Age effects on diel activity patterns of juvenile Atlantic salmon: parr are more nocturnal than young-of-the-year

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In the summer Atlantic salmon *Salmo salar* parr were predominantly active at night, while young-of-the-year were equally active during day and at night. These findings are consistent with the prediction that larger animals should be less willing to risk predation for a certain increase in size than smaller animals. © 2004 The Fisheries Society of the British Isles

Key words: diurnal; habitat use; nocturnal density; population assessment; *Salmo salar*.

Stream-dwelling juvenile salmonids have been considered to be visual sit-and-wait predators that feed mainly on drift during dawn, full daylight and dusk in the summer (Elliott, 1970). In the late autumn and winter, at water temperatures <8–10° C, juvenile salmonids shelter passively in the substratum or vegetation during the day and become more active at night (Rimmer *et al.*, 1983; Fraser *et al.*, 1993; Riehle & Griffith, 1993). More recently, the nocturnal activity of juvenile Atlantic salmon *Salmo salar* L. has been documented in the summer at high water temperatures (13–23° C), indicating that the nocturnal activity does not take place only in the winter (Gries *et al.*, 1997). A plausible explanation for this observation, as suggested for lower water temperatures (Fraser *et al.*, 1993, 1995), is that juvenile salmonids try to avoid diurnal avian predators by foraging predominantly at night.

Gries *et al.* (1997) found that both young-of-the-year (YOY) and parr of *S. salar* were more active at night than during the day. This result is unexpected because animals with higher level of accumulated fitness assets (*e.g.* larger body size) should be less willing to risk predation when foraging (asset protection principle, Clark, 1994). The mortality rate of YOY stream salmonids is very high for 1 or 2 months after emergence due to intraspecific competition for feeding territories (Elliott, 1994). Most of this mortality is thought to be due to starvation (Elliott, 1994). Also, fishes may not survive their first winter, unless

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they reach a threshold size (Smith & Griffith, 1994). Hence, to grow as quickly as possible, YOY salmonids are expected to take greater risks when foraging than older fishes. The objective of this study was to test the prediction that YOY *S. salar* are more active during the day than at night, while *S. salar* parr are predominantly nocturnal. Day and night underwater observations were conducted in a natural stream and all visible YOY and parr of *S. salar* were counted.

Sampling was conducted in three 40 m long sites selected along the main branch of Sainte-Marguerite River, a tributary of Saguenay River, Québec, Canada. The lowermost site (hereafter known as lower; $70°13'318''$ W; $48°23'206''$ N) was a riffle habitat (mean ± s.d. water depth = $0.37 ± 0.09$ m; mean ± s.d. water velocity = $0.78 ± 0.30$ m s^{-1}), characterized by a substratum composed of mostly cobble, boulder, pebble and some gravel. The middle site was a run habitat (mean ± s.d. water depth = $0.71 ± 0.20$ m; mean ± s.d. water velocity = $0.43 ± 0.13$ m s^{-1}), located 1290 m upstream from the lower site. The substratum of the middle site was predominantly composed of boulder, gravel and pebble, with some cobble and sand. The upper site, located 7170 m upstream from the lower site, was also a run habitat (mean ± s.d. water depth = $0.77 ± 0.24$ m; mean ± s.d. water velocity = $0.34 ± 0.07$ m s^{-1}). The substratum of the riverbed ranged from sand to cobble, but it was mostly composed of sand and gravel. The wetted width for all three sites ranged from 20 to 25 m.

Paired day–night underwater visual surveys were conducted between 28 July and 13 August 2002 at the three sampling sites to quantify the abundance of YOY and parr of *S. salar*. Each site was sampled on three consecutive occasions (28 July, 7 August and 11 August). These sites were not always sampled on the same day. During the last survey, daytime data for all sites were collected on 11 August. Due to unfavourable conditions, however, the corresponding night-time data were collected 2 days later.

