes. It is approximately 8 km in length, with an average width of 9 m, and has a coarse substrate consisting primarily of gravel,

Fig. 1 Map of study areas for case study 1 (Western Brook and Stag Brook, Newfoundland), case study 2 (Miramichi River and Otter Brook, New Brunswick), and case study 3 (Kennebecasis River, New Brunswick)



cobble and boulders. The estimated average summer discharge was 1.36 m³/s (Dietrich 2001). SBK is an important spawning and nursery habitat for Atlantic salmon and brook trout.

Two fyke traps (18 mm mesh size) were set in SBK (approximately 1.5 km upstream from its confluence with the pond) and monitored daily between late May and early July in 1999 and 2000. Together, they covered approximately 90% of the stream width and most of the flow. In the larger WBK, three fyke traps were situated approximately 60 m downstream of the WPD outflow in 1999. This configuration sampled ~50% of the river width and ~25% of the flow. In 2000, five fyke traps were situated approximately 440 m downstream from WPD between June 14, 2000 and July 28, 2000 (site R, Fig. 1). The nets covered approximately 65% of the stream width and 58% of the stream flow (hence, they were not as effective at capturing migrating fishes as in SBK). This site was about 5 km downstream from where smolts were marked in SBK (site M, Fig. 1). All captured parr and smolts were anesthetized using a 40 ppm clove oil bath, measured (fork-length), weighed, and checked carefully for marks administered in SBK.

A Panjet dye inoculator was used to apply Alcian Blue tattoos (Hart and Pitcher 1969) to the ventral body surface, just anterior to the pelvic girdle. Individually numbered Carlin tags were also used to mark migrating

smolts. These green plastic tags were attached just anterior of the dorsal fin with double polyethylene monofilament thread. Approximately half of the smolts were given Panjet tattoos and the other half were Carlin tagged. Marking occurred throughout the smolt run in SBK. Marked fish were held for 24 h, in live-boxes before release, to detect if mortalities may have resulted from marking.

Scale samples were taken from all juvenile salmon > 9 cm in length that were captured in SBK in 1999 and 2000. Scales were also collected from all smoltified individuals caught at the outflow of the lake. A second scale sample was collected from smolts when recaptured after having exited WPD.

For stable isotope analysis, dried macroinvertebrates (whole individuals or pooled samples, n = 2-20) were ground and caudal fin clips (salmon parr and smolts) were cut to appropriate weights. Approximately 0.2 mg of sample was weighed into a tin capsule and combusted in a Carlo Erba NC2500 elemental analyzer. Resultant gases (CO2 and N2) delivered via continuous flow to a Finnigan Mat Delta Plus isotope ratio mass spectrometer were analyzed for stable isotopes of carbon and nitrogen, and presented as delta values (or differences $\begin{array}{l} [(^{\dot{1}\dot{3}}C/^{\dot{1}\dot{2}}C_{sample} - \\ [(^{\dot{1}\dot{5}}N/^{\dot{1}\dot{4}}N_{sample} - \\ \end{array}]$ standard) following $^{13}\text{C}/^{12}\text{C}_{\text{PDB}})-1]\times1,000$ and $^{15}N/^{14}N_{AIR})-1]\times 1,000$. Analytical error over the course of the study was monitored using IAEA standards (CH6: $-10.4\pm0.14\%$ SD, CH7: $-31.8\pm0.11\%$ SD, N1: $0.4\pm0.11\%$ SD, N2: $20.3\pm0.11\%$ SD). One standard deviation of IAEA standards within a run was never >0.23% and 0.22% for C and N, respectively.

Results and discussion

Atlantic salmon smolts emigrated each spring from SBK, two to three weeks earlier than from WPD, with the commencement of movement coincident with mean daily water temperatures reaching 10°C (Fig. 2). The number of smolts captured emigrating from the pond was approximately twice the number entering the pond from SBK (Fig. 2), the only rearing tributary. Median age of smolts from the two locations was age-3 (for 1999 and 2000, Dietrich 2001) indicating that smolts from SBK emigrated seaward in the same year but many delayed in the pond for several weeks.

For Atlantic salmon parr, there was a significant number of individuals that moved downstream from SBK into WPD in late May and early June, especially in 2000, following the smolt emigration (Table. 1, 2). Of the 679 parr captured emigrating from SBK in 2000, 80% (n = 546) were < 9 cm in length and aged 1 +; the remainder were mostly 2 +. This movement from SBK was followed by the subsequent emigration of similarly

aged (1+), but fewer, parr from the pond (WPD) 1–3 weeks later (Table 2). The absence of recaptured SBK parr in the WPD traps in both years suggested that, upon entering the pond, most salmon parr stayed there for a considerable time. The absence of upstream migrating parr in fyke traps (oriented to capture fish moving against the current) indicated limited to no movement from WBK into WPD (Dietrich 2001).

Once in the pond, smolts foraged on local invertebrate prey as evidenced by the isotopic signatures that matched local prey items (Fig. 3). Very few of the smolts sampled leaving the pond (3 of 22) or exiting the river mouth (2 of 23) had tributary-specific (SBK) stable carbon 'signatures' that would have indicated a quick passage and lack of foraging in the pond or lower river reaches (Fig. 3). This was further confirmed by the mark-recapture data where smolts tagged in SBK and subsequently recaptured in the WPD traps in both years (n=32; Table 1) took 20 days, on average, to travel between the two locations (Dietrich 2001). During this protracted stay in the pond, smolts foraged (Fig. 3) and accrued considerable biomass (Dietrich 2001) from WPD prey, typical of smolts passing through ponds in Newfoundland (Hutchings 1986; O'Connell and Ash 1989).

