WINTER MOVEMENT, ACTIVITY AND HABITAT USE OF ATLANTIC SALMON Salmo salar L. PARR IN NEWFOUNDLAND

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Winter movement, activity and habitat use of Atlantic salmon *Salmo salar* L. parr in Newfoundland

by

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A thesis submitted to the School of Graduate Studies in partial fulfilment of the requirements for the degree of Doctor of Philosophy in the Faculty of Science

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Abstract

Knowledge of Atlantic salmon *Salmo salar* L. parr behaviour in wintering habitat is limited to a few studies suggesting that they are largely sedentary and primarily nocturnal in winter. In a series of field studies, radiotelemetry was used to investigate winter movement, activity and habitat use of Atlantic salmon parr in Newfoundland. In the natural rivers studied, Northeast Brook and Stoney River, Atlantic salmon parr remained active throughout the diel cycle in winter and utilised a variety of mesohabitats, even under stable environmental conditions. Based on the age of parr captured in fluvial habitats in early and mid-winter, young parr (2-3 yrs) appeared to overwinter in fluvial habitat while pre-smolts (4-6 yrs) did so in lacustrine habitat. In the regulated river studied, West Salmon River, landlocked Atlantic salmon parr were active throughout the diel cycle in winter. However, there was significantly less daytime than nighttime movement and movement declined significantly with increased fish size. Increases in flow from 1.3 $m^3 s^{-1}$ (low) to 5.2 $m^3 s^{-1}$ (high) for 24 hour periods did not affect fish habitat use, displacement or prey consumption. However, fish activity rates in late winter were lower at high flow than at low flow. The results of these studies supported recent laboratory research indicating that parr are not strictly nocturnal in winter and that individual variation in time spent foraging during the day may result from differences in the benefits of enhanced feeding and growth. The traditional view that Atlantic salmon parr are sedentary stream dwellers in winter, moving only in response to adverse stream conditions, was not supported by the results of the present studies.

Acknowledgements

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Chapter 1.0 General Introduction

1.1 Background

Vertebrates living in temperate seasonal environments are exposed to periods where conditions favour growth, 'summer' (i.e., moderate temperatures and abundant resources) and periods where conditions limit growth, 'winter' (i.e., freezing temperatures and limited resources; Fretwell, 1972; Boyce, 1979). For many vertebrate species, the winter season is considered to be a critical period for survival as it is associated with reduced growth, depletion of energy resources and increased mortality risk (Lord, 1960; Bednekoff & Houston, 1994; Schultz *et al.*, 1998).

Many vertebrate species avoid harsh environmental conditions and/or reduce metabolic requirements during the winter season through migration, hibernation or torpor (Begon *et al.*, 1996). Vertebrate species remaining active throughout the winter season within temperate environments have evolved life history traits that minimize overwinter mortality, which is primarily caused by a size dependent risk of starvation (Ojanguren *et al.*, 1996; Murie & Boag, 1984; Ekman & Hake, 1990; Piper & Wiley, 1990). These traits include large body sizes (Bergmann's rule; Ray, 1960; Kendeigh, 1969; Murphy, 1985; James, 1991; Lindstedt & Boyce, 1985; Holcik & Jedlicka, 1994; Kurzava & Morin, 1994) and fast growth rates (Conover & Present, 1990; Williamson & Carmichael, 1990;

Nicieza *et al.*, 1994; Shultz *et al.*, 1996; Power & McKinley, 1997; Brown *et al.*, 1998).

Atlantic salmon are a primary example of a vertebrate species that must adapt to seasonal conditions. These fish reproduce in the fresh waters around the North Atlantic Ocean. Juveniles remain in the rivers until they smolt and migrate downstream to the sea after 1 to 8 years (Scott & Crossman 1973; Metcalfe & Thorpe 1990). Post-smolts remain at sea for 1 to 3 years before returning to their natal rivers to reproduce (Scott & Crossman 1973). A threshold body size is required to trigger smolting 7-10 months prior to migration to sea in the spring (Metcalfe 1998). Therefore, juvenile growth rates in fresh water determine the age at which individuals make their smolt migration to sea (Alm 1959).

Atlantic salmon parr have been traditionally viewed as sedentary stream dwellers spending their freshwater lives within a small stream reach (Keenlyside, 1962; Gibson, 1993). Researchers now acknowledge that parr may migrate between preferred winter and summer habitat (Gibson, 1978; Rimmer *et al.*, 1983). However, once within preferred habitats, parr will remain sedentary unless forced to move due to adverse stream conditions (i.e. competition for suitable habitat, reduced water level, ice formation: Cunjak & Randall, 1993; Whalen *et al.*, 1999). Gowan *et al.* (1994) coined the term 'restricted movement paradigm' for many adult salmonids that are considered to be sedentary throughout their lives. Restricted movement has been used by scientists as the standard null hypothesis for fish movement studies. It has been suggested that the common acceptance of this null hypothesis is related to mark recapture study designs that are biased against detecting movement (Porter & Dooley, 1993). Research on the movement of stream fish should use radio telemetry to allow for the detection of individual fish over large spatial scales (Gowan *et al.*, 1994).

The winter season for stream resident Atlantic salmon parr, defined in temperate and arctic climates as the period immediately following egg deposition in autumn until the loss of surface ice and concurrent rising water temperature the following spring, is considered a critical period to survival (Cunjak *et al.*, 1998). Overwinter mortality of parr, primarily due to starvation, has been estimated to range from 23-57% (Cunjak & Randall, 1993). Therefore, parr must continue to forage throughout the winter in order to minimize the risk of starvation (Cunjak *et al.*, 1998). Foraging activity is costly during the winter as cold water temperatures reduce a fish's escape response to diurnal endothermic predators (i.e., bird and mammal species; Webb, 1978; Johnson *et al.*, 1996; Valdimarsson & Metcalfe, 1998; Metcalfe *et al.*, 1999). Atlantic salmon parr balance the trade-off between starvation and predation in winter by becoming predominantly nocturnal (Rimmer & Paim, 1989; Valdimarsson *et al.*, 1997). Parr spend the day concealed in interstitial spaces beneath the substrate and emerge at night to forage (Gibson, 1978; Rimmer & Paim, 1989; Fraser *et al.*, 1993, 1995). Nighttime activity has also been associated with a cost in terms of energy intake. Salmonid parr are visual foragers and feeding efficiency at nighttime light levels is reduced 65 % as compared to daytime light levels (Fraser &

Metcalfe, 1997). Fraser and Metcalfe (1997) suggested the cost of nocturnal foraging, in terms of reduced energy intake, may be offset by reduced energy requirements at cold water temperatures. Hence, fish may be able to meet metabolic demands through nocturnal feeding in winter. Recent research indicates that salmonid parr may be active throughout the diel cycle in winter but the level of daytime activity will vary among individual fish (Metcalfe *et al.*, 1998, 1999; Bradford & Higgins, 2001).

At present, knowledge of the mesohabitat (i.e., stream reach; e.g., pool, riffle) and microhabitat (i.e., physical characteristics of habitat used; e.g., water velocity and depth) requirements and behaviour of Atlantic salmon parr in winter is limited. Atlantic salmon are an important recreational species world-wide and wild populations are rapidly declining throughout their range. Two North American populations, Gulf of Maine and Inner Bay of Fundy, have been listed as endangered [U.S. Fish & Wildlife Service, Committee on the Status of Endangered Species in Canada (COSEWIC)]. Marine survival has been suggested to be the primary factor threatening the Inner Bay of Fundy population (Amiro, 2003), however, given the low densities of parr (Amiro, 1998) other factors that affect freshwater systems such as habitat alteration (i.e. fragmentation, flow) through road and dam construction may limit population recovery and should not be dismissed. Understanding the habitat requirements necessary for the survival of a species (i.e. critical habitat) is crucial for successful conservation and recovery strategies. This thesis examines winter movement, activity and habitat use (meso- and microhabitat) of

Atlantic salmon parr in both natural and regulated rivers in southern Newfoundland.

1.2 Chapter Outlines

In Chapter 2, I examined the effects of surgically implanted radio transmitters on wild Atlantic salmon parr. Similar tagging studies found no significant effect on hatchery-reared parr and smolts (McCleave & Stred, 1975; Moore *et al.*, 1990), whereas, significant adverse tagging effects have been demonstrated for wild juvenile rainbow trout *Oncorhynchus mykiss* (Peake *et al.*, 1997). Consequently, no assumptions could be made on the effects of surgically implanted transmitters on wild Atlantic salmon parr based on previous studies. Therefore, I conducted a laboratory experiment comparing the swimming performance, food consumption rate and growth of individually tagged and non-tagged (control) fish.

In Chapters 3 & 4, I examined winter movement, activity and habitat preference of radio-tagged Atlantic salmon parr in southeastern Newfoundland. In Chapter 3, I used manual tracking of tagged fish during the day and night. In Chapter 4, I developed a technique using fixed automatic data logging receivers (Lotek SRX 400) and cable antennas (i.e., stripped coaxial cables) to record parr movement continuously throughout the diel cycle. I determined the timing and frequency of fish movement using fluctuations in signal strength received from the radio transmitters. This study represents the first recording of individual movements of Atlantic salmon parr continuously throughout the diel cycle in a natural watershed in winter.

In Chapter 5, I examined winter activity patterns of landlocked Atlantic salmon parr in a regulated river in Newfoundland, West Salmon River. The study site was located just downstream from a fisheries compensation gate that released water into the river but prevented fish movement upstream into the reservoir. Discharge within this site was maintained at a regulated minimum of 1.3 $m^3 s^{-1}$ for the winter months (30 November to 1 June).

In Chapter 6, I examined the effect of experimental flow fluctuations in West Salmon River on activity, displacement, stranding and habitat use of Atlantic salmon parr in winter. Flow fluctuations have been shown to have minimal effects on the behaviour of salmonid fishes in summer (Heggenes, 1988; Simpkins *et al.*, 2000). However, similar flow studies in winter resulted in increased fish displacement and stranding rates (Vehanen *et al.*, 2000; Salveit *et al.*, 2001). Winter is a critical period for Atlantic salmon parr survival (Cunjak *et al.*, 1998) and habitat alterations during this time period may reduce survival. Determining the effect of flow fluctuations on Atlantic salmon parr in winter will assist the producers and regulatory agencies of hydroelectricity in reducing potential impacts.

Chapter 7 reviews the results of Chapters 2-6 and discusses the implications they may have to the successful management of Atlantic salmon populations.

1.3 Co-authorship Statement

I am the principal author (nee Hiscock) of the following chapters that have been published. These publications represent research in which I took the lead on study design, data collection and analysis, and preparation of the manuscript.

Chapter 2:

Robertson, M. J., Scruton, D. A. & Brown, J. A. (2003). Effects of surgically implanted transmitters on swimming performance, food consumption and growth of wild Atlantic salmon parr. *Journal of Fish Biology* **62**, 673-678.

Chapter 3:

Hiscock, M. J., Scruton, D. A., Brown J. A. & Clarke, K. D. (2002). Winter movement of radio-tagged juvenile Atlantic salmon in Northeast Brook, Newfoundland. *Transactions of the American Fisheries Society* **131**, 577-581.

Chapter 4:

Robertson, M. J., Clarke, K. D., Scruton, D. A. & Brown, J. A. (2003). Interhabitat and Instream Movements of Large Atlantic Salmon Parr in a Newfoundland Watershed in Winter. *Journal of Fish Biology* **63**, 1208-1218.

Chapter 5:

Hiscock, M. J., Scruton, D. A., Brown, J. A. & Pennell, C. J. (2002). Diel activity pattern of juvenile Atlantic salmon (*Salmo salar*) in early and late winter. *Hydrobiologia* **483**, 161-165.

Chapter 6:

Robertson, M. J., Pennell, C. J., Scruton, D. A., Robertson G. J., & Brown, J. A. (2004). Effect of increased flow on the behaviour of Atlantic salmon parr in winter. *Journal of Fish Biology*, in press.

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Chapter 2.0 Effects of surgically implanted transmitters on swimming performance, food consumption and growth of wild Atlantic salmon parr

2.1 Abstract

Experiments were conducted on wild Atlantic salmon *Salmo salar* L. parr to determine the effect of surgically implanted dummy transmitters on swimming performance, food consumption and growth. Swimming performance of tagged fish (tag 1.7-3.7 % of fish mass) was similar to that of control fish 1, 5 and 10 days after surgery. Negative effects on growth, however, were found up to day 36 of a 45 day experiment (tag 0.9-2.6 % of fish mass). Consumption rates were similar between tagged and control fish and did not explain differences in growth.

2.2 Introduction

Surgically implanted radio transmitters have been used to examine the movement and behaviour of Atlantic salmon *Salmo salar* L. adults (Begout-Anras *et al.*, 2001), smolts (Aarestrup *et al.*, 1999) and parr (Hiscock *et al.*, 2002). However, general population statements made from data collected on tagged fish assumes that fish are unaffected by the transmitters.

Studies have indicated that the swimming performance, feeding behaviour and growth of surgically tagged parr and smolts are similar to that of untagged controls (McCleave & Stred, 1975; Moore *et al.*, 1990). These studies were conducted on hatchery-reared fish and the results for wild conspecifics may differ. Peake *et al.* (1997) studied the swimming performance of hatchery-reared and wild tagged Atlantic salmon smolts and found that only the wild tagged smolts were affected by the transmitter. Therefore, no assumptions could be made on the effects of surgically implanted transmitters on wild Atlantic salmon parr based on previous studies.

The present study was conducted to examine the effect of surgically implanted dummy transmitters on the swimming performance, food consumption and growth of wild Atlantic salmon parr.

2.3 Materials and Methods

Fish and Surgical Procedure

Atlantic salmon parr were collected from rivers on the Avalon Peninsula (47° 50' N, 53°12' W), Newfoundland, Canada, with a backpack electrofisher (Smith-Root Model 12). Fish were transported to the laboratory (~ 1.5 h) and held in 1m^2 holding tanks for 1 week prior to experimentation. Fish were fed chopped dew-worms *Lumbricus terrestris* daily to satiation during this period.

A surgical procedure similar to Adams *et al.* (1998) and Moore *et al.* (1990) was used to implant dummy transmitters (Lotek Wireless Inc., 7 x 12 mm, 0.75 g in air, 0.5 g in water, with a 28 cm whip antenna) into the peritoneal cavity of test fish. Fish were anaesthetized with clove oil (Anderson *et al.*, 1997) and placed ventral side up on a foam pad. The transmitter was inserted through a 10 mm incision on the mid-ventral line anterior to the pelvic girdle. The transmitter antenna was fed through a needle (Jelco; 18 G, 38 mm) inserted through the body wall approximately 5 mm posterior and dorsal to the incision. The incision was closed with two sutures (USSC; 4-0 coated braided silk and C-13 needle). Surgery took approximately 2-3 min, and during this time, water was intermittently poured over the fish's gills. Tagged fish were placed in recovery tanks until the effects of the anaesthetic disappeared.

Swimming Performance

Eighty fish were randomly selected and placed in one of four treatment groups. Three groups underwent surgical implantation of dummy transmitters and were placed individually in 76 l flow-through aquaria until testing. The fourth group had no procedure and was used as the control group (mean ± S.E., mass 29.2 ± 1.3 g, 142.6 ± 0.19 mm fork length, L_F). Fish were fed chopped worms daily to satiation. Fish were not fed 24 h prior to testing. The swimming performance of the first tagged group was tested 1 day after surgery (mass 31.9 ± 1.5 g, 144.0 ± 2.2 mm L_F, tag 2.4 ± 0.1 % of fish mass), the second tagged group was tested 5 days after surgery (mass 31.2 ± 1.58 g, 143.8 ± 2.3 mm L_F , tag 2.5 ± 0.1 % of fish mass), and the third tagged group was tested 10 days after surgery (31.1 ± 1.4 g, 143.6 ± 1.9 mm L_F, tag 2.5 ± 0.1 % of fish mass). Control fish were tested after each tagged fish. Each fish was only tested once. Control and tagged fish were similar in both mass and fork length (ANOVA, $P > 0.05$). Critical swimming speed (maximum velocity a fish maintained for a defined period of time; Brett, 1964) was determined using a modified Blazka swim chamber (Smith & Newcomb, 1970). A test fish was acclimated to the swim chamber for 1 h at a speed of 15 cm s^{-1}, approximately 1 body length per second (BL s^{-1}). The speed was then increased at increments of 20 cm s^{-1} every 10 min until the fish fatigued. Fatigue was determined as the condition when a fish rested against the back screen of the chamber and was unable to return to a free-swimming position (Brett, 1964). The experiment was conducted between 9 and 31 July 2000 and water temperature in the aquaria and swimming chamber ranged from 15.9 to 16.8°C (mean ± S.E., 16.3 ± 0.1° C) throughout the study.

Critical swimming speeds were converted to B.L. s^{-1} and analysed using one-way ANOVA to explore differences within the four treatment groups.

Food Consumption and Growth

A 45 day experiment was conducted between 27 August and 11 October 1999 and repeated between 27 July and 10 September 2000. Fish randomly selected for the tagged group were weighed and measured prior to surgery and control fish were anaesthetized, weighed and measured (Table 1). The water temperature in the aquaria ranged from 13.8 to 17.3° C in 1999 and 16.2 to 18.4°C in 2000.

Table 1. Mean ± S.E. (range in parentheses) initial sizes of tagged and control wild Atlantic salmon parr used in the food consumption and growth experiments.

