

Nocturnal activity of juvenile Atlantic salmon (*Salmo salar*) in late summer: evidence of diel activity partitioning

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Abstract: Paired day–night underwater counts of juvenile Atlantic salmon (*Salmo salar*) were completed on tributaries of the West River, Vermont, U.S.A., between 28 August and 10 September 1995. At water temperatures ranging from 13 to 23°C, the relative count of juvenile salmon was greater at night. Nocturnal counts differed for young-of-the-year and post-young-of-the-year (PYOY) salmon, with PYOY exhibiting almost exclusive nocturnal activity. Nocturnal activity in late summer may enable salmon to maintain population densities when space and suitable feeding areas may be limited. Nocturnal activity of juvenile salmon should be considered in studies of habitat use, competition, time budgets, and associated bioenergetic processes.

Résumé : Des dénombrements appariés jour-nuit du saumon atlantique (*Salmo salar*) ont été réalisés dans les tributaires de la rivière West, au Vermont, É.-U., entre le 28 août et le 10 septembre 1995. À des températures de l'eau variant de 13 à 23°C, le dénombrement relatif de saumons juvéniles était plus élevé la nuit. Les dénombrements nocturnes ont différé pour les saumons qui sont des jeunes de l'année et les saumons qui ne sont plus des jeunes de l'année, ces derniers montrant une activité presque exclusivement nocturne. L'activité nocturne à la fin de l'été peut permettre au saumon de maintenir des densités de population lorsque l'espace et les aires d'alimentation convenables sont limités. L'activité nocturne du saumon juvénile devrait être prise en considération dans les études sur l'utilisation de l'habitat, la compétition, l'emploi du temps et les processus bioénergétiques connexes.

[Traduit par la Rédaction]

Introduction

Nocturnal activity of juvenile Atlantic salmon (*Salmo salar*) is a temperature-dependent behavior involving in part an increase in nighttime feeding at decreasing laboratory water temperatures (Fraser et al. 1993). Laboratory and field analyses further confirmed that nocturnal activity is controlled by water temperature rather than photoperiod or a predetermined circannual rhythm (Fraser et al. 1995), as suggested by Rimmer et al. (1983, 1984). Fraser et al. (1995) found that juvenile salmon increase their daytime occupation of shelters with decreasing water temperatures but remain nocturnally active at laboratory water temperatures ranging from 2 to 18.5°C.

While Fraser et al. (1995) provided evidence for a temperature-dependent basis of diel activity patterns, several points warrant further consideration. All field work in their study was

completed at water temperatures $\leq 8.4^\circ\text{C}$; therefore, patterns of day and nighttime activity that they observed in the laboratory at water temperatures ranging from 9 to 18°C may not apply in the wild. In addition, young-of-the-year (YOY) salmon were used in their laboratory experiment, yet older juvenile salmon (parr) from three seasonal periods (April, June, October) were described in the field analysis; no distinction was made between the diel activity patterns of these life stages. Although juvenile Atlantic salmon have been observed to be active at night in the winter (Fraser et al. 1993), summer nocturnal activity at seasonal water temperatures in the natural environment has not been documented. Our objectives were to determine the level of nocturnal activity of juvenile Atlantic salmon and if YOY and post-young-of-the-year (PYOY) salmon exhibit similar diel activity patterns in the wild during late summer.

Materials and methods

Study area and species

Underwater surveys were completed in tributaries of the West River, Vermont: Rock River, Marlboro Branch, Wardsboro Branch, and Utley and Greendale brooks (43°08'N, 73°25'W; Fig. 1). The West River is a tributary of the Connecticut River. Eight survey sites were selected on the five study streams (Fig. 1). Discharge (cubic metres per second) determined on 7 September 1995 in each tributary was 0.19 for the Rock–Marlboro system, 0.094 for Wardsboro, 0.088 for Utley, and 0.042 for Greendale. Water depth was recorded at 0.5-m intervals across transects spaced 4 m apart at each survey site on 6 September 1995. Maximum water depth along each transect was also determined and the mean maximum water depth for each survey site was calculated for comparison purposes (Table 1).