The relatively high number of smolts coming from the pond and the fact that capture efficiency in the WPD traps was poorer than in SBK (where 85% of smolts

Fig. 2 Daily counts of Atlantic salmon smolts emigrating from Stag Brook (top panel) and Western Brook Pond (bottom panel) in 1999 relative to mean water temperatures. The 10°C line is shown for reference

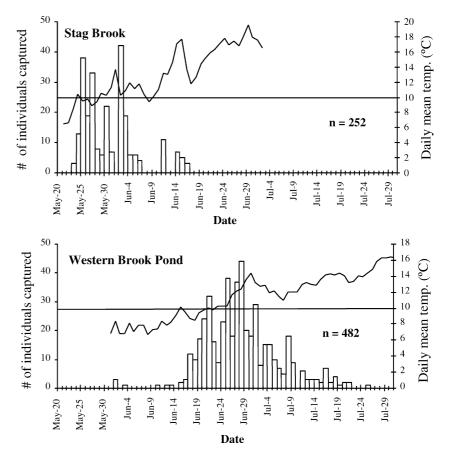


Table 1 Duration and peak of Atlantic salmon smolt movement and the number of smolts captured, marked and recaptured in Stag Brook (SBK), and Western Brook Pond (WPD) in 1999 and 2000

Year	Site of marking	Duration of smolt migration	Peak in smolt migration	Captured	Marked	Site of recapture	
						SBK	WPD
1999 2000	Stag Brook (SBK) Western Brook Pond (WPD) Stag Brook (SBK) Western Brook Pond (WPD)	23 May 1999–16 June 1999 1 June 1999–25 July 1999 28 May 2000–30 June 2000 17 June 2000–28 July 2000	25–27 May 1999 25–28 June 1999 1, 7, 18 June 2000 3–7 July 2000	252 482 470 916	236 0 470 0	16 NA 0 NA	4 NA 28 NA

Table 2 Duration and peak of movement of Atlantic salmon parr and the number of parr captured, marked and recaptured in Stag Brook (SBK), and Western Brook Pond (WPD) in 1999 and 2000

Year	Site	Duration of sampling	Peak in parr captures	Captured	Marked	No. of recaptures	
						SBK	WPD
1999 2000	Stag Brook (SBK) Western Brook Pond (WPD) Stag Brook (SBK) Western Brook Pond (WPD)	21 May 1999–2 Jul 1999 31 May 1999–2 Aug 1999 26 May 2000–27 July 2000 14 June 2000–28 July 2000	13 June 1999 21 July 1999 24 June 2000 2 July 2000	21 118 679 114	11 0 343 0	0 NA 58 NA	0 NA 0 NA

were presumed to have been captured) suggests a large proportion of the smolts emigrating from WPD originated from parr rearing in the pond for 1–2 years. The age data of parr and smolts support such a recruitment mechanism. The median age for smolts was 3, for both years, and the median age of parr captured at the various traps was 1+ (80% were 1+, 20% 2+; Dietrich 2001). The absence of SBK parr recaptured in WPD traps in 1999 or 2000 (Table 2) further supports the concept of smolt recruitment from salmon parr rearing in WPD the previous year(s).

If salmon parr were rearing in the pond prior to emigrating as smolts, there should be evidence of foraging on resident macroinvertebrate (prey) species. This was the case where SIA of parr tissue reflected the isotopic signature of local prey species (Fig. 3). Atlantic salmon parr captured in the pond (Jardine et al. 2005) or emigrating from the pond (both years; this study) showed δ^{13} C signatures that were enriched relative to SBK or the lower river reaches (WBK) and reflected the signatures of prey species captured in the pond (Fig. 3). A small proportion (only 1 of 46) of parr caught in SBK showed pond-specific stable carbon signatures (Figure 3); this finding supports our contention that very few parr in the pond move upstream into SBK to forage.

Therefore, for Atlantic salmon parr in the Western Brook system, there was a significant downstream movement (emigration) by parr from SBK into WPD in May/June where they subsequently resided and foraged before contributing to smolt production 1–2 years later. This research demonstrates the utility of combining two techniques for understanding parr and smolt movement

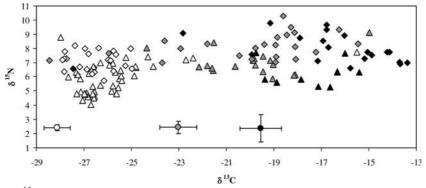


Fig. 3 Combined δ^{13} C and δ^{15} N signatures of individual Atlantic salmon smolt (*diamonds*) and parr (*triangles*) fin tissue in relation to macroinvertebrate food sources (*circles*, mean values \pm SE) in three distinct rearing environments of the Western Brook system,

Newfoundland, Canada. Stag Brook (white symbols, tributary), Western Brook Pond (black symbols, lake), Western Brook (grey symbols, lower river). Modified from Jardine et al. (2005)

and differentiating habitat use at the scale of sub-basins (SBK versus WPD and WBK). That so few recaptured individuals from tagging were found is a common problem of mark-recapture experiments (Hobson 1999) and limits the ability to infer meaningful conclusions but, in conjunction with SIA, the explanation is made more plausible. So, in the case of Atlantic salmon in the Western Brook system, the lake is an important foraging area for parr, and for smolts. Further, this extended opportunity for growth (Dietrich 2001; Jardine et al. 2005) may increase sea survival as suggested by other studies (Lundqvist et al. 1988).

