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Diel activity patterns of juvenile Atlantic salmon in rivers with summer water temperature near the temperature-dependent suppression of diurnal activity

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Direct day and night underwater observations of juvenile Atlantic salmon *Salmo salar* during summer and autumn showed a duality in response to temperature between 7 and 11° C for young-of-the-year (YOY) Atlantic salmon. They were predominantly diurnal in early summer and nocturnal in late summer although water temperatures were similar. Post-YOY Atlantic salmon did not show a strong response to temperature as they were mostly nocturnal during the study period. It is suggested that the difference in activity patterns between YOY and post-YOY Atlantic salmon can be explained by size-dependent trade-off between growth and predation risk.

Key words: diel patterns; nocturnal activity; *Salmo salar*.

INTRODUCTION

Juvenile Atlantic salmon *Salmo salar* L., as well as other juvenile salmonids, display complex diel activity patterns. Unlike most animals, they cannot be considered as being entirely diurnal, nocturnal or crepuscular. During summer, juvenile Atlantic salmon are active and they feed during the day but also during hours of darkness (Higgins & Talbot, 1985; Fraser *et al.*, 1993; Gries *et al.*, 1997; Valdimarsson *et al.*, 1997; Amundsen *et al.*, 1999, 2000). During autumn and winter, they suppress their daytime activity when water temperature drops below a threshold of 8–12° C. They then conceal themselves within streambed interstices during the day (Rimmer *et al.*, 1983; Cunjak, 1988; Heggenes & Saltveit, 1990) and emerge only at dusk to feed (Fraser *et al.*, 1993, 1995; Valdimarsson & Metcalfe, 1999). Because juvenile Atlantic salmon are visual foragers, such exclusive nocturnal activity is unexpected due to the reduced feeding efficiency at night-time light intensities (Fraser & Metcalfe, 1997; Valdimarsson & Metcalfe, 1998).

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It has been suggested that juvenile Atlantic salmon become predominantly nocturnal in order to minimize predation risk (Fraser *et al*., 1993; Valdimarsson & Metcalfe, 1998). Since position holding performance, and thus escape reaction, drops sharply in cold water (Rimmer *et al*., 1985), juvenile Atlantic salmon become very vulnerable to predation by warm-blooded predators such as piscivorous birds and mustelids (Contor & Griffith, 1995; Fraser *et al*., 1995; Valdimarsson & Metcalfe, 1998). Because avian predators are only active by day, it has been proposed that it may be adaptive for fish to hide during the day when predation risk is highest (Fraser *et al*., 1993). Thus, low feeding efficiency at night is possibly offset by reduced predation risk and by increased food availability (Fraser *et al*., 1993, 1995; Rader, 1997; Valdimarsson & Metcalfe, 1998). Furthermore, maximum food intake rates decrease at low water temperature due to slower metabolic and digestion rates (Brett & Groves, 1979; Higgins & Talbot, 1985), making a reduction of feeding efficiency less costly in winter (Fraser *et al*., 1993). An alternative explanation for this nocturnal activity is that juvenile Atlantic salmon may move out of streambed refuges to avoid being trapped by ice, since decreasing water temperature at night often induces very dynamic ice conditions (Heggenes *et al*., 1993). This explanation, however, cannot account for the adoption of a nocturnal activity pattern in environments where ice rarely forms, such as in U.K. rivers (Metcalfe *et al*., 1999).

Previous observations of diel activity patterns of juvenile Atlantic salmon in the wild were completed either in glacial rivers at water temperatures $<8{\cdot}4^\circ$ C from spring to autumn (Fraser *et al*., 1995) or in temperate streams during late summer at temperatures $>13^\circ$ C (Gries *et al*., 1997). Yet, it is not known which activity pattern is adopted by wild juvenile Atlantic salmon when faced with summer water temperature between 8 and 12° C. Such information is important for the understanding of feeding rhythms and growth opportunities of juvenile Atlantic salmon. Thus, the objective of this study was to examine the diel activity patterns of juvenile Atlantic salmon in rivers with summer water temperatures within the 8–12° C range. It also aimed to assess whether, in such environment, young-of-the-year (YOY, age 0 year juveniles) and post-YOY Atlantic salmon (age 1 year or older juveniles) display similar activity patterns through the growth season and the summer-autumn transition.

