Individual variability in activity patterns of juvenile Atlantic salmon (*Salmo salar*)

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A Thesis

in

The Department

of

Biology

Presented in Partial Fulfilment of the Requirements

For the Degree of Master of Science at

Concordia University

Montréal, Québec, Canada

January 2003

0-612-77663-8

Abstract

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To describe the activity patterns of juvenile Atlantic salmon, I monitored the behaviour of 35 age-0+ (emerged from gravel in the spring) and eight age-1+ (emerged from gravel in the spring of the previous year) fish over an eight-week-summer field season. Active fish were visible on their home range whereas inactive fish were assumed to be sheltering. My data were consistent with the prediction of the Asset Protection Principle that larger individuals will take fewer chances in order to reduce risk of predation. Indeed, 1+ fish (larger and older) were more active at night than during the day, whereas 0+ fish were almost exclusively active during the day. In contrast to my expectations, however, daytime activity did not peak at the optimal water temperature of 17°C found in laboratory studies of other populations. Rather, the activity of 1+ fish peaked at 20.7°C, whereas the activity of 0+ fish continued to increase until 23°C and then leveled off between 23-27°C. Once individuals were active, season and light intensity were the variables that most influenced their foraging rate. There was considerable individual variability within an age-class in how fish responded to environmental variables. The causes of this individual variability and the consequences for growth deserve further study.

Acknowledgments

I am very grateful to my supervisor Dr. J.W.A. Grant for being so helpful and guiding me in my master program. I would also like to acknowledge Laura K. Weir without whom data collection would not have been that much fun and as successful. I really appreciate the work you have put in this study. I would like to thank Dr. Widden, Dr. Dayanandan and Dr. G. Brown for being on my committee and giving useful comments on earlier versions of the thesis. I would like to thank Stefán O. Steingrimsson for comments on the methods and the thesis. Also, I would like to thank Istvan Imre for advice on the statistical analyses. A special thank to Ian Hamilton, Cheryl Johnson, Isabelle Girard, Michel Noël and Ivan Dolinsek for interesting discussions.

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Introduction

All organisms are constrained by a set of environmental factors that help define their ecological niche (Huntchinson 1957; Willmer 1991). Ectothermic organisms rely on the environment to regulate their body temperature, so environmental temperature is an important factor influencing their physiology, behaviour and growth (Feminella and Resh 1990, Magnuson and Destasio 1996). Thus, activities such as foraging and movement can be greatly reduced in low temperature conditions (Fry 1971, Johnston and Ball 1996), leading to changes in behaviour and habitat choice (Cunjak 1988).

In fishes, the biological effects of temperature have been well studied under laboratory conditions (e.g. Fry 1971). The optimal temperature for a fish is typically defined in two ways: behaviourally as the temperature preferred by the fish (Richard et al. 1977; Magnuson et al 1979) or physiologically as the temperature that maximizes growth (Elliott and Hurley 1997). Studies comparing the relationship between these two optima have shown that the preferred temperature selected by fish corresponds closely to the temperature that maximizes growth (Magnuson et al. 1979). Based on the preferred temperature of fishes, three thermal guilds of fishes have been defined: coldwater (< 19°C), coolwater (19 - 25°C) or warmwater fishes (> 25°C) (Coker et al. 2001).

Like most salmonid fishes, the Atlantic salmon (*Salmo salar*) is classified as a coldwater species because juveniles prefer a temperature of 17°C (Magnuson et al. 1979) and the optimal temperature for growth varies between 16°C to 19°C under laboratory conditions (Jensen et al. 1989; Elliott and Hurley 1997). However, the behavioural response of juvenile Atlantic salmon to thermal gradients in the wild has not received much attention (Valdimarsson et al. 1997).

The first field studies on the effects of water temperature on salmonids focused on seasonal changes in activity. Because juvenile Atlantic salmon are visual foragers (Hoar 1942), it was assumed that they feed during the day and are inactive at night (e.g. Metcalfe et al. 1998). Hence, describing seasonal patterns in activity focused on daytime activity. The first general pattern observed in the field is that juvenile Atlantic salmon are active most of the day during the summer (see Rimmer et al. 1983) and are dormant, sheltering beneath the substrate, during the day in the winter (Allen 1940, Cunjak 1988). The key water temperature for this switch in behaviour is thought to be 10°C; below and above this temperature fish are inactive and active, respectively (Fraser et al. 1993).

The focus of recent research shifted from studying seasonal activity patterns to diel activity patterns after Heggenes et al. (1993) observed that brown trout feed actively at night in winter. This finding was unexpected because salmonids are visual foragers and, therefore, are assumed not to forage at night. Since then, further research has demonstrated that salmonids are often nocturnally active during the winter (Heggenes et al. 1993; Riehle and Griffith 1993) and inactive during the day (Fraser et al. 1995).

Because salmon are assumed to be active all day during warmer summer temperatures (Metcalfe et al. 1998), few studies have investigated their activity patterns during the summer. However, Gardiner (1984) noticed that about 50% of salmon were inactive at temperatures of 14-15°C during the day in the summer. More recently, counts of juvenile salmon were observed to be greater at night for both 0+ and 1+ fish (Gries et al. 1997). But, 1+ salmon were relatively more abundant at night than were 0+ salmon. Hence, the notion of a single switch point for activity at 10°C may be overly simplistic.

The most likely explanation for these diel activity patterns is a trade-off between foraging efficiency and predator avoidance (Fraser and Metcalfe 1997). When water temperatures are low, some fish forgo the higher foraging opportunities during the day due to the higher risk of predation. Age-0+ chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*) are also active during the day whereas older fish are active at dusk, and presumably at night, leading to the suggestion that the diel activity patterns might be a function of fish size or age (Bradford and Higgings 2001). These observations are consistent with the Asset Protection Principle, predicting that larger individuals closer to reproductive size/age will take fewer chances in order to reduce their risk of predation (Clarke 1994).

Differences in diel activity patterns also occur between individuals of different size within an age-class (Metcalfe et al. 1986). Larger, dominant individuals within and between age-classes may occupy the best foraging sites, enabling them to forage only when conditions are optimal (e.g. dusk) and hide during the day when the risk of predation is high (Bradford and Higgings 2001). Hence, larger or dominant individuals may feed at the most profitable times of day to maximize growth and minimize predation risk. Curiously, the opposite trend was noted in juvenile Atlantic salmon. During the day, the faster growing individuals of an age-class feed actively whereas the slower growing individuals shelter in the substrate (Valdimarsson et al. 1999). The slower growing individuals were presumably trying to minimize their risk of predation because they cannot reach the critical size for smolting in the present year.

No detailed field study has yet quantified the activity patterns of wild 0+ Atlantic salmon during their active growing season. I will compare the activity patterns of two age-classes to determine whether the differences in diel activity patterns found by Gries et al. (1997) on a stocked population also occurred in a naturally reproducing population. The specific goals of my study were: 1) to compare the diel activity patterns of 0+ and 1+ salmon to test the prediction of the Asset Protection Principle that smaller fish (0+) are relatively more active during the day and larger fish (1+) relatively more active at night; 2) to test whether activity in the wild peaked at the optimal temperature determined in laboratory studies; 3) to determine the variables that influence the foraging rate of fish; and 4) to explore the magnitude of individual variation in activity patterns of fish in the wild. To achieve these goals, I tagged 85 juvenile Atlantic salmon and followed the activity of 43 of these fish over an eight-week field season in Catamaran Brook, N.B.

Material and methods

Study site and species

The study was conducted during the summer of 2001 in the Little Southwest Miramichi River, New Brunswick, and in one of its tributaries, Catamaran Brook (46°52'42"N, 66°06'00"W). Sixteen fish species are present in the two streams (Cunjak et al. 1993), the anadromous Atlantic salmon being the most abundant (Cunjak et al. 1990). In mid-June, 0+ Atlantic salmon emerge from their nests at a total length of about 2.6 cm (Randall 1982). They reside in the stream for a period of 2 to 3 years (Cunjak et al. 1993) where their diet is composed mainly of invertebrates (Keeley and Grant 1995), primarily chironomid larvae (Keeley and Grant 1997).

Eight study sites ($\bar{x}$ = 26m^2, range = 20 - 36m^2) were used, with a minimum distance of 20m between sites. Sites were chosen based on whether they could be snorkeled and according to the salmon densities. Four sites were located in the Gorge Reach (see Cunjak et al. 1993 for details), which is approximately 5km upstream from the mouth of Catamaran Brook, one site was located 5m upstream from the mouth of Catamaran Brook and three sites were in the Little Southwest Miramichi River all within 500m from the mouth of Catamaran Brook (Fig. 1). Hereafter, I will refer to these reaches as the Gorge, Mouth and River, respectively.

Tagging

Seven 0+ (i.e. fertilized in the fall of 2000 and emerged from the gravel in June 2001) Atlantic salmon were tagged per site between June 25 and June 29, 2001 for a total of 56 fish. On July 9, two additional 0+ fish were tagged per site and 13 age-1+ fish were also tagged: six in the Gorge, three in the Mouth and four in the River. Age-0+ salmon were tagged approximately 2 weeks after emergence at fork lengths of 25.6-34.6 mm, whereas the 1+ salmon were 68.2-78.7 mm. Beginning below a study site, I snorkeled upstream until I located a fish, observed it for one minute to ensure that it was feeding normally, and then captured it using two aquarium dip-nets. The position of each fish was marked with an identification flag that was pushed into the substrate where the fish was first seen. On shore, each fish was anesthetized using clove oil (2 drops per 250ml of water) (Keene et al. 1998) and measured for fork length to the nearest 0.05mm using a hand-held caliper. Each fish was individually tagged with a subcutaneous injection of fluorescent elastomer paint (Dewey and Zigler 1996) in two of eight possible tagging locations (left and right pectoral fin, front and back of the dorsal fin, and top left, bottom left, top right, bottom right side of the caudal peduncle) with three different paint colors (red, green and orange). The fish were allowed to recover in a bucket of water for 5-10 minutes.

To return the fish to their home range, I began with the fish that was farthest upstream in each site; it was released 15cm downstream of the flag. I watched the fish until it regained its home range. Using the same technique, I recaptured and re-measured all active fish in the Gorge on July 31 and in the Mouth and River on August 1. The sites were sampled by a four-person crew, using a Smith-Root Model XI electrofisher on August 21 and 22; all the tagged fish that were recaptured were again measured for fork length.

Behavioural observations

I collected data on the activity, foraging rate and growth rate of the individually tagged fish between June 25 and August 22, 2001. On any particular day, I collected data in only four of the eight sites (Gorge or Mouth/River) in a four day rotation: day 1, Gorge 07:00-13:00 and 23:00; day 2, Mouth/River 15:00-21:00; day 3, Gorge 15:00-21:00; day 4, Mouth/River 07:00-13:00 and 23:00. Each observer (C.B. or Laura K. Weir) snorkeled upstream within a site to collect the data for two of the four sites for a particular time period. The observers alternated for each time period. I attempted to observe each fish eight times over the summer in each of the eight time periods during the day (07:00, 09:00, 11:00, 13:00, 15:00, 17:00, 19:00 and 21:00) and three times at night (23:00) for a total of 67 observations. No observations were made in the Mouth from August 15-22 because the water level was too shallow for snorkeling. Each fish that was present for the complete 8-week study (see below) was observed 48 to 67 times during the study period. Each time I snorkeled a site, the number of 'active' (see below) juvenile Atlantic salmon was counted. For each site, I obtained seven density measurements per time period during the day and three at night (23:00).