Case Study 2—Atlantic salmon parr, Miramichi River

The Miramichi River of New Brunswick is considered to produce more Atlantic salmon (smolts and returning adults) than any other river in North America. During spring to late summer, the juvenile, freshwater stage (parr) typically occupy fast-flowing sections of rocky streams, where they are strongly territorial (Gibson 1993), preferring water temperatures between 16°C and 20°C for optimal growth (Jonsson et al. 2001). The species is also renowned for using different rearing habitats as parr (Hutchings 1986; Cunjak 1992) and for its variable life history strategies (Hutchings and Jones 1998)

Despite the voluminous literature devoted to the study of the behaviour of salmon parr in freshwater, our understanding of small-scale, individual movements and the causal mechanisms underlying the behaviour is limited (McCormick et al. 1998). Of importance to conservation and salmon management is an appreciation of the role of cool tributary streams as sites of thermal refuge and/or foraging for parr populations inhabiting large river corridors. Erkinaro et al. (1998) detailed the differential habitat use of large river and tributary habitats by salmon parr in response to various environmental stimuli, including water temperature. Earlier work by Gibson (1966) in the Miramichi River noted that parr abandoned territories to aggregate at small groundwater seeps during periods of thermal stress. Also in the Miramichi system, Cunjak et al. (1993) observed the aggregation and upstream movement of parr and brook trout from a large river into a cool tributary during a period when water temperatures exceeded 22– 24°C in the former. During the past 5 years, we have observed salmon parr moving in both directions between a small thermally stable tributary (Otter Brook, OBK, annual temperature range = $1-17^{\circ}$ C) and the larger, more dynamic receiving river, the Little Southwest (LSW) Miramichi River (0-30°C) at different periods from spring to late summer. With the aid of SIA and PIT technology, our aim was to explain the reasons for these movement patterns. Earlier work by Doucett (1994) established that fishes and macroinvertebrate prey from these two watercourses were isotopically distinct, and Roussel et al. (2000) and Barbin Zydlewski et al. (2001) demonstrated that stationary and portable PIT detection systems were feasible for use in monitoring the movement of individually tagged fish in streams. Specifically, we asked the question: do Atlantic salmon parr move between OBK and the LSW to seek thermal refuge or to forage?

Methods

The field work was carried out in OBK, a second-order tributary of the LSW in central New Brunswick, Canada (46°52′N, 66°06′W; Fig. 1) over two years. OBK is a 4 km long stream running through mixed deciduous and coniferous forest. Groundwater discharge stabilizes flow and moderates water temperature in the brook. The channel width is 4 m at its mouth, whereas the LSW is approximately 80 m wide. OBK is disrupted by a beaver dam (0.5 km) and suitable habitats for juvenile Atlantic salmon are located primarily in the lower 150 m of the stream.

Twenty-six wild, Atlantic salmon parr (FL range = 7.0-9.8 cm) were captured in OBK, and in the LSW within a 50-m radius from the confluence of OBK on May 28, 2001, using a backpack electrofisher (Smith-Root type 12,500 V, 60 Hz). They were individually anaesthetised in a solution of 2-phenoxy ethanol (0.03%), measured (nearest mm), pelvic fin clipped for stable isotope analysis, and then released after recovery. The same procedure was performed on May 29 in 2002, 28 salmon parr (FL range = 7.0–10.7 cm) were captured and PIT-tagged before being released back into the habitat from where they had been captured (13 and 15 parr from OBK and LSW, respectively). The transponders used for the experiment were 23-mm long (Texas Instruments, TIRIS series 2000, RI-TRP-WRHP); details about surgical implantation were outlined in Roussel et al. (2000). Macroinvertebrates representing various foraging strategies (shredders, scrapers, filterers and predators) were sampled using kick nets in OBK and LSW (upstream from the confluence) to measure isotopic variations in food sources between the two streams.

Movements of PIT-tagged parr were monitored using a stationary antenna system (Barbin Zydlewski et al. 2001) set up across the channel, a few metres upstream from the confluence. In addition, 15 tracking surveys were conducted from May 30, 2002 to October 2, 2002, using a portable PIT-tag detector (Roussel et al. 2000) to identify and locate PIT-tagged parr in OBK. By combining results from the stationary and the portable systems, it was possible to monitor fish movements between the river and the brook. During the same period, water temperature was recorded on an hourly basis in LSW (10 m upstream from the confluence) and in OBK using Vemco Minilog 8-bit data loggers.

For stable isotope analysis, macroinvertebrates (whole individuals and pooled samples, n = 2-20) and fin tissue were analyzed for stable isotopes of carbon and

nitrogen as described above (Case Study 1). Precision of IAEA standards (CH6: $-10.4\pm0.25\%$ SD, CH7: $-31.8\pm0.12\%$ SD, N1: $0.4\pm0.26\%$ SD, N2: $20.3\pm0.46\%$ SD) and repeats within runs (SD=0.28–0.55%) were acceptable for this study due to the large gradient that exists in stable carbon ratios between LSW and OBK.

Student's *t*-tests were used to test isotopic differences between samples from OBK and the LSW (δ^{13} C and δ^{15} N). When heteroscedasticity was detected among two samples (*F*-tests), we used the Welch modified two-sample *t*-test with weighted average degrees of freedom (Sokal and Rohlf 1995). When deviations from normality were detected (Kolmogorov-Smirnow tests), non-parametric Kruskal-Wallis rank tests were used. Statistical significance was set at $\alpha = 0.05$.