Juvenile salmon in the study streams originated from annual

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Fig. 1. Location of survey sites in the West River Basin, Vermont. The Connecticut River Basin is shaded.

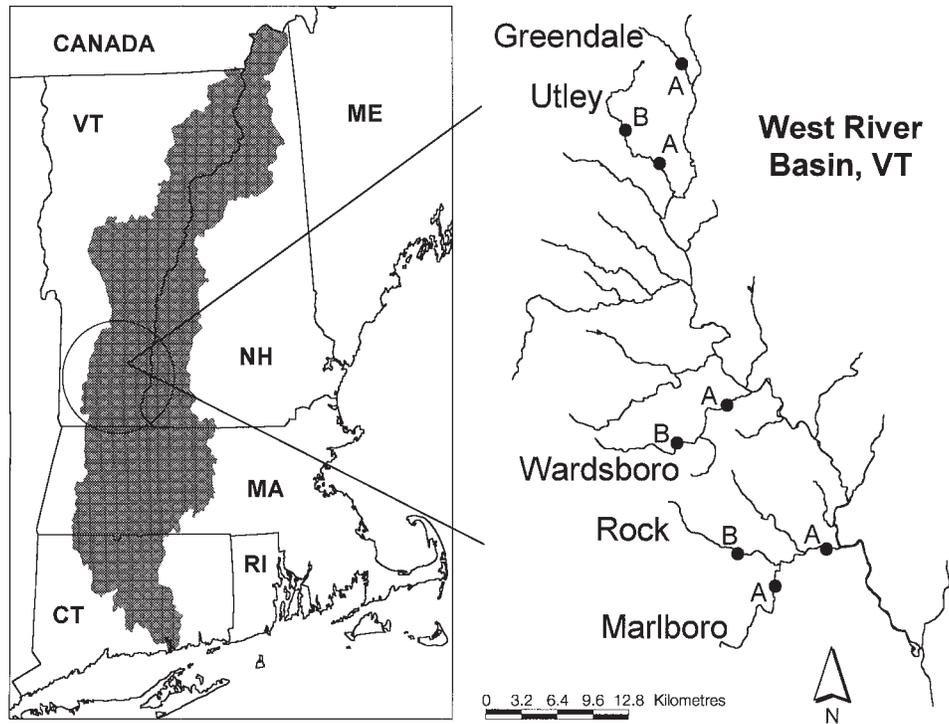


Table 1. Number of paired day–night snorkeling surveys completed and mean (± 1 SE) physical characteristics of the survey sites (see Fig. 1 for location of survey sites).

Stream	Survey site	Number of paired snorkeling surveys	Mean water depth (cm)	Mean maximum water depth (cm)	Mean width (m)	Length (m)
Rock River	A	3	14.8 (0.9)	27.6 (0.9)	5.01 (0.35)	33.4
Rock River	B	3	18.6 (1.1)	34.7 (0.9)	9.41 (0.50)	32.3
Marlboro Branch	A	3	14.2 (0.8)	23.2 (0.4)	6.67 (0.33)	22.0
Wardsboro Branch	A	1	17.9 (1.2)	28.5 (1.1)	7.18 (0.33)	42.0
Wardsboro Branch	B	1	14.6 (0.7)	25.2 (0.6)	8.02 (0.55)	28.0
Utley Brook	A	1	18.2 (1.3)	27.1 (0.8)	5.99 (0.31)	32.0
Utley Brook	B	1	10.5 (0.7)	21.2 (0.4)	8.89 (0.28)	32.0
Greendale Brook	A	3	7.9 (0.4)	14.6 (0.2)	6.01 (0.44)	45.0

stockings of unfed fry during April and May at target densities of 30–50–100 m⁻². Although stocking densities in individual tributaries differ, they generally result in yearling parr densities of 6–100 m⁻² (McMenemy 1995). Most juvenile salmon spend two winters in these tributaries before migrating as smolts (K.G. Whalen and D.L. Parrish, unpublished data). Several adult salmon have been observed in the West River system, but the extent of natural spawning is assumed to be minimal. Other species commonly encountered in the study streams included brook trout (*Salvelinus fontinalis*), longnose dace (*Rhinichthys cataractae*), blacknose dace (*Rhinichthys atratulus*), white sucker (*Catostomus commersoni*), and slimy sculpin (*Cottus cognatus*).