	1999	2000
Tagged	n = 11	n = 10
(Tag mass) (fish mass)$^{-1}$ (%)	0.9-2.6	1.4-2.5
Mass (g)	45.5 ± 5.1	37.8 ± 2.6
L_F (mm)	152 ± 5 (134-191)	150 ± 3 (143-162)
Control	n = 10	n = 9
Mass (g)	41.2 ± 5.2	39.2 ± 1.9
L_F (mm)	149 ± 6	151 ± 2 (144-164)

Tagged and control fish were placed individually in separate 76 l flow-through aquaria. Starting 24 h after surgery, day 1 of the experiment, fish were fed a weighed quantity of chopped worms exceeding satiation levels every second day. Remaining worms were removed from the tank 24 h after feeding and weighed. Worm mass was reduced 24% to compensate for water absorbed overnight in the tank. This 24% adjustment was determined in preliminary trials where a known quantity of worms were placed in 10 tanks for 24 hrs and then removed and weighed (% weight increase, 23.7 ± 1.2). Fish were anaesthetized, weighed and measured after every fourth feeding (i.e., days 9, 18, 27, 36 and 45 of the experiment).

Consumption rate was calculated as grams consumed per gram fish mass and growth rate as percent body mass change through each 9 day feeding period. To analyse growth, a General Linear Model (GLM) was developed with year, treatment and feeding period, as well as their interaction terms, as categorical variables and consumption rate as the covariate.

2.4 Results

No fish died during the experiments. During the food consumption and growth experiments, transmitters were expelled from two fish on days 27 and 29 in 1999 and three fish on days 20, 27 and 29 in 2000. Two of these transmitters were observed emerging through the antenna hole, which later appeared slightly swollen. Transmitters in two fish in 1999 (day 8 and 9) and one in 2000 (day 11) moved toward the posterior end of the body cavity, flipping the antenna toward the fish's head. All tagged fish were necropsied at the end of the 45 day experiment. All incisions were completely healed and transmitters were encapsulated in fibrous tissue on the body wall. No external or internal infections were apparent.

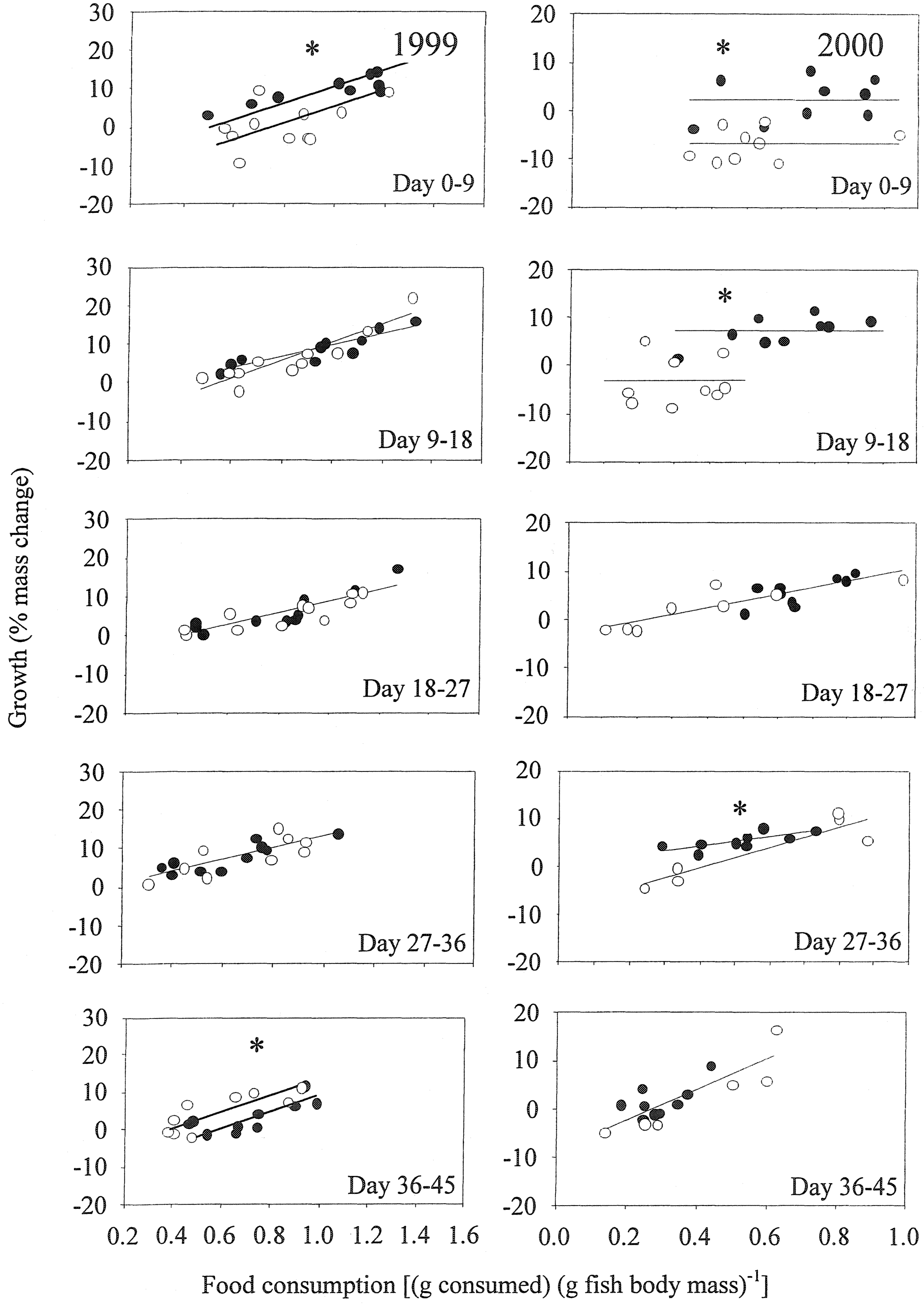
Swimming Performance

Swimming performance was similar between control fish (8.8 ± 0.4 B.L. s^{-1}) and tagged fish tested 1 day after surgery (7.8 ± 0.4 B.L. s^{-1}), 5 days after surgery (8.2 ± 0.5 B.L. s^{-1}) and 10 days after surgery (8.1 ± 0.4 B.L. s^{-1}; ANOVA, $P > 0.05$).

Food Consumption and Growth

Due to a strong year and feeding period interaction term in the original model (repeated measures ANCOVA, $F_{9,157} = 10.95$, $P < 0.0001$), the 1999 and 2000 data were analysed separately. In 1999, control fish had significantly greater growth rates than tagged fish on day 9. Growth rates were then similar up to day 36 and tagged fish outgrew control fish on day 45 (Fig. 1). In 2000, control fish had significantly greater growth rates than tagged fish up to day 18 and on day 36 (Fig. 1).

Figure 1. The relationship between individual food consumption rate and growth of surgically tagged wild Atlantic salmon parr (○) and non-tagged controls (●) over 9 day feeding periods. Tagged and control fish were compared using GLM. *, a significant difference between tagged and control fish at $P < 0.05$.


1999
2000
*
Day 0-9
Day 9-18
Day 18-27
Day 27-36
Day 36-45
30
20
10
0
-10
-20
Growth (% mass change)
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
0.0
0.2
0.4
0.6
0.8
1.0
Food consumption [(g consumed) (g fish body mass)$^{-1}$]

2.5 Discussion

Surgically implanted dummy transmitters did not affect the swimming performance of wild Atlantic salmon parr over a 10 day period. Negative effects on growth, however, were found in both the 1999 and 2000 experiments. The longer duration of growth rate effects in 2000 may be related to the smaller size of fish used that year as tagging effects can be inversely related to fish size (McCleave & Stred, 1975; Greenstreet & Morgan, 1989).

Food consumption rates were similar between tagged and control fish. Therefore, energy intake could not explain differences in growth rate between groups. Tagged fish may have expended more energy than control fish as a result of the physiological stress response to surgery (Jepsen *et al.*, 2001), protein synthesis for wound healing and transmitter encapsulation (Brafield & Llewellyn, 1982; Marty & Summerfelt, 1986) and higher activity levels (Adams *et al.*, 1998). In 1999, tagged fish grew faster than control fish in the last 9 days of the experiment, possibly indicating compensatory growth (Maclean & Metcalfe, 2001; Morgan & Metcalfe, 2001).

The results from the present study suggest that researchers can be confident making general population statements based on the swimming performance of surgically tagged wild Atlantic salmon parr > 120 mm using one of the smallest transmitters currently available. Although sample sizes in the growth rate experiment were low, the results suggest that caution is needed when interpreting growth data collected on surgically tagged wild Atlantic salmon parr.

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Chapter 3.0 Winter movement of radio-tagged Atlantic salmon parr in Northeast Brook, Newfoundland

3.1 Abstract

In winter, Atlantic salmon *Salmo salar* L. parr move to habitats with increased water depth, reduced water velocity and larger substrate than preferred summer habitat and become predominantly nocturnal. However, knowledge of their behaviour in winter habitat is limited. In this study, radiotelemetry was used to investigate winter movement, activity and habitat preference of Atlantic salmon parr. Data on fish position, corresponding habitat variables, and fish activity (i.e., active or nonactive) were collected on 14 days and 9 nights between 21 January and 10 February 1999. Due to mild winter air temperature, the study river remained ice free and water temperature ranged from 0.5 to 1.4°C. Habitat preference differed between active and non-active states. Fish were observed in an active state only at night and preferred smaller substrate and higher water velocity than the same fish in a non-active state. Selecting higher water velocity while active may give fish access to more prey. The number, distance, and direction of movements were highly variable and unexpected, given that the river was ice free and had relatively stable flow.

3.2 Introduction

Atlantic salmon *Salmo salar* L. parr move to preferred winter habitat in response to decreasing water temperature in the fall (< 8-10°C: Gibson, 1978; Rimmer *et al.*, 1983). Winter habitats are generally characterized by increased water depth, reduced water velocity, and larger substrate than preferred summer habitat (Cunjak, 1996; Whalen *et al.*, 1999). However, movement in and out of preferred habitats may continue throughout winter in response to ice formation and build-up, reduced water level and competition for suitable habitat (Cunjak & Randall, 1993; Whalen *et al.*, 1999). Atlantic salmon parr also switch from being active throughout the diel cycle in summer to being predominantly nocturnal in winter (Rimmer & Paim, 1989; Gries *et al.*, 1997; Valdimarsson *et al.*, 1997). Fish spend the day concealed in interstitial spaces beneath the substrate and emerge at night to forage (Gibson, 1978; Rimmer & Paim, 1989; Fraser *et al.*, 1993, 1995). The adaptive function of this behaviour has been associated with predator avoidance, minimizing energy expenditure, and avoiding harsh environmental conditions (Cunjak *et al.*, 1998; Valdimarsson & Metcalfe, 1998).

At present, knowledge of Atlantic salmon behaviour in winter habitat is limited. The objective of this study was to investigate the winter movement and activity (i.e., active or nonactive) of radio-tagged Atlantic salmon parr in Northeast Brook, Newfoundland.

3.3 Study Site

Northeast Brook, Trepassey, is a third-order river located in south-eastern Newfoundland, Canada (46° 46' N, 53° 21' W; Fig. 1). The study site, located on the main stem, extended from a high gradient riffle, about 200 m above the river mouth, to the first small lake (Miller's Pond) located about 800 m upstream. The study site consisted of five main mesohabitat types, which were categorized as glides, pools, riffles, deep pools, or runs (Scruton & Gibson, 1995; Sooley *et al.*, 1998; Fig. 1). The mean width (± S.E.) of the river within these habitat types was 12.6 ± 0.4 m. Species diversity within Northeast Brook, as within most eastern Newfoundland rivers, was low and consisted of anadromous Atlantic salmon, anadromous/resident brook trout *Salvelinus fontinalis* (Mitchell) and American eel *Anguilla rostrata* (Lesueur).

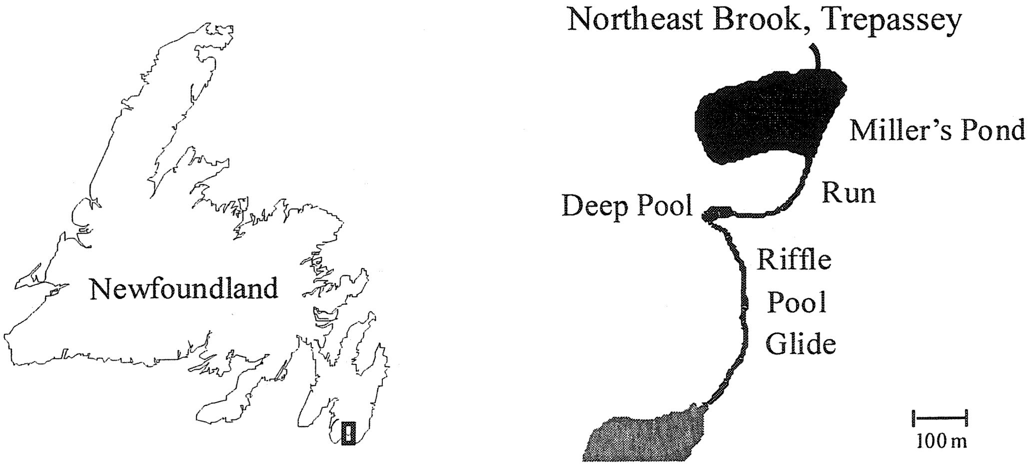

Figure 1: Study site: Northeast Brook, Trepassey. The 800-m study reach consisted of five main habitat types including a glide, pool, riffle, deep pool, and run.

3.4 Materials and Methods

Ten fish [mean weight (± S.E.) = 21.6 ± 1.8 g, mean fork length = 129.7 ± 4.6 mm, and mean age = 3.5 ± 0.3 years] were caught from various habitat types on 18 January 1999 with a backpack electrofisher (Smith-Root Model 12). Fish were anaesthetized with clove oil (Anderson *et al.*, 1997) and transmitters (Advanced Telemetry Systems Model 2-377 transmitters, 7 x 7 x 18 mm, 1.3 g in air) were surgically implanted into the body cavity using a procedure similar to Adams *et al.* (1998) and Moore *et al.* (1990). A transmitter was inserted through a 10-mm incision made on the midventral line anterior to the pelvic girdle. The transmitter antenna was fed through a needle (Jelco; 18 guage, 38 mm) inserted through the body wall approximately 5 mm posterior and dorsal to the incision. The incision was closed with two sutures (USSC; 4-0 coated braided silk and C-13 needle). Fish were held for 24 h after surgery before release back into their respective habitats on 19 January 1999.

All fish were tracked (Lotek SRX 400 receiver) for 9 consecutive days and 6 nights starting 20 January 1999, and for 5 days and 3 nights between 3 February and 10 February 1999. After this time, signals from the transmitters were too weak to allow further tracking of the fish. Daytime observations were collected between 0900 and 1400 hours and nighttime observations between 1900 and 2200 hours.

The general position of each fish was determined using a handheld H-antenna; the precise position was pinpointed with a dipole antenna that was submerged and placed on the substrate. Fish were approached slowly from downstream of their position to minimize disturbance. Active fish were only approached to a distance of approximately 3 m, which allowed visual contact and habitat use to be determined. Lights were required at night; however, observed fish did not respond to the light (e.g., flee or move toward cover). The position of each fish within a marked habitat was recorded relative to the transect number and bank. Changes in position less than or equal to 50 m were measured directly with a measuring tape and positions greater than 50 m or outside the marked habitats were determined using a Garmin Differential Global Positioning System (DGPS), which was accurate to approximately 6 m.

Once the position of each fish was determined, the corresponding habitat variables were recorded. These included bottom and mean column water velocity (Marsh-McBirney model 2000 portable flowmeter), water depth, and substrate [sand (< 2 mm), gravel (2 mm - 3 cm), cobble (3 - 25 cm), boulder (> 25 cm): modified from Scruton & Gibson, 1995 and Sooley *et al.*, 1998]. Fish activity and visibility of the fish or antenna were also recorded. Fish were considered to be in an active state if they were moving or holding position in the water column. Fish in a nonactive state were on the bottom, either partially or fully concealed under cover. An underwater viewing tube was used to confirm the presence of nonactive fish or their antennas. Movements in and out of the small lake and deep pool were recorded, but detailed observations were not conducted. Thermographs (Vemco minilog TR) placed along the study reach recorded water temperature throughout the study period.

3.5 Results

The movements of the 10 radio-tagged Atlantic salmon parr in Northeast Brook are displayed in Figure 2. The number of recorded movements throughout the study ranged from 3 to 17. The mean proportion of upstream and downstream movements (± S.E.) were equal, 0.50 ± 0.05. The distance moved upstream (median = 9 m) and downstream (median = 12 m) did not differ significantly (Mann-Whitney, W = 1,606.0, n = 76, P = 0.778). Movement declined throughout the study period (r = 0.587, n = 23, P = 0.003; Fig. 3). Net distance moved from initial to final recorded position was highly variable, ranging from 4 to 669 m. Net movement occurred in both the upstream (n = 7) and downstream (n = 3) directions. A comparison of initial recorded habitat type to the final recorded habitat type indicated that fish from shallower habitats (i.e., riffle and run) tended to move to deeper habitats (i.e., pool, deep pool, and small lake), while those originally in deeper habitats (i.e., glide or pool) tended to remain there.

Eight of the 10 tagged fish were active at least once during the study. Fish were only observed to be active at night. To determine if habitat preference differed between active and nonactive states, the habitat variables recorded for fish in an active state were paired with the habitat variables recorded earlier that day when the same fish was in a nonactive state. Substrate preference differed between active and nonactive fish (G-test:

$G_2 = 22.33$, $P < 0.001$; Fig. 4). Active fish preferred gravel-cobble substrate, and nonactive fish preferred cobble-boulder substrate. There was no significant differences in water depths used by active and nonactive fish ($W = 286.5$, $n = 16$, $P = 0.406$). However, active fish preferred higher bottom and mean column water velocity than nonactive fish ($W = 325.0$, $n = 16$, $P = 0.017$ for active fish and $W = 328.5$, $n = 16$, $P = 0.015$ for nonactive fish; Fig. 5). Nonactive fish, including their antennas, were seldom visible (proportion occurrence = 0.12). The water temperature ranged from 0.5 to 1.4°C throughout the study period.