MATERIALS AND METHODS

STUDY AREA

The study was conducted on the Petite Cascapédia River (48°12′ N; 65°50′ W) and on the Bonaventure River (48°02′ N; 65°28′ W), located on the Gaspé Peninsula, Québec, Canada (Fig. 1). The Petite Cascapédia River drains an area of 1463 km^2 and has a mean annual discharge of $33{\cdot}2\ m^3\ s^{-1}$ [Water survey of Canada (National Water Data Archive, Government of Canada) gauge 010902, 1996–2002]. The river is organized into an east and a west branch merging to form a main stem of 35 km. The Bonaventure River has a catchment area of 2391 km^2 and a mean annual discharge of $39{\cdot}9\ m^3\ s^{-1}$ (Water survey of Canada gauge 010802, 1996–2002). Many tributaries supply the river, among which the West Bonaventure River is the most important one. Water temperature in these two rivers is largely influenced by important groundwater contributions. As a result, summer water temperatures are generally cool, with mean monthly water temperature ranging

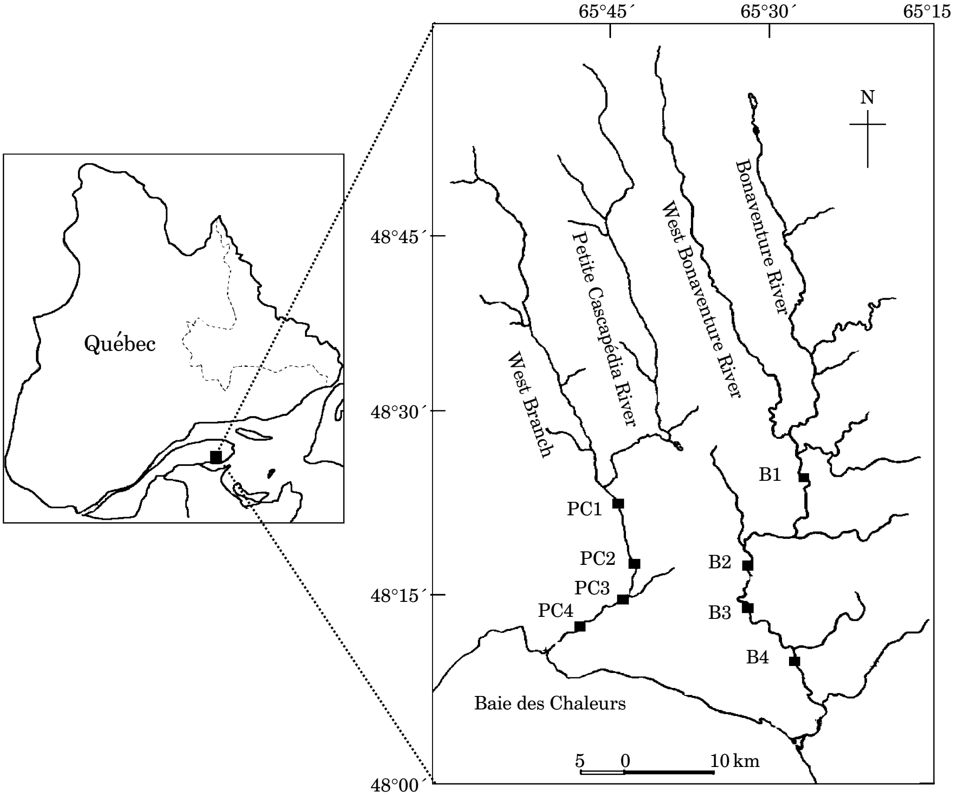

FIG. 1. Location of study sites on the Petite Cascapédia (PC1–PC4) and Bonaventure Rivers (B1–B4), in the province of Québec, Canada.

from 7·6 to 11·0° C from June to September on both rivers, depending on the position within the drainage basin.

Fish species composition is roughly the same for both rivers: Atlantic salmon, brook trout *Salvelinus fontinalis* (Mitchill), blacknose dace *Rhinichtys atratulus* (Hermann), shiners *Notropis* sp., three-spined stickleback *Gasterosteus aculeatus* L., longnose sucker *Catostomus catostomus* (Forster), white sucker *Catostomus commersoni* (Lacépède) and American eel *Anguilla rostrata* (LeSueur). Slimy sculpin *Cottus cognatus* Richardson is very abundant in the Petite Cascapédia River but completely absent in the Bonaventure River. Longnose dace *Rhinichtys cataractae* (Valenciennes) were found only in the Bonaventure. Avian and mammalian predators of juvenile Atlantic salmon present on both rivers are the common merganser *Mergus merganser* L., the belted kingfisher *Ceryle alcyon* L., the great blue heron *Ardea herodias* L., the mink *Mustela vison* L. and the river otter *Lutra canadensis* (Schreber).

