The effects of abiotic factors and intraspecific versus interspecific competition on the diel activity patterns of Atlantic salmon (*Salmo salar*) fry

Simon Blanchet, Géraldine Loot, Louis Bernatchez, and Julian J. Dodson

Abstract: We conducted semi-natural experiments to measure the relative contribution of various environmental factors and intraspecific and interspecific competition with an exotic invader on the daytime and crepuscular activity levels of Atlantic salmon (*Salmo salar*) fry. We demonstrated that interspecific competition with the exotic rainbow trout (*Oncorhynchus mykiss*) significantly increases the daytime activity of Atlantic salmon. The effect of intraspecific competition on the daytime activity of salmon was half that of interspecific competition. This indicates that the effect of rainbow trout was a combination of increasing density and the identity of the competitor. We also demonstrated that the effect of rainbow trout was probably the result of territorial interference between species. Moreover, we showed that water temperature simultaneously played an important role in explaining daytime activity of Atlantic salmon. During twilight, we observed no effect of competition on salmon activity, but environmental cues other than temperature (e.g., invertebrate drift, cloud cover) became significant predictors of activity. Feeding and growth rates of Atlantic salmon were not affected by the different levels of competition. Nevertheless, the exotic species may have a major impact by exposing the native species to increased risks of daytime predation.

Résumé : Nous avons mené des expériences en milieu semi-naturel pour mesurer les contributions relatives de divers facteurs du milieu, de la compétition intraspécifique et de la compétition interspécifique avec un envahisseur exotique sur les niveaux d'activité durant le jour et le demi-jour chez des alevins de saumons atlantiques (*Salmo salar*). Nous démontrons que la compétition interspécifique avec la truite arc-en-ciel (*Oncorhynchus mykiss*) exotique augmente significativement l'activité diurne de saumon atlantique. L'effet de la compétition intraspécifique sur l'activité diurne du saumon est la moitié de celui de la compétition interspécifique. Cela indique que l'effet de la truite arc-en-ciel est dû à une combinaison d'une densité accrue et de l'identité du compétiteur. Nous démontrons aussi que l'effet de la truite arc-en-ciel est probablement le résultat d'une interférence territoriale entre les espèces. De plus, nous montrons qu'au même moment la température de l'eau permet d'expliquer une partie importante de l'activité diurne chez le saumon atlantique. Au demi-jour, nous n'observons aucun effet de la compétition sur l'activité des saumons, mais des signaux du milieu autres que la température (par ex., la dérive des invertébrés, la couverture de nuages) deviennent des variables prédictives significatives de l'activité. Les taux d'alimentation et de croissance du saumon atlantique ne sont pas affectés par les différents niveaux de compétition. Les espèces exotiques peuvent néanmoins avoir un impact important en exposant les espèces indigènes à des risques accrus de prédation durant la journée.

[Traduit par la Rédaction]

Introduction

Within a complex and dynamic environment, individual activity patterns may vary at both spatial and temporal scales (Reebs 2002; Kronfeld-Schor and Dayan 2003) to optimize the trade-off between growth and survival (Kotler et al. 1994; Biro et al. 2003; but see Railsback and Harvey 2002). For most animals, the temporal partitioning of resource acquisition seems to be largely shaped by predation risk (Flecker 1992; Kronfeld-Schor and Dayan 2003; Fraser et al. 2004). Indeed, during daytime, food is generally easier to detect but the risk of being eaten by a predator is higher (Fraser and Metcalfe 1997; Metcalfe et al. 1999; Kronfeld-Schor and Dayan 2003). However, competition has also been demonstrated to influence daily activity patterns (for a review, see Kronfeld-Schor and Dayan 2003). For instance, at the intraspecific level, Alänära et al. (2001) demonstrated in the laboratory that dominant individual brown trout (*Salmo trutta*) fed mainly at the most beneficial times of dusk and in the early part of the night; whereas subordinate fish fed at other times.