Snorkeling observations

We used snorkeling observations to quantify the number of YOY and PYOY juvenile Atlantic salmon holding position on or above the substrate during the day and night at the eight survey sites. We could not visit all sites on the same day or visit all sites the same number of times (Table 1) during the 28 August to 10 September 1995 survey period. Sampling throughout the study period was performed by two snorkelers, with each snorkeler surveying individual sites. Each site

was always sampled by the same individual to reduce observational bias (Hankin and Reeves 1988). In addition to Atlantic salmon, the number of brook trout, white sucker, slimy sculpin, and longnose dace holding position on or above the substrate was also quantified; blacknose dace were too numerous to count accurately. The survey procedure was as follows. The snorkeler entered the water downstream of the survey site and moved upstream while searching for and counting all target species holding position on or above the substrate. The survey course included both midstream and peripheral habitats. YOY and PYOY salmon were readily distinguishable based on size (YOY < 90 mm TL, PYOY > 110 mm TL; K.G. Whalen and D.L. Parrish, unpublished data), as were brook trout and white sucker. Search time was directed at enumeration, not behavioral observations. Because water depth limitations precluded our ability to search the entire wetted area of each survey site and a significant difference in time spent on snorkeling observations between day and night surveys was detected (Wilcoxon paired-sample test; mean difference ± 1 SE = 3.4 \pm 1.1 min; night > day; $p = 0.009$), we adjusted snorkeling counts relative to the time spent searching (i.e., relative count = total number of fish observed per minute spent snorkeling). To compare patterns of diel activity among YOY and PYOY Atlantic salmon and

between other species, we standardized relative count data by calculating a nocturnal index (Fraser et al. 1995):

$$\text{Nocturnal index} = 100 \times \frac{RC_n}{RC_n + RC_d}$$

where RC_n = night relative count and RC_d = day relative count.

Water temperature was recorded at the beginning of each survey with a hand-held thermometer. Only trace precipitation (<1 cm) occurred during the study period. Underwater visibility was a minimum of 3 m on each sampling occasion, with vision being more commonly obstructed by underwater structure than water clarity. All sampling was performed during relatively cloudless days and nights. All surveys were completed between 13:30 and 00:30. Night surveys were performed with the aid of an underwater hand-held white light. We minimized fish displacement by directing the light beam at the underside of the water surface (Contor and Griffith 1995). During the survey period, sunrise occurred between 05:08 and 05:23 and sunset occurred between 18:11 and 18:34. Darkness generally occurred approximately 45 min after sunset (i.e., 19:00). Day and night observations at each survey site were paired; both observations were completed during the same 24-h period. The total underwater search time for the survey period was 12.9 h (day = 6.0 h and night = 6.9 h).