Before entering a site, both the water temperature and the light intensity were measured. I recorded water temperature at the downstream end of each site using a MultiLine P4-F/set-3/110V digital hand-held thermometer (± 0.1°C). Light intensity was measured (± 50 lx) using an Extech Instruments model 401027 (range 0 - 20 000 lx). Light intensity was measured 5cm above the water surface with the probe facing towards the water surface. Three periods of the diel cycle were defined based on light intensity: night (< 0.01 lx), dawn or dusk (0.01 lx - 100 lx) and day (> 100 lx) (see Valdimarsson et al. 1999). Sunrise was always before 7:00, but on 51 of 260 observations 7:00 was defined as dawn in the heavily forested Gorge sites. Under the more open canopy at the Mouth/River sites, 7:00 was always defined as day. Similarly, 21:00 was always day or dusk in the Mouth/River sites but in the Gorge sites, 41 of 202 observations were defined as night.

After locating a marked individual, the observer waited for three minutes before collecting data to allow the fish to resume its normal behaviour (see Grant and Noakes 1987). The activity of tagged individuals was first categorized as being active or not on the home range. A fish was scored as active if it was swimming, foraging or holding position on or near the substrate anywhere within its original site. Individuals that were not seen were assumed to be sheltering within the substrate (see below), but may also have died or relocated. To guard against counting a dead or relocated fish as 'inactive', a fish that was not observed was only scored as inactive if it was subsequently observed in its original site.

If an individual was active on its home range, I collected data on foraging. Because it was difficult to determine if an organism was eaten by a fish, I counted the number of foraging attempts in a 2 minute period. A foraging attempt was defined as a quick movement by the fish towards an item (Grant and Noakes 1987). Foraging data were collected 9 - 27 times per fish, depending on its activity.

Statistical analysis

Each fish was potentially observed at 8 times of day, 8 times over the season (except only 3 times for 23:00). Hence, I always included time of day and season as factors in any analyses. For each of these observations, I also monitored light intensity and water temperature.

To examine the overall patterns of activity of all fish with respect to an environmental variable, I calculated the percentage of times that an individual was active at a particular value for a particular environmental variable. For example, with respect to time of day, I calculated the percentage of times (n = 5-8 observations for each time of day except n = 3 for 23:00) each fish was active at a particular time of day and used it as a datum in the analysis. For the overall analyses of time of day, I used a 2-way ANOVA to determine whether there was an interaction between age class and time of day. Because 0+ and 1+ fish differed in diel activity, I analyzed the daytime activity of each age class separately using a randomized complete block design with individual fish as blocks. Specific linear or dome-shaped trends were tested using polynomial contrasts. Quantitative trends were described using standard linear and polynomial regression.

Because activity is an attribute variable (sensu Sokal and Rohlf 1995; i.e. active or not), I analyzed the activity of each individual using a simple logistic regression for each of the four main variables (time of day, day of year, water temperature, light intensity) (i.e. 43 fish x 4 = 172 logistic regressions). For each fish, I also calculated a multiple logistic regression to evaluate which of the four variables was most significantly related to activity. Quadratic terms were included in the logistic regression models only if significant after the linear term was first entered in the model.

I used the same statistical approach for analyzing foraging rate as I used for activity, except that I used linear regressions rather than logistic regressions. Only individuals with at least 15 foraging observations were included in the analyses of individual fish; therefore, 27 age-0+ fish and seven 1+ fish were used for foraging analyses.

To meet the assumptions of parametric tests, light intensity and foraging rate were $\log_{10}$ transformed. The activity of fish was arcsine square-root transformed for statistical analyses; however, the untransformed data are presented in the figures.

Results

Density

The diel patterns in the density of juvenile Atlantic salmon that were counted during snorkeling surveys differed between the two age-classes (2-way ANOVA, interaction effect: $F_{(8,126)} = 12.61$, $P < 0.0001$, Fig. 2). The density of 0+ fish exhibited a dome-shaped relationship (ANOVA with sites as blocks, quadratic polynomial contrast: $F_{(1,63)} = 62.55$, $P < 0.0001$); the number was low in the morning, peaked in the early afternoon and then decreased at night (quadratic regression for 0+: density = 0.076 * time of day - 0.0026 * time of day^2 - 0.34, $r^2 = 0.54$, $n = 72$, $P < 0.0001$). In contrast, the density of 1+ fish increased linearly over the day (ANOVA with sites as blocks, linear polynomial contrast: $F_{(1,63)} = 83.89$, $P < 0.0001$) and was highest at night (linear regression for 1+: density = 0.013 * time of day - 0.055, r^2 = 0.46, n = 72, P < 0.0001).

Activity of tagged fish - univariate analyses

Of the original tagged fish, 51 of 72 0+ fish and 10 of 13 1+ fish were seen at least once after tagging and 35 age-0+ and 8 age-1+ fish were followed throughout the study period. The mean displacement from the initial tagging location to the location observed at the end of the study did not differ significantly for 0+ ($\bar{x}$ ± SE = 0.53 ± 0.10m, range = 0 - 3m) and 1+ ($\bar{x}$ ± SE = 0.39 ± 0.11m, range = 0 - 1m) fish (Fig. 3; 2 sample t-test: t = 0.68, df = 42, P = 0.50). On average, 0+ and 1+ salmon were observed on 46.1% (n = 35, range = 22.0 - 82.9) and 36.8% (n = 8, range = 11.9 - 70.2) of the snorkeling surveys over the study period (Mann-Whitney U test: U = 221, n = 43, P = 0.064).

Activity and time of day

Overall, the diel patterns of activity of the tagged fish (Fig. 4) were similar to the diel patterns in density; the two age-classes showed different diel activity patterns (2-way ANOVA, interaction effect: $F_{(8,369)}$ = 10.49, P < 0.0001). The 0+ fish were most active in the late morning and afternoon (ANOVA with individuals as blocks, quadratic polynomial contrast: $F_{(1,272)}$ = 173.37, P < 0.0001; quadratic regression for 0+: arcsine square-root activity = 0.78 * time of day - 0.026 * time of day^2 - 5.65; r^2 = 0.33, n = 315, P < 0.0001) whereas 1+ fish were most active at night (ANOVA with individuals as blocks, linear polynomial contrast: $F_{(1,64)}$ = 39.90, P < 0.0001; linear regression for 1+: arcsine square-root activity = 0.12 * time of day - 2.27; $r^2 = 0.27$, n = 81, $P < 0.0001$).

However, there was considerable variation in the diel activity patterns among individuals within an age-class (Fig. 5). To investigate this individual variability, I used separate logistic regressions for each fish. Three basic patterns of diel activity were detected for 0+ fish: linear increase, dome-shaped relationship and non-significant relationship. Of 35 age-0+ fish, 22 exhibited a significant diel activity pattern: 17 showed a significant quadratic relationship with activity peaking in the late morning or early afternoon and five showed a significant increase over the day with their activity highest at night. Of the 13 fish whose activity did not differ significantly with time of day, six exhibited a positive trend and seven a negative trend with time of day. Curiously, none of the four fish at the Mouth exhibited a dome-shaped relationship.

The diel activity patterns of 1+ fish differed from most 0+ fish (Fig. 5d). Of the eight 1+ fish, six increased their activity with time of day, four of which were significant. Two fish in the Gorge exhibited a significant U-shaped relationship, being most active at dawn and at dusk/night. Because the activity of most 0+ and 1+ fish differed between day (> 100 lx) and night (< 0.01 lx), I treated the day and night data separately below. In addition, because the diel activity patterns of 0+ and 1+ fish differed significantly, I also treated them separately below.

Daytime activity and season

Overall, the patterns of daytime activity changed little over the season (Fig. 6). The activity of 0+ fish was initially low and then changed little over the season (ANOVA with individuals as blocks, quadratic polynomial contrast: $F_{(1,235)} = 7.98$, P

= 0.0051; quadratic regression: arcsine square-root activity = 9.29 * day of year - 0.022 * day of year^2 - 946.85, r^2 = 0.050, n = 268, P = 0.0009). The activity of 1+ fish was initially high, decreased and then changed little over the season (ANOVA with individuals as blocks, quadratic polynomial contrast: $F_{(1,44)}$ = 7.07, P = 0.011; quadratic regression: arcsine square-root activity = -28.31 * day of year + 0.065 * day of year^2 + 3090, r^2 = 0.11, n = 65, P = 0.027). On July 15 (day 210), no 1+ fish were observed during these morning observations, presumably because the mean water temperature was 14.8°C (see below).

Individual patterns were again variable and revealed no overall patterns (Fig. 7a-d). There were four basic patterns of activity over the season: linear increase, linear decrease, dome-shaped and non-significant relationship. Of the 35 0+ fish, 16 changed their activity significantly over the season; five were more active, six were less active, four exhibited dome-shaped curves (i.e. were most active on July 5, day 200, and one fish exhibited an odd activity pattern). This last fish was active 100% of the time until July 13 (day 208), when its activity decreased markedly, followed by an increase (Fig. 7a). This fish was not seen for a period of 2 days (day 208 and 211) (8 observations) suggesting that it might have moved out of the site for a few days and then returned. Of the 19 individuals with non-significant relationships, 12 tended to decrease their activity whereas seven tended to increase their activity with season (Sign test P > 0.10). Of the eight 1+ fish, seven were less active over the season (Sign test P > 0.10), three of which were significantly less active (Fig. 7d).

Daytime activity and water temperature

Overall, the daytime activity of 0+ fish increased with increasing water temperature and then leveled off at about 23°C (ANOVA with individuals as blocks, quadratic polynomial contrast: $F_{(1,365)} = 4.50$, $P = 0.035$; quadratic regression: arcsine square-root activity = 10.96 * water temperature - 0.20 * water temperature^2 - 98.27, $r^2 = 0.15$, $n = 414$, $P < 0.0001$, Fig. 8). In contrast, the daytime activity of 1+ fish exhibited a dome-shaped relationship with a peak in activity at 20.7°C (ANOVA with individuals as blocks, quadratic polynomial contrast: $F_{(1,77)} = 16.32$, $P = 0.00013$; quadratic regression: arcsine square-root activity = 30.71 * water temperature - 0.71 * water temperature^2 - 288.96, $r^2 = 0.31$, $n = 99$, $P < 0.0001$).

Once again, there was considerable variability among the tagged fish (Fig. 9). Four patterns emerged: linear increase, linear decrease, dome-shaped and non-significant. Daytime activity was significantly related to water temperature in 18 of 35 0+ fish. Of these 18 fish, 11 fish were more active with increasing water temperature, six exhibited dome-shaped relationships with peaks in activity at about 21°C, and one was less active with increasing water temperature. Of the 17 age-0+ fish whose activity was not significantly related to water temperature, 15 increased their activity with water temperature (Sign test, $P = 0.01$). Hence, overall 33 fish (Sign test, $P < 0.01$) increased their activity as water temperature increased from 13 to 20°C. Unlike the 0+ fish, there was no consistent pattern with the 1+ fish. The activity of only three of eight 1+ fish was significantly related to water temperature: two increased their activity and one showed a dome-shaped relationship with a peak at 20°C (Fig. 9d). Of the five fish with non-significant relationships, one was less active and three were more active with increasing water temperature.