SNORKELLING OBSERVATIONS

Direct day and night underwater observations of juvenile Atlantic salmon were used to determine the temporal and spatial variation of activity patterns during summer and autumn 2001. Four study sites were selected on both rivers in order to reflect longitudinal variations of water temperature along the main stem of each river (Fig. 1). Distance between sites was *c.* 7 and 14 km on the Petite Cascapédia and Bonaventure Rivers respectively. At each site, two survey sections covering an area of 500 m^2 each (width: 5 m, length: 100 m) were chosen along the right (R) and left (L) bank of the channel. The sections were located along the river margins because previous snorkelling observations on the Petite Cascapédia River showed that 98·1% ($n = 160$) of juvenile Atlantic salmon were found within a distance of 5 m from the banks during the night and that during the day very few fish were seen throughout the channel (N.E. Bergeron, unpubl. data).

Physical characteristics of the sections were determined in September 2000 at discharges similar to those observed during the study period in summer–autumn 2001 (7–11 $m^3 s^{-1}$) (Water survey of Canada gauge 010802 and 010902, 1996–2002). Water depth, water velocity and substratum size were quantified at 2 m intervals along transects spaced every 10 m. Water velocities were visually assessed by trained operators and classified as being $<10 cm s^{-1}$, between 10 and $40 cm s^{-1}$ or $>40 cm s^{-1}$. Size of the median stone (median axis) found in an area of $1 m^2$ centred on each measurement location was also estimated by eye according to the technique described by Latulippe *et al.* (2001). Mean substratum diameter of the sections was generally comprised of the pebble-cobble grain size classes (4·0 to 10·0 cm) except for site B3-L (Fig. 1) where particle size was in the cobble-boulder classes (>12·8 cm) (Table I). Mean water velocity was generally $<40 cm s^{-1}$ with the exception of sections PC1-L and PC2-R where it was higher (Table I). Mean water depth varied from 16 to 74 cm and maximum water depth was between 34 and 132 cm. Thermographs continuously monitored water temperatures at the upstream and downstream sites of both rivers during the entire study period. Water temperatures of the other sites (PC2, PC3, B2 and B3) were calculated from significant relationships obtained between temperatures measured with a hand-held thermometer at those sites on several occasions during the study period and temperatures recorded by the closest thermograph. For all sites, water temperature was also measured by hand at each snorkelling survey.

TABLE I. Physical characteristics of the study sites on the Petite Cascapédia and Bonaventure Rivers (see Fig. 1) as measured in September 2000

Site and section	Maximum water depth (cm)	Mean water depth (cm)	Mean width (m)[a]	Mean substratum diameter (cm)[b]	Water velocity classes[c]	Distance to river mouth (km)
PC1 R	43	21	34	7·5	1	34
L	83	44		7·5	2–3	
PC2 R	68	42	30	8·0	2–3	25
L	87	43		7·5	2	
PC3 R	42	27	20	9·0	1	18
L	42	26		5·0	1–2	
PC4 R	98	74	20	6·0	2	12·5
L	50	31		4·0	1	
B1 R	68	30	36	8·0	1	56
L	51	40		10·0	2	
B2 R	63	25	85	6·0	1–2	44
L	40	27		7·0	1	
B3 R	34	16	36	9·0	1	37
L	132	47		>12·8	1	
B4 R	NA	NA	32	8·5	NA	15
L	NA	NA		NA	NA	

[a]Mean wetted width of the river at this site.
[b]Visual estimation.
[c]Visual estimation of mean water velocity, categorized in three classes: 1) $<10 cm s^{-1}$, 2) 10 to $40 cm s^{-1}$ and 3) $>40 cm s^{-1}$.
NA, not available.

Snorkelling surveys were conducted at 3 to 4 week intervals from June to October 2001 (26–29 June, 19–22 July, 27–30 August, 24–27 September and 26–29 October) in order to encompass most of the growth season as well as the summer to autumn transition. At each site, data were collected as paired day-night observations completed within a 12 h period. Daytime snorkelling observations were made between 1000 and 1500 hours and night-time observations were made between 2200 and 0300 hours. A diving light was used at night-time. The light beam was directed to the underside of the water surface to reduce displacement of fish (Contor & Griffith, 1995). Two snorkellers performed the observations, with each section of a site being surveyed by the same person throughout the entire study period to reduce observational bias (Hankin & Reeves, 1988). Divers entered the water downstream of their sections and moved upstream to minimize fish disturbance. To avoid counting the same individual twice, snorkellers displaced fish slightly downstream by hand as they continued their upstream survey. Juvenile Atlantic salmon holding position on or above the substratum were enumerated and YOY were distinguished from post-YOY Atlantic salmon based on a visual estimation of their length. Juveniles <65 mm in total length (L_T) were considered as YOY while those ≥ 65 mm were classified as post-YOY, according to Boudreau & Bourdages (2000) and Bourdages & Boudreau (2001). Underwater visibility was at all times >8 m in both rivers.