Sampling was performed by four snorkellers, who sampled separate count strips (*c*. 5 m wide × 40 m long) at each site (four strips per site). The count strips included both nearshore and midstream areas. The snorkellers entered the river downstream from the site and counted all visible YOY and parr while slowly moving upstream. Snorkellers used a waterproof hand-held white light during night sampling. In order to minimize the potential disturbance to the fish, the light beam was directed at the water surface (Gries *et al.*, 1997). The fish did not appear to be disturbed by the light; no fish were observed to leave from, or to be attracted to, the observation area during the night surveys.

The sampling was performed between 1400 and 1815 hours during the day and between 2200 and 0130 hours at night. Water temperature and cloud cover were recorded at the beginning of sampling at each site. Each survey was completed within 1·5 h. No sampling was performed during rain. Sampling resumed when the discharge of the river and the underwater visibility returned to values prior to the rain.

The number of fish visible in each counting strip during the day and night was analysed with a three factor repeated measures ANOVA. This test was performed separately for YOY and parr of *S. salar*. Site was considered an independent variable, while time of day (day, night) and sampling date were treated as repeated measures factors. Only significant interactions were

reported. To meet the assumptions of the repeated measures ANOVA, all data were $\ln(x+1)$ transformed. As the homogeneity of variances assumption was violated for some groups, the data were also analysed using Kruskal–Wallis ANOVA (comparison between sites) and Friedman ANOVA (day–night and sampling date comparisons). The non-parametric tests confirmed the results of the parametric tests.

Over the sampling period, the number of YOY Atlantic salmon observed in the individual counting strips varied between zero to six fish ($CV = 1.87$, $n = 36$) during the day and zero to two fish ($CV = 2.03$, $n = 36$) at night. In total, 27 YOY *S. salar* were observed during the day and 12 at night. While there seemed to be more YOY *S. salar* visible during the day than at night [Fig. 1(a)], the difference between day and night counts was not significant ($F_{1,9}$, $P = 0.142$). Similarly, there were no significant differences between sites ($F_{2,9}$, $P = 0.581$), or between sampling dates ($F_{2,18}$, $P = 0.353$).

Overall, 65 *S. salar* parr were observed during the day and 140 at night. The number of parr observed in individual count strips during the sampling period ranged from zero to 15 ($CV = 1.87$, $n = 36$) during the day and from zero to 12 ($CV = 0.89$, $n = 36$) at night. There were significantly more visible *S. salar* parr at night than during the day [Fig. 1(b)] ($F_{1,9}$, $P = 0.004$). Atlantic salmon parr counts differed significantly between sites ($F_{2,9}$, $P = 0.021$) and between sampling dates ($F_{2,18}$, $P = 0.004$). There were significant differences in the pattern of day and night counts depending on sampling date (Fig. 2) (interaction term $F_{2,18}$, $P = 0.007$). There was no significant difference between the night counts obtained at the three sampling dates (repeated measures ANOVA on the night counts only, $F_{2,18}$, $P = 0.136$). The day counts, however, did vary among the three sampling dates (repeated measures ANOVA on the day counts only, $F_{2,18}$, $P < 0.001$). During the day, the number of visible *S. salar* parr was significantly higher at the third sampling date than on the first (Tukey HSD test, $P < 0.001$) or second sampling date (Tukey HSD test, $P < 0.001$) (Fig. 2).

The water temperature and cloud cover varied between 16 and $21.5°$C and 5–75% during the day and 14–$20°$C and 0–85% at night, respectively. The day or night mean site counts of YOY and parr of *S. salar* were not related to the cloud cover or water temperature measured at the time of sampling ($r = 0.03$–0.62, $P = 0.08$–0.93, $n = 9$).