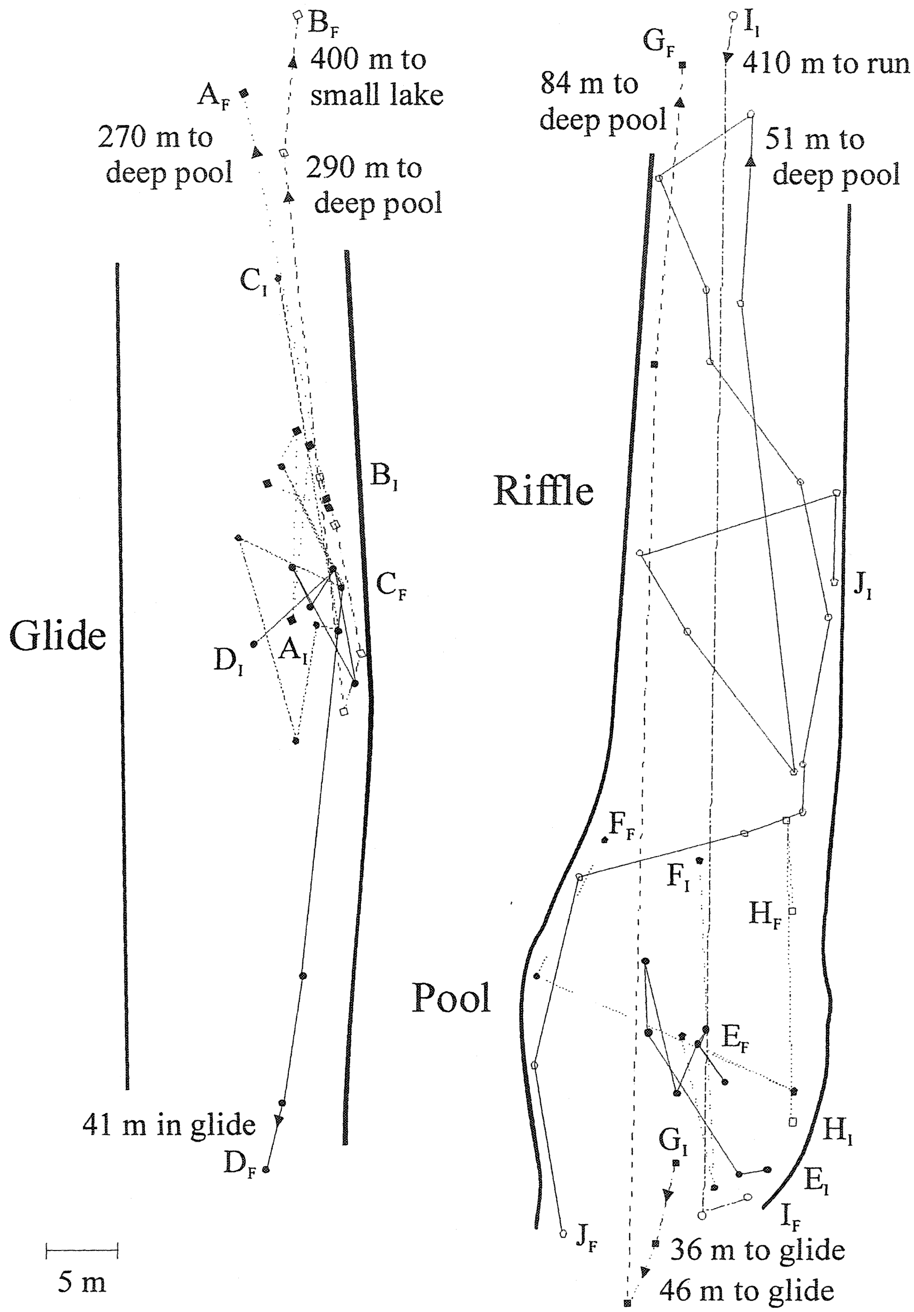

Figure 2: Movement of 10 radio-tagged Atlantic salmon parr in Northeast Brook, Newfoundland. Each fish is represented by a letter and I and F in subscript indicate initial and final position respectively.

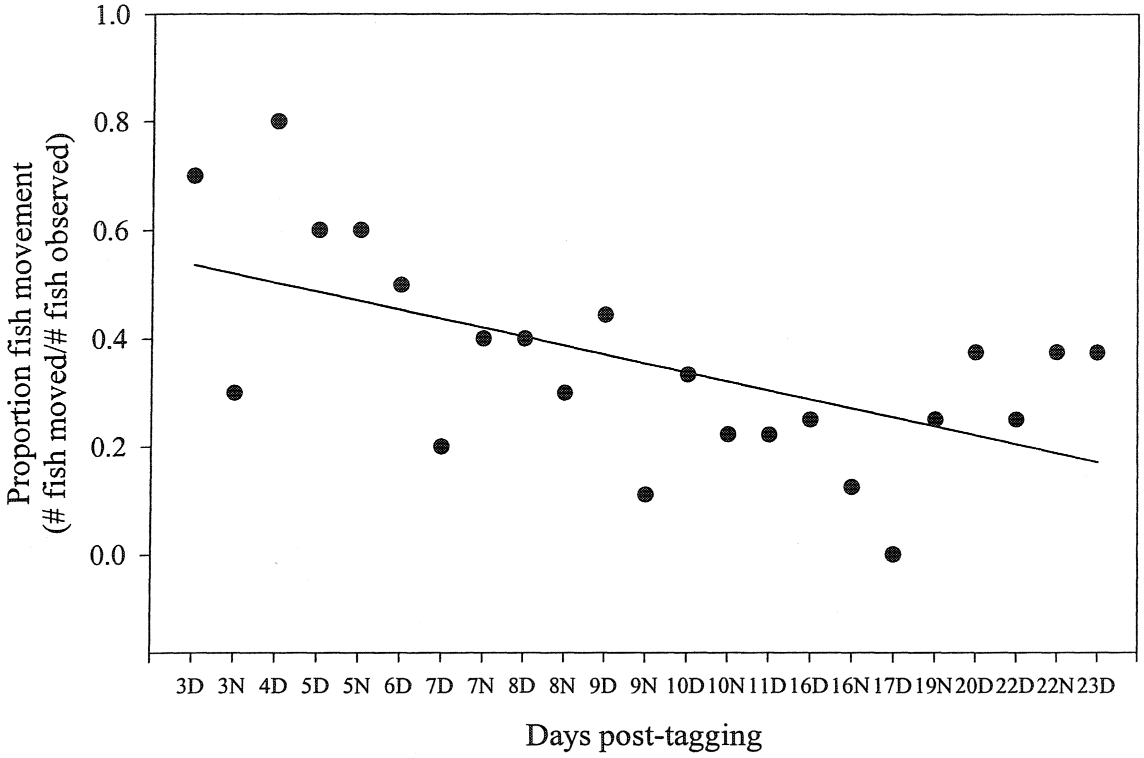

Figure 3: Proportion of radio-tagged Atlantic salmon parr displaying movement throughout the study period (r = 0.587, n = 23, P = 0.003). The letter D represents the daytime observation period; N represents the nighttime observation period.

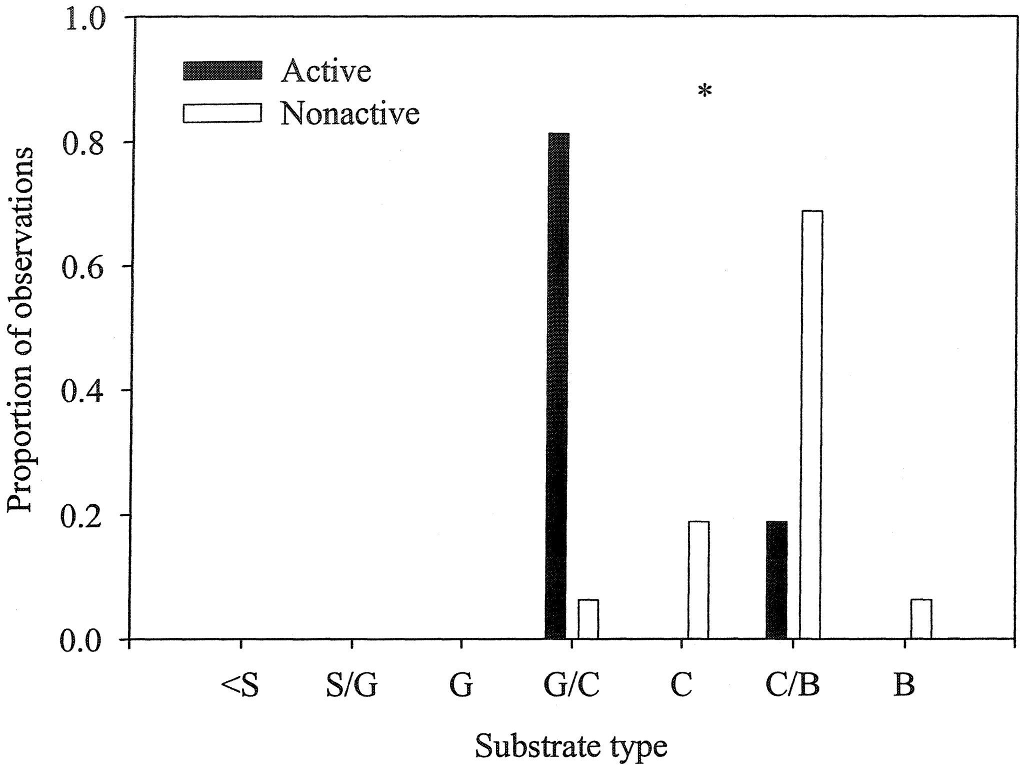

Figure 4: Comparison of substrate used by radio-tagged Atlantic salmon parr in active and non-active states. Substrate type: <S = sand, S/G = sand-gravel, G = gravel, G/C = gravel-cobble, C = cobble, C/B = cobble-boulder, and B = boulder (see text for particle sizes of substrate types). *, denotes a significant difference between active and nonactive states ($P < 0.05$).

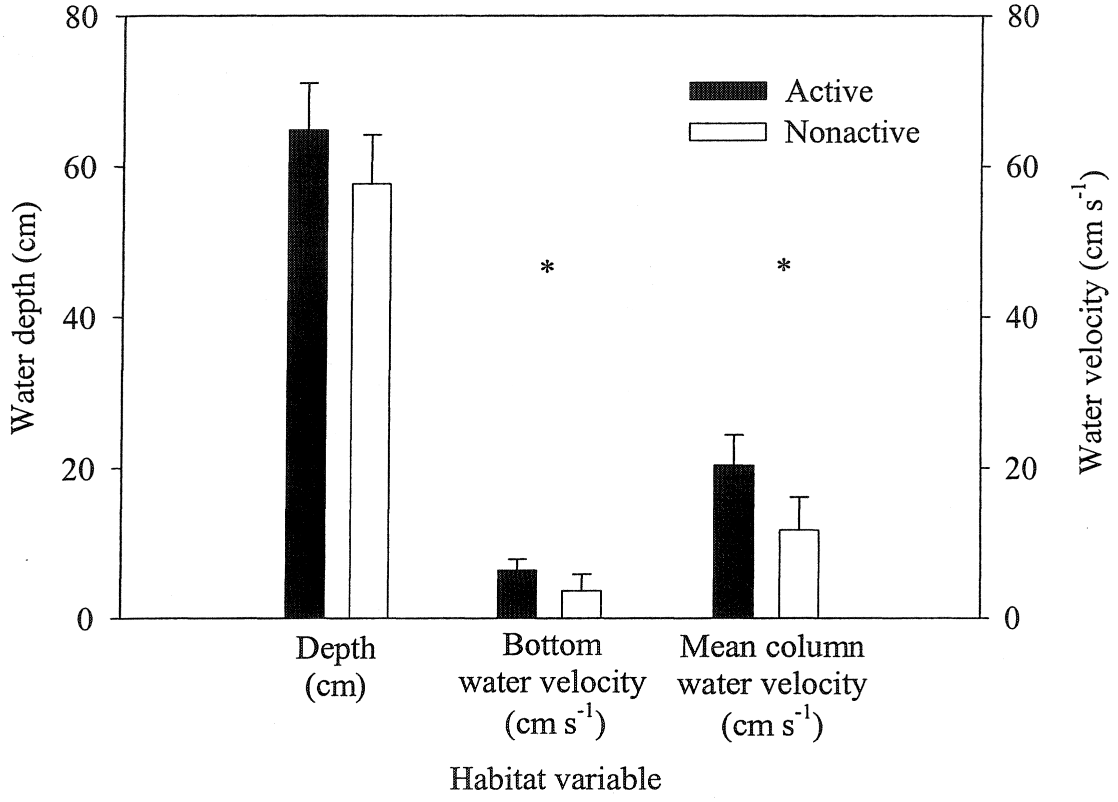

Figure 5: Comparison of mean (+ S.E.) water depth and velocity used by radio-tagged Atlantic salmon parr during active and nonactive states. *, denotes significant differences between active and nonactive states ($P < 0.05$).

3.6 Discussion

The number, distance, and direction of movements were highly variable and unexpected, given that the river was ice free and had relatively stable flow throughout the study period. Mild winter conditions are common for this area of Newfoundland, especially over the last 10 years (hydrological modelling, Department of Environment, Government of Newfoundland and Labrador, unpublished data). Fish in this study were not forced to move due to ice formation and build-up, increased water velocity, or reduced water level. It is also unlikely that movement was a result of high interspecific or intraspecific competition for limited suitable habitat, given that (1) larger brook trout were not found in the stream reach while electrofishing, and (2) due to the nature of the radio transmitters, larger, likely dominant parr were selected for the study (Kalleberg, 1958; Abbott *et al.*, 1985). Movement declined throughout the study period and fish tended to move toward deeper habitat. These results may indicate that these fish delayed settling into preferred winter habitat, possibly due to the mild winter conditions.

The present study also investigated habitat preference between active and nonactive states. Fish in a nonactive state, observed both day and night, used predominately cobble-boulder substrate. Nonactive fish appeared to be burrowing into the substrate, given that the fish nor their antennas, approximately 25 cm in combined length, were usually visible. This behaviour may indicate that the fish are not only seeking low velocity habitat but also using cover to be completely concealed from potential predators.

Fish in an active state, only observed at night, used predominantly gravel-cobble substrate and higher water velocity than the same fish in a nonactive state. Given that increased flow is associated with increased invertebrate drift (Wańkowski & Thorpe, 1979; Fausch, 1984), selecting higher water velocity while active may give fish access to more prey.

Two of the 10 fish with transmitters were lost to predation during the study. One fish (F in Fig. 2) was found partially consumed within 2 m of the pool bank on 27 January. The other fish (H in Fig. 2) was found in faeces from a mink *Mustela vison* S. approximately 40 m from the riffle bank on 3 February. Although predation was a prevalent factor in this study, no conclusions can be made on the natural level of winter predation in these habitats, given that the tagged fish may have been more susceptible to predation. Increased predation rates were demonstrated on surgically tagged juvenile chinook salmon *Oncorhyncus tshawytscha*, possibly due to reduced burst swimming performance and increased visibility from the transmitter antenna (Adams *et al.*, 1998).

The results of this study are based on a small sample size within one river and may not be broadly applicable. The movement observed in this study may be a result of mild winter conditions. More research is required to determine the general movement pattern of Atlantic salmon parr under various winter conditions.

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Chapter 4.0 Interhabitat and Instream Movements of Large Atlantic Salmon Parr in a Newfoundland Watershed in Winter

4.1 Abstract

Radiotelemetry was used to investigate movement of large, mainly mature male (80%) Atlantic salmon *Salmo salar* L. parr in Stoney River, Newfoundland during early winter (November; water temperature 6.0 ± 0.1 °C) and mid-winter (January to February, 0.8 ± 0.0 °C). Site fidelity of parr in early winter was low. Parr moved between fluvial and lacustrine habitats and were active throughout the diel cycle. Parr caught in fluvial habitats in mid-winter were smaller and younger than parr caught in early winter. Site fidelity of parr in mid-winter was greater than in early winter. Parr in mid-winter moved between fluvial and adjacent small lacustrine habitats, but avoided a larger pond: inhabited by piscivorous fishes. Instream movement rates in mid-winter were lower than in early winter and occurred primarily during hours of darkness (dawn, dusk, night). Fluvial habitats were ice free and had relatively stable flow throughout the study periods. These results suggested that large Atlantic salmon parr utilize a variety of habitats and remain active throughout the winter, even under stable environmental conditions.

4.2 Introduction

Atlantic salmon *Salmo salar* L. parr have been traditionally viewed as sedentary stream dwellers (Keenlyside, 1962; Gibson, 1993). In river systems with few competing or predatory fish species, however, Atlantic salmon use lakes for parr rearing and smolt production (Hutchings, 1986; Gibson, 1993; Gibson *et al.*, 1993). Lake use by parr is widespread in Newfoundland, Canada (Pepper, 1976; Chadwick & Green, 1985; Hutchings, 1986; O'Connell & Ash, 1993) and has been documented in Iceland (Einarsson *et al.*, 1990), Norway (Halvorsen & Jørgensen, 1996; Halvorsen & Svenning, 2000), Finland (Erkinaro *et al.*, 1995; 1998; Jørgensen *et al.*, 1999) and Ireland (Matthews *et al.*, 1997).

In Newfoundland, seasonal habitat shifts between fluvial and lacustrine habitats are common for Atlantic salmon parr (Hutchings, 1986; Ryan, 1986; Erkinaro & Gibson, 1997). Parr may enter lakes in the spring or early summer and remain there until they emigrate to reproduce after maturing (mainly males) or migrate to sea as smolts (predominantly females; Hutchings, 1986). Migration to lakes may be of adaptive significance, as growth and survival rates are greater in lacustrine habitats compared to fluvial habitats (Hutchings, 1986; Dempson *et al.*, 1996; Erkinaro & Gibson, 1997; Erkinaro *et al.*, 1998; Halvorsen & Svenning, 2000).