DATA ANALYSIS

The extent to which juvenile Atlantic salmon were nocturnal was expressed in terms of a nocturnal index (I_N), $I_N = 100E_n(E_n + E_d)^{-1}$, where E_n and E_d are the number of fish observed at night and day, respectively (Fraser *et al.*, 1993). An I_N of 100% indicates complete nocturnal behaviour. Separate nocturnal indices were calculated for YOY and post-YOY Atlantic salmon. These indices were calculated at every site for each snorkelling survey. A Wilcoxon matched pairs test was used to test the null hypothesis that the proportion of fish holding position on or above the substratum at night was the same for YOY and post-YOY Atlantic salmon for each monthly sampling survey, with YOY and post-YOY Atlantic salmon of the same site being paired together. Kruskal–Wallis ANOVA by ranks was employed to compare the proportion of fish holding position on or above the substratum at night between months for YOY and post-YOY Atlantic salmon. For this analysis, the nocturnal index of all sites were pooled together for a given month since the overall result was of greater interest than the comparison between sites. Spearman's rank correlation (r_S) was used to test for the presence of a relationship between I_N and water temperature. Statistical analyses were performed using STATISTICA (StatSoft, 1997).

RESULTS

WATER TEMPERATURE

During the sampling period between 26 June and 29 October 2001, mean daily water temperature ranged from 0·5 to 15° C (Fig. 2). The majority of snorkelling surveys were performed at temperatures between 8 and 12° C. Temporal variation of water temperature was comparable on both rivers although the Petite Cascapédia River was generally cooler than the Bonaventure River, especially during summer (Fig. 2).

SNORKELLING COUNTS

During the 105 h of underwater searching of this study, a total of 1393 juvenile Atlantic salmon (934 YOY and 459 post-YOY) were observed during the day while 4967 individuals were observed at night (359 YOY and

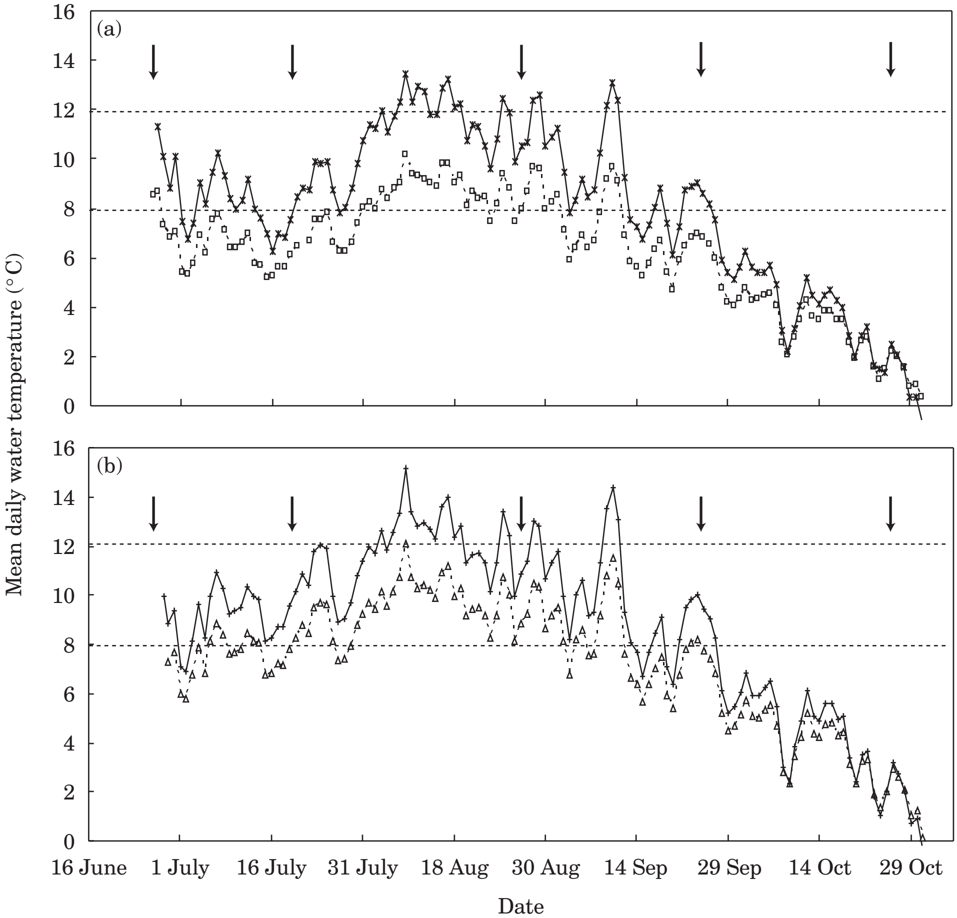

FIG. 2. Mean daily water temperature at the upstream and downstream study sites of both rivers from 26 June to 31 October 2001. (a) Sites PC1 (□) and PC4 (×) of the Petite Cascapédia River and (b) sites B1 (△) and B4 (+) of the Bonaventure River. ↓, snorkelling surveys; ----, the 8 to 12° C interval.