Daytime activity and light intensity

The overall pattern of daytime activity was not significantly related to light intensity for 0+ fish (ANOVA with individuals as blocks: $F_{(1,155)} = 2.57$, $P = 0.11$)

whereas 1+ fish became less active at higher light intensities (linear polynomial contrast: $F_{(1,32)} = 20.18$, $P < 0.0001$; linear regression: arcsine square-root: 13.97 * $\log_{10}$ light + 1.68, $r^2 = 0.094$, $n = 45$, $P = 0.041$, Fig. 10).

There was less variability among fish in how they responded to light (Fig. 11). Only the activity of six of 35 0+ fish varied significantly with light intensity: five were more active, one less active and one had a dome-shaped relationship with increasing light. Of the 29 non-significant curves, 17 increased and 12 decreased with light intensity. Daytime activity of 1+ fish was significantly related to light intensity in only one out of eight fish. Of the non-significant relationships, three of seven were less active with increasing light while four were more active (Fig. 11d).

Daytime activity of tagged fish – multivariate analyses

A complete multiple logistic regression was used for each individual fish to determine which environmental variables had significant effects on daytime activity independent of all other variables (Table 1). For the 0+ fish, water temperature and day of year were the most important variables influencing daytime activity. Of the 35 fish, the daytime activity of 13 and 11 were significantly affected by water temperature and season, respectively. Twelve fish initially increased their activity with increasing water temperature, five of which showed a decrease in activity at higher temperatures. While season was the second most important factor affecting daytime activity, there was no consistent seasonal pattern in activity. Time of day and light intensity had significant independent effects on the activity of only five fish each. The general pattern was an initial increase in activity with time of day and light intensity.

The daytime activity of 1+ fish appeared to be mainly influenced by water temperature and time of day. Six and four fish were significantly affected by water temperature and time of day, respectively. Six fish increased their activity with increasing water temperature, one of which decreased at higher water temperatures. Four fish increased their daytime activity with time of day, being most active towards the end of the day. Light intensity and day of year had independent effects on the daytime activity of only two and one fish, respectively.

Dawn, dusk and nighttime activity

Age-0+ fish were significantly more active at dusk ($\bar{x}$ = 35.3%, range = 0 - 100) than at dawn ($\bar{x}$ = 18.5%, range = 0 - 100) (Wilcoxon signed ranks test: Z = 2.43, n = 13, P = 0.015) or at night ($\bar{x}$ = 11.4%, range = 0 - 100) (Wilcoxon signed ranks test: Z = 3.43, n = 23, P = 0.00061) but there was no significant difference between dawn and night (Wilcoxon signed ranks test: Z = 0.80, n = 13, P = 0.93). The activity of 1+ fish, however, did not differ significantly between dusk and dawn (Z = -0.18, n = 5, P = 0.85) and night ($\bar{x}$ = 71.2%, range 0 - 100) (Wilcoxon signed ranks test: Z = 0.51, n = 8, P = 0.61).

Daytime foraging

In general, the foraging rate of active fish was only weakly related to the environmental variables (Table 2). The two most important variables influencing the foraging rate of 0+ fish were day of year and light intensity; of 27 fish, the foraging rate of only nine and 11 fish were significantly related to day of year and light intensity, respectively. However, 24 of 27 (Sign test, P < 0.01) decreased their foraging rate with day of year, 20 of 27 initially increased their foraging rate with light intensity (Sign test, P = 0.02) and 20 increased their foraging rate with water temperature (Sign test, P = 0.02). While the overall trends were significant, the foraging rate of even fewer fish was significantly related to environmental variables in the multiple regressions.

Because of the smaller sample size, the trends between foraging rate and the environmental variables was even weaker for 1+ fish. (Table 2b). As for 0+ fish, the two most important variables were day of year and light intensity. Of the 7 1+ fish, all 7 initially decreased their foraging rate over the season (Sign test, P = 0.02) and 6 initially increased their foraging rate with light intensity (Sign test, P > 0.10). In the multiple regressions, only two fish significantly decreased their foraging rate with day of year and only one fish increased its foraging rate with increasing light intensity.

Discussion

The most striking finding of my study is how inactive 0+ fish were during the summer, the period of active growth. They were active on average 46% of the time with a peak of only 56% early in the afternoon. On average, 1+ fish were active 37% of the time, but 74% were active at night.

Both the density and the activity data were consistent with the prediction of the Asset Protection Principle. The 1+ fish were more active at night than during the day, whereas 0+ fish were mainly active during the day. Age-1+ fish grow little during July and August (Swansburg et al. 2002), perhaps because the abundance of drift declines over the summer (Keeley and Grant 1997; Steingrimsson and Grant 1999). Hence, given their limited opportunities for growth, 1+ fish probably maximized their fitness by feeding at night to minimize their risk of predation during the day. In contrast, 0+ fish grow primarily in July and August (Girard 2002). Presumably, they maximize their fitness by feeding during the day when conditions are optimal for visual foraging (Wilzbach et al. 1986) to maximize their growth rate. They accept a higher predation risk while feeding during the day in order to grow fast.

Previous laboratory work has provided support for the Asset Protection Principle. Larger fish avoid predator more than smaller fish under similar conditions (Reinhardt and Healey 1999). In some salmon populations, larger individuals, who have a chance of reaching the minimum size for migration to sea the following spring, continue foraging and growing over the fall and winter, whereas smaller fish, who require another year to reach the minimum size, 'protect their assets' by not feeding during the fall and winter (Valdimarsson and Metcalfe 1999). A consequence of this differential willingness to accept predation risk is the divergence of the population into a bimodal size distribution (Metcalfe et al. 1988).

During late August and early September, Gries et al. (1997) also noted that 1+ fish were active at night and inactive during the day. Interestingly, their 0+ fish were almost as active at night as during the day, in contrast to my findings. These divergent findings may be the result of seasonal differences in the two studies. I observed 0+ salmon during the growing season whereas they observed fish after the growing season.

My estimates of activity depend crucially on the assumption that the fish were hiding in the substrate when I did not see them. For three reasons, I am confident in this assumption. First, tagged and untagged fish were observed sheltering underneath cobbles (sensu Hynes 1970) in the substrate. By chance, I discovered four tagged 0+ and one tagged 1+ fish sheltering in the substrate on their home range (also see

Bachman 1984). Second, the tagged fish in my study were very sedentary with the average seasonal displacement being only 0.51m (also see Steingrimsson, unpublished data). Third, I carefully searched the whole site, plus 1m upstream and downstream of the site, for an average of 34m^2, for each tagged fish. Therefore, it seems unlikely that a fish was active at another location.

Contrary to my expectations, 0+ and 1+ fish did not show a strong daytime peak in activity at their optimal water temperature. On average, the activity of 0+ fish did not decline at warm water temperatures but leveled off between 23°C and 27°C. For 1+ fish, a peak in daytime activity was detected at 20.7°C, much higher than the preferred temperature of 17°C under laboratory conditions (Magnuson et al. 1979). Hence, my data suggest that laboratory optima may not directly apply to the salmon population of the Miramichi River. The most likely explanation for these differences is that my fish were acclimatized to the warmer daytime temperatures in the field. Optimal temperature studies usually use fish subjected to maximum rations of food (Magnuson and Destasio 1996). The differences I observed are unlikely due to food ration, because the optimal temperature for growth typically increases with ration (Wootton 1990). Elliott and Hurley (1997) studied a Scottish stock of salmon, which may have been adapted to cooler water temperatures. Hence, their optimal temperature might be lower than in the population I studied.

It was surprising to observe how much individual variability was present within an age-class. Three 0+ fish in the Gorge and two in the Mouth were most active at night and resembled 1+ fish in their activity patterns Three of these fish, for which body length measurements were available, were larger (55.0mm, 54.9mm, 50.4mm) than the average fish at these sites ($\bar{x}$ = 49.7mm). Perhaps these fish had reached a body size at which it was more beneficial to trade off a lower growth rate for a lower risk of predation. Similarly, two 1+ fish exhibited a U-shaped daily activity pattern; they were active at dawn and dusk/night but were almost totally inactive during the day. One of these fish, for which body length was available (85.7mm) was also much larger than the average 1+ fish ($\bar{x}$ = 75.5mm). This anecdotal information suggests that some of the individual variability in daily activity patterns may be explained by body size.

Interestingly, the two variables that most influenced the activity of 0+ fish, time of day and water temperature, had little effect on foraging rate. Once individuals were active, foraging rate varied primarily with season and light intensity. The decrease in foraging rate over the season has been observed in other studies (Bachman 1984; Steingrimsson unpublished data) and may be related to the decline in drift over the season in Catamaran Brook (Keeley and Grant 1997; Steingrimsson and Grant 1999). Overall, foraging rate increased with increasing daytime light intensity in my study and in previous work (Fraser and Metcalfe 1997). This is not surprising because salmonids are visual foragers and hence, can better detect and intercept prey at higher light intensities (Wilzbach et al. 1986).

The advantage of monitoring marked individuals is the ability to detect individual variation. Sometimes overall patterns will be an accurate representation of individuals in the population. For example, the overall dome-shaped diel activity pattern of 0+ fish reflected the behavioural patterns of most individuals. In other cases, however, overall patterns obscure individual patterns. For example, the overall relationship between daytime activity and water temperature for 1+ fish was a dome-shaped curve, whereas only one of eight individuals exhibited such a relationship. The overall pattern was an artefact caused by some fish being more active with increasing water temperature and others being less active.

In summary, the single most important factor affecting the activity of juvenile Atlantic salmon is the diel cycle of light intensity. These diel activity patterns of 0+ and 1+ fish are consistent with the Asset Protection Principle; 1+ fish were most active at night whereas 0+ fish were most active during the day. The daytime activity of individual 0+ and 1+ fish was affected primarily by water temperature and season; their activity initially increased with increasing water temperature. The activity of my fish did not peak at the optimal water temperature determined in laboratory studies of other populations. Curiously, the foraging rate of active fish was largely unrelated to water temperature. The best predictor of foraging rate was season; for both age-classes foraging rate decreased over the season.

Most importantly, I show marked individual variation within an age-class in both activity and foraging rate. Because this variation may be related to individual differences in body size and/or dominance and may have consequences for growth and mortality, it deserves further study.

Figure 1 Map of the area and the location of the study sites in the Little Southwest Miramichi River, N.B. and Catamaran Brook, one of its tributaries.