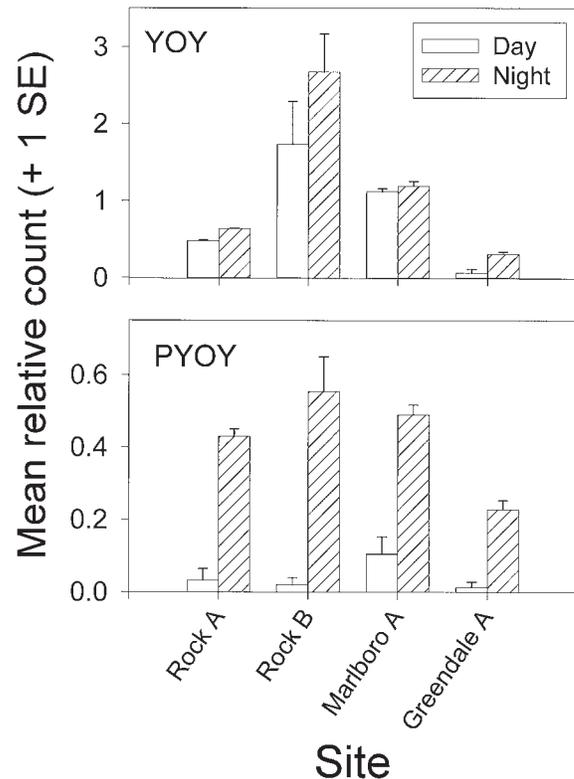
Statistical analyses

Two approaches were used in the analysis of the salmon data: (i) day and night comparisons, for which we defined discrete time periods of 13:00–17:00 for day and 20:15–23:30 for night, and (ii) hour of the day analysis, for which we treated the hour of the day the sample was taken as a continuous measure that encompassed the entire range of times (13:30–00:30) when surveys were completed. Using these two approaches allowed us to compare day and night relative counts and also to examine how relative counts changed over time. Data from all eight survey sites were included in the hour of the day analysis, while data from the four survey sites visited on three occasions were used for day and night comparisons (Table 1).

To compare day and night relative counts of YOY and PYOY juvenile Atlantic salmon, we used a three-factor repeated measures analysis of variance (ANOVA; Cody and Smith 1991). The ANOVA was blocked by survey site with repeated measures on both phase (day, night) and sample date (early, middle, late). This approach enabled us to account for variation associated with the survey site, which was significant, yet maintain pairing in the day and night samples as well as balance in the design. A logarithmic transformation ($\ln(x+1)$) was applied to the YOY and PYOY salmon relative count data to meet the assumptions of the repeated measures ANOVA (Neter et al. 1990). Statistical tests reported for the YOY and PYOY salmon relative count data are from transformed data, but means and cumulative percentages reported in the text and figures are pretransformed. To compare the nocturnal index of YOY and PYOY salmon, we used the same approach and design as above but with stage (YOY, PYOY) replacing phase in the analysis. As before, only the nocturnal index values calculated from relative count data collected from 13:30 to 17:00 and from 20:15 to 23:30 were used in the analysis. We evaluated the influence of daytime water temperature on nocturnal activity by plotting the nocturnal index of YOY and PYOY salmon and daytime water temperature. Nocturnal index values for this relationship were calculated using relative count measures from the discrete periods of the day and night.

For hour of the day comparisons between YOY and PYOY salmon, we computed a weighted hourly relative count index based on the division of the total count of salmon, either YOY or PYOY, by the total time spent searching over all sites in the respective hour of the day. Sampling was conducted during every hour of the day between 13:30 and 00:30 except 16:00 (± 0.5 h). We then calculated a cumulative relative count measure to facilitate comparisons in the diel relative count pattern between YOY and PYOY salmon. All statistical

Fig. 2. Day and night mean relative counts of YOY and PYOY juvenile Atlantic salmon at survey sites visited on three occasions.



tests were performed using SAS (SAS 1988). Significance of tests was determined at the 0.05 α level.

Results

During the survey period, 212 juvenile Atlantic salmon were observed during the day and 534 were observed at night. Marginal differences in relative counts between day and night were found for YOY salmon ($p = 0.08$) and large differences for PYOY salmon ($p = 0.007$) at water temperatures ranging from 13 to 23°C. Relative counts at all sites were greater at night for both YOY and PYOY salmon (mean difference ± 1 SE: YOY = 0.35 ± 0.12 , PYOY = 0.38 ± 0.04 ; Fig. 2).

From 13:00 to 19:00, YOY salmon were much more abundant than PYOY salmon, which was followed by a threshold-like increase in cumulative relative counts for both YOY and PYOY salmon as darkness progressed (>19:00; Fig. 3).

The nocturnal index of PYOY salmon was consistently larger than that for YOY salmon at all sites ($p = 0.021$; mean difference ± 1 SE: $28 \pm 4\%$; Fig. 4). PYOY salmon were almost exclusively nocturnal, while YOY salmon became increasingly nocturnal at lower daytime water temperatures (Fig. 5). Thus, as daytime water temperature decreased, so did the disparity between the nocturnal index of YOY and PYOY salmon.