Results and discussion

The fin tissue of Atlantic salmon parr from LSW showed a distinct and relatively enriched δ^{13} C signature $(-23.57 \pm 0.96\% \text{ SD})$ and a range between -22.17 and -27.14% that reflected the similarly enriched values for potential invertebrate prey from the same site (Fig. 4). By contrast, δ^{13} C values for salmon parr from OBK were wide-ranging (-22.88 to -33.73%) as attested by heteroscedasticity detected between samples from the two sites (F = 0.0908, p = 0.0001). Parr from OBK had a depleted δ^{13} C significantly more signature $(-29.11 \pm 10.11\%$ SD) relative to LSW parr (t = 8.39,p < 0.0001). Similarly, macroinvertebrates from OBK were distinctly more depleted than those from LSW (Fig. 4). Doucett (1994) found a similar separation in the δ^{13} C signatures of biota from LSW and OBK, and a nearby tributary, Catamaran Brook, as well as

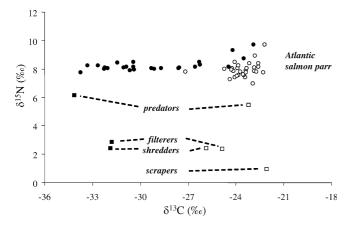


Fig. 4 Combined δ^{13} C and δ^{15} N signatures of aquatic biota sampled from the LSW Miramichi River (*open symbols*) and Otter Brook (*solid symbols*), May 2001 and May 2002. *Circle* symbols represent individual Atlantic salmon parr, based on fin tissue samples. Macroinvertebrates (*square symbols*) include: filterers (Simuliidae), scrapers (Glossosomatidae), shredders (*Pteronarcys*) and predators (Rhyacophilidae + Odonata + perlid nymphs); *symbols* represent composite samples (2–20 individuals pooled)

wide-ranging $\delta^{13}C$ signatures in the tissues of salmon parr. There were no obvious differences in $\delta^{15}N$ values between sites, for pairings of the functional feeding groups of macroinvertebrates or fish (Fig. 4). The increasing $\delta^{15}N$ values from scrapers to invertebrate predators to fish reflect a classic step-wise enrichment with each trophic level increase (Fry 1991).

The wide ranging and overlapping values of $\delta^{13}C$ for salmon parr leads us to hypothesize that these individuals represent different life history tactics. If some parr were moving between, and feeding in, the two watercourses, then we might expect intermediate isotopic signatures. Similarly, the occurrence of "OBK fish" with ^{13}C signatures overlapping those of LSW parr (and invertebrates) may indicate that these parr either foraged regularly in the large river or that they were LSW parr that entered OBK for reasons other than to forage (e.g., refuge). These predictions were tested by examining the results of the PIT-tag tracking with portable and stationary antennae.

Three different foraging tactics were obvious based on the tracking of individually tagged parr. One group of parr resided and foraged in OBK for the spring and part or all of the summer, and was designated "OBK residents". They are represented by the tracking of 3 parr at the stationary antenna (Fig. 5a) and repeated recaptures in the brook during the summer surveys with the portable antenna. Despite one of the parr emigrating in mid-July, these fish foraged and grew during the period of maximum invertebrate drift and salmonid growth from May until the end of June (Keeley and Grant 1995). The mean δ^{13} C signature (\pm SD) for these tagged parr was -32.5% (\pm 0.7), similar to the depleted values for macroinvertebrates from OBK (Fig. 4).

A second group of tagged parr (n=4) were designated "transient parr" because of their repeated forays between OBK and LSW during June and July before eventually returning to the larger river habitat (Fig. 5b). These fish likely foraged in both habitats as indicated by the intermediate mean δ^{13} C signature of -30.6% (± 2.1).

The third foraging tactic was referred to as "LSW resident" parr in that they obviously resided and foraged in the larger river. Their tissue had a distinctly enriched mean δ^{13} C signature of -23.4% (± 0.9). These tagged parr (n=5) entered the field of the stationary antennae in OBK for brief periods in each of early July and mid August before quickly returning to the large river (Fig. 5c). We believe that these parr were not foraging; rather, they were entering the cooler brook to seek thermal refuge during brief periods of thermal stress. This suggestion was supported by the thermistor records for the summer, showing that OBK maintained a 3-10°C cooler temperature than the river, and the fact that maximum summer temperatures > 22°C in LSW coincided with the periods of movement by these fish (Fig. 5d). Previous research on salmon parr in the Miramichi River has identified that water temperatures >22°C stimulated changes in movement and behaviour

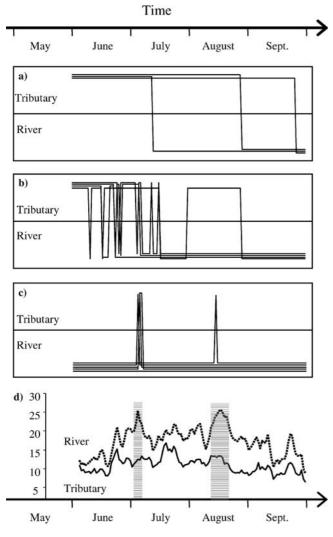


Fig. 5 Temporal movements of PIT-tagged Atlantic salmon parr between the Little Southwest Miramichi River (LSW) and Otter Brook (Tributary), 2002. a Parr residing in the tributary in spring and early summer before emigrating to the river, b parr moving back and forth between river and its tributary, c parr from the river that moved to the tributary during a high temperature event, d temporal variations in water temperatures during the study period; grey bars represent water temperatures > 22°C in LSW

(Cunjak et al. 1993), and induced a heat shock (physiological) response indicative of protein damage (Lund et al. 2002). When comparing the isotopic signatures of the three groups (OBK residents, transient parr and LSW residents), a significant difference was found for δ^{13} C (p=0.0144), but not for δ^{15} N (p=0.1753).