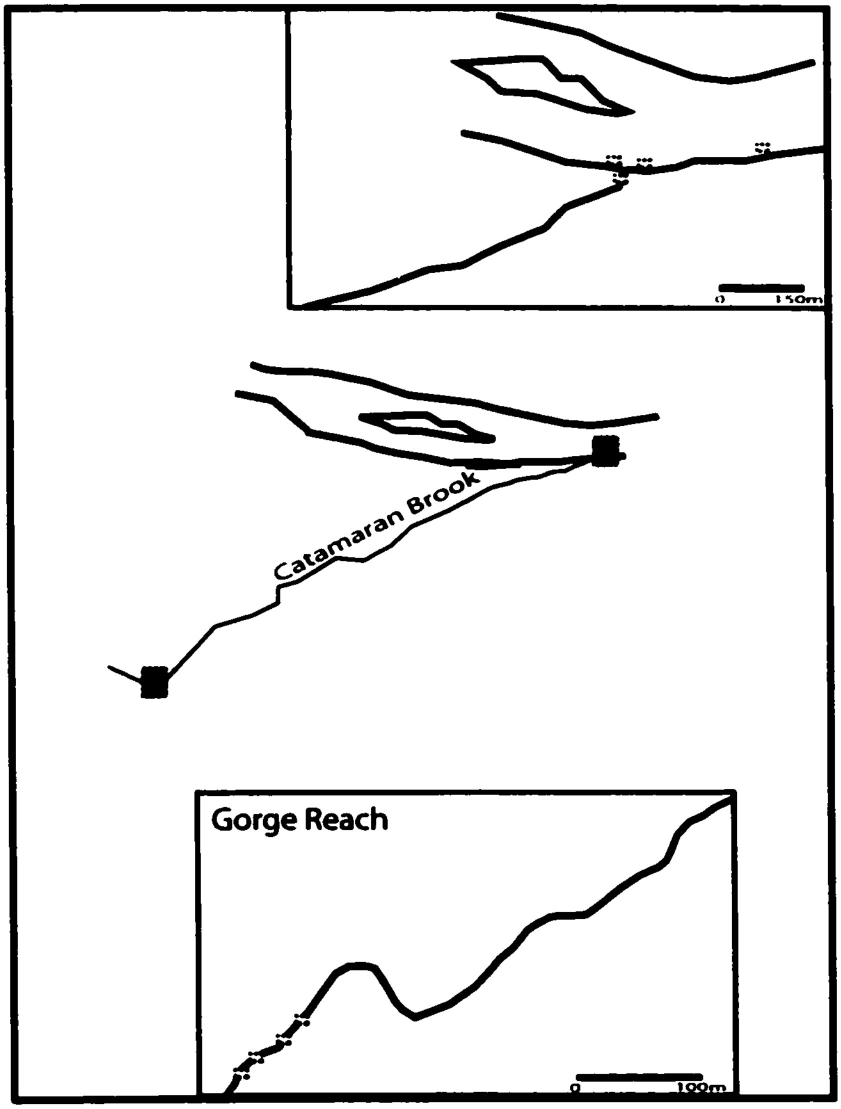
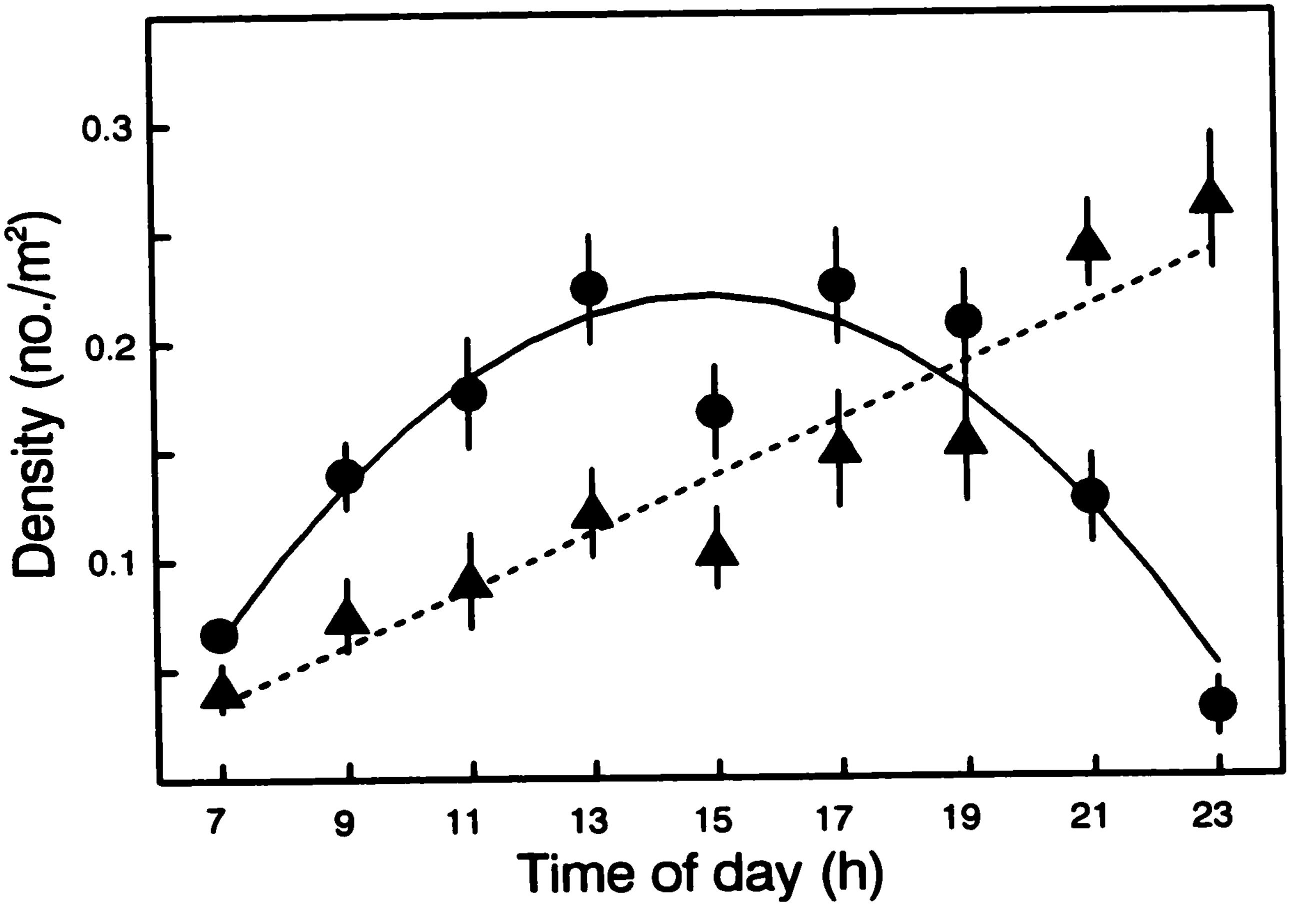

0
150m
Catamaran Brook
Gorge Reach
0
100m

Figure 2 Mean density (± SE, n = 8 sites) of 0+ (●) and 1+ (▲) Atlantic salmon counted during snorkeling surveys at different times of the day. A datum in the analysis was the average density at a particular site and time of day based on 8 counts over the season (except n = 3 for 23:00).



Density (no./m²)
0.3
0.2
0.1
7
9
11
13
15
17
19
21
23
Time of day (h)

Figure 3 Mean displacement of tagged fish from the initial tagging location to the location observed at the end of the study period. Solid bars represent 0+ fish and open bars 1+ fish.

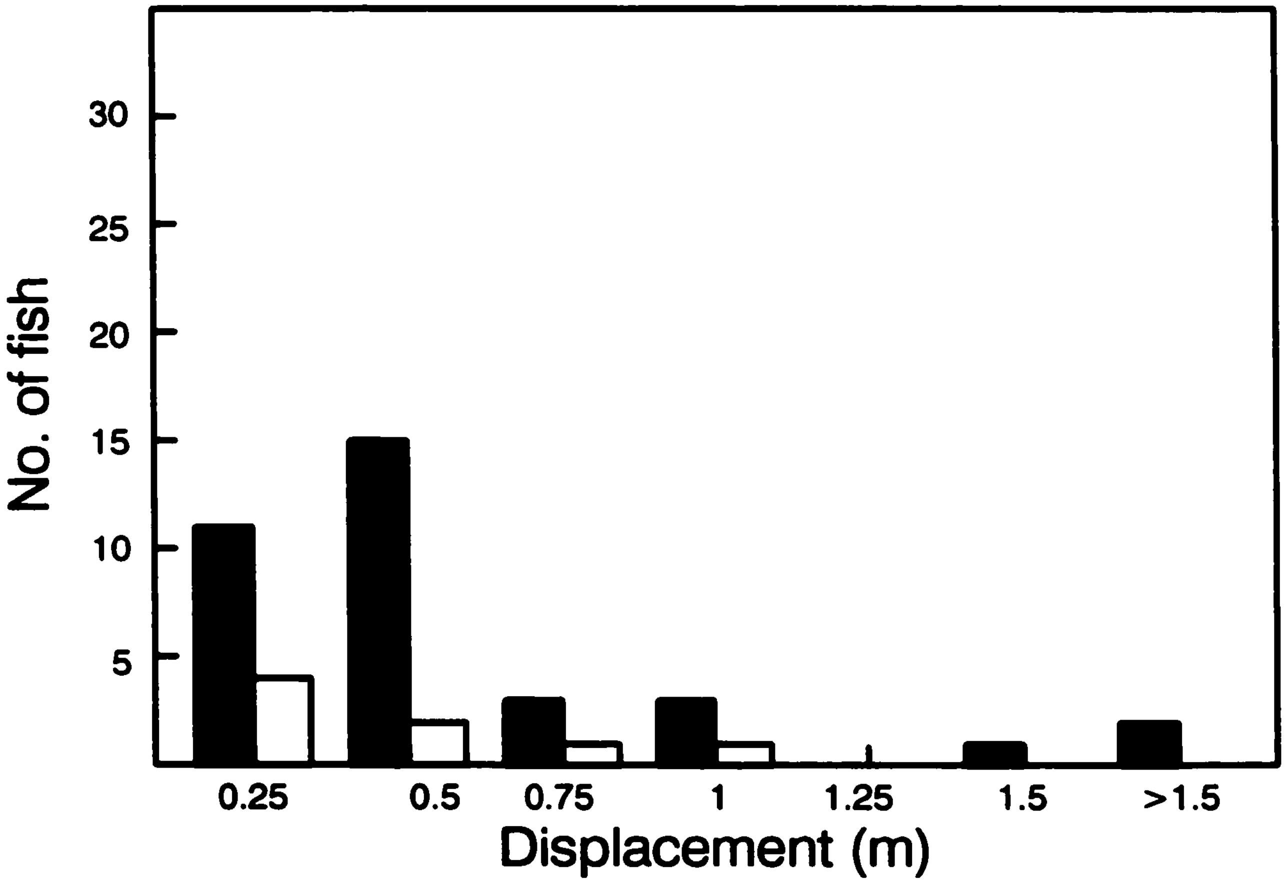
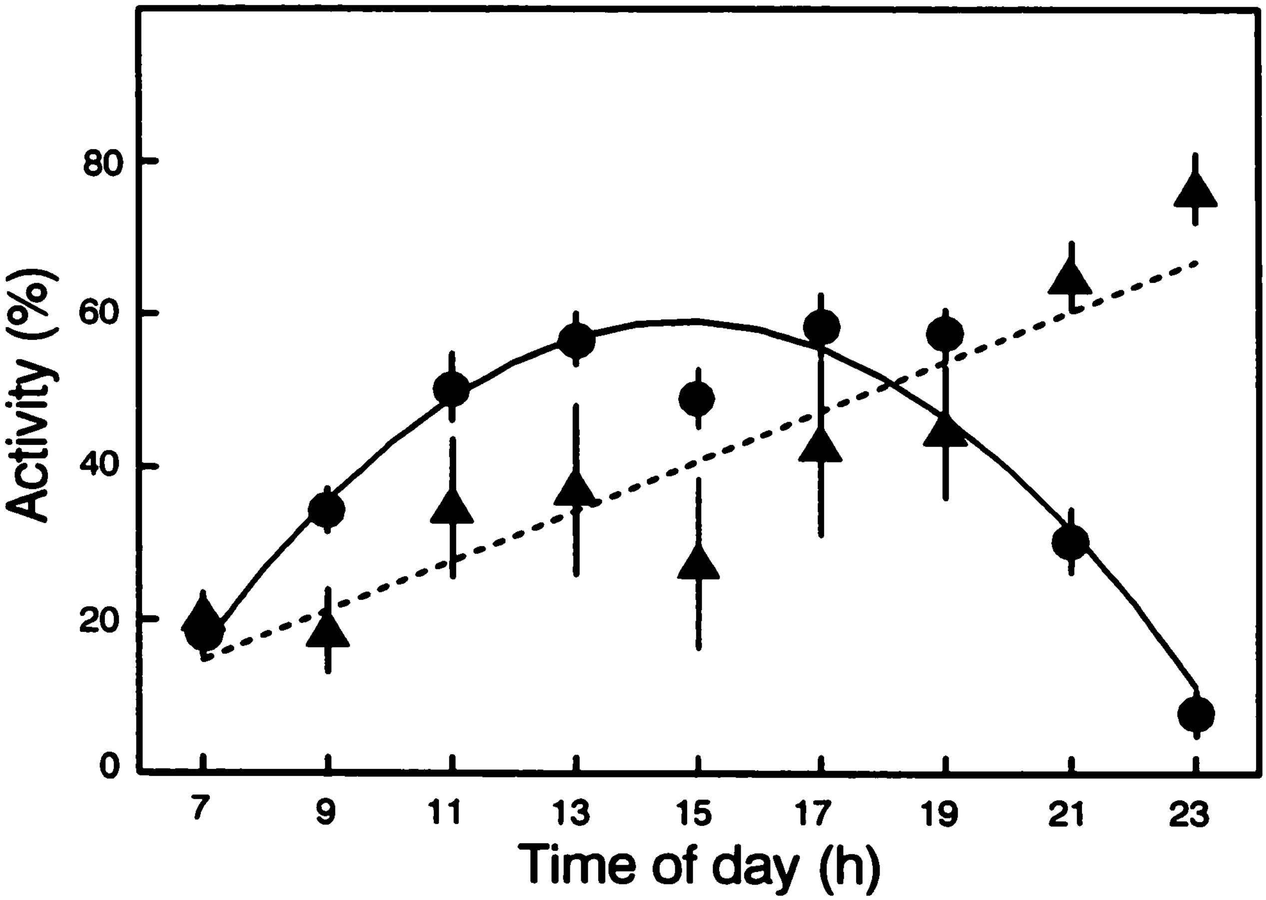