The winter season for stream resident Atlantic salmon parr, defined in temperate and arctic climates as the period immediately following egg deposition in autumn until the loss of surface ice the following spring, is generally considered a critical period for survival (Cunjak *et al.*, 1998). Parr overwintering in streams exhibit a variety of behavioural adaptations to reduce predation risk from diurnal endothermic predators (i.e., avian or mammalian), conserve energy, and avoid adverse environmental conditions. These behaviours include use of large substrate for daytime concealment, switching from primarily diurnal to nocturnal activity and moving in response to ice formation or reduced water levels (Gibson, 1978; Rimmer *et al.*, 1983; Cunjak & Randall, 1993; Fraser *et al.*, 1995; Valdimarsson & Metcalfe, 1998; Metcalfe *et al.*, 1999; Whalen *et al.*, 1999).

The objective of this study was to examine winter site fidelity, mesohabitat use and diel movement patterns of Atlantic salmon parr in Stoney River, Newfoundland using radiotelemetry. Given the size of the radio transmitters currently available, only large parr (> 125 mm fork length, L_F) could be studied. Parr movement was recorded continuously throughout the diel cycle within fluvial habitats (instream) and between fluvial and lacustrine habitats (interhabitat). The study was conducted in early winter and mid-winter to examine variations in movement between the two periods. This study represents the first recording of individual movements of Atlantic salmon parr continuously throughout the diel cycle in a natural watershed in winter.

4.3 Study Area

Stoney River is located in south-eastern Newfoundland, Canada and empties into the Atlantic Ocean via Trepassey Bay. The study area included Stoney Pond (25 ha) and adjacent fluvial and smaller lacustrine habitats (1-2 ha; Fig. 1). The lacustrine habitats, including Stoney Pond, were shallow (maximum depth 4.6 m), with cobble, gravel and organic substrate. Fluvial habitats (mean ± S.E. wetted width, 9.4 ± 0.2 m) were characterized as predominantly riffle-run habitat with cobble and boulder substrate (see Scruton & Gibson, 1995). Fluvial habitats had stable flow conditions and remained relatively ice free throughout the winter. In contrast, lacustrine habitats were ice-covered in mid-winter. Stoney River supports populations of Atlantic salmon and brook trout *Salvelinus fontinalis* (Mitchill), brown trout *Salmo trutta* L., three-spine stickleback *Gasterosteus aculeatus* L., rainbow smelt *Osmerus mordax* (Mitchill) and American eel *Anguilla rostrata* (Lesueur).

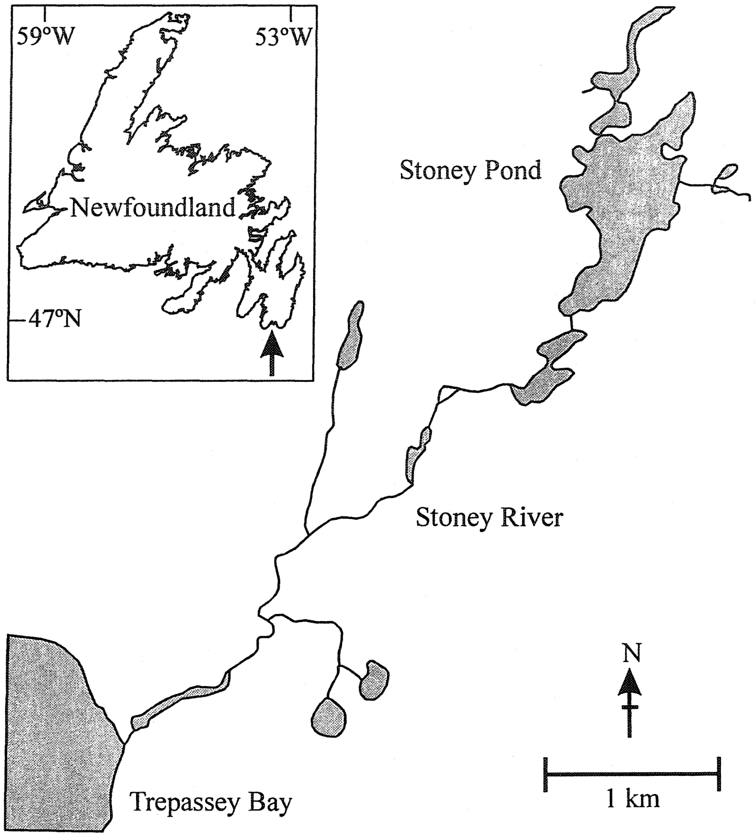


Figure 1: The location of the study area in Stoney River, Newfoundland, Canada.

4.4 Materials and Methods

Research was conducted over two winters immediately following spawning in early winter (3-17 November 2000 and 6-16 November 2001) and after freeze-up of lacustrine habitats in mid-winter (22 January to 2 February 2001 and 21 January to 3

February 2002). Thermographs (Vemco minilog TR) placed in fluvial habitats and Stoney Pond recorded water temperature hourly throughout the study periods. Fish were caught with a backpack electrofisher (Smith-Root Model 12) from fluvial habitats within the study area and, in early winter, with fyke nets in Stoney Pond. The surgical procedure used by Robertson *et al.* (2003) was used to implant the radio transmitters (Advanced Telemetry Systems Model 377, 7 x 7 x 18 mm, 1.3 g in air) into the fish's peritoneal cavity. Fish were anaesthetised with clove oil (Anderson *et al.*, 1997) and placed ventral side up on a foam pad. The transmitter was inserted through a 10 mm incision on the midventral line anterior to the pelvic girdle. The transmitter antenna was fed through a needle (Jelco; 18 G, 38 mm) inserted through the body wall approximately 5 mm posterior and dorsal to the incision. The incision was closed with two sutures (USSC; 4-0 coated braided silk and C-13 needle). Tagged fish were placed in flow-through recovery buckets within the river and released back into the habitat in which they were caught approximately 1 to 2 h after surgery. Recent laboratory research on wild Atlantic salmon parr, using the same surgical method, found no differences in swimming performance and food consumption between tagged and control parr (tag 0.9-3.7 % fish mass; Robertson *et al.*, 2003). Therefore, data collected on tagged parr in the present study should be representative of similar wild parr within the population.

Tracking commenced 24 h after tagging. No fish died as a result of the tagging procedure. Tagged fish were tracked manually using a hand held H-antenna once per day. Cable antennas (i.e., striped coaxial cables) taped to small rocks were placed in arrays on the substrate within fluvial habitats and placed adjacent to tagged fish concealed under the substrate. The detection range of each cable antenna was approximately 5 m (100 m^2) and the antenna arrays were placed so that all movements within fluvial habitats could be detected. Cable antennas placed between fluvial and lacustrine habitats were used as gates to record interhabitat movements. The cable antennas were attached to fixed automatic data logging receivers (Lotek Inc., SRX 400) that recorded movement continuously throughout the diel cycle (Fig. 2). Instream movements were determined through fluctuations in signal strength recorded by the receiver. Due to technological limitations, movements < 1 m from the cable antenna could not be detected and the distance fish moved from the cable antennas could not be quantified. Therefore, instream movements were defined as movements > 1 m. Recent publications have used similar techniques for determining fish movement (David & Closs, 2001; Hiscock *et al.*, 2002).

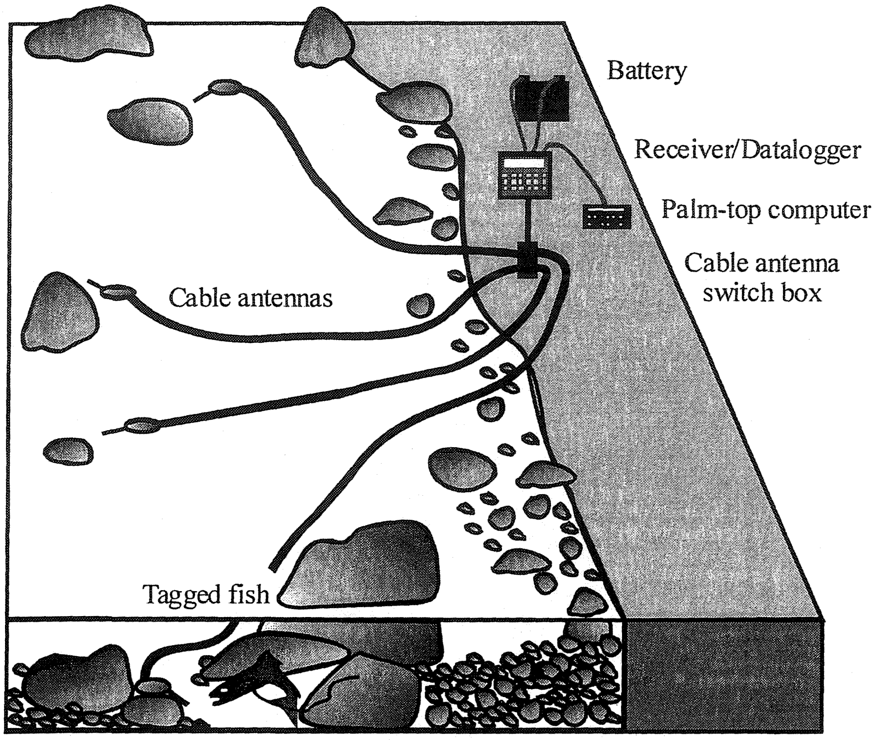


Figure 2: Schematic diagram of the telemetry system used to record parr movement throughout the diel cycle.

4.5 Results

A total of 63 Atlantic salmon parr were tagged with radio transmitters. The size and age of parr tagged in early winter from fluvial habitats (n = 25, mean ± S.E.; L_F, 161.1 ± 3.7 mm; mass, 45.7 ± 3.3 g; age, 4.2 ± 0.2 years, age range 3-6 years; tag 3.2 ± 0.2 % of fish mass) and Stoney Pond (n = 11, L_F, 159.2 ± 3.1 mm; mass, 43.1 ± 3.2 g; age, 3.8 ± 0.2 years, age range 3-5; tag 3.2 ± 0.2 % of fish mass) were similar (Wilcoxon two-sample test, $P > 0.05$). Parr tagged from fluvial habitats in mid-winter were smaller

(Fig 3; n = 27, L_F, 144.1 ± 3.1 mm; mass, 31.6 ± 2.2 g, age, 3.1 ± 0.2 years, age range 2-5 years; tag 4.5 ± 0.3 % of fish mass: L_F; Wilcoxon test, W = 845.5, $P < 0.001$) and younger than parr caught in early winter (age 4.2 ± 0.2 years; W = 797, $P < 0.001$). Most parr (81%) in early winter were mature males with free-flowing milt. Ten tagged parr were killed and sexed at the end of the mid-winter study periods. Of these fish, 80% were mature males and 20% were immature females.

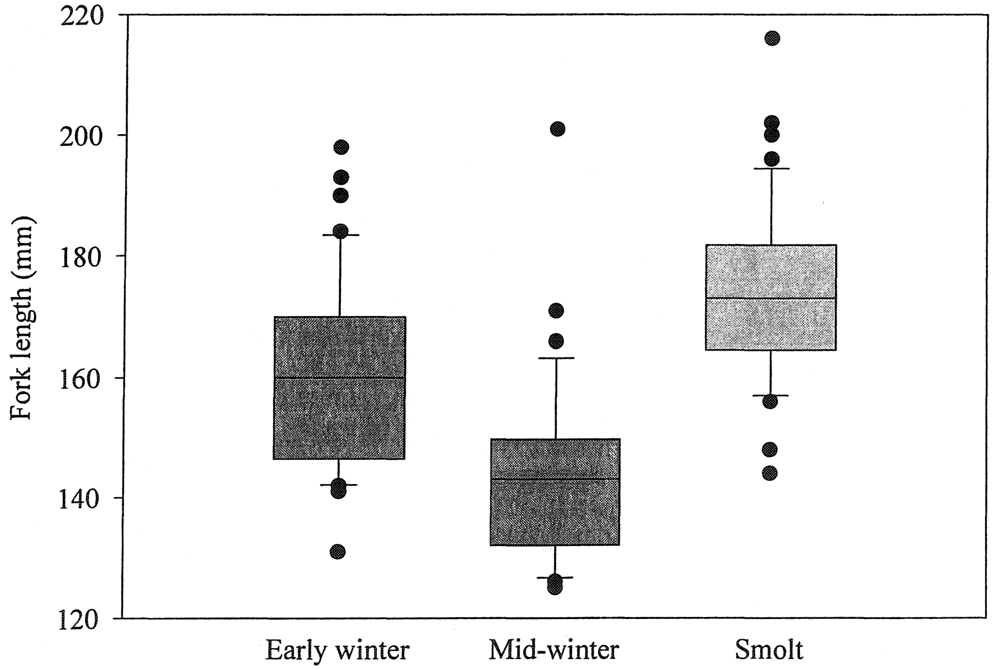


Figure 3: Fork length of Atlantic salmon parr tagged from fluvial habitats in Stoney River in winter. Smolt size is included for comparison. Smolts were collected from a smolt fence installed during the spring of 2001 and 2002. Vertical boxes with error bars indicate the median, 10th, 25th, 75th, and 90th percentiles and dots represent outliers.

Water temperatures in fluvial habitats and Stoney Pond were similar during the study periods (t-test, $P > 0.05$). However, mean daily water temperature differed between years in early winter, with higher temperatures in 2000 (range 7.4 – 10.8 °C, mean ± S.E., 8.8 ± 0.3 °C) than in 2001 (2.9 - 8.3 °C, 6.0 ± 0.6 °C; $t = 3.98$, d.f. = 15, $P = 0.001$). Water temperatures were similar between years in mid-winter (0.7 ± 0.03 °C, t-test, $P > 0.05$).

Interhabitat movements (movements day^{-1}) were similar for parr tagged from fluvial habitats and Stoney Pond in early winter, occurring approximately once every third day (0.39 ± 0.07 movements day^{-1}). However, interhabitat movements in mid-winter were 4.5 times less frequent than in early winter, usually occurring only once during the study period (0.09 ± 0.02 movements day^{-1}; $t = 4.38$, d.f. = 40, $P < 0.0001$). In early winter, 76% of fish tagged from fluvial habitats moved to lacustrine habitats including Stoney Pond, whereas, 45% of fish tagged in Stoney Pond moved to fluvial habitats (Fig. 4). In mid-winter, 48% of fish tagged from fluvial habitats moved to small lacustrine habitats and 4% (i.e., one fish) moved into Stoney Pond (Fig. 4). Total distance of interhabitat movements appeared to be greater in early winter than in mid-winter. However, due to high variability and low sample size in mid-winter, statistically significant differences between winter periods and years were not detected (Fig. 5; repeated measures ANOVA, $P > 0.05$).

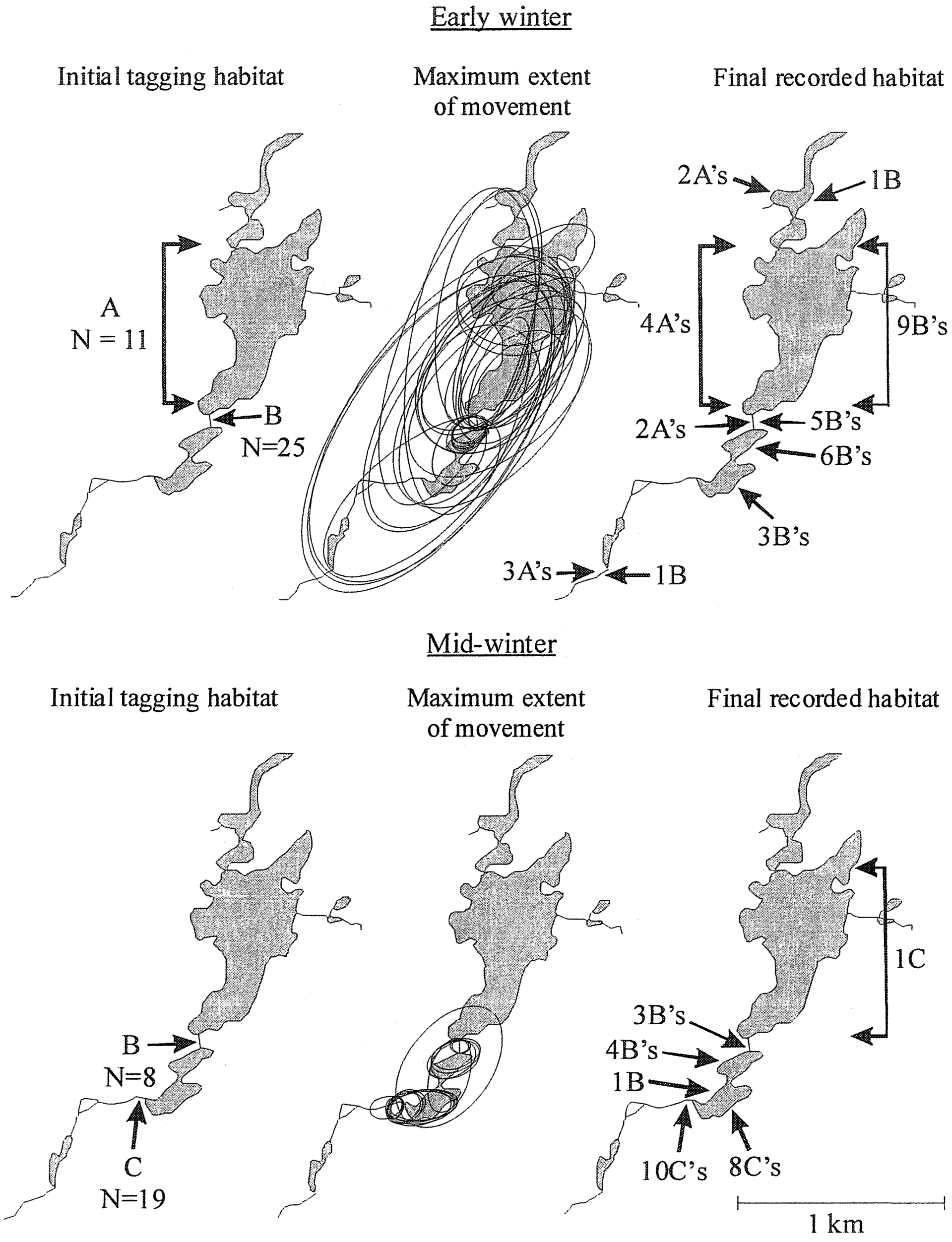


Figure 4: Initial tagging habitat (A = Stoney Pond, B and C = fluvial habitat), maximum extent of movement, and final recorded habitat (number of fish present from initial tagging habitats) of radio-tagged Atlantic salmon parr in Stoney River, Newfoundland in winter.