All other species observed were active both diurnally and nocturnally. Data for these species were collected between 13:30 and 00:30 (± 0.5 h), with 19:00 as the demarcation between day and night. The nocturnal index, pooled over all survey sites, was 61% for slimy sculpin ($n = 59$), 80% for longnose dace ($n = 91$), 52% for white sucker ($n = 43$), and

Fig. 3. Cumulative percent of relative counts of YOY and PYOY juvenile Atlantic salmon by hour of the day sampled using relative count data pooled over all survey sites. No observations were made at 16:00 (± 0.5 h). Darkness occurred after 19:00.

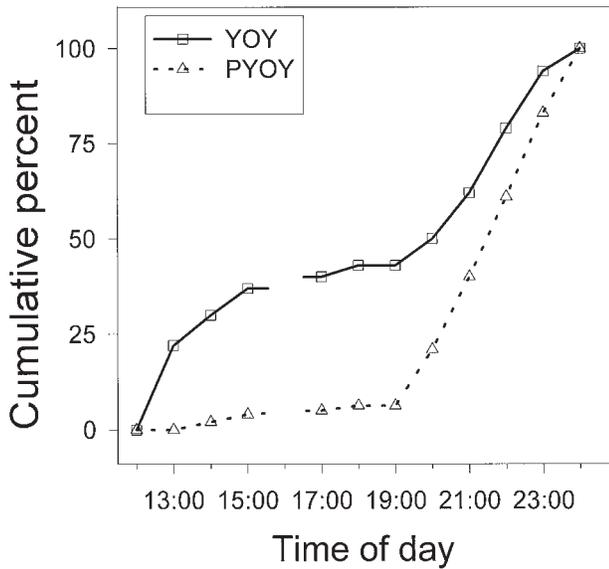
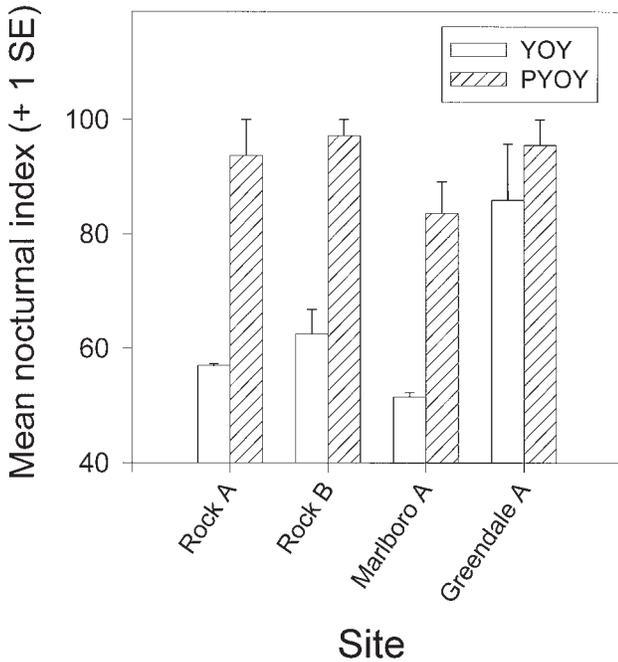


Fig. 4. Mean nocturnal index of YOY and PYOY juvenile Atlantic salmon at survey sites visited on three occasions.