30
25
20
15
10
5
No. of fish
0.25
0.5
0.75
1
1.25
1.5
>1.5
Displacement (m)

Figure 4 Mean (± SE) percentage of snorkeling surveys in which 0+ (●, n = 35) and 1+ (▲, n = 8) Atlantic salmon were observed at various times of day. A datum in the analysis was the percentage of surveys (n = 5-8 over the season, except n = 3 for 23:00) in which an individual salmon was active at a particular time of day.



Activity (%)
80
60
40
20
0
7
9
11
13
15
17
19
21
23
Time of day (h)

Figure 5 Logistic regressions of the diel activity of 35 tagged 0+ salmon found in the a) Gorge, b) River, c) Mouth and d) 8 tagged 1+ salmon found in all four sites. The solid lines represent significant linear or quadratic logistic regressions whereas dashed lines were not significant. Sample size varied between 48 and 67 observations for each fish.

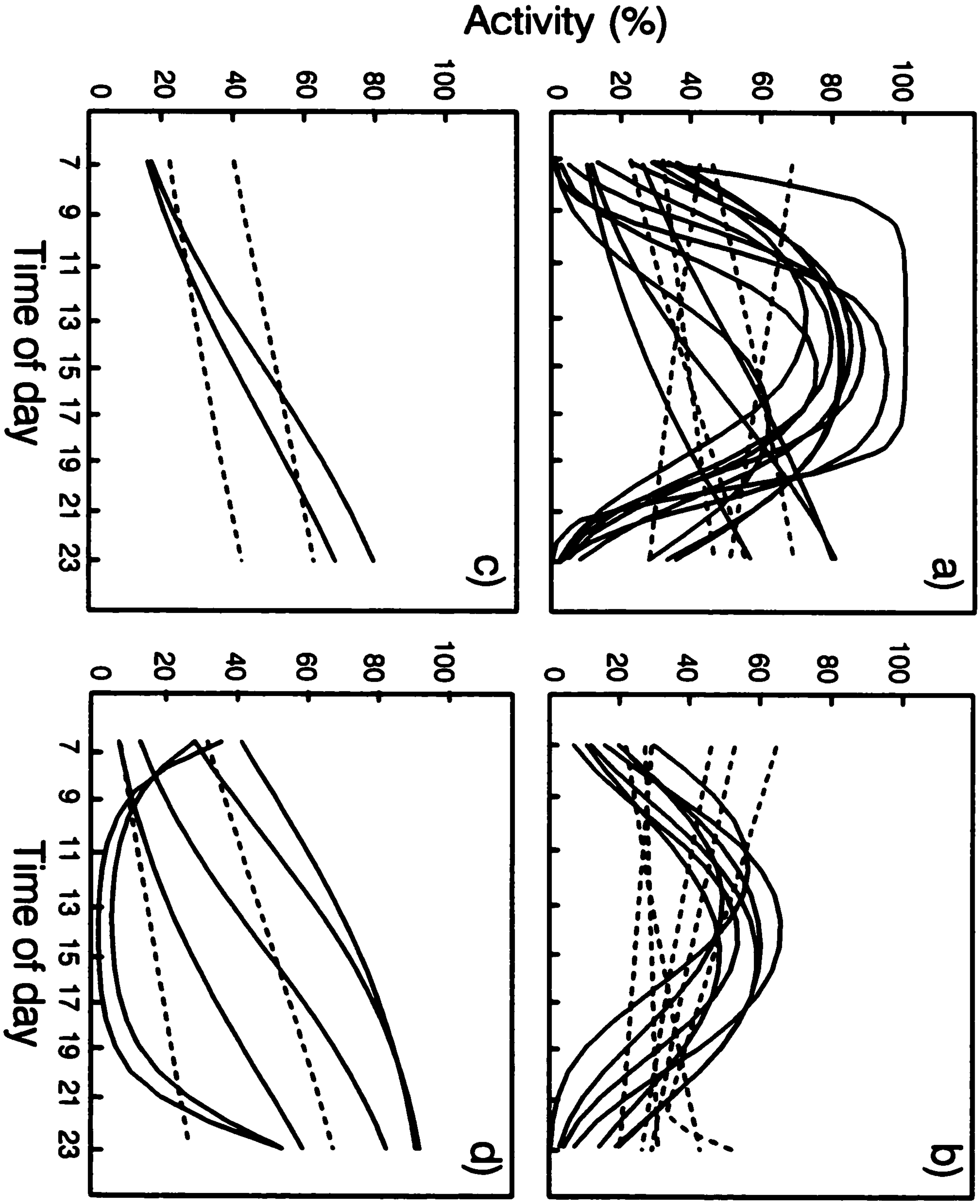

Activity (%)
0
20
40
60
80
100
7
9
11
13
15
17
19
21
23
Time of day
a)
b)
c)
d)

Figure 6 Mean (± SE) percentage of daytime (light intensity > 100 lx) snorkeling surveys in which 35 0+ (●, n = 35, except n = 12 for day 183 and n = 11 for day 194) and 8 1+ (▲, n = 8, except n = 4 for day 183 and n = 3 for day 210) Atlantic salmon were observed over the season. A datum in the analysis was the percentage of 8 surveys in a day for which an individual salmon was active.

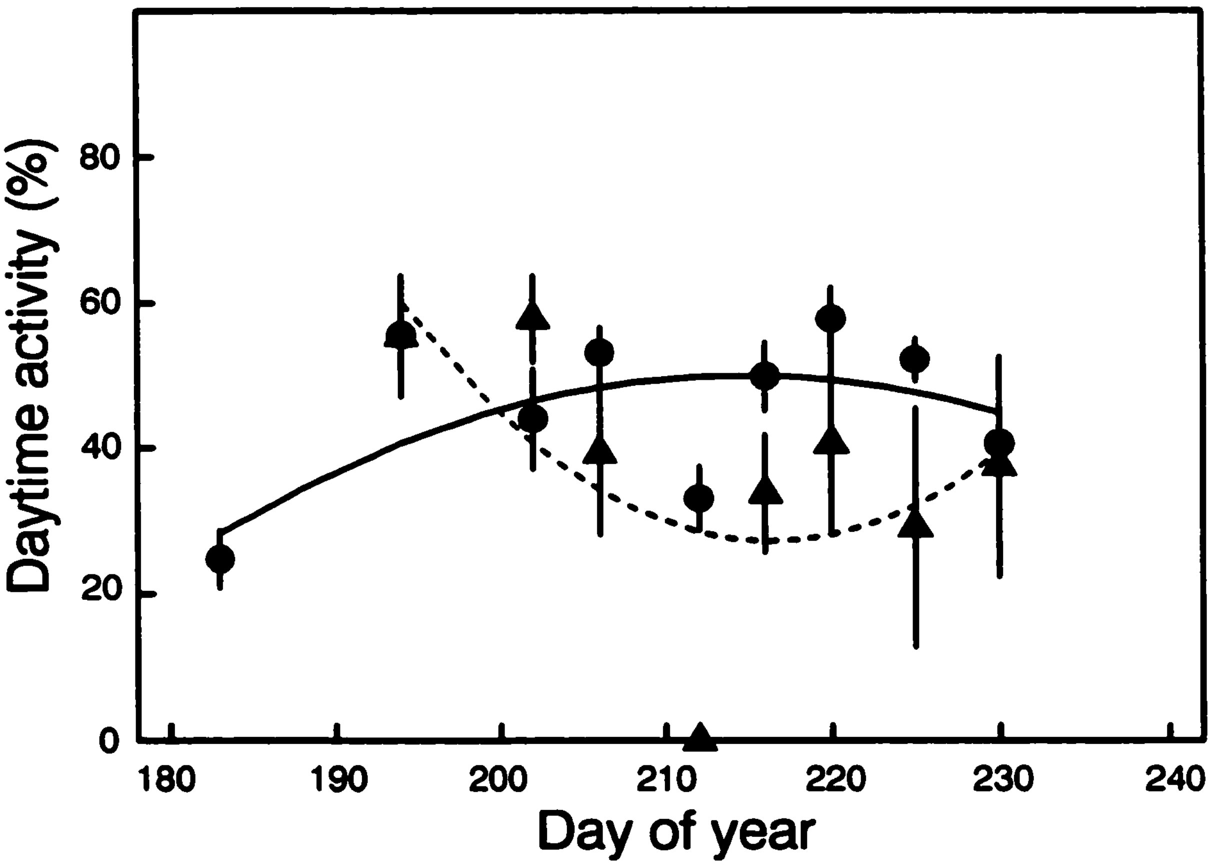

Daytime activity (%)
0
20
40
60
80
180
190
200
210
220
230
240
Day of year

Figure 7 Logistic regressions of the daytime activity of 35 tagged 0+ fish found in a) the Gorge, b) the River and c) the Mouth and d) 8 tagged 1+ salmon versus day of the year. The solid lines represent significant linear or quadratic logistic regression whereas dashed lines were not significant. Sample size varied between 48 and 67 observations for each fish.