Consistent with the asset protection principle ('when desperate, gamble; when well-off, play safe'; Clark, 1994), *S. salar* parr in this study were predominantly nocturnally active. While there was no significant difference between the diurnal and nocturnal counts for YOY *S. salar*, the trend toward higher diurnal counts exhibited by the data was consistent with the prediction that younger or smaller animals should accept higher predation risks in order to maximize their growth rate (Grant & Noakes, 1987; Clark, 1994). The findings of this study may not be unexpected in the light of evidence that stream salmonids show size- and age-dependent changes in their tactics that decrease the risk of encountering predators (Grant & Noakes, 1987); reactive distance, latency to forage, use of cover (Grant and Noakes, 1987) and the extent of nocturnal activity (Gries *et al.*, 1997) increase with body size or age. The findings of this study and the above evidence suggests that size- or age-dependent differences in wariness could be a general pattern for stream salmonids. In contrast to this study, Gries *et al.*
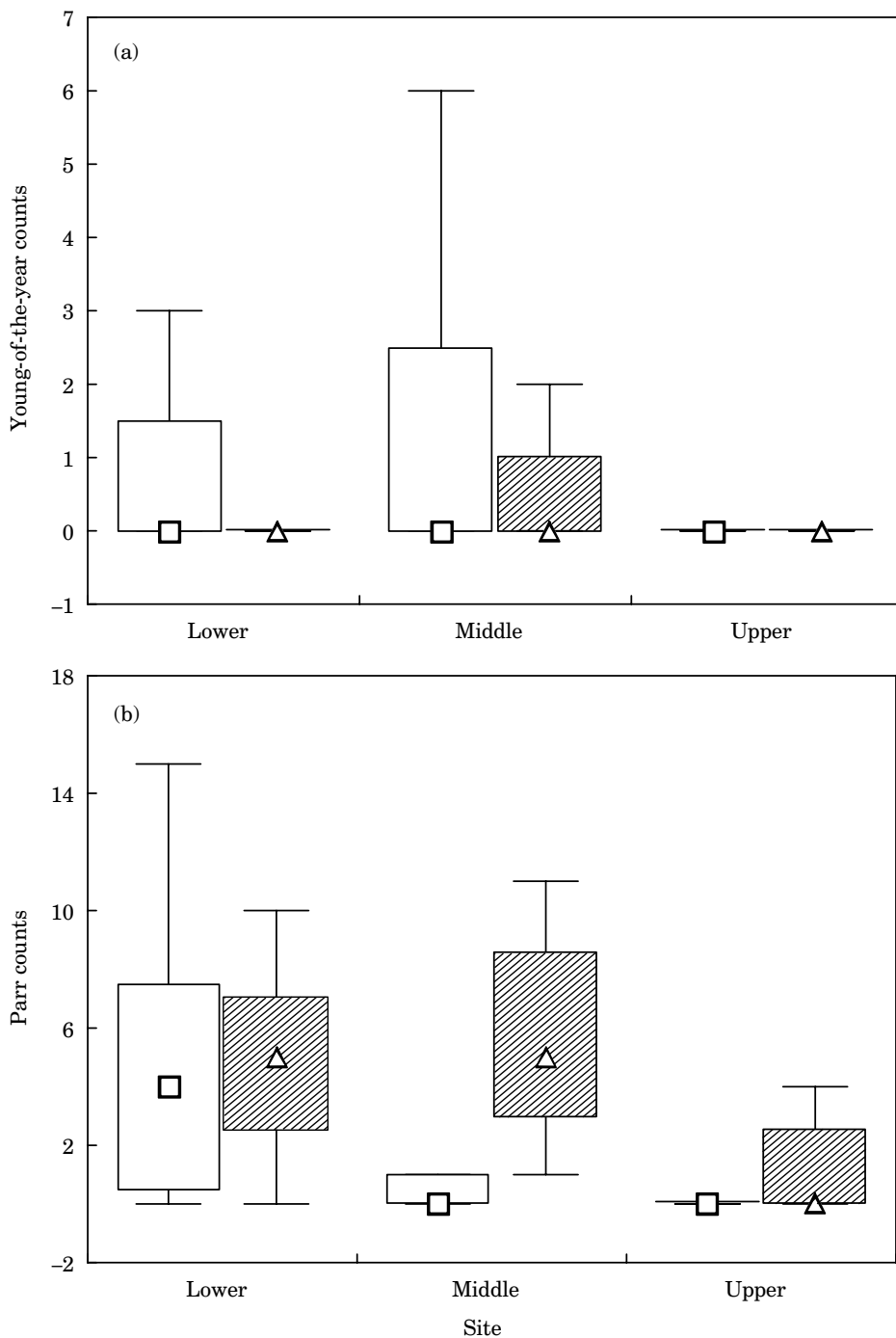
FIG. 1. Day (□, □) and night (▧, Δ) median (box: 25%, 75%; whisker: non-outlier minimum, non-outlier maximum) counts of Atlantic salmon (a) young-of-the-year and (b) parr at the three sites sampled on three occasions in the Sainte-Marguerite River. The descriptive statistics are based on non-transformed data from all counting strips at each site over the three sampling occasions ($n = 12$).