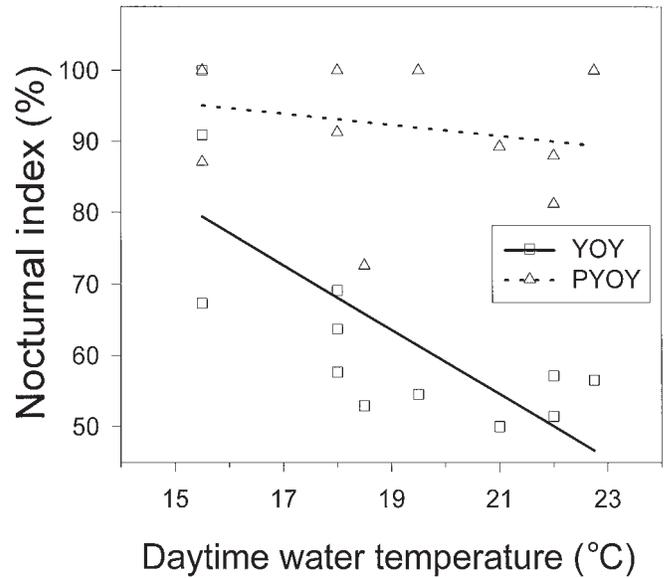


84% for brook trout ($n = 14$). YOY white sucker and brook trout were observed during both day and night, yet PYOY white sucker and brook trout were only seen at night.

Discussion

We observed differences in the relative counts of YOY and PYOY juvenile Atlantic salmon between day and night during underwater surveys at water temperatures ranging from 13 to

Fig. 5. Relationship between daytime water temperature and the nocturnal index of YOY and PYOY juvenile Atlantic salmon. Regression lines are drawn to help present general trends. $n = 12$ for both YOY and PYOY salmon.



23°C, which extends observations above the maximum of 8.4°C previously assessed in the natural environment (Fraser et al. 1995). Our results indicate that YOY salmon daytime relative count continuously decreases with declining daytime water temperatures without an apparent threshold effect. Moreover, the diel relative counts of YOY and PYOY salmon were skewed towards nocturnal activity at water temperatures where Fraser et al. (1995) observed equal daytime activity. This suggests that within certain seasonal periods and water temperature ranges, other factors in addition to water temperature may interact to determine diel patterns of activity.

Differences in the pattern of the nocturnal index of YOY and PYOY salmon were found, with PYOY salmon exhibiting almost exclusive nocturnal activity during the survey period. Unlike YOY salmon, most male PYOY salmon in our system in late summer mature in the fall, undergo a parr-smolt transformation in the spring, or both (K.G. Whalen and D.L. Parrish, unpublished data). Because differences in life stage influence other behaviors of juvenile Atlantic salmon in the fall (e.g., feeding; Huntingford et al. 1988; Metcalfe et al. 1988), it is not surprising that the diel activity of YOY and PYOY salmon differed. In addition to juvenile Atlantic salmon, we observed differences in the day and night relative counts of YOY and PYOY brook trout and white sucker. For each of these species, PYOY were observed almost exclusively at night, while YOY were observed during both day and night. We term this allocation of a fish's activity to either the day or night as diel activity partitioning (DAP). The similar pattern of DAP we observed for these three species indicates that this phenomenon is not exclusively an anadromous life history feature and may be unrelated to salmon life history.

Nocturnal activity has been associated with predation risk in both temperate freshwater stream (Culp 1989) and lake (Emery 1973; Helfman 1981; Hanych et al. 1983) fish. DAP where larger individuals are primarily nocturnal has been

observed in temperate freshwater lake fish (Helfman 1981; Magnan and FitzGerald 1984), where it has been suggested to be related to the greater predation risk for larger individuals during the day (Cerri 1983). Similarly, under increasing predation risk, larger baetid mayflies become increasingly nocturnal (Allan 1978; Culp and Scrimgeour 1993). Because diel activity patterns are influenced by water temperature (this study; Fraser et al. 1993, 1995) and potentially affected by seasonal and diel patterns of food availability and feeding motivation (Allen 1940; Wankowski 1981; Metcalfe et al. 1986, 1988; Adams et al. 1988), predation risk must be considered within a larger context of factors that may affect diel activity. Predation risk as the cause of nocturnal activity will therefore require further evaluation and careful consideration of potentially important interacting factors.