4608 post-YOY). Day and night inspections of the central part of the channel not covered by the surveyed sections confirmed that most of the observed fish in the sites were located in the study sections. On the Petite Cascapédia River, the total number of observations of YOY Atlantic salmon were low (one to 75 individuals per site per survey) and generally decreased throughout the study period [Fig. 3(a)]. On the Bonaventure River, the number of YOY observations was larger (one to 159 individuals per site per survey), and fairly constant throughout summer except for a peak in August [Fig. 3(c)]. Between August and October, snorkelling observations of YOY Atlantic salmon decreased steadily. For post-YOY Atlantic salmon, the total number of observations on the Petite Cascapédia River generally decreased from June to October and varied from zero to 154 individuals per site per survey [Fig. 3(b)]. On the Bonaventure River, the total number of observations of post-YOY Atlantic salmon was relatively constant during summer despite a large variation around the median

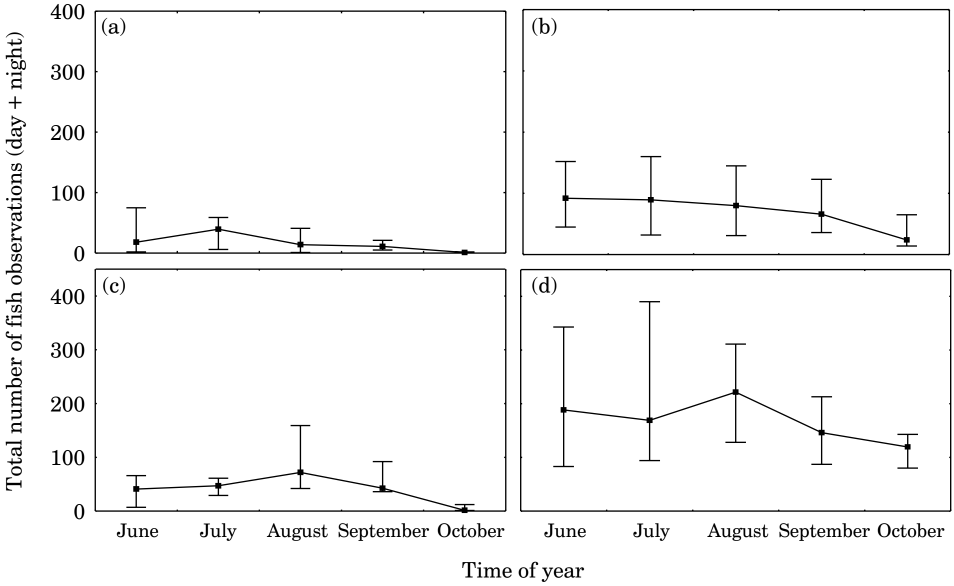

FIG. 3. Total number of fish observations (day + night) (median, minimum and maximum) of (a) young-of-the-year (YOY) and (b) post-YOY Atlantic salmon of the Petite Cascapédia River, (c) YOY and (d) post-YOY Atlantic salmon of the Bonaventure River observed at each snorkelling survey.

value for the months of June and July and a slight peak in August [Fig. 3(d)]. This relative stability was followed by a steady decrease until October. The total number of observations of post-YOY on this river was considerable, from 80 to 284 individuals per site per survey. On both rivers, the total number of observations of YOY and post-YOY Atlantic salmon showed a steady increase in the downstream direction, the maximum number of observations being always at the downstream site and the lowest number being at the upstream site. Furthermore, total numbers of YOY observed were constantly lower than those of post-YOY Atlantic salmon (Fig. 3).