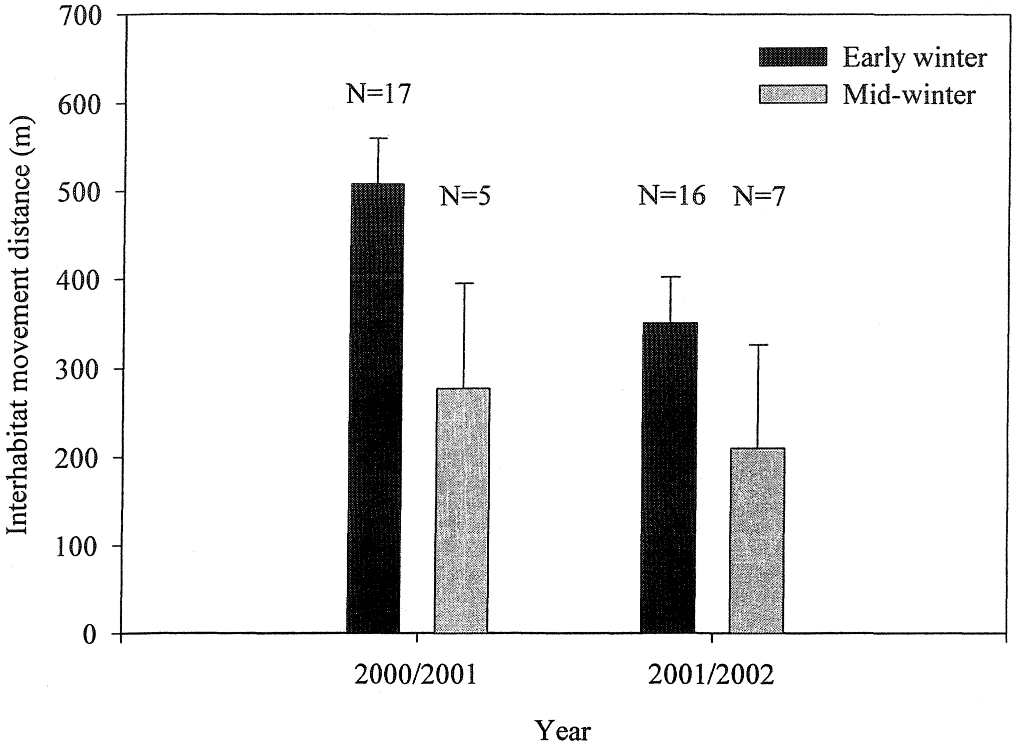


Figure 5: Interhabitat movement distance (least squared means + S.E. adjusted for fork length) of radio-tagged Atlantic salmon parr in early and mid-winter.

Instream movement rates (movements h^{-1}) were positively related to fish size in early winter (t = 2.7, d.f. = 19, P = 0.001; Fig. 6), while no trend was apparent in mid-winter (P > 0.05). Instream movement rates were also 2.4 times greater in early winter (3.1 ± 0.1 movements h^{-1}) than in mid-winter (1.3 ± 0.1 movements h^{-1}; repeated measures ANOVA controlled for fish length: $F_{1,33} = 126.5$, P < 0.0001).

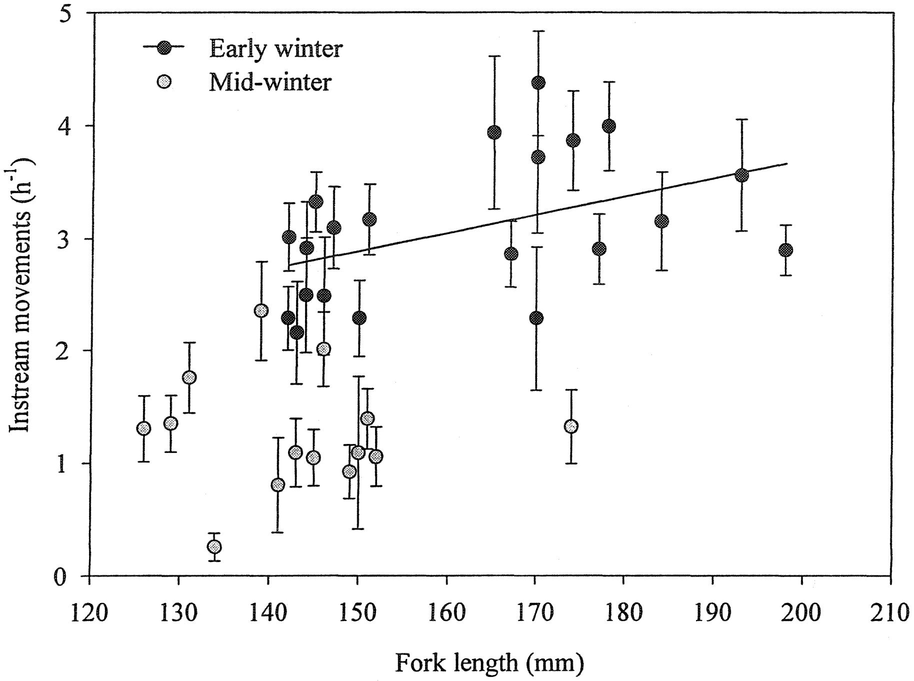
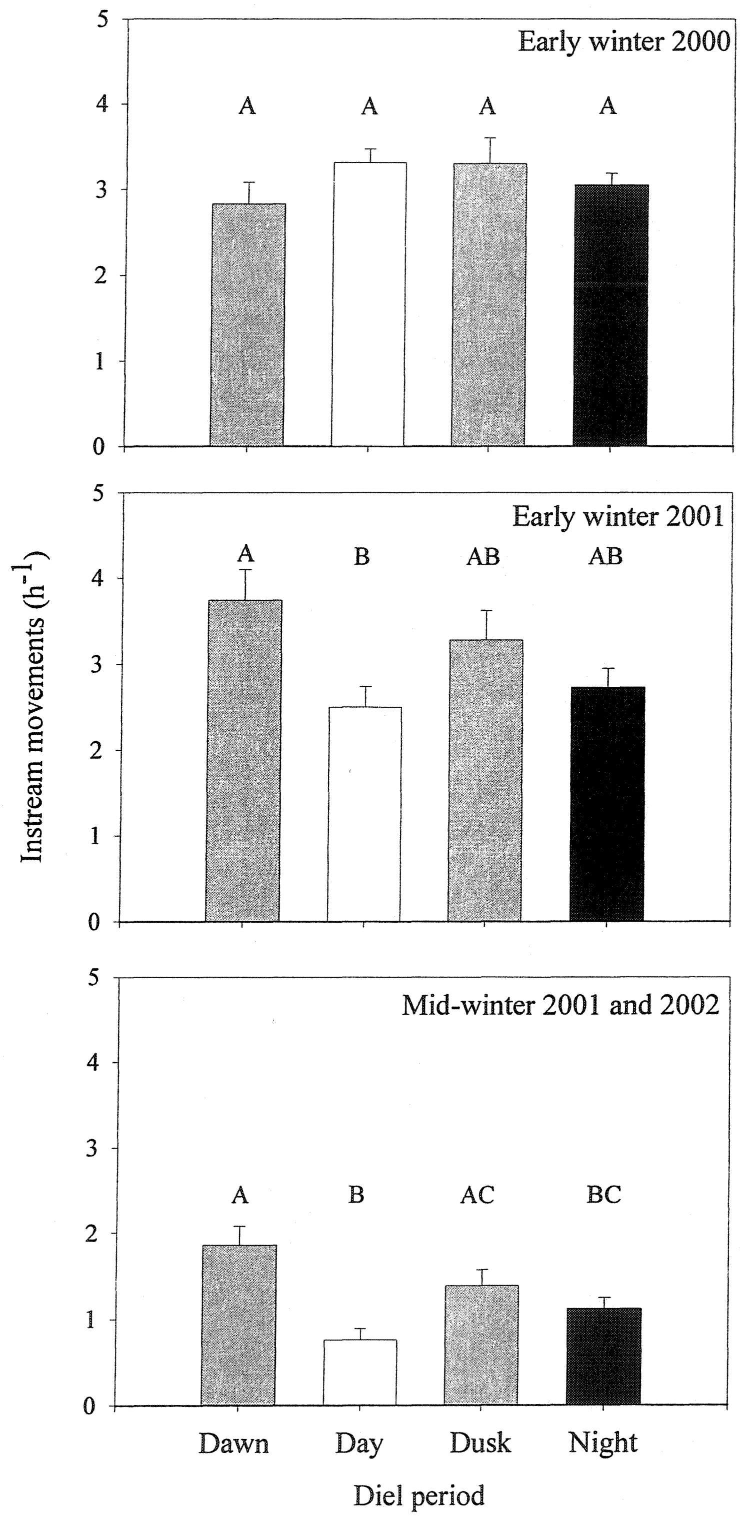


Figure 6: Relationship between instream movement rate (mean ± S.E.) and fork length of radio-tagged Atlantic salmon parr in early and mid-winter.

Instream movements were divided into four diel periods; dawn (civil twilight), day, dusk (civil twilight) and night. Instream movements between diel periods were significantly different between years in early winter (repeated measures ANOVA, $F_{3,59}$ = 3.4, P = 0.025; Fig. 7). In early winter 2000, instream movements occurred throughout the diel cycle. In early winter 2001, the diel pattern of instream movements was more similar to mid-winter, with lowest movement occurring during the day and greatest movement occurring at dawn (Fig. 7). Low water temperature in early winter 2001 may have been responsible for the mid-winter movement pattern observed. Diel movement patterns were similar between years in mid-winter (P > 0.05).

Figure 7: Instream movement rate (mean + S.E.) of radio-tagged Atlantic salmon parr in early and mid-winter. Means with the same letter are not significantly different from each other (repeated measures ANOVA, $P > 0.05$). P-values were corrected using sequential Bonferroni adjustments.


Early winter 2000
A
A
A
A
Early winter 2001
A
B
AB
AB
Mid-winter 2001 and 2002
A
B
AC
BC
Instream movements (h^{-1})
0
1
2
3
4
5
Dawn
Day
Dusk
Night
Diel period

4.6 Discussion

Site fidelity of parr tagged in early winter was low. Parr moved between fluvial and lacustrine habitats and were active throughout the diel cycle. Site fidelity in mid-winter was greater than in early winter. Parr in mid-winter moved between fluvial and adjacent small lacustrine habitats, but avoided Stoney Pond. Instream movement rates in mid-winter were lower than in early winter and occurred primarily during hours of darkness (dawn, dusk, night). The results of the present study are based on large ($L_F >$ 125 mm), predominantly mature male parr (80 %) and may not be applicable to individuals exhibiting different life history strategies.

Early maturation of male parr is a common life history strategy in Newfoundland river systems (Dalley *et al.*, 1983; Myers, 1984; Chadwick & Green, 1985). Mortality rates of mature male parr have been estimated to be approximately double that of immature male parr (Mitans, 1973; Myers, 1984). Emaciation upon maturation and increased activity during the spawning season are probable factors contributing to the increased mortality of mature male parr (Mitans, 1973). Therefore, maximizing energy intake and replenishing post-spawning energy loss in early winter would have been crucial for overwinter survival. Parr in the present study may have enhanced energy intake rates in early winter by foraging throughout the diel cycle and by utilizing large lacustrine habitats that provide greater growth opportunities than fluvial habitats (Hutchings, 1986; Dempson *et al.*, 1996; Erkinaro & Gibson, 1997; Erkinaro *et al.*, 1998;

Halvorsen & Svenning, 2000). Enhanced growth rates of parr foraging in lakes may be associated with increased food resources and reduced energy required for maintaining position and territorial behaviour (Hutchings, 1986). Mature male parr caught in fluvial habitats in early winter may have emigrated from lakes to spawn in autumn (Hutchings, 1986; Erkinaro & Gibson, 1997). Therefore, early winter movement to lacustrine habitat observed in the present study, may reflect the return of mature male parr back to lakes after spawning. The extent of interhabitat movements in early winter may also be explained by continued movement in and out of spawning areas in search of late spawning opportunities or to forage on highly nutritious salmonid eggs drifting in the water column. The increase in instream movement with fish size observed in early winter may indicate greater post-spawning energy losses for larger parr.

The age difference between parr caught in fluvial habitats in early winter and mid-winter suggested that 2 to 3 year old parr remained in fluvial habitats to overwinter, whereas 4 to 6 year old parr overwintered in lacustrine habitats. The predominance of mature male parr in fluvial habitats in winter suggested that large female parr (i.e., pre-smolts) overwintered in lacustrine habitats. Given that smolt size has been correlated with survival at sea (Hansen & Lea, 1982; Dieperink *et al.*, 2002; Klemetsen *et al.*, 2003), maximizing winter growth rates in lacustrine habitats would be beneficial for large parr that will smolt in the spring. Research has indicated that, in some river systems, lacustrine habitats are responsible for the majority of smolt production (Chadwick & Green, 1985; Ryan, 1986; Hutchings, 1986). Alternatively, large parr may overwinter in lacustrine habitat because adequate substrate for daytime concealment in fluvial habitats may be limited (Cunjak, 1988).

In contrast with previous research on the winter movement of Atlantic salmon parr, interhabitat movement observed in the present study could not be explained by adverse stream conditions (Cunjak & Randall, 1993; Cunjak *et al.*, 1998; Whalen *et al.*, 1999). Parr were not forced to move due to reduced water levels or ice formation. Mid-winter movements from fluvial to small lacustrine habitats in the present study may have occurred as stored energy reserves became depleted and parr needed to increase energy intake to avoid starvation. Only one parr in mid-winter moved into the largest lacustrine habitat in the study area (Stoney Pond). Parr caught in fluvial habitats in mid-winter were smaller than parr caught in early winter and may not attain sufficient size to smolt in the spring (see Fig. 2). Therefore, the predation risks from piscivorous fish overwintering in large lacustrine habitats, such as the large brook trout and brown trout in the present study (K. Clarke, unpublished data), may outweigh the benefits of enhanced growth rate in those parr that will not smolt in the spring.

Instream movements occurred predominantly during hours of darkness (dawn, dusk, night) in mid-winter, as was found in previous research (Gibson, 1978; Rimmer *et al.*, 1983; Fraser *et al.*, 1995; Valdimarsson & Metcalfe, 1998). The presence of daytime activity, however, supports recent research suggesting that parr are not strictly nocturnal in winter (Metcalfe *et al.*, 1998; 1999; Hiscock *et al.*, 2002). Salmonid parr are visual foragers and feeding efficiency at daytime light levels is 65% greater than at nighttime light levels (Fraser & Metcalfe, 1997). Parr foraging during the day may increase growth rate but, due to a reduced escape response at cold water temperatures, doing so increases the risk of predation from diurnal endothermic predators (Valdimarsson & Metcalfe, 1998; Metcalfe *et al.*, 1999). Therefore, diel activity patterns in winter may reflect a trade-off between the benefits of increased energy intake and the risk of predation.

The results of the present study indicated that large Atlantic salmon parr are not sedentary stream dwellers in winter. Parr remained active throughout the winter and moved between fluvial and lacustrine habitats. Utilizing a variety of habitat types and adjusting diel activity patterns in winter may increase parr survival. Therefore, assuming this movement is adaptive, anthropogenic activities resulting in fish habitat fragmentation (i.e., improper culvert installation; Langill & Zamora, 2002) will restrict parr movement, especially during low water levels in winter, and may reduce overwinter survival of large parr.

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Chapter 5.0 Diel activity pattern of Atlantic salmon parr in early and late winter

5.1 Abstract

Radiotelemetry was used to investigate the diel activity pattern of Atlantic salmon *Salmo salar* L. parr in early and late winter. Fish were active throughout the diel cycle. However, there was significantly less daytime than nighttime movement and movement declined significantly with increasing fork length. Maximizing winter growth rate, through an overall increase in foraging activity, may reduce the risk of starvation in smaller fish. The results of the present study provide evidence that the activity patterns of salmonid parr are quite complex and support the suggestion that individual variation in activity patterns are, at least, partially driven by body size.

5.2 Introduction

Salmonid parr switch from being active throughout the diel cycle in summer to predominantly nocturnal behaviour in winter (Gibson, 1978; Rimmer & Paim, 1990; Heggenes *et al.*, 1993; Riehle & Griffith, 1993; Gries *et al.*, 1997). At water temperatures less than 8 to 10 °C, fish generally spend the day concealed in interstitial spaces beneath the substrate and emerge at night to forage (Gibson, 1978; Fraser *et al.*, 1993, 1995). Nocturnal feeding behaviour in winter has been primarily associated with avoiding diurnal endothermic predators including various bird and mustelid species (Valdimarsson & Metcalfe, 1998; Metcalfe *et al.*, 1999). Fish, being ectotherms, become sluggish at cold water temperatures and their ability to escape predation is reduced (Webb, 1978; Johnson *et al.*, 1996). Therefore, it may be adaptive to be active at night when the risk of predation is lowest (Fraser *et al.*, 1993). However, nighttime activity has also been associated with a cost in terms of energy intake. Salmonid parr are visual foragers and feeding efficiency at nighttime light levels is reduced 65 % as compared to daytime light levels (Fraser & Metcalfe, 1997). Fraser and Metcalfe (1997) suggested the cost of nocturnal foraging, in terms of reduced energy intake, may be offset by reduced energy requirements at cold water temperatures. Hence, fish may be able to meet metabolic demands through nocturnal feeding in winter.