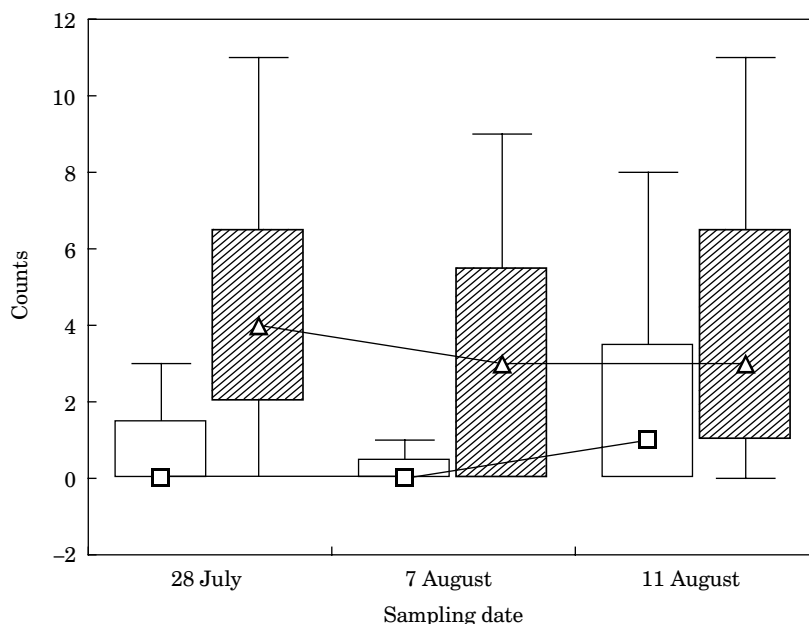
FIG. 2. Day (□, □) and night (▨, Δ) median (box: 25%, 75%; whisker: non-outlier minimum, non-outlier maximum) counts of Atlantic salmon parr sampled on three consecutive occasions in the Sainte-Marguerite River. The descriptive statistics are based on the non-transformed number of fish in the individual counting strips from all three sites sampled during a sampling occasion ($n = 12$).

(1997) recently found that the relative counts for YOY *S. salar*, similar to parr of *S. salar*, were greater at night than during the day. Both this study and their study observed juvenile *S. salar* over periods of similar length, at similar temperatures in the summer. The study of Gries *et al*. (1997), however, was conducted later in summer (28 August to 10 September), than the present study (28 July to 13 August). A plausible explanation for the differences in YOY *S. salar* diel activity patterns between the two studies is that fish become more risk averse and forage more at night as their body size ('asset') increases over the summer season. To reconcile the two studies, further study of juvenile *S. salar* diel activity patterns over summer and autumn is required. The present study also found that, in contrast with daytime sampling, the nocturnal counts of parr were not different between sampling occasions. Hence, night surveys of parr may be temporally more stable than daytime surveys.

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