This case study highlights the complexity of behavioural tactics displayed by stream fishes, like salmon parr, and the importance of tributary streams for serving as foraging and/or refuge sites under different situations. The work also demonstrates the benefits of combining investigative tools to address ecological questions. With only one of the two tools, the picture was not nearly as clear. Increasing water temperature trends over the past 20 years in the Miramichi

(Swansburg et al. 2002) and other rivers near the southern limit of the species' distribution has raised concern about the future of coolwater fishes in the region. In the past 15 years, maximum temperatures between 28°C and 31°C have been recorded in the Miramichi River with consequent impacts on parr movement and physiology (Cunjak et al. 1993; Lund et al. 2002). A predicted 2–6°C increase in air temperatures of eastern Canada over the next 100 year (Parks Canada 1999) is expected to adversely affect growth potential and parr and smolt production (Power and Power 1994; Swansburg et al. 2002). Future research on movements and thermal refuge use by parr is recommended for developing management policies to protect the species and its habitat.

Case Study 3—Slimy sculpin, St. John River

Establishing an organism's residency in an area of possible exposure to a stressor or disturbance is a significant challenge for effective environmental monitoring (Munkittrick et al. 2000). The mobility of the species in question will affect the feasibility of using reference sites adjacent to or immediately upstream of the impact area when no natural barriers are present. The use of a fish with high spatial and temporal residency for monitoring ensures confidence that the target species was exposed to conditions at the site under study. It has been suggested that the slimy sculpin (*Cottus cognatus*), a small benthic fish, may be a useful sentinel species (Gray et al. 2002; Gray 2003) although little is known about its residency and site fidelity.

Recent research by Gray et al. (2004) in the Little River of northern New Brunswick showed that there was an incremental enrichment of approximately 5% in δ^{13} C in the muscle tissue of slimy sculpin, from headwaters to sites downstream (a 30-km distance). The site-specific signatures suggested that slimy sculpin were not moving long distances among sites, and were incorporating their isotopic signatures over a small spatial scale. To confirm that sculpin display high site fidelity, and hence are suitable sentinel species for environmental monitoring, it was necessary to carry out field experiments to monitor tagged individuals within a stream. Therefore, the objective of this study was to assess the residency and site fidelity of slimy sculpin in a natural system.

Methods

To assess site fidelity, all sculpin to be tagged were collected in late July, 2001, using a backpack electrofisher (Smith-Root Model C-15) in the Kennebecasis River, New Brunswick (45°49′37″N, 65°13′8″W; Fig. 1). The 140 m long study reach was 5–12 m wide with a mean depth of 20 cm. Riffle and run habitats each represented approximately 50% of the study area.

The study design incorporated five 10 m long treatment sections (labeled A through E in an upstream direction) within the study reach (see Gray 2003 for full description). Treatment sections were separated from each other by 15 m long "buffer zones", in which no fish were disturbed on the tagging date. The minimum sculpin size for tagging was set at 65 mm based on previous laboratory experimentation on survival and tag retention (Gray 2003).

Tags used in this study were 11.5 mm long, 2 mm diameter, glass encapsulated PIT tags (Destron Fearing Corp., South St. Paul, MN, USA). Tags were surgically implanted in the body cavity and fish were allowed to recover in an aerated bucket for at least 30 min before being placed in flow-through live boxes, set in the stream, for a minimum of 24 h to monitor post-surgery effects. After 24 h, the incision of each fish was examined, and fish were subsequently released at the mid-point of the treatment sections where they were captured. There were no mortalities of tagged fish observed after 24 h.

The term 'movement' hereafter refers to the spatial displacement between the last known release point and the recapture point. Attempts to locate tagged fish were made on five separate occasions (11, 48, 93, 129, and 306 days post-release). The entire study area (treatment sections and buffer zones) was electrofished with one complete pass in the upstream direction. All sculpin > 65 mm TL were retained, scanned using a handheld PIT tag reader, and examined for an incision scar. There was never a case where a fish with an incision mark had no detectable tag.

When a tagged sculpin was recaptured, the tag number and location was noted by visual reference to flags located at 1 m intervals along the bank, and by estimating position within five strata subdividing the stream width. The minimum and maximum measurable distance of movement was 0.5 and 120 m. At 93 days and 129 days post-release, 15 m of river above and below the study area was also electrofished; at 306 days post-release, an additional 15 m below the entire study area was electrofished. (amounting to a total length of 155 m).

As fish size and distance data were not normally distributed, non-parametric Kruskal-Wallis or Mann Whitney U-tests were used. Statistical significance was set at $\alpha = 0.05$.