Analysis of I_N indicated that YOY Atlantic salmon were predominantly diurnal in early summer and became increasingly nocturnal as summer progressed, while post-YOY Atlantic salmon were almost exclusively nocturnal at all times (Fig. 4). The proportion of post-YOY Atlantic salmon out at night was consistently greater than that of YOY Atlantic salmon for all surveys (Table II). From August to October, the disparity between I_N of YOY and post-YOY Atlantic salmon decreased, as YOY fish switched to nocturnal activity but the difference was still large enough to stay significant (Table II). The transition of YOY Atlantic salmon to nocturnal activity occurred in August and September, as indicated by an increase in the values of the I_N and by an increased variation of the index [Fig. 4(a), (c)]. The effect of months in the proportion of YOY holding position on or above the substratum at night was significant (Kruskal–Wallis test, d.f. = 4, $n = 40$, $P < 0{\cdot}01$), indicating that the change in the activity pattern was significant. The I_N of post-YOY Atlantic salmon was always between 71·4 and 100%, showing that age-1 year and older juveniles were almost exclusively nocturnal throughout the study period. On the Petite

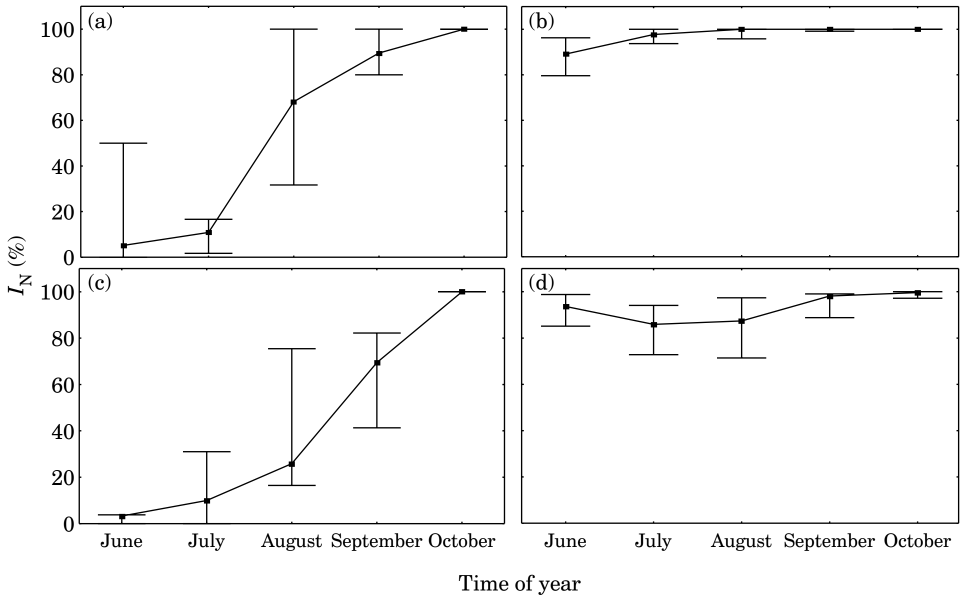

FIG. 4. Nocturnal index (I_N; median, minimum and maximum) of (a) young-of-the-year (YOY) and (b) post-YOY Atlantic salmon of the Petite Cascapédia River, (c) YOY and (d) post-YOY Atlantic salmon of the Bonaventure River for each snorkelling survey ($I_N = 100\%$ indicates nocturnal behaviour).

Cascapédia River, post-YOY Atlantic salmon were slightly less nocturnal in June than in any other month [Fig. 4(b)] while on the Bonaventure River, they were generally less nocturnal in July and August [Fig. 4(d)]. With both rivers taken together, the I_N of post-YOY Atlantic salmon increased significantly throughout the study period (Kruskal–Wallis test, d.f. = 4, $n = 40$, $P < 0{\cdot}01$).

For YOY Atlantic salmon, the switch from diurnal to nocturnal activity occurred at temperatures ranging from 7 to 11° C [Fig. 5(a)]. They were completely nocturnal at <7° C while they were predominantly diurnal at >11° C. In the 7 to 11° C temperature range, a duality in the response to temperature was observed. For similar temperatures, YOY Atlantic salmon were almost exclusively diurnal in

TABLE II. Wilcoxon matched pairs test results for testing the difference in the proportion of fish holding position above the substratum at night (expressed with the nocturnal index, I_N) for young-of-the-year (YOY) and post-YOY Atlantic salmon for each monthly sampling survey

	Median I_N		Median I_N			
Survey	YOY	Range	Post-YOY	Range	n	P
June	3·2	0·0–50·0	91·8	79·6–98·7	8	0·01
July	9·9	0·0–31·0	93·9	72·8–100·0	8	0·01
August	34·0	16·5–100·0	96·6	71·4–100·0	8	0·03
September	81·1	41·3–100·0	99·1	88·8–100·0	8	0·02
October	100·0	100·0	100·0	97·2–100·0	8	–