Recent research indicates that salmonid parr may be active throughout the diel cycle in winter but the level of daytime activity varies among individual fish (Metcalfe *et al.*, 1998, 1999; Bradford & Higgins, 2001). Given that daytime foraging is positively correlated with growth rate, individual variation in the time spent foraging during the day may result from differences in the benefits of enhanced feeding and growth (Metcalfe *et al.*, 1998, 1999).

The purpose of the present study was to investigate the winter activity patterns of Atlantic salmon parr continuously throughout the diel cycle in the field. The study was conducted in early and late winter in order to examine intra-seasonal variations in diel activity patterns.

5.3 Study Site

West Salmon is a regulated river (Upper Salmon Hydroelectric Development, Newfoundland and Labrador Hydro) in south-central Newfoundland, Canada (48°12' N, 56°15' W; Fig. 1). The study site was located approximately 80 m downstream from the fisheries compensation gate used in regulating the river flow from the reservoir. The site was 90 m long and ranged from 28 to 56 m wetted width. The habitat was predominantly riffle, run and flat with cobble boulder substrate (Scruton & Gibson, 1995). Water discharge was maintained at 1.3 $m^3 s^{-1}$ throughout the study periods and the resulting water depth ranged from 1 to 78 cm (median, 20 cm). In early winter the study site was ice free and water temperature decreased from 3.1 to 0.2 °C (mean ± S.E., 1.36 ± 0.05 °C). In late winter the study site was 30 % ice covered and water temperature increased from 0 to 1.3 °C (0.51 ± 0.01 °C).

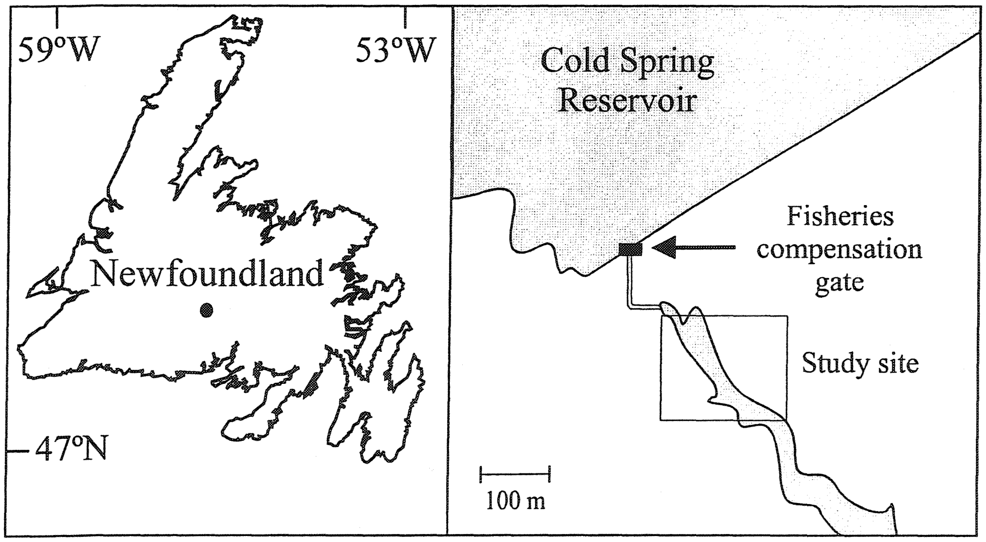

Figure 1: Location of West Salmon River and diagram of study site.

5.4 Materials and Methods

Radiotelemetry was used to investigate the diel activity patterns of Atlantic salmon parr in early and late winter, 28 November to 9 December 2000 and 7 to 17 March 2000 respectively. Fish were caught with a backpack electrofisher (Smith-Root Model 12) from within the study site. Fish were anaesthetized with clove oil (Anderson *et. al.*, 1997) and radio transmitters (Advanced Telemetry Systems Model 377, 7 x 7 x 18 mm, 1.3 g in air) were surgically implanted into the body cavity using a procedure similar to Adams *et al.* (1998) and Moore *et al.* (1990). A transmitter was inserted through a 10 mm incision made on the midventral line anterior to the pelvic girdle. The transmitter antenna was fed through a needle (Jelco; 18 guage, 38 mm) inserted through the body wall approximately 5 mm posterior and dorsal to the incision. The incision was closed with two sutures (USSC; 4-0 coated braided silk and C-13 needle). Given the size of the radio transmitter, fish > 13.5 cm fork length (L_F) were selected for tagging. Seven fish (mean ± S.E., $L_F = 14.9 \pm 0.3$ cm, mass = 33.7 ± 2.4 g) were tagged in early winter and twelve fish ($L_F = 14.1 \pm 0.4$ cm, mass = 26.0 ± 2.0 g) were tagged in late winter. Fish were held for 4 to 5 hours after surgery to insure full recovery and tracking commenced 24 h after being released back into the study site.

Tagged fish were manually tracked using a hand held H-antenna. Once the fish□s location was pinpointed, a cable antenna (i.e., stripped coaxial cable) taped to a small rock was placed on the substrate adjacent to the fish's cover stone. The cable antennas were connected to fixed automatic data logging receivers (Lotek, SRX 400) located on the river bank. Data from the fixed stations was downloaded daily between 0900 and 1000 hours and the cable antennas were moved if the fish changed location. Movement was determined through fluctuations in signal strength recorded by the receiver. Using a transmitter taped to the bottom of a wooden rod, the relationship between transmitter distance from the cable antenna and signal strength received was investigated. It was determined that a change in signal strength of 30 represented a movement of approximately 1 m from the cable antenna (signal strength ranges from 0 to 236). Therefore, any fluctuation in signal strength greater than 30 was considered a movement. It should be noted that the transmitter test was conducted on cobble substrate at a water depth of 30 cm. Substrate type and water depth will influence the relationship between transmitter distance from the cable antenna and signal strength. Therefore, the distance fish move from the cable antenna was not quantified. A similar technique for determining fish movement was recently published by David & Closs (2001). Movement between sunrise and sunset (i.e., daylight hours) was considered daytime movement and movement between sunset and sunrise (i.e., dark and civil twilight hours) was considered nighttime movement.

Circular statistics were used in analysing the general diel activity patterns displayed in early and late winter (Batschelet, 1981; Brown & Downhower, 1988). Circular statistics are used for data arrayed along a circular scale such as the diel cycle. The data were transformed into sines and cosines in order to accommodate the nature of circular data. The test was used to determine whether the diel activity patterns observed were random, and allowed mean activity times to be calculated. A repeated measures ANCOVA, to control for multiple measures of individuals, was used to examine variation in movements per hour in relation to study period (early winter, late winter), day within study, time (day, night) and fork length of tagged fish. Higher order interaction terms were sequentially removed from the model at $P > 0.05$. All means are reported with standard errors (± S.E.).

5.5 Results

Eighteen of the 19 tagged fish were active throughout the diel cycle, while one fish was strictly nocturnal. Movement time was not random, clustering around mean activity times of 0100 and 2148 hours for early and late winter respectively (Fig. 2; early winter, $W = 6.23$, $P < 0.05$; late winter, $W = 140.50$, $P < 0.05$). The mean movement time was significantly later in early winter than in late winter ($F_{1, 998} = 146.1$, $P < 0.05$).

There was no significant relationship between movements per hour and study period (early winter, late winter) or day within study, while there were significantly less daytime than nighttime movements per hour and movements per hour declined significantly with increasing fork length (Table 1; Fig. 3).

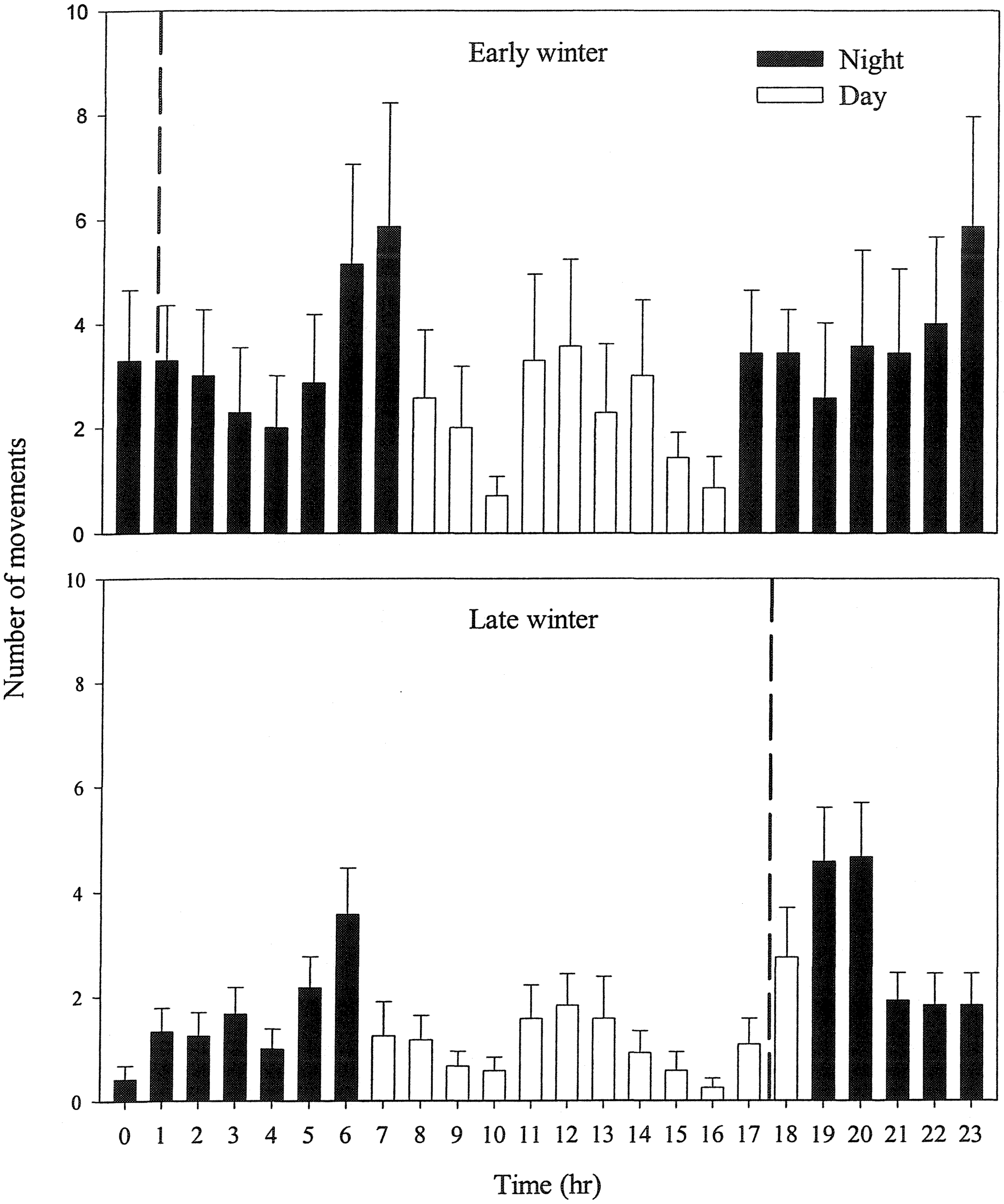

Figure 2: Movements (mean + S.E.) of radio-tagged Atlantic salmon parr occurring hourly throughout the diel cycle in early winter (n = 7) and late winter (n = 12). Dashed line indicates mean movement time.

Table 1: Repeated measures ANCOVA statistics to test the relationship between movements h^{-1} of Atlantic salmon parr and the study period (early winter, late winter), day within study, time (day, night) and fork length.

Effect	d.f.	F	P
Study period	116	0.0	0.99
Day within study	1236	0.1	0.72
Time	118	8.1	0.01
Fork length	116	5.7	0.03

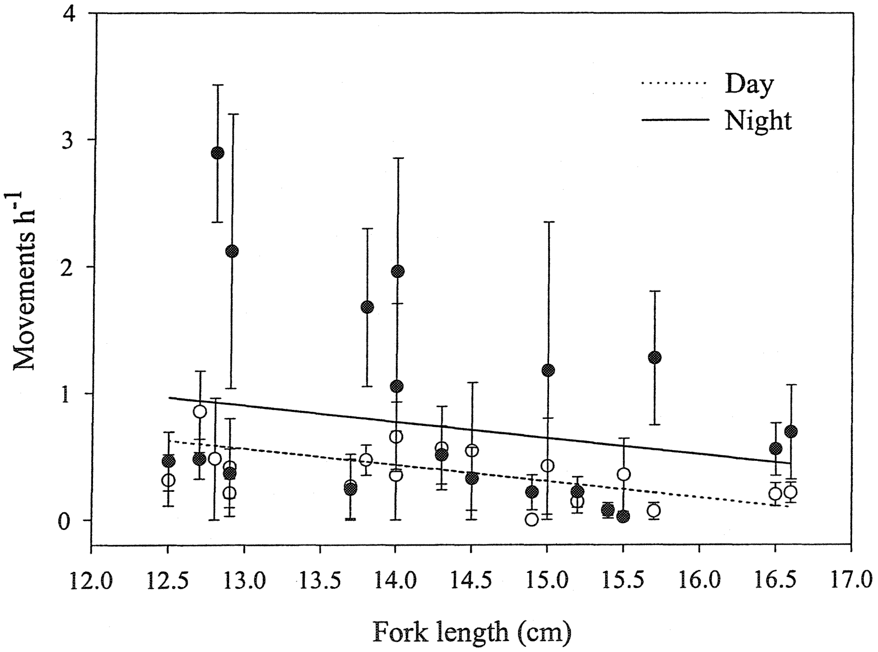

Figure 3: Movements h^{-1} (mean ± S.E.) of 19 radio-tagged Atlantic salmon parr during the day (○) and night (●) as a function of fork length. Lines fitted according to the final model.

5.6 Discussion

Wintering Atlantic salmon parr in the present study were active throughout the diel cycle. Activity levels were greater at night and peaked shortly before sunrise and after sunset. These nighttime peaks in activity correspond to earlier reported activity peaks in salmonid parr (Gibson, 1978; Rimmer & Paim, 1990; Heggenes *et al.*, 1993; Riehle & Griffith, 1993). The diel activity patterns were similar in early and late winter. However, the number of movements per hour appeared to be reduced in late winter but this difference was not significant. More movement may have been expected in early over late winter due to higher metabolic demands at warmer water temperatures and the need to replenish lipid reserves that are suggested to be rapidly depleted during acclimatization to winter conditions (Cunjak & Power, 1987; Cunjak, 1988). The mean movement time also occurred later in the night in early winter than in late winter. This difference may have resulted from the longer period of darkness and thus a greater amount of safe (i.e., reduced predation risk) activity time in early winter.

Daytime and nighttime activity levels increased with decreasing body size. Similarly, Metcalfe *et al.* (1998) and Bradford & Higgins (2001) demonstrated increased activity in smaller fish, however, they only found this relationship during the day. Maximizing winter growth rates, through daytime foraging, may reduce the risk of starvation in smaller fish or those fish that experienced the greatest rate of weight loss during the acclimation to winter conditions (Metcalfe *et al.*, 1998). Assuming that activity levels in the present study were associated with foraging movements, smaller fish may maximize growth rates through an increase in both daytime and nighttime foraging activity. Moreover, digestive rates decline with increasing body size and consequently, smaller fish may need to forage more often than larger fish (Brett & Groves, 1979).

The results of the present study, along with other recent studies, provide evidence that the activity patterns of salmonid parr are quite complex (Metcalfe *et al.*, 1998; 1999; Bradford & Higgins, 2001) and support the suggestion that individual variation in activity levels are, at least, partially correlated with body size.

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Chapter 6.0 Effect of short-term flow fluctuations on the behaviour of Atlantic salmon parr in winter

6.1 Abstract

The effect of increased flow on movement and microhabitat use of Atlantic salmon *Salmo salar* L. parr in winter was investigated using radiotelemetry. To simulate hydropeaking operations, flow was increased four-fold from 1.3 $m^3 s^{-1}$ to 5.2 $m^3 s^{-1}$ for 24 hour periods. Flow did not affect fish habitat use or displacement and had little effect on fish activity within diel periods. During high flow periods in late winter, fish reduced nighttime activity. Stranding rates during flow reduction were also very low (1 fish).

6.2 Introduction

Hydroelectric facilities often generate power using 'hydropeaking' operations (Ward & Stanford, 1979). These facilities maintain water discharge at a regulated minimum and rapidly increase discharge rates through the turbines to meet short-term demands in electricity. Therefore, changes in flow occur at irregular intervals (i.e., daily, weekly) and discharge below the dam can vary by many orders of magnitude. These variable and unpredictable flow regimes create unstable aquatic habitats below the dam that modify the physical and chemical conditions of the water (Ward & Staford, 1979; Gore *et. al.*, 1989; 1994) and may decrease the density and diversity of benthic invertebrate communities and fish communities (Bain *et al.,* 1988; Garcia de Jalon *et al.*, 1988; Casado *et al.*, 1989; Fraley *et al.*, 1989; Weisberg *et al.*, 1990; Moog, 1993; Valentin *et al.*, 1994; Céréghino & Lavandier, 1998; McKinney *et al.*, 2001).