Results and discussion

Of 37 movements detected for slimy sculpin (based on recapture of 25 of 57 tagged sculpin), two were lateral movements, 24 movements were upstream and 11 downstream (Table 3). The median movements were 16.8 m upstream and 6.8 m downstream, but there was no statistical difference between the direction of movement (p=0.19). Over the total study period of 10 months (306 days), the recaptured fish moved a minimum distance of 0.5 m, and a maximum distance of 101 m. In no case was a tagged fish found outside of the 170 m study area. Seventy-five percent of recaptured fish moved <38 m. The median absolute distance moved from the point of release for all recaptured sculpin was 9.2 m. There were no significant differences in lengths (p=0.68) or weights (p=0.24) of sculpin tagged in different sections of the study area.

Therefore, adult slimy sculpin tagged with passive integrated transponder (PIT) tags showed limited movements in the Kennebecasis River although there was moderate variability in the degree of individual movements (0.5–101 m). The apparent concentration of recapture locations at upper and lower ends of the study area (Table 3) may have been habitat-related because release locations were distributed throughout the study site. Dry conditions in the summer resulted in very low water within the riffle habitats (middle section of study area). This may have caused fish to move into the deeper run habitats where more tagged fish were recaptured.

Previous research on freshwater sculpin movements has indicated that cottids are not likely to move long distances. Using a variety of marking and collecting techniques, most slimy sculpin, and the closely related mottled sculpin (*Cottus bairdi*), were found to stay within stream areas ranging from 1 m to 50 m (Hill and Grossman 1987; Morgan and Ringler 1992). In our study, the single sculpin responsible for the longest downstream movement (101 m) was also responsible for the longest upstream movement (99.5 m) resulting in an absolute displacement of only 0.5 m from its original release point 10 months earlier. Eight of the 15 PITtagged sculpin that were recaptured more than once were found < 5 m from their previous recapture points.

One of the shortcomings of mark-recapture studies is accounting for those fish not recaptured after initial release. There are four possible explanations: (a) the

Table 3 Median total length (range) for slimy sculpin collected and PIT tagged in the Kennebecasis River, NB. Number of sculpin recaptured from each section and the mean \pm SE distances [number of movements] are given for upstream/downstream movements

Section	Median fish length (mm)	Number recaptured	Upstream movements (m)	Downstream movements (m)
A 9 B 11 C 11 D 11 E 15	67 (65–84)	7	$27.4 \pm 19 [5]^a$	31.0 ± 23 [4]
	70 (65–85)	8	$32.7 \pm 11 [9]$	7.3 ± 1 [4]
	73 (65–84)	2	$43.8 \pm 14 [3]$	[0]
	68 (65–77)	3	$30.5 \pm 7 [4]$	[0]
	72 (65–83)	5	$6.2 \pm 2 [3]$	14.8 ± 11 [3]

^a There were two lateral movements (2 and 4 m)

fish died, (b) the fish moved out of the study area, (c) they remained in the study site but were not captured during tracking, or (d) tags were lost. Based on previous capture success experiments and modeling of the mark-recapture data, the combined mortality and emigration for sculpin during the 10-month study period was estimated to be low (Gray 2003). Although there was variability in the degree of individual movements (0.5–101 m), results from the study in the Kennebecasis River provide evidence that slimy sculpin display a relatively high degree of both spatial and temporal residency. These conclusions of low mobility corroborate the findings of Gray et al. (2004) in another river using stable isotope data. In that study, low variance and absence of large outliers in sculpin carbon data from the Little River indicated that few sculpin moved between sites, and they were not feeding over a broad spatial scale. Discrete patterns in δ^{13} C in riverine biota were also found by Finlay (2001), Bunn et al. (2003) and Forsberg et al. (1993) and further indicate the potential for identifying foraging and habitat use at the sub-basin and basin scales.

In this case study, then, distinct isotopic signatures (Gray et al. 2004) and PIT-tracking data (this study) collectively suggest that slimy sculpin display strong site fidelity and reflect local environmental conditions. These attributes endorse the species as a suitable sentinel for environmental research when residency is an important factor.

In summary, stable isotope analysis in conjunction with PIT technology and traditional mark-recapture data are useful tools for understanding individual movement and foraging behaviour of stream fishes. Appreciating the degree of movement by stream fishes (Rodriguez 2002) can improve the modeling of population dynamics because immigration and emigration can significantly influence estimates of population abundance (Cunjak and Therrien 1998) and the impacts of biological invasions (Peterson and Fausch 2003). Other combined approaches involving relatively new technological tools have similarly advanced our understanding of life history variants and animal movements (e.g., Clegg et al. 2003). Recent research using molecular tools (mDNA) in conjunction with SIA has provided insights to the complex of life history morphs of smelt (Osmerus mordax) in a catchment in eastern Canada (Curry et al. 2004). In addition to the recommendation of inter-disciplinary research and analyses involving multiple isotopes for studying animal movement patterns (Hobson 1999), we further suggest that a combination of appropriate tools like SIA and telemetry can improve our understanding of complex aspects of animal ecology.

Acknowledgements We are grateful to the following individuals and agencies: R. Doucett, A. McGeachy, M. Savoie, C. Paton for lab analyses; the Catamaran Brook crew (especially A. Fraser), V. Bujold, and technicians and students from the Canadian Rivers Institute for field assistance. Funding was provided by the Natural Sciences and Engineering and Research Council, the Canada Research Chairs program, and Parks Canada (to RAC); la Mission

des Relations Internationales (INRA) to JMR; and, the Toxic Substances Research Initiative (TSRI) to KRM. Contribution no. 79 of the Catamaran Brook research project.