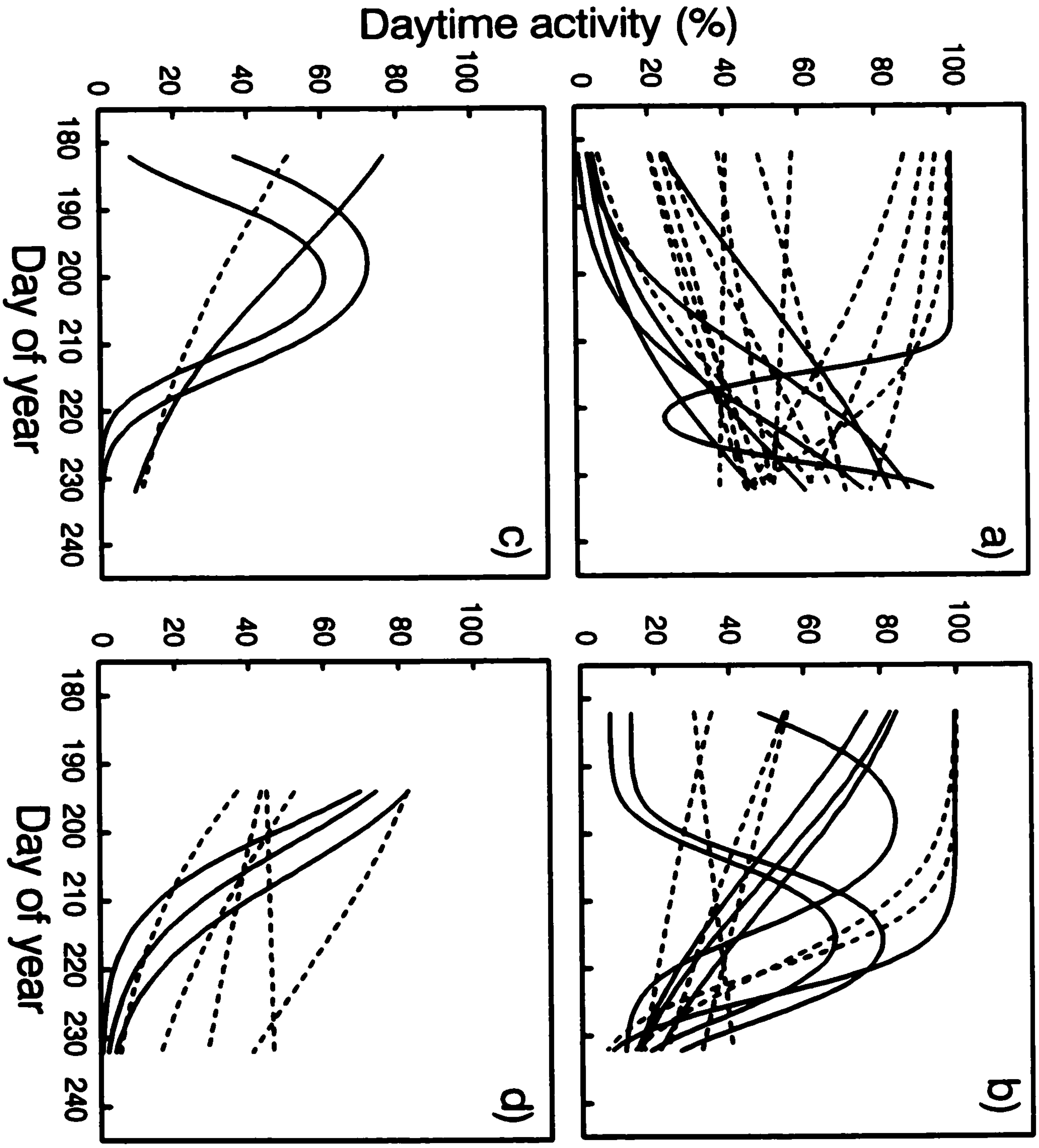
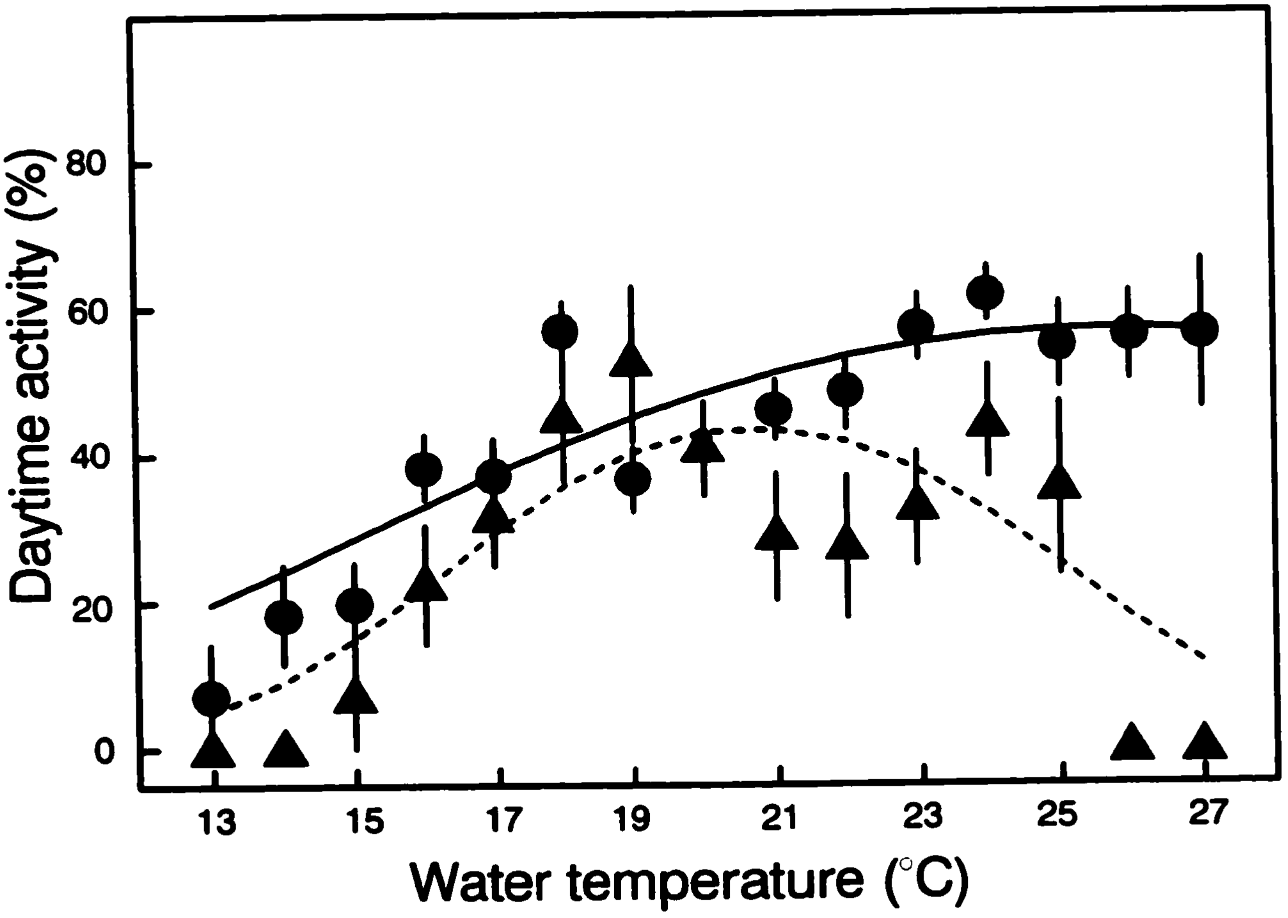

Daytime activity (%)
0
20
40
60
80
100
180
190
200
210
220
230
240
Day of year
a)
b)
c)
d)

Figure 8 Mean daytime (light intensity > 100 lx) activity of 0+ (●, n = 35 for 17 - 21°C and 23 - 24°C, n = 32 for 16°C, n = 30 for 22 and 25°C, n = 23 for 14°C, n = 19 for 15°C, n = 15 for 13°C, n = 13 for 26°C and n = 11 for 27°C) and 1+ (▲, n = 8 for 17, 19, 21 and 23°C, n = 3 for 13 - 16, 20 and 24 - 27°C) fish in relation to water temperature. Each datum was the mean activity for each tagged fish at each water temperature.



Daytime activity (%)
0
20
40
60
80
13
15
17
19
21
23
25
27
Water temperature (°C)

Figure 9 Logistic regressions of the daytime activity in relation to water temperature of 35 tagged 0+ fish found in the a) Gorge, b) River and c) Mouth and d) of 8 tagged 1+ fish at all sites. The solid lines represent significant linear or quadratic logistic regressions whereas dashed lines were not significant. Sample size varied between 48 and 67 observations for each fish.