Research has shown that flow fluctuations have minimal effects on the behaviour of salmonid fishes in summer (Heggenes, 1988; Simpkins *et al.*, 2000). However, studies in winter have demonstrated that hydropeaking can increase fish displacement and stranding rates (Vehanen *et al.*, 2000; Saltveit *et al.*, 2001). These effects have been attributed to reduced swimming ability (Webb, 1978; Johnson *et al.*, 1996) and increased use of cover beneath the substrate by salmonids at low water temperatures (Gibson, 1978; Rimmer & Paim, 1989; Fraser *et al.*, 1993; 1995). The winter studies cited above were conducted under laboratory conditions (Vehanen *et al.*, 2000) or within a small enclosure in the river (75 m^2; Saltveit *et al.*, 2001). The present study was conducted in a regulated river without enclosures to examine the effect of increased flow on activity, displacement, stranding and habitat use of wild landlocked Atlantic salmon parr in winter.

6.3 Materials and Methods

Study Site and Flow Regime

The West Salmon River is a regulated river (Upper Salmon Hydroelectric Development, Newfoundland and Labrador Hydro) in south-central Newfoundland, Canada (48°12'N, 56°15'W; Fig. 1). Water is released from Cold Spring Pond reservoir into the river through a fisheries compensation gate. Discharge is maintained at a regulated minimum of 1.3 $m^3 s^{-1}$ from 30 November to 1 June and increased to 2.6 $m^3 s^{-1}$ for the remainder of the year. The study site was located approximately 50 m downstream from the reservoir outlet. The site was 240 m long and ranged from 28 to 68 m wetted width at 1.3 $m^3 s^{-1}$ and was dominated by riffle, run and flat habitats with cobble boulder substrate (Scruton & Gibson, 1995). To simulate hydropeaking operations, flow was increased four-fold from a base level of 1.3 $m^3 s^{-1}$ (low flow) to 5.2 $m^3 s^{-1}$ (high flow) for a 24 hour period starting at either sunrise or sunset, followed by a 24 hour period of low flow. The flow was increased 8 times within each seasonal period. The time required to reach stable high flow conditions within the study site was approximately 30-45 minutes. Water depth ranged from 1-76 cm (mean ± S.D., 24.2 ± 13.3 cm) at low flow to 4-85 cm (40.6 ± 14.3 cm) at high flow. Mean column water velocity ranged from 0-129 cm s^{-1} (21.2 ± 21.6 cm s^{-1}) at low flow to 0-158 cm s^{-1} (42.0 ± 31.9 cm s^{-1}) at high flow. The water temperature ranged from 0.0-3.1 °C (1.8 ± 0.8 °C, 27 November to 14 December 2001) in early winter, 0.0-1.0 °C (0.3 ± 0.2 °C, 19 February to 9 March 2002) in mid-winter and 1.6-4.0 °C (2.4 ± 0.5 °C, 22 April to 9 May 2002) in late winter. The study site was ice free in early and late winter. Ice cover was initially 20% in mid-winter but was removed from the main channel of the river after the first increase in discharge; remaining only in shallow areas adjacent to the banks.

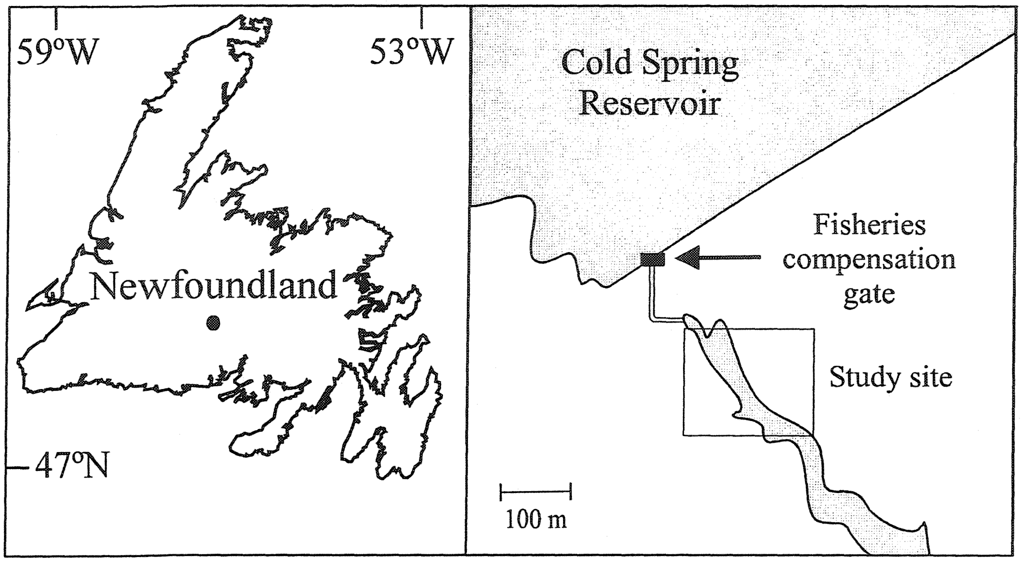


Figure 1: Location of West Salmon River and diagram of study site.

Fish Sampling and Surgical Procedure

Radiotelemetry was used to investigate movement and habitat use of Atlantic salmon parr in early winter, mid-winter and late winter. Fish were caught with a backpack electrofisher (Smith-Root Model 12) from within the study site. Given the size of the radio transmitters currently available, only large parr (> 125 mm fork length, L_F) could be tagged. A total of 36 Atlantic salmon parr were tagged with radio transmitters, 10 in early winter (L_F: 149.4 ± 1.8 mm; mass: 34.0 ± 1.0 g; age: 3.9 ± 0.2 years; tag 3.8 ± 0.1 % fish mass), 11 in mid-winter (L_F: 159.2 ± 12.3 mm; mass: 45.3 ± 12.0 g; age: 3.9 ± 0.3 years;

tag 4.6 ± 0.7 % fish mass) and 15 in late winter (L_F: 150.0 ± 3.3 mm; mass: 32.3 ± 2.6 g; age: 3.7 ± 0.2 years; tag 4.3 ± 0.3 % fish mass) The size and age of parr tagged between the seasonal periods were similar (ANOVA, $P > 0.05$). Fish were anaesthetized with clove oil (Anderson *et al.*, 1997), measured (L_F, mm) and weighed (g). A radio transmitter (Advanced Telemetry Systems, Model 377, 7 x 7 x 18 mm, 1.3 g in air) was implanted into the fish's peritoneal cavity using standard methods (see Hiscock *et al.*, 2002 for details). Tagged fish were placed in flow-through cages within the river and released back into the study site approximately 1 to 2 h after surgery.

Tracking and Microhabitat Measurements

Manual tracking, using a hand held H-antenna, commenced 24 h after tagging. Once the fish's location was identified beneath the substrate, a cable antenna (i.e., stripped coaxial cable) was taped to a small rock and placed on the substrate adjacent to the fish's position. The cable antennas were connected to fixed automatic data logging receivers (Lotek, SRX 400) located on the river bank. Data from the fixed stations were downloaded daily between 09:00 and 10:00 h. Cable antennas were adjusted if necessary during the receiver download period and prior to flow change. The detection range of each cable antenna was calibrated to be approximately 5 m. Small-scale movement around the cable antennas was determined through fluctuations in signal strength recorded by the receiver. Using a transmitter taped to the bottom of a wooden rod, the relationship between transmitter distance from the cable antenna and signal strength received was investigated. It was determined that a change in signal strength of 30 represented a movement of approximately 1 m from the cable antenna (signal strength ranges from 0 to 236). Therefore, any fluctuation in signal strength greater than 30 was considered a movement. It should be noted that the transmitter test was conducted on cobble substrate at a water depth of 30 cm. Substrate type and water depth influence the relationship between transmitter distance from the cable antenna and signal strength. Therefore, the distance fish moved from the cable antenna was not quantified. A similar technique for determining fish movement was recently published by David & Closs (2001) and Hiscock *et al.* (2002). Small-scale movements have been reported as any movements between 1 and 5 m from the cable antenna. When fish moved to a new position or beyond the 5 m range of the cable antenna, fish were relocated with a hand held H-antenna. The distance moved was measured and recorded relative to a transect number on the bank and the distance to the nearest bank. Fish positions were later plotted in MapInfo (Professional 7.0) to generate the home range size for each fish (i.e., minimum convex polygon: White & Garrott, 1990).

Microhabitat use was recorded for each fish during the receiver download period and prior to flow change. The habitat variables measured included water depth, mean column water velocity (Marsh-McBirney model 2000 portable flowmeter) and substrate [gravel (0.2-3 cm), cobble (3-25 cm), boulder (>25 cm): modified from Scruton & Gibson, 1995; Sooley *et al.*, 1998]. Habitat availability during low and high flow was determined by measuring the same habitat variables at 1 m intervals across 30 equally spaced transects along the length of the study site.

Statistical Analyses

The sample unit for the small-scale movement analysis was the hour and all movements within each hour were tallied. Data collected during the hour in which a flow change occurred were not included in the data set. Data were analysed using a General Linear Model (GLM) with a repeated measure using PROC MIXED in SAS (SAS Institute Inc., 1996) because the data had an unbalanced design and missing data. The initial model constructed was a saturated model with movements h^{-1} as the response variable and fish as the individual subjects with repeated measures. Seasonal period (early winter, mid-winter, late winter) was treated as a between-subject factor, and diel period (dawn, day, dusk, night) and flow (low, high) were treated as within-subject factors. All higher order interaction terms of the three categorical factors were included and fish fork length was included as a within-subject covariate. It was not possible to examine the within-subject variance-covariance matrix (i.e., test for sphericity), as the size and complexity of the data set and the models used precluded fitting complex variance-covariance matrices. However, examination of a subset of time series for individual fish with ARMA models showed little evidence that these time series did not differ from white noise, so the variance components option (i.e., constant variance across subjects and no covariance) in PROC MIXED was used (SAS Institute Inc., 1996). When higher-order interactions were significant, further analyses within each level of one of the factors were conducted to examine sources of variation without the confound of significant interactions. To test for differences between flows within seasons and diel periods, Bonferroni adjustment to the critical alpha were used ($\alpha_{crit} = 0.05/12 = 0.0042$).

Similar analyses, using general linear models and repeated measures, were undertaken when comparing water depth and mean column velocity used by fish to that available. For the purposes of the analysis, all data for available habitat was treated as a single subject.

Dawn and dusk were defined as the hour in which sunrise and sunset occurred, respectively. Herein, small-scale movement rates (movements h^{-1}) are referred to as fish activity. The home range data were examined graphically and nonparametric statistics were used when the data were not normally distributed. All means have been reported with corresponding standard errors (i.e., mean ± S.E.).

6.4 Results

Small-scale Movement

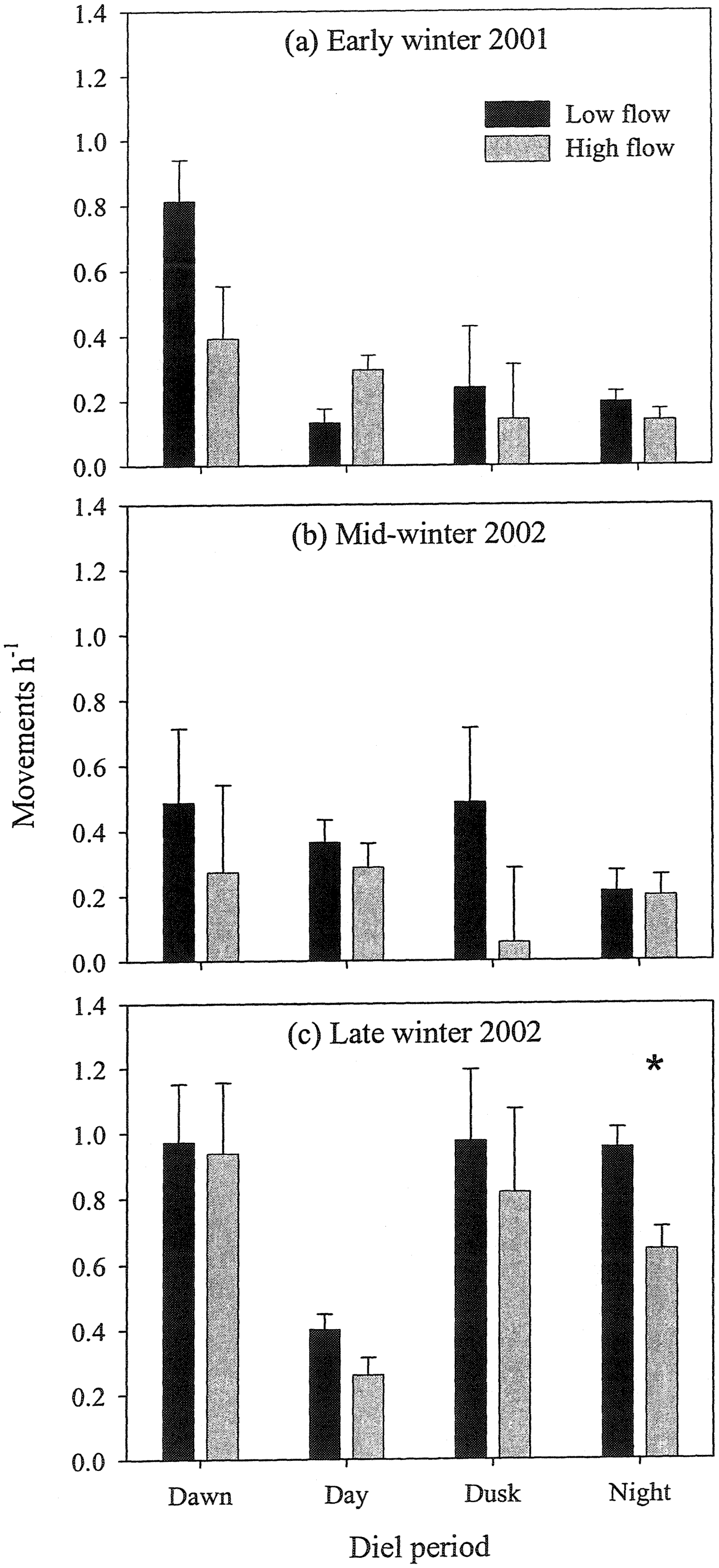
In the global saturated model, the covariate fish fork length was not related to fish activity (GLM, $F_{1,33} = 1.36$, $P = 0.25$) and was not considered in further analyses. The three way interaction of diel period, season and flow was not significant ($F_{6,80} = 1.12$, $P =$

0.36), nor was the interaction between flow and season ($F_{2,33}$ =0.11, P = 0.90) and flow and diel period ($F_{3,80}$ =1.23, P = 0.31). However, the interaction between diel period and seasonal period was significant ($F_{6,97}$ =12.1, P < 0.0001), with late winter showing highest fish activity (Fig. 2). Therefore, each seasonal period was analysed separately.

In early winter, there was a significant interaction between diel period and flow ($F_{3,20}$ = 4.15, P = 0.019). Fish activity among diel periods was significantly different at low flow ($F_{3,24}$ = 8.15, P = 0.001) with highest activity at dawn, while at high flow ($F_{3,26}$ = 3.27, P = 0.037), the highest fish activity was at dawn and during the day (Fig. 2). Within diel periods, there were no differences in activity between flow rates.

In mid-winter (Fig. 2), there were no significant differences in fish activity among diel periods ($F_{3,28}$ = 1.21, P = 0.33) and between flows ($F_{1,9}$ = 2.19, P = 0.17), nor was there an interaction between flow and diel period ($F_{3,22}$ = 0.60, P = 0.62).

In late winter, there was a significant difference in fish activity among diel periods ($F_{3,40}$ = 26.0, P = 0.0001), with activity during the day being lowest (Fig. 2). No flow effect ($F_{1,14}$ = 2.00, P = 0.18) or interaction between flow and diel period ($F_{3,37}$ = 0.83, P = 0.49) was detected. However, fish activity was significantly reduced during high flow at night ($F_{1,37}$ = 11.47, P = 0.0017).