References

- Baras E, Malbrouck C, Houbart M, Kestemont P, Mélard C (2000) The effect of PIT-tags on growth and physiology of age-0 cultured Eurasian perch *Perca fluviatilis* of variable size. Aquaculture 185:159–173
- Barbin Zydlewski G, Haro A, Whalen KG, McCormick SD (2001) Performance of stationary and portable passive transponder detection systems for monitoring of fish movements. J Fish Biol 58:1471–1475
- Bourgeois CE, O'Connell MF (1986) Observations on the seaward migration of Atlantic salmon smolts through a large lake as determined by radiotelemetry and Carlin tagging studies. Can J Zool 66:685–691
- Brännäs E, Lundqvist H, Prentice E, Schmitz M, Brännäs K, Wilklund B-S (1994) Use of the Passive Integrated Transponder (PIT) in a fish identification and monitoring system for fish behavioural studies. Trans Am Fish Soc 123:395–401
- Bridger CJ, Booth RK (2003) The effects of biotelemetry transmitter presence and attachment procedures on fish physiology and behavior. Rev Fish Sci 11:13–34
- Bunn SE, Davies PM, Winning M (2003) Sources of organic carbon supporting the food web of an arid zone floodplain river. Freshw Biol 48:619–635
- Carlin B (1955) Tagging of salmon smolts in the River Lagan. Institute of Freshwater Research, Drottningholm, Annual Report 1954, No. 36. pp 57–74
- Castro-Santos T, Haro Â, Walk S (1996) A passive integrated transponder (PIT) tag system for monitoring fishways. Fish Res 28:253–261
- Chadwick EMP, Green JM (1985) Atlantic salmon (Salmo salar L.) production in a largely lacustrine Newfoundland watershed. Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie 22:2509–2515
- Clegg SM, Kelly JF, Kimura M, Smith TB (2003) Combining genetic markers and stable isotopes to reveal population connectivity and migration patterns in a neotropical migrant, Wilson's warbler (*Wilsonia pusilla*). Mol Ecol 12(4):819–30
- Cooke SJ, Hinch SG, Wikelski M, Andrews RD, Kuchel LJ, Wolcott TG, Butler PJ (2004) Biotelemetry: a mechanistic approach to ecology. Trends Ecol Evol 19:334–343
- Cunjak RA (1992) Comparative feeding, movements, and growth of Atlantic salmon (*Salmo salar*) parr from riverine and estuarine environments. Ecol Freshw Fish 1:26–34
- Cunjak RA, Therrien J (1998) Inter-stage survival of wild juvenile Atlantic salmon, Salmo salar L. J Fish Manage Ecol 5:209–224
- Cunjak RA, Caissie D, El-Jabi N, Hardie P, Conlon JH, Pollock TL, 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
- Curry RA, Currie SL, Bernatchez L, Saint-Laurent R (2004) The rainbow smelt, *Osmerus mordax*, complex of Lake Utopia: threatened or misunderstood? Environ Biol Fishes 69:153–166
- Dempson JB, O'Connell MF, Shears M (1996) Relative production of Atlantic salmon from fluvial and lacustrine habitats estimated from analyses of scale characteristics. J Fish Biol 48:329–341
- Dietrich JP (2001) The behaviour, survival and production of Atlantic salmon (*Salmo salar* L.) smolts in the Western Brook system. MSc thesis, University of New Brunswick
- Doucett RR (1994) Stable isotope analysis of food pathways in the Miramichi River system, New Brunswick. M.Sc. thesis, University of Waterloo
- Doucett RR, Hooper W, Power G (1999) Identification of anadromous and nonanadromous brook trout and their progeny in

- the Tabusintac River, New Brunswick, by means of multiple-stable-isotope analysis. Trans Am Fish Soc 128:278–288
- Dussault C, Rodríguez MA (1997) Field trials of marking stream salmonids by dye injection and coded-wire-tagging. North Am J Fish Manage 17:451–456
- Erkinaro J, Gibson RJ (1997) Interhabitat migration of juvenile Atlantic salmon in a Newfoundland river system. J Fish Biol 51:373–388
- Erkinaro J, Julkunen M, Niemelä E (1998) Migration of juvenile Atlantic salmon *Salmo salar* in small tributaries of the subarctic river Teno, northern Finland. Aquaculture 168:105–119
- Finlay JC (2001) Stable-carbon ratios of river biota: implications for energy flow in lotic food webs. Ecology 82:1052–1064
- Forsberg BR, Araujo-Lima CARM, Martinelli LA, Victoria RL, Bonassi JA (1993) Autotrophic carbon sources for fish of the central Amazon. Ecology 74:643–652
- Fry B (1991) Stable isotope diagrams of freshwater food webs. Ecology 72:2293–2297
- Gibson RJ (1966) Some factors influencing the distribution of brook trout and young Atlantic salmon. J Fish Res Board Canada 23:1977–1980
- Gibson RJ (1993) The Atlantic salmon in fresh water: spawning, rearing and production. Rev Fish Biol Fish 3:39–73
- Gray MA (2003) Assessing non-point source pollution in agricultural regions of the upper St. John River basin using the slimy sculpin (*Cottus cognatus*). Ph.D. thesis, University of New Brunswick
- Gray MA, Curry RA, Munkittrick KR (2002) Non-lethal sampling methods for assessing environmental impacts using a small-bodied sentinel fish species. Water Quality Res J Canada 37:195–211
- Gray MA, Cunjak RA, Munkittrick KR (2004) Site fidelity of slimy sculpin: insights from stable isotope analysis. Can J Fish Aquatic Sci 61:1717–1722
- Halvorsen M, Svenning MA (2000) Growth of Atlantic salmon parr in fluvial and lacustrine habitats. J Fish Biol 57:145–160
- Hansen LP, Jonsson B, Doving KB (1984) Migration of wild and hatchery reared smolts of Atlantic salmon, *Salmo salar* L., through lakes. J Fish Biol 25:617–623
- Hart PJB, Pitcher TJ (1969) Field trials of fish marking using a jet inoculator. J Fish Biol 1:383–385
- Hershey AE, Pastor J, Peterson BJ, Kling GW (1993) Stable isotopes resolve the drift paradox for *Baetis* mayflies in an Arctic river. Ecology 74:2315–2325
- Hesslein RH, Capel MJ, Fox DE, Hallard KA (1991) Stable isotopes of sulfur, carbon, and nitrogen as indicators of trophic level and fish migration in the Lower Mackenzie River Basin, Canada. Can J Fish Aquatic Sci 48:2258–2265
- Hill J, Grossman GD (1987) Home range estimates for 3 North American stream fishes. Copeia 2:376–380
- Hobson KA (1999) Tracing origins and migrations of wildlife using stable isotopes: a review. Oecologia 120:314–326
- Hobson KA, Wassenaar LI (1997) Linking breeding and wintering grounds of neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. Oecologia 109:142–148
- Hobson KA, Wassenaar LI, Taylor OR (1999) Stable isotopes (δD and δ¹³C) are geographic indicators of natal origins of monarch butterflies in east North America. Oecologia 120:397–404
- Hutchings JA (1986) Lakeward migrations by juvenile Atlantic salmon, *Salmo salar*. Can J Fish Aquatic Sci 43:732–741
- Hutchings JA, Jones M (1998) Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. Can J Fish Aquatic Sci 55(Suppl 1):22–47