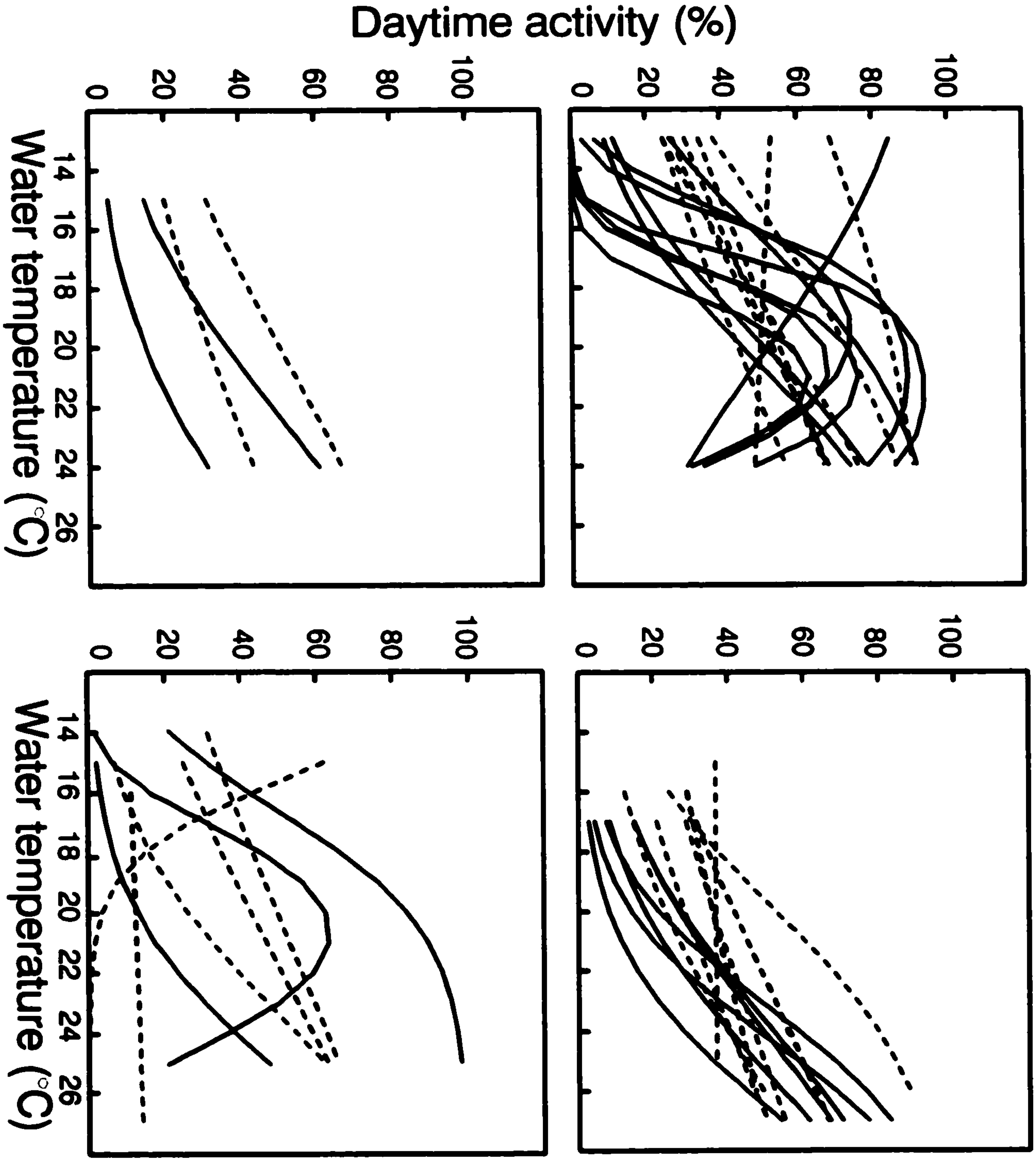

Daytime activity (%)
0
20
40
60
80
100
14
16
18
20
22
24
26
Water temperature (°C)
Water temperature (°C)

Figure 10 Mean percentage of daytime (light intensity > 100 lx) snorkeling surveys in which 0+ (●, n = 35 for 160 – 2560 lx and n = 15 for 5120 lx) and 1+ (▲, n = 8) fish were observed at different light intensity. A datum was the percentage of surveys in which a fish was active at a particular category of light intensity (categories: 100-215, 216-430, 431-861, 862-1722, 1723-3444, > 3444 lx).

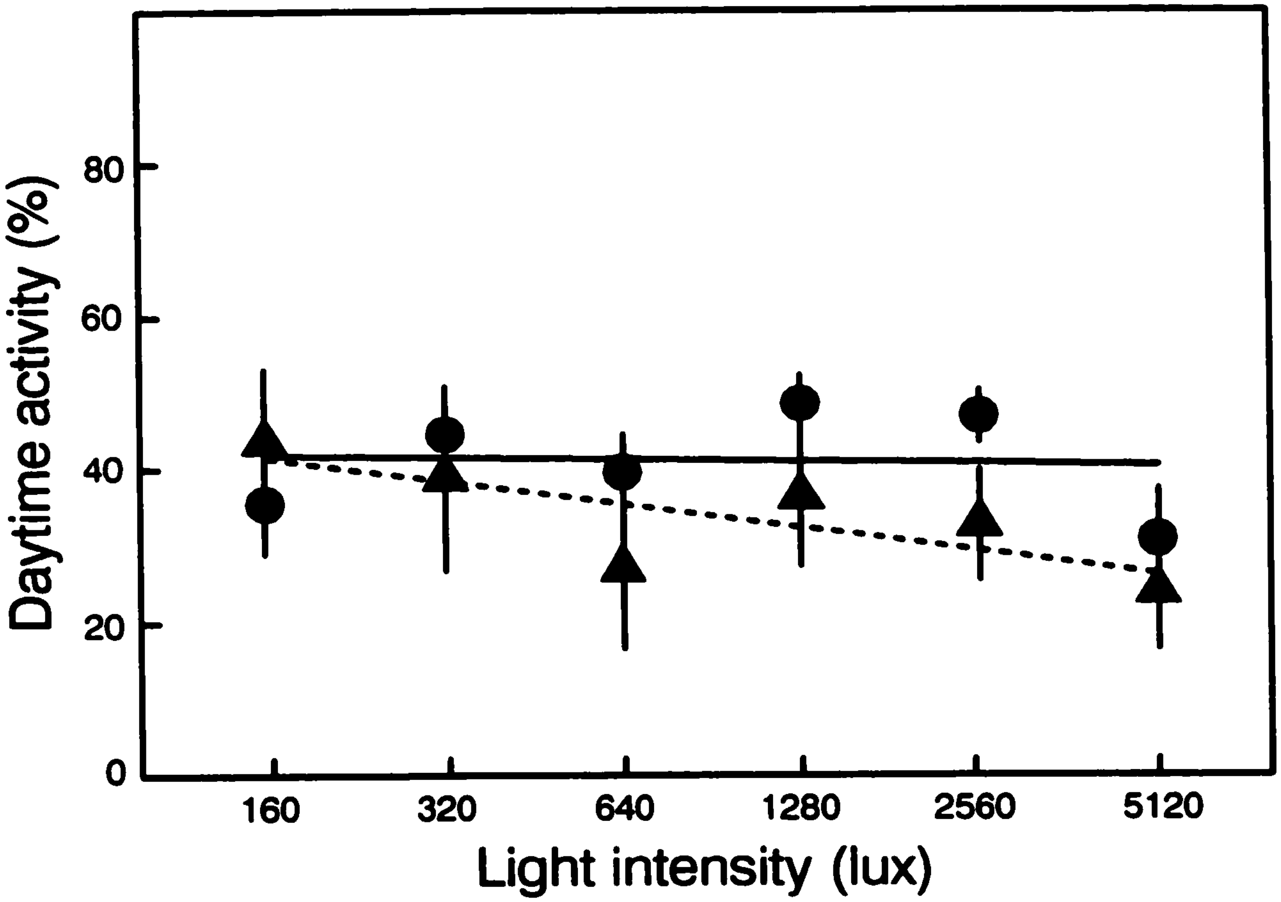

Daytime activity (%)
80
60
40
20
0
160
320
640
1280
2560
5120
Light intensity (lux)

Figure 11 Logistic regressions of daytime activity of tagged 0+ fish found in the a) Gorge, b) River, c) Mouth and d) of tagged 1+ fish at all sites across different light intensity. The solid lines represent significant linear or quadratic logistic regression and the dashed lines were not significant. Sample size varied between 48 and 67 observations for each fish.

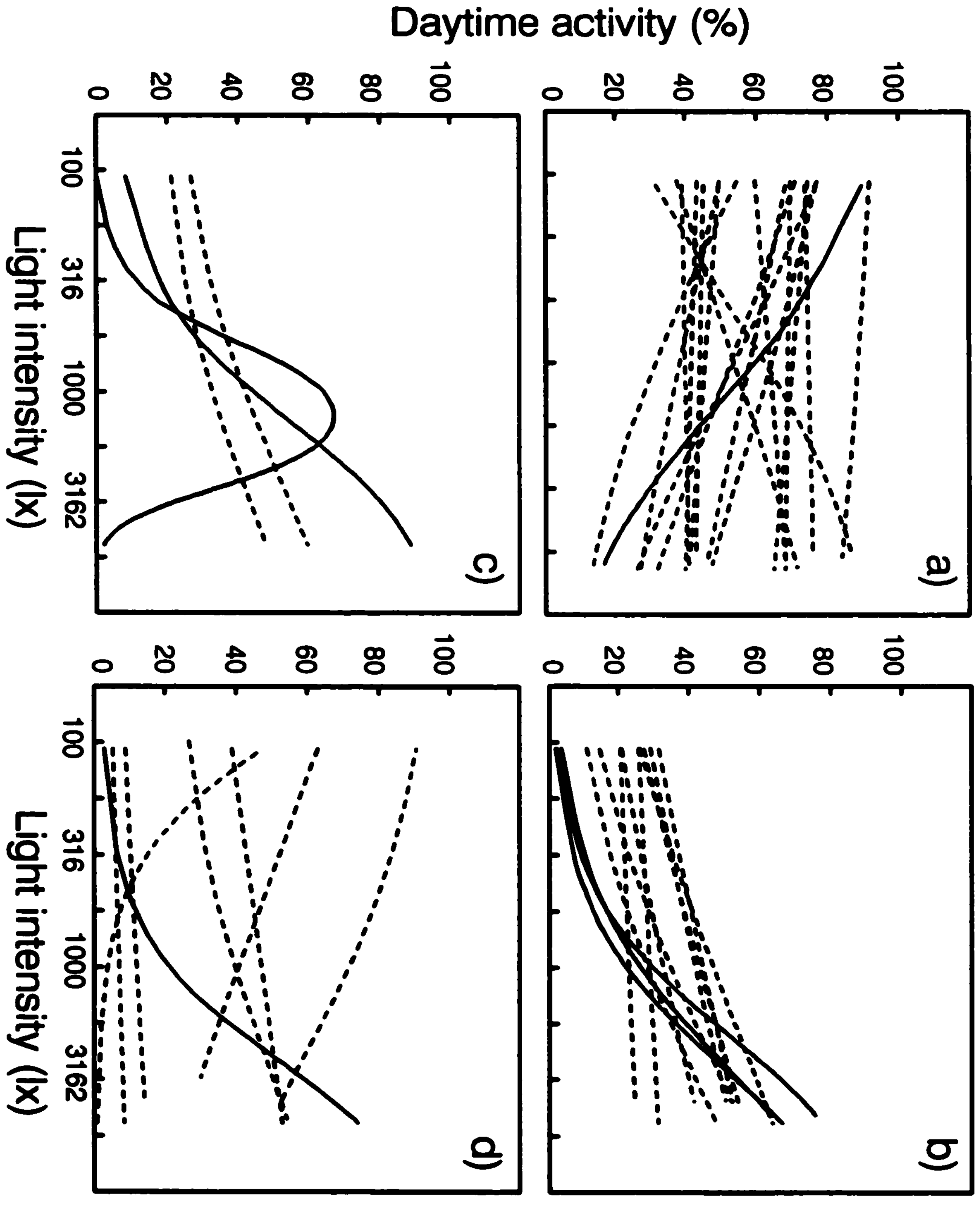

Daytime activity (%)
0
20
40
60
80
100
100
316
1000
3162
Light intensity (lx)
a)
b)
c)
d)

Table 1. Multiple logistic regressions of the daytime activity of a) 35 0+ and b) 8 1+ fish in relation to each environmental variable. The numbers represent the number of fish for which a particular environmental variable was significantly related to activity when entered last in the model.