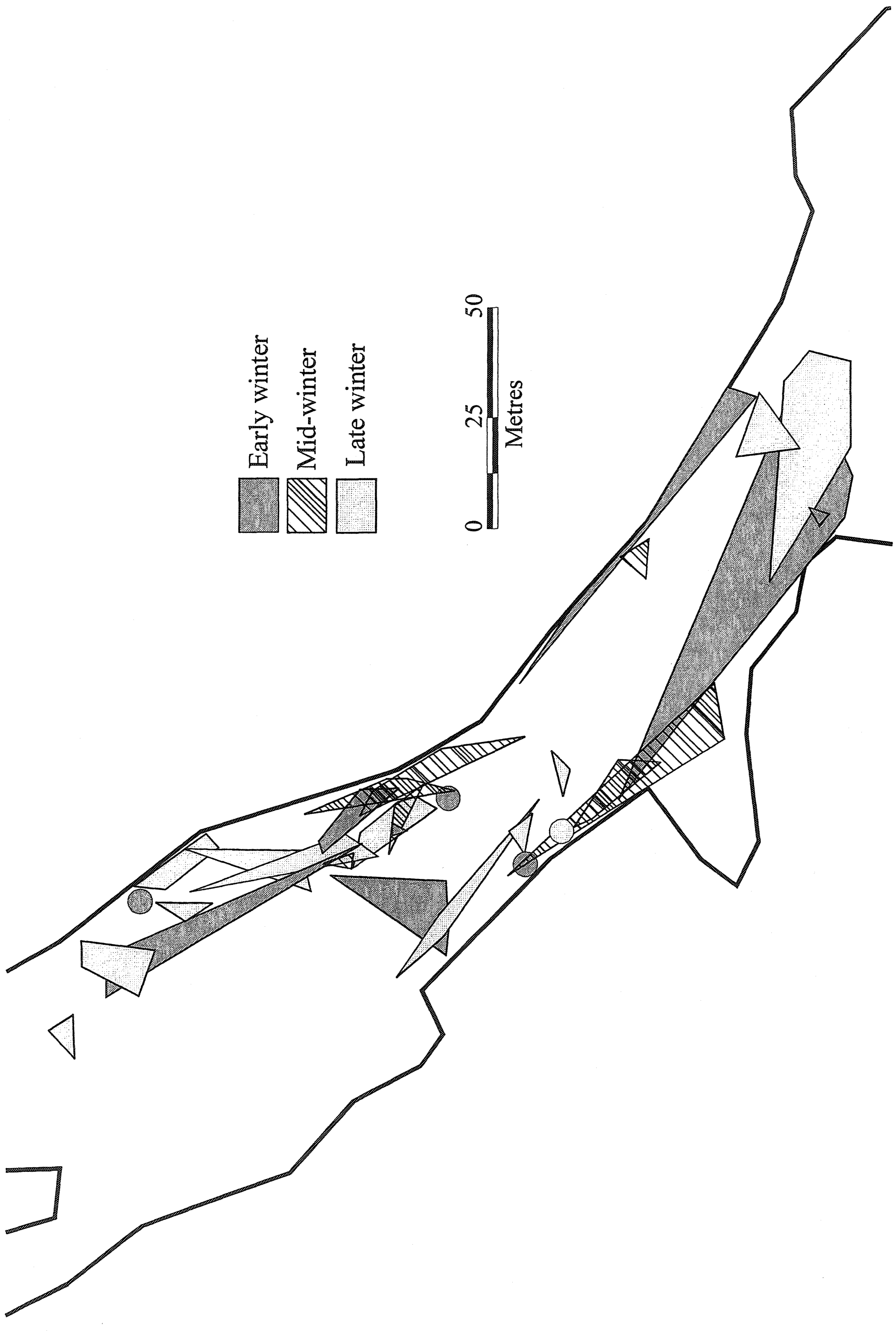

(a) Early winter 2001
Low flow
High flow
(b) Mid-winter 2002
(c) Late winter 2002
*
Movements h^{-1}
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
Dawn
Day
Dusk
Night
Diel period

Home Range

Home range size did not differ between seasonal periods (range 5-1270 m^2, 160 ± 50 m^2: GLM, $F_{2,23} = 1.36$, $P = 0.28$) and was not related to fish size ($F_{1,24} = 0.13$, d.f. = 1, $P = 0.72$: Fig. 3). The number of fish locations within each home range did not differ between seasonal periods (range 1-11, 4.0 ± 0.4: $F_{2,27} = 1.03$, $P = 0.37$). The number of fish movements to new locations were similar during high and low flow (G-test, $P > 0.05$) but did occur more during hours of darkness (dawn, dusk, night) in mid-winter ($G = 4.37$, d.f. = 1, $P = 0.03$) and late winter ($G = 8.34$, d.f. = 1, $P = 0.004$). The distance from the centre point of each home range to the nearest bank was 10.0 ± 1.0 m (range 0.5-21.5 m). Fish appeared to avoid the centre channel of the river (Fig. 3).

Six fish moved greater than 300 m downstream from the study site (1 early winter, 3 mid-winter, 2 late winter). These movements did not occur due to an increase in flow (i.e., displacement) because they occurred equally during both low and high flows. Only one fish was stranded during the study, in late winter. The fish survived the low flow period in approximately 3 cm of water. Four fish were lost to mink *Mustela vison* S. predation during the day, 2 in early winter (high flow) and 2 in mid-winter (low flow). Transmitters from these fish were found near the river bank in mink faeces or located adjacent to mink dens.

Figure 3: Comparison of home range size (minimum convex polygons) of radio-tagged Atlantic salmon parr in early winter (n = 10), mid-winter (n = 7) and late winter (n = 13). Circles represent fish that used one cover stone for the duration of the study period.


Early winter
Mid-winter
Late winter
0
25
50
Metres

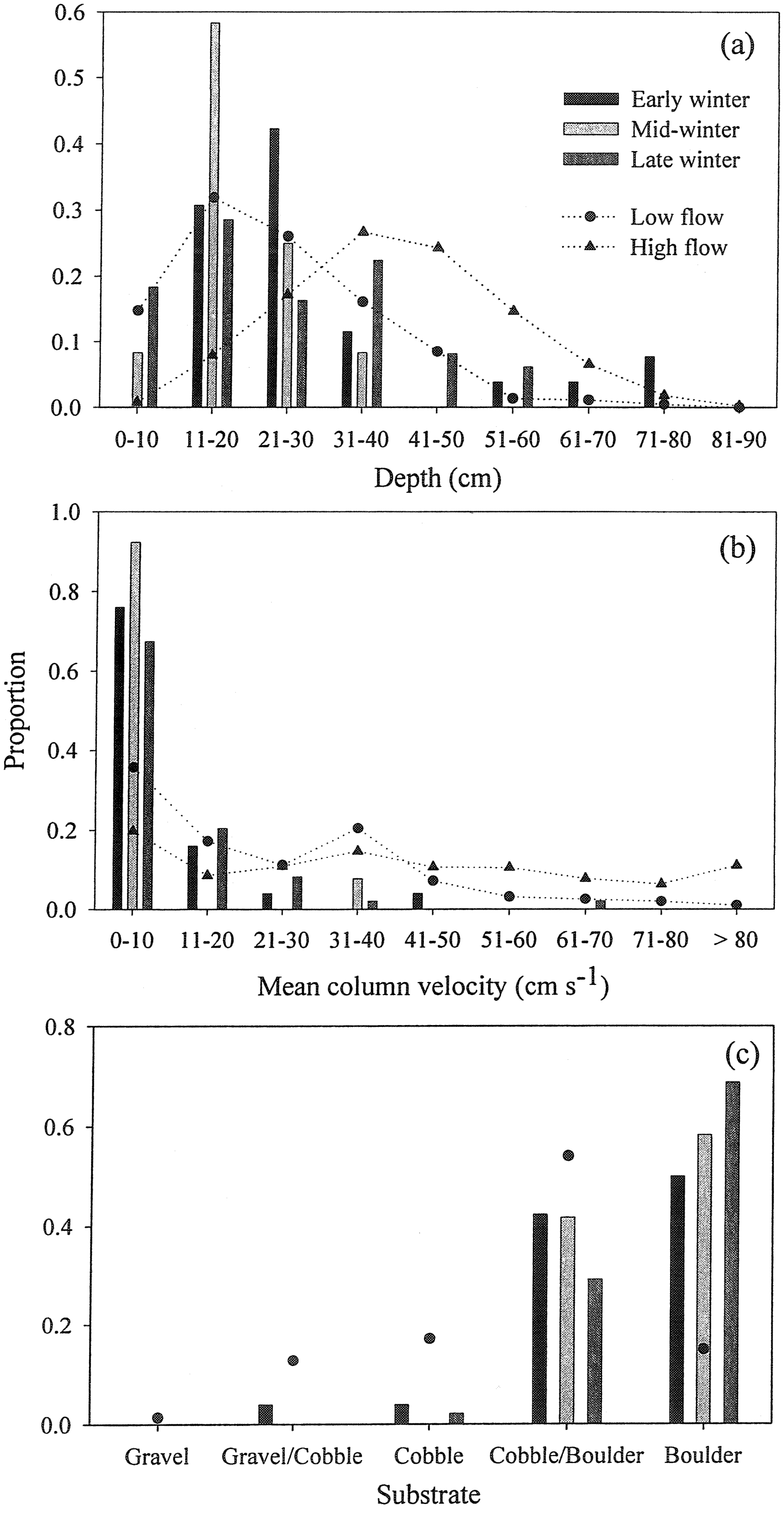
Microhabitat Use

Fish used the same position at low and high flows (i.e., flow did not influence fish movement to new locations). Given that habitat preferences would have been relatively similar between low and high flow, comparisons of fish habitat use between seasonal periods and to availability were conducted on data collected during low flow.

Water depth used by fish did not differ among seasonal periods [range 6-74 cm, 26.6 ± 1.6 cm: GLM, $F_{2,32} = 2.25$, $P = 0.12$: Fig. 4(a)]. No preference for water depth was detected in early winter (29.5 ± 2.6 cm, $F_{1,32} = 3.83$, $P = 0.06$), mid-winter (18.4 ± 4.0 cm; $F_{1,32} = 0.45$, $P = 0.51$) or late winter (25.5 ± 1.9; $F_{1,32} = 2.01$, $P = 0.17$) comparing habitat use to availability (24.2 ± 0.6 cm).

Fish in all three seasonal periods were found in mean column water velocities not detectably different from one another [early winter: 8.2 ± 4.0 cm s^{-1}; mid-winter: 3.0 ± 6.2 cm s^{-1}; late winter: 8.9 ± 2.9 cm s^{-1}: $F_{2,32} = 0.91$, $P = 0.41$: Fig. 4(b)]. However, fish in all seasonal periods preferred the lowest mean column water velocities available (available = 21.2 ± 1.0 cm s^{-1}: early winter; $F_{1,32} = 9.88$, $P = 0.004$; mid-winter: $F_{1,32} = 16.7$, $p = 0.0003$; late winter; $F_{1,32} = 8.48$, $P = 0.007$). Substrate use did not differ between seasonal periods [G-test, $G = 4.87$, d.f. = 6, $P = 0.56$: Fig. 4(c)] and fish preferred the largest substrates available ($G = 91.8$, d.f. = 4, $P < 0.0001$).

Figure 4: Comparison of (a) water depth, (b) mean column water velocity and (c) substrate used by radio-tagged Atlantic salmon parr during low flow in early winter, mid-winter and late winter. The line and scatter plots show the availability of each habitat variable at low and high flow.


(a)
Early winter
Mid-winter
Late winter
Low flow
High flow
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0-10
11-20
21-30
31-40
41-50
51-60
61-70
71-80
81-90
Depth (cm)
(b)
Proportion
1.0
0.8
0.6
0.4
0.2
0.0
0-10
11-20
21-30
31-40
41-50
51-60
61-70
71-80
> 80
Mean column velocity (cm s-1)
(c)
0.8
0.6
0.4
0.2
0.0
Gravel
Gravel/Cobble
Cobble
Cobble/Boulder
Boulder
Substrate

6.5 Discussion

The increase in flow used in the present study (1.3 $m^3 s^{-1}$ to 5.2 $m^3 s^{-1}$) did not affect fish habitat use, displacement or noticeably increase stranding rates. Flow also had little effect on fish activity within diel periods. The only detectable difference in activity between flows occurred in late winter where fish reduced nighttime activity at high flow.

Fish in the present study had the highest overall activity rates during late winter, although daytime activity remained suppressed. Late winter is a period of energy replenishment after the cold winter months and the increased activity rates may have reflected increased foraging activity. Given that water temperatures remained low in late winter (1-4 °C), daytime activity would be expected to be minimized to avoid diurnal endothermic predators (birds and mammals: Valdimarsson & Metcalfe, 1998; Metcalfe *et al.*, 1999), such as the mink *M. vison* observed in the present study. The effect of flow on fish activity may be based on foraging decisions that reflect trade-offs between swimming cost, prey availability, prey accessibility and the fish's internal state (Huntingford *et al.*, 1988; Metcalfe *et al.* 1999). Reduced fish activity at high flow during the night in late winter may suggest that the increased swimming cost and reduced prey accessibility at low light levels did not outweigh the benefits of increased prey availability. Atlantic salmon parr are visual drift feeders and feeding efficiency at nighttime light levels has been shown to be reduced 65% as compared to daytime light levels (Fraser & Metcalfe, 1997).

Atlantic salmon parr used cobble and boulder substrates in low water velocity areas away from the main channel of the river. Previous studies have shown similar preferences for winter habitat (Cunjak, 1996; Whalen *et al.*, 1999). Flow did not influence movement to new locations, however these movements did occur during hours of darkness (dawn, dusk, night) when predation risk would be minimized. Fish may not have been forced to move to new locations in response to changes in flow because increases in water depth and velocity at high flow fell within the range used by fish under low flow conditions. Given that long distance movements downstream (> 300m) occurred equally at low and high flow, fish did not appear to be displaced by the increase in flow. The cobble and boulder substrate, predominant within the study area, would have provided opportunities for fish to avoid displacement (Heggenes, 1988).

The increase in flow used in the present study (1.3 $m^3 s^{-1}$ to 5.2 $m^3 s^{-1}$) had minimal effects on the behaviour of Atlantic salmon parr in winter. This flow change, although common to many hydro facilities (Pert & Erman, 1994), is very small and further research would be necessary to determine the effect of more severe flow changes.

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7.0 Summary

The series of papers contained within this thesis addressed the activity patterns and meso- and microhabitat requirements of Atlantic salmon parr in winter. These papers also demonstrate the usefulness of applying radiotelemetry techniques to monitor the behaviour of relatively small animals within natural systems.

7.1 Chapter Summaries

The results of Chapter 2 suggest that researchers can be confident making general population statements based on data collected from surgically tagged wild Atlantic salmon parr > 120 mm using one of the smallest transmitters currently available (Lotek Wireless Inc., 7 x 12 mm, 0.75 g in air, 0.5 g in water). The radio transmitters used in this study did not affect the swimming performance (tag 1.7-3.7 % of fish mass) or consumption rate (tag 0.9-2.6 % of fish mass) of wild parr. Negative effects on growth, however, were found up to day 36 of a 45 day experiment. Therefore, caution is needed when interpreting growth data collected on surgically tagged wild Atlantic salmon parr.

The observed movement of Atlantic salmon parr in Chapters 3 indicated that parr are not necessarily sedentary stream dwellers in winter. The number, distance, and direction of movements in this study were highly variable and unexpected, given that the river was ice free and had relatively stable flow. A similar, more extensive study on an adjacent river was conducted in Chapter 4. Atlantic salmon parr, in this study, remained active throughout the winter, utilising a variety of mesohabitats, even under stable environmental conditions. Based on the age of parr captured in fluvial habitats in early and mid-winter, young parr (2-3 yrs) appeared to overwinter in fluvial habitats while pre-smolts (4-6 yrs) did so in lacustrine habitat. Instream movement was recorded throughout the diel cycle indicating that parr were not strictly nocturnal in winter.

Landlocked Atlantic salmon parr in Chapter 5 were also active throughout the diel cycle. There was, however, significantly less daytime than nighttime movement and movement declined significantly with increasing fork length. Maximizing winter growth rate, through an overall increase in foraging activity, may reduce the risk of starvation in smaller fish or those fish that experienced the greatest rate of weight loss during acclimation to winter conditions.

The results of Chapter 6 demonstrated that short-term fluctuations in flow did not significantly affect habitat use, consumption, displacement or stranding rates of landlocked Atlantic salmon parr. However, flow did affect activity within diel periods in early and late winter. During high flow periods, fish in early winter increased daytime activity whereas fish in late winter reduced both daytime and nighttime activity. These results were discussed in relation to the benefits of enhanced feeding and growth.

7.2 General Conclusions

This thesis has: 1) advanced the ability to apply new radiotelemetry technologies to the study of fish movement, 2) furthered the knowledge of Atlantic salmon parr movement, activity and habitat use in winter, and 3) provided recommendations with respect to habitat for management agencies.

The radiotelemetry system used in Chapters 4-6 recorded fish movement throughout the diel cycle. The system was able to detect fish movements > 1 m in shallow habitats (< 1 m depth) with predominantly cobble-boulder substrate. However, the distance fish moved from the cable antenna was difficult to quantify as substrate type, water depth, and transmitter antenna orientation influenced the signal strength detected by the receiver. Radio transmitters currently available limit research to large parr (> 125 mm fork length, L_F) and typically have an operational life < 30 days. The size of transmitters is currently limited by battery size but the operational life can now be extended using transmitters with pre-programmed activation times. These pre-programmed transmitters would enable researches to study individual fish intermittently throughout the year. In spite of the current limitations, the radiotelemetry system used in this thesis proved to be very useful for studying the movement and behaviour of large Atlantic salmon parr in winter.

Previous research on the diel activity patterns of Atlantic salmon parr in winter was limited to laboratory studies using hatchery-reared fish (Metcalfe *et al.*, 1998; 1999). The results of the present studies supported previous laboratory research indicating that parr are not strictly nocturnal in winter and that individual variation in time spent foraging during the day may result from differences in the benefits of enhanced feeding and growth (Metcalfe *et al.*, 1999). The traditional view that Atlantic salmon parr are sedentary stream dwellers in winter, moving only in response to adverse stream conditions (Cunjak & Randall, 1993; Whalen *et al.*, 1999), was not supported by the results of the present studies. Atlantic salmon parr in the present studies utilized both fluvial and lacustrine habitats and remained active even under stable environmental conditions (i.e., ice free, stable flow).

There are two main management implications resulting from the present studies. The first is that Atlantic salmon parr in Newfoundland did not remain sedentary within wintering habitat. Atlantic salmon parr remained active throughout the winter and moved between fluvial and lacustrine habitats. Therefore, assuming this movement is adaptive, anthropogenic activities resulting in fish habitat fragmentation (i.e., improper culvert installation; Langill & Zamora, 2002) will restrict parr movement, especially during low water levels in winter, and may reduce overwinter survival of parr. Further winter research on younger parr (1-2 yrs) is needed as these parr may have different habitat requirements than the large parr studied in this thesis. The second management implication is that increases in flow from 1.3 $m^3 s^{-1}$ to 5.2 $m^3 s^{-1}$ for 24 hours in winter had little impact on Atlantic salmon parr. Changes in flow did not affect fish habitat use, displacement or noticeably increase stranding rates. Flow also had little effect on fish activity within diel periods. This flow change, although common to many hydro facilities (Pert & Erman, 1994), is very small and further research would be necessary to determine the effect of more severe flow changes.

7.3 References

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