- Jardine TD, Cartwright DF, Dietrich JP, Cunjak RA (2005) Resource use by salmonids in riverine, lacustrine and marine environments: evidence from stable isotope analysis. Env Biol Fish 000–000 (in press)
- Johnson WE, Groot C (1963) Observations on the migration of young sockeye salmon (*Oncorhynchus nerka*) through a large complex lake system. J Fish Res Board Canada 20:919–938
- Jonsson B, Forseth T, Jensen AJ, Naesje TF (2001) Thermal performance of juvenile Atlantic salmon Salmo salar L. Funct Ecol 15:701–711
- Keeley ER, Grant JWA (1995) Allometric and environmental correlates of territory size in juvenile Atlantic salmon (Salmo salar). Can J Fish Aquatic Sci 52:186–196
- Kerekes JJ (1994) Western brook pond. In: Allan RJ (ed) The book of Canadian lakes. Canadian Association on water quality, Monograph no. 3, CCIW, Burlington, pp 284–293
- 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 strain Atlantic salmon (Salmo salar) parr. Can J Fish Aquatic Sci 59:1553–1562
- Lundqvist H, Clarke WC, Johansson H (1988) The Influence of precocious sexual maturation on survival to adulthood of river stocked Baltic salmon Salmo salar smolts. Holarctic Ecol 11:60– 60
- Martin-Smith KM, Armstrong JD (2002) Growth rates of wild stream-dwelling Atlantic salmon correlate with activity and sex but not dominance. J Anim Ecol 71:413–423
- Matthews B, Mazumder A (2004) A critical evaluation of intrapopulation variation of δ13C and isotopic evidence of individual specialization. Oecologia 140:361–371
- McCormick SD, Hansen LP, Quinn TP, Saunders RL (1998) Movement, migration and smolting in Atlantic salmon. Can J Fish Aquatic Sci 55(Suppl 1):77–92
- Metcalfe NB, Fraser NHC, Burns MD (1999) Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. J Anim Ecol 68:371–381
- Morgan CR, Ringler NH (1992) Experimental manipulation of sculpin (*Cottus cognatus*) populations in a small stream. J Freshw Ecol 7:227–232
- Munkittrick KR, McMaster ME, Van Der Kraak G, Portt C, Gibbons WN, Farwell A, Gray M (2000) Development of methods for effects-driven cumulative effects assessment using fish populations: Moose River project. Society of Environmental Toxicology and Chemistry (SETAC), Pensacola, FL, 256p
- Peterson DP, Fausch KD (2003) Testing population-level mechanisms of invasion by a mobile vertebrate: a simple conceptual framework for stream salmonids. Biol Invasions 5:239–259
- Power M, Power G (1994) Modeling the dynamics of smolt production in Atlantic salmon. Trans Am Fish Soc 123:535–548
- Roussel J-M, Haro A, Cunjak RA (2000) Field-test of a new method for tracking small fishes in shallow rivers using passive integrated transponder (PIT) technology. Can J Fish Aquatic Sci 57:1326–1329
- Sokal RR, Rohlf, FJ (1995) Biometry: the principles and practice of statistics in biological research, 3rd edn. WH Freeman and Co., New York, p 887
- Swansburg E, Chaput G, Moore D, Caissie D, El-Jabi N (2002) Size variability of juvenile Atlantic salmon: links to environmental conditions. J Fish Biol 61:661–683
- Thorpe JE, Ross LG, Struthers G, Watts W (1981) Tracking Atlantic salmon smolts, *Salmo salar* L., through Loch Voil Scotland. J Fish Biol 19:19–537