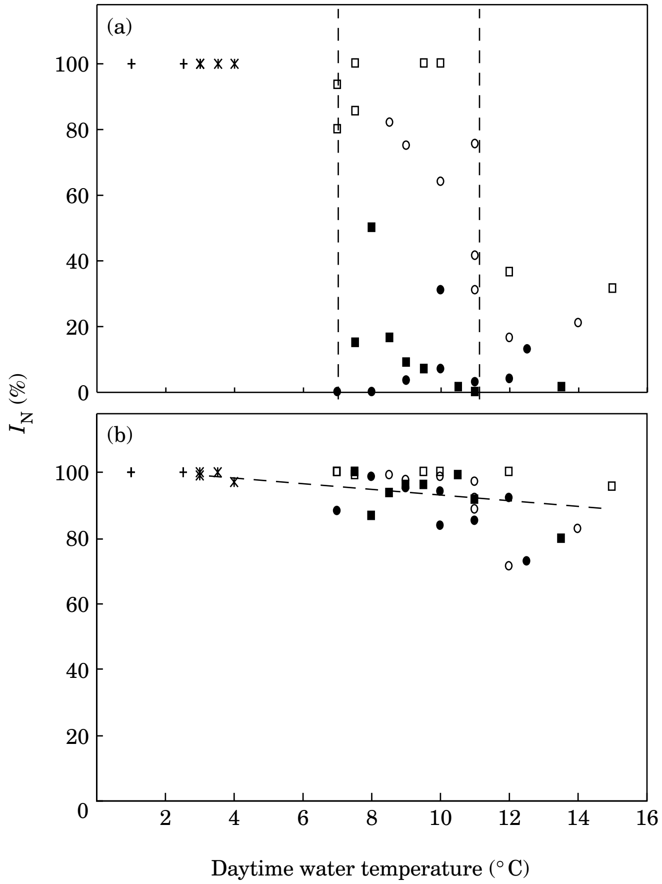

FIG. 5. The relationship between daytime water temperature and the nocturnal index of (a) young-of-the-year (YOY) and (b) post-YOY juvenile Atlantic salmon. $n = 40$ (two rivers, each with four sites surveyed five times) for both YOY and post-YOY. [Petite Cascapédia: early summer (June to July) (■), late summer (August to September) (□) and autumn (October) (+) and Bonaventure: early summer (June to July) (●), late summer (August to September) (○) and autumn (October) (×)]. The broken vertical lines in (a) indicate the 7 to 11° C interval and the broken line in (b) indicate the relationship between the nocturnal index and daytime water temperature ($y = -1{\cdot}1658x + 104{\cdot}21$).

early summer (June and July) while they became predominantly nocturnal in late summer (August and September) [Fig. 5(a)]. Post-YOY Atlantic salmon did not show a strong response to the range of water temperatures documented in this study [Fig. 5(b)]. Even though post-YOY Atlantic salmon were predominantly nocturnal, Spearman's rank correlation between the nocturnal index and water temperature was significant both for daytime ($r_s = -0{\cdot}58$, $n = 40$, $P < 0{\cdot}01$) and night-time water temperature ($r_s = -0{\cdot}49$, $n = 40$, $P < 0{\cdot}01$).

DISCUSSION

For YOY Atlantic salmon, a duality in response to water temperature was observed between 7 and 11° C, where they were predominantly diurnal in early summer and nocturnal in late summer. Below this temperature range, they were exclusively nocturnal while above this range they were mostly diurnal. In contrast, post-YOY fish were predominantly nocturnal during the entire summer and autumn period on both rivers. The observed disparity in diel activity patterns displayed by YOY and post-YOY Atlantic salmon can be viewed in terms of a trade-off between growth and predation risk. Since the scope for growth declines with increasing body size (Brett & Groves, 1979) and predation risk may be higher for larger individuals (Cerri, 1983), nocturnal feeding activity may offer an optimal trade-off for larger fish. Conversely, diurnal feeding activity may be more profitable for smaller individuals with higher metabolic rates and lower predation risk. The asset protection principle (Clark, 1994) predicts that there should be a threshold size below which small individuals should adopt a riskier diurnal strategy in order to increase their 'asset' (*i.e.* body mass) whereas individuals larger than the threshold size should adopt a nocturnal strategy to protect their accumulated 'asset' and, hence, future fitness. The results of this study agree with this principle in two ways. Firstly, for similar water temperature, YOY Atlantic salmon were diurnal in early summer while they had a small body size and they gradually switched to nocturnal activity while their body size became larger. Secondly, post-YOY Atlantic salmon (having a relatively large body size) were nocturnal at all times, suggesting that they adopted a nocturnal strategy allowing the protection of their accumulated asset. These results and their interpretation are consistent with a growing body of evidence that post-YOY Atlantic salmon display nocturnal activity under a wide range of conditions and that they are almost always nocturnal (Fraser *et al.*, 1995; Gries *et al.*, 1997; Amundsen *et al.*, 1999, 2000). Since the size of the fish seen during snorkelling observations was not measured, the results provide only an indirect support to Clark's (1994) principle.