Hypotheses for why juvenile Atlantic salmon evolved certain patterns of diel activity are limited by the range of data from which they are formulated. For juvenile Atlantic salmon, daytime selection of substrate shelters in autumn (Rimmer et al. 1983) and winter (Cunjak 1988) has been suggested to be a response to a reduction in swimming performance at low water temperatures (Rimmer et al. 1985). The nighttime emergence of juvenile salmon at low water temperatures to feed (Fraser et al. 1993) was hypothesized to be a behavioral response to increased daytime predation risk because of temperature-induced energetic constraints, as well as to nightly patterns of ice formation (Heggenes et al. 1993). Our findings of nocturnal activity at high water temperatures, in conjunction with concordant results from the laboratory (Fraser et al. 1995), indicate that nocturnal activity is not exclusively a winter behavior and occurs when these fish are likely not energetically constrained or affected by ice formation.

Our study was limited to a short seasonal period and results should be interpreted within the context of a potential late summer, low flow, high water temperature interaction. Further analysis of juvenile Atlantic salmon diel activity patterns over a broader seasonal period and diversity of stream habitats would be prudent. Because we found nocturnal activity to represent a significant component of the diel activity pattern of juvenile Atlantic salmon, nighttime behavior should be considered in studies of competition, habitat use, self-thinning, time budgets, and associated bioenergetic processes.

Juvenile Atlantic salmon share the riverine environment with fish known to exhibit nocturnal behavior in summer (Cerri 1983; Fraser and Emmons 1984; Reeb et al. 1995) and we found nocturnal activity to be a community-wide phenomenon for the assemblage of stream fish we analyzed. We also observed trends in day and night activity similar to those reported in other regions of North America for longnose dace (Culp 1989) and white sucker (Campbell 1971; Emery 1973; Reeb et al. 1995). That nocturnal activity is both commonly exhibited and broadly distributed suggests that it is important to stream fish communities and therefore should be addressed at a community level. Understanding the evolution and importance of nocturnal activity in juvenile Atlantic salmon will probably be enhanced by assessing nocturnal behavior in other geographical areas and by continuing to address salmon behavior within the context of the entire fish community.

Diel abundance patterns may be critical to population regulation in stream salmonids (Fraser et al. 1995). Population density of stream salmonids is thought to be limited by territory

size (Chapman 1966; Allen 1969; Grant and Kramer 1990) where territories are defended from intruders by agonistic behaviors (Kalleberg 1958; Keenleyside and Yamamoto 1962; Hartman 1965). We noted, however, that juvenile salmon at night seemed docile and tolerant of neighboring conspecifics, as has been observed under winter conditions for Atlantic salmon in the laboratory (Fraser et al. 1993) and for the closely related brown trout (*Salmo trutta*) in the wild (Heggenes et al. 1993). Because juvenile salmon appear tolerant of conspecifics at night, far higher densities may be maintained through nocturnal activity than would be possible with strict diurnal activity. Thus, nocturnal activity may be a response that enables these fish to maintain population densities during a period of the year when space and suitable feeding areas are limited. In this regard, the observed DAP among YOY and PYOY salmon may also prove to be advantageous by enabling YOY salmon access to resources and feeding opportunities that may otherwise be suppressed in the presence of PYOY salmon.

The consistency in night relative counts of PYOY Atlantic salmon that we observed may have practical applicability for management purposes because of the importance of indexing in their population assessment (Crozier and Kennedy 1995). Cunjak et al. (1988) assessed the reliability of underwater observations to estimate juvenile Atlantic salmon abundance by completing daytime (08:30–15:00) snorkeling and electrofishing surveys in late summer at high water temperatures (15–20°C). Generally poor agreement was found between visual and electrofishing estimates of juvenile salmon abundance (Cunjak et al. 1988). This difference was attributed to the habitat preference of young salmon and to the heterogeneity of surveyed habitats. Based on our results, the disparity that Cunjak et al. (1988) observed may also have been related to late summer patterns of nocturnal activity. Our data suggest that visual estimation via night snorkeling may be a useful technique for estimating the abundance of juvenile Atlantic salmon, especially in areas that are difficult to sample using a traditional method such as electrofishing or when minimal fish disturbance is a goal.

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