Environmental variable[a]	Linear + [b]	Linear - [b]	Quadratic + [c]	Quadratic - [c]
a) water temperature (°C)	7	1	5	0
day of year	2	3	6	0
time of day (hour)	3	0	2	0
light intensity (lx)	2	1	2	0
b) water temperature (°C)	5	0	1	0
time of day (hour)	4	0	0	0
light intensity (lx)	0	1	0	1
day of year	0	1	0	0

[a] Logistic regressions are based on $\log_{10}$-transformed data for light intensity.

[b] Linear + is a positive increase and linear – is a linear decrease.

[c] Quadratic + is asymptotic positive or dome-shaped curve, quadratic – is asymptotic negative or U-shaped curve.

Table 2. Simple and multiple linear regressions of the daytime foraging rate of a) 27 0+ and b) 7 1+ fish in relation to each environmental variable. The numbers and the number in brackets represent the number of fish for which a particular environmental variable was significantly related to foraging rate in a simple linear regression and when entered last in a multiple regression model, respectively.

Environmental variable[a]	Linear +[b]	Linear -[b]	Quadratic +[c]	Quadratic -[c]	NS +	NS -
a) day of year	0	7(4)	0	2(1)	3	15
light intensity (lx)	6(1)	1(1)	2(2)	2	12	4
time of day (hour)	0	0	0	4(3)	12	11
water temperature (°C)	2	0	1(1)	0	17	7
b) day of year	0	3(2)	0	1	0	3
light intensity (lx)	1(1)	0	1	1	4	0
water temperature (°C)	1	0	0	0	4	2
time of day (hour)	0	0	0	0	3	4

[a] Linear regressions are based on $\log_{10}$-transformed data for foraging rate and light intensity.

[b] Linear + is a positive increase and linear – is a linear decrease.

[c] Quadratic + is asymptotic positive or dome-shaped curve, quadratic – is asymptotic negative or U-shaped curve.

References

Allen, K.R. 1940. Studies on the biology of the early stages of the salmon (*Salmo salar*). 1. Growth in the River Eden. J. Anim. Ecol. **9**: 1-23.

Bachman, R.A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Trans. Am. Fish. Soc. **113**: 1-32.

Bradford, M.J., and Higgins, P.S. 2001. Habitat-, season-, and size-specific variation in diel activity patterns of juvenile chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*). Can. J. Fish. Aquat. Sci. **58**: 365-374.

Clarke, C.W. 1994. Antipredator behaviour and the asset-protection principle. Behav. Ecol. **5**: 159-170.

Coker, G.A., Portt, C.B. and Minns, C.K. 2001. Morphological and Ecological Characteristics of Canadian Freshwater Fishes. Can. MS Rpt. Fish. Aquat. Sci. **2554**: iv+89p.

Cunjak, R.A., Caissie, D., El-Jabi, N., Hardie, P., Conlon, J.H., Pollock, T.L., Giberson, D.J., and Komadina-Douthwright, S. 1993. The Catamaran Brook (New-Brunswick) habitat research project: biological, physical, and chemical conditions (1990-1992). Can. Tech. Rep. Fish. Aquat. Sci. No. 1914.

Cunjak, R.A., Caissie, D., and El-Jabi, N. 1990. The Catamaran Brook habitat research project: description and general design of study. Can. Tech. Rep. Fish. Aquat. Sci. No.1751.

Cunjak, R.A. 1988. Behaviour and microhabitat of young Atlantic salmon (*Salmo salar*) during winter. Can. J. Fish. Aquat. Sci. **45**: 2156-2160.

Dewey M.R., and Zigler S.J. 1996. An evaluation of fluorescent elastomer for marking bluegills in experimental studies. The progressive fish-culturist. **58**:219-220.

Elliott, J.M., and Hurley, M.A. 1997. A functional model for maximum growth of Atlantic salmon parr, *Salmo salar*, from two populations in northwest England. Funct. Ecol. **11**: 592-603.

Feminella, J.W., and Resh, V.H. 1990. Hydrologic influences, disturbance, and intraspecific competition in a stream caddisfly population. Ecology **71**: 2083-2094.

Fraser, N.H.C. and Metcalfe, N.B. 1997. The cost of becoming nocturnal: feeding efficiency in relation to light intensity in juvenile Atlantic salmon. Funct. Ecol. **11**: 385-391.

Fraser, N.H.C., Heggenes, J., Metcalfe, N.B., and Thorpe, J.E. 1995. Low summer temperatures cause juvenile Atlantic salmon to become nocturnal. Can. J. Zool. **73**: 446-451.

Fraser, N.H.C., Metcalfe, N.B., and Thorpe, J.E. 1993. Temperature-dependant switch between diurnal and nocturnal foraging in salmon. Proc. R. Soc. Lond. B. Biol. Sci. **252**: 135-139.

Fry, E.J. 1971. The effect of environmental factors on the physiology of fish in Fish Physiology, Vol. VI. eds W.S. Hoar and D.J. Randall, Academic Press, London, pp. 1-98.

Gardiner, W.R. 1984. Estimating population densities of salmonids in deep water in streams. J. Fish Biol. **24**: 41-49.

Girard, I. 2002. Foraging and growth in relation to habitat use of young-of-the-year Atlantic salmon (*Salmo salar*). MSc thesis, Concordia University, Montréal, Canada.

Grant, J.W.A. and Noakes, D.L.G. 1987. Escape behaviour and use of cover by young-of-the-year brook trout, *Salvelinus fontinalis*. Can. J. Fish. Aquat. Sci. 44: 1390-1396.

Gries, G., Whalen, K.G., Juanes, F., and Parrish, D.L. 1997. Nocturnal activity of juvenile Atlantic salmon (*Salmo salar*) in late summer: evidence of diel activity partitioning. Can. J. Fish. Aquat. Sci. 54: 1408-1413.

Heggenes, J., Krog, O.M.W., Lindås. O.R., Dokk, J.G., and Bemnes, T. 1993. Homeostatic behavioural responses in a changing environment: brown trout (*Salmo trutta*) become nocturnal during winter. J. Anim. Ecol. 62: 295-308.

Hoar, W.S. 1942. Diurnal variations in feeding activity of young salmon and trout. J. Fish. Res. Board Can. 6: 90-101.

Hutchinson, G.E. 1957. An introduction to population ecology. New Haven, Yale University Press. p.415-427.

Hynes, H.B.N. 1970. The ecology of running waters. University of Toronto Press. Toronto 555p.

Jensen, A.J., Johnsen, B.O. and Saksgard, L. 1989. Temperature requirements in Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), and Artic char (*Salvelinus alpinus*) from hatching to initial feeding compared with geographic distribution. Can. J. Fish. Aquat. Sci. 46: 786-789.

Johnston, I.A., and Ball, D. 1996. Thermal stress and muscle function in fish. Society for experimental biology seminar series 61. Eds C.M. Wood and D.G. McDonald. p.79-104.

Keeley, E.R., and Grant, J.W.A. 1997. Allometry of diet selectivity in juvenile Atlantic salmon (*Salmo salar*). Can. J. Fish. Aqua. Sci. 54: 1894-1902.

Keeley, E.R., and Grant, J.W.A. 1995. Allometric and environmental correlates of territory size in juvenile Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **52**:186-196.

Keene, J.L., Noakes, D.L.G., Moccia, R.D., and Soto, C.G. 1998. The efficacity of clove oil as an anaesthetic for rainbow trout, *Oncorhynchus mykiss* (Walbaum). Aquaculture Research. **29**: 89-101.

Magnuson, J.J., and Destasio, B.T. 1996. Thermal niche of fishes and global warming. Society for experimental biology seminar series 61. Eds C.M. Wood and D.G. McDonald. p.377-408.

Magnuson, J.J., Crowder, L.B., and Medvick, P.A. 1979. Temperature as an ecological resource. Am. Zool. **19**: 331-343.

Metcalfe, N.B., Fraser, N.H.C., Burns, M.D. 1998. State-dependent shifts between nocturnal and diurnal activity in salmon. Proc. R. Soc. Lond., Ser. B: Biol. Sci. **265**: 1503-1507.

Metcalfe, N.B., Huntingford, F.A., and Thorpe, J.E. 1988. Feeding intensity, growth rates, and the establishment of life-history patterns in juvenile Atlantic salmon *Salmo salar*. J. Anim. Ecol. **57**: 463-474.

Metcalfe, N.B., Huntingford, F.A., and Thorpe, J.E. 1986. Seasonal changes in feeding motivation of juvenile Atlantic salmon (*Salmo salar*). Can. J. Zool. **64**: 2439-2446.

Randall, R.G. 1982. Emergence, population densities, and growth of salmon and trout fry in two New Brunswick streams. Can. J. Zool. **60**: 2239-2244.

Reinhardt, U.G. and Healy, M.C. 1999. Season and size-dependent risk taking in juvenile coho salmon: experimental evaluation of asset protection. Anim. Behav. **57**: 923-933.

Richards, F.P., Reynolds, W.W., and McCauley, R.W. 1977. Temperature preference studies in environmental impacts assessments: an overview with procedural recommendations. J. Fish. Res. Board Can. **34**: 728-761.

Riehle, M.D. and Griffith, J.S. 1993. Changes in habitat utilization and feeding chronology of juvenile rainbow trout (*Oncorhynchus mykiss*) in fall and the onset of winter in Silver Creek Idaho. Can. J. Fish. Aquat. Sci. **50**: 2119-2128.

Rimmer, D.M., and Paim, U. 1983. Autumnal habitat shift of juvenile Atlantic salmon (*Salmo salar*) in a small river. Can. J. Fish. Aquat. Sci. **40**: 671-680.

Sokal, R.R. and Rohlf, F.J. 1995. Biometry: the principles and pratice of statistics in biological research. 3rd. ed. by W.H. Freeman and Compagny, New York p.859.

Steingrímsson, S.Ó. and Grant, J.W.A. 1999. Allometry of territory size and metabolic rate as predictors of self-thinning in young-of-the-year Atlantic salmon. J. Anim.Ecol. **68**: 17-26.

Swansburg, E., Chaput, G., Moore, D., Caissie, D., and El-Jabi, N. 2002. Size variability of juvenile Atlantic salmon: links to environmental conditions. J. Fish Biol. **61**: 661-683.

Valdimarsson, S.K., and Metcalfe, N.B. 1999. Effect of time of day, time of year, and life history strategy on time budgeting in juvenile Atlantic salmon, *Salmo salar*. Can. J. Fish. Aquat. Sci. **56**: 2397-2403.

Valdimarsson, S.K., Metcalfe, N.B., Thorpe, J.E., and Huntingford, F.A. 1997. Seasonal changes in sheltering: effect of light and temperature on diel activity in juvenile salmon. Anim. Behav. **54**: 1405-1412.

Willmer, P. 1991. Thermal biology and mate acquisition in ectotherms. Trends Ecol. Evol. **6**: 396-399.

Wilzbach, M.A., Cummins, K.W., and Hall, J.D. 1986. Influence of habitat manipulations on interactions between cutthroat trout and invertebrate drift. Ecology. 67: 898-911.

Wootton, R.J. 1990. Ecology of teleost fishes. Fish and Fisheries Series 1. eds. Chapman and Hall. New York. pp. 117-157.