Feeding motivation and seasonal fluctuations in nutritional state of fish may also have affected the observed diel activity patterns. In fact, feeding motivation of YOY Atlantic salmon has been shown to decline steadily from July to September regardless of temperature, food supply and competition (Metcalfe *et al.*, 1986; Metcalfe & Thorpe, 1992). The YOY Atlantic salmon might minimize the costs of obtaining a maintenance ration in late summer, whereas earlier in the summer their strategy may have been one of maximizing the net intake rate. For post-YOY Atlantic salmon, seasonal fluctuations in nutritional state of the fish might account for the fluctuations in the nocturnal index that were observed in June on both rivers and in July to August on the Bonaventure River. In early summer, fish can become hyperphagic when water temperature rises in order to restore fat lost during the winter (Higgins & Talbot, 1985; Cunjak, 1988; Bull *et al.*, 1996; Simpson *et al.*, 1996). In fact, post-YOY Atlantic salmon of both rivers may maximize feeding in June and then, while they adopted a safer feeding strategy by becoming more nocturnal on the Petite Cascapédia River, they may have adopted a different strategy on the Bonaventure River due to higher water temperatures and thus, metabolic rates.

Another interesting result is that a steady decrease in the number of observations was noticed for both YOY and post-YOY Atlantic salmon from August to October. This general decrease in snorkelling observations may indicate that some fish were sheltering during both night and day, although emigration or mortality may also partially account for the decline of fish numbers. Riehle & Griffith (1993) also monitored a similar decline in daytime and night-time relative densities for juvenile rainbow trout *Oncorhynchus mykiss* (Walbaum) at decreasing temperatures in autumn and early winter. In the present study, it was also noticed that the number of observations of both YOY and post-YOY Atlantic salmon generally increased in the downstream direction. This could be related to the gradually increasing water temperature from upstream to downstream sites. In these rivers where water temperature is rarely $>12^\circ$ C, the downstream sites with higher water temperatures may offer better conditions for growth and survival of juvenile Atlantic salmon.

In this study, the total numbers of observations of YOY Atlantic salmon were constantly lower than those of post-YOY fish, which may reflect the lower accuracy of underwater counts for YOY Atlantic salmon. In fact, YOY fish generally tended to select stations in shallow water where snorkellers had difficulty in accessing. This could lead to a constant underestimation of fish numbers (Cunjak *et al.*, 1988; Hillman *et al.*, 1992). Moreover, YOY Atlantic salmon are harder to locate than post-YOY due to their small size, especially in coarse substratum habitats (Cunjak *et al.*, 1988). It is difficult to assess to what extent the number of YOY Atlantic salmon were underestimated by snorkelling counts because most of the other usable census techniques (*i.e.* electrofishing, seining and toxicants) allow the estimation of a 'total' number of fish (sheltering + active fish) and not an estimation of the number of fish holding position in the water column. Thus, the results obtained by the snorkelling method cannot be compared with those obtained by a different method. Another explanation for the low numbers of YOY Atlantic salmon observed could be that a larger proportion of them were constantly sheltering compared to post-YOY fish, as observed previously by Gries & Juanes (1998). This hypothesis, however, cannot be confirmed, since substratum stones were not overturned to search for sheltering fish.

The traditional understanding of temperature-dependent 'summer' and 'winter' activity patterns may not apply in the wild where fishes must make a trade-off according to the relative importance of feeding, growth and predation on survival. For YOY Atlantic salmon, growth appeared to be a major concern in early summer when they adopted a diurnal activity pattern, while in late summer, they seemed to minimize predation risk by becoming almost exclusively nocturnal. This trade-off was quite different for post-YOY Atlantic salmon, since avoiding predation seemed to be of greater importance than growth at all times. While salmonids are known to defend feeding territories during the day in summer (Grant & Kramer, 1990) but not during the night in either winter or summer (Fraser *et al.*, 1993; Heggenes *et al.*, 1993; Gries *et al.*, 1997), further investigation is needed to understand implications of this behaviour on population dynamics. In the two river systems studied here, competition for feeding territories may be a major concern for YOY Atlantic salmon during their first summer, while in winter and for the remainder of their in-stream life, competition for interstitial refuges may control survival and, hence, the carrying capacity of streams (Armstrong & Griffiths, 2001). Thus, carrying capacity of those rivers may be more related to general habitat characteristics and to availability of shelters than to feeding territory size (Gries *et al.*, 1997; Armstrong & Griffiths, 2001; Bradford & Higgins, 2001).

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