In the same way, the effect of interspecific competition on diel activity has been demonstrated (e.g., desert rodents; Ziv et al. 1993; Wasserberg et al. 2006) and has been proposed

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as an important mechanism influencing population dynamics and species coexistence (Kronfeld-Schor and Dayan 2003). In fish, only Harwood et al. (2001) has provided evidence that the competitive interactions between two species (brown trout and Atlantic salmon, *Salmo salar*) modified individual diel activity patterns. However, in most of the studies designed to evaluate the effect of interspecific competition, authors used simple additive designs that do not allow the measurement of the strength of interspecific competition relative to intraspecific competition (Connell 1983; Fausch 1998). Therefore, to gain insight into the effect of interspecific competition on the temporal activity of fish, the use of a more adequate design (i.e., combined additive and substitutive design; Fausch 1998) is needed to discriminate between the confounding effects of increasing density and the identity of competitors.

In addition, several interacting ecological forces (including both biotic and abiotic factors) may also influence individual foraging decisions. Indeed, Hansen and Closs (2005) compared daily activity patterns within the hierarchy of an endemic New Zealand fish (the giant kokopu, *Galaxias argenteus*) under different food supply conditions. Under normal food densities, dominant fish were mainly nocturnal; whereas subdominants were diurnal. In contrast, when food density was artificially limited, dominant fish increased diurnal activity while simultaneously reducing the overall activity of subdominants.

Understanding the influence of interspecific competition on diel activity patterns may be particularly relevant in the context of invasion biology. Analysis of competition between indigenous and exotic species has been considered in a spatial context (e.g., Mills et al. 2004; Morita et al. 2004; Blanchet et al. 2007*a*), but the effect of exotic species on the diel activity patterns of native species has rarely been investigated.

Thus, the main objective of the present study was to assess the relative influence of intra- versus inter-specific competition with an exotic invader, food availability, and selected abiotic factors in shaping the diel activity patterns of a native species. We also aimed to verify whether changes in the patterns of diel activity of the native species might alter its subsequent growth performance.

To address these issues, we used the salmonid model system, native Atlantic salmon (*Salmo salar*) – invasive rainbow trout (*Oncorhynchus mykiss*). Worldwide stocks of Atlantic salmon are declining, and in this context, interaction with exotic species may represent an additional risk to such weakened populations (Fausch 1998). Juvenile Atlantic salmon are territorial sit-and-wait predators living in streams and feeding on invertebrate drift (Klemetsen et al. 2003). Feeding activity generally exposes the fish to predators, and salmon are thus confronted with the competing demands of gaining energy and sheltering under a refuge for protection from predators. Several natural observations (e.g., Gries et al. 1997; Johnston et al. 2004; Breau et al. 2007) and laboratory experiments (e.g., Fraser et al. 1993; Metcalfe et al. 1999; Alanärä et al. 2001) have shown that fish daily activity patterns varied according to season and (or) water temperature. In many rivers of the eastern coast of North America, Atlantic salmon now coexists with the exotic rainbow trout (Crawford and Muir 2008). In sympatry, juveniles of both species occupy similar macro- and micro-habitats and are likely to compete for resources (Hearn and Kynard 1986; Blanchet et al. 2007*b*), but the effect of rainbow trout on the diel activity of Atlantic salmon has never been investigated.

To study the influence of competition and selected environmental variables (invertebrate drift, water temperature, cloud cover, moon phase, water depth, and water velocity) on the diel activity patterns of the native Atlantic salmon, we placed juvenile salmon in field enclosures (outdoor channels) subjected to natural environmental fluctuations and to three competitive conditions: low intraspecific competition, high intraspecific competition, and interspecific competition with the rainbow trout. We first compared the effect of intraspecific competition versus interspecific competition on the diel activity of Atlantic salmon. Then, we assessed the relative contribution of competition and other ecological forces on daytime and crepuscular activity separately to verify whether biotic and abiotic factors acted synergistically in shaping individual activity patterns. Finally, we compared the growth rate and behaviour (feeding rate and aggression rate) of Atlantic salmon among the different competitive treatments to evaluate the fitness consequences of potential change in diel activity patterns.

Materials and methods

Sampling sites

During the summers of 2005 and 2006, young-of-the-year (YOY) Atlantic salmon and rainbow trout were sampled by electrofishing in the Malbaie River (Québec, Canada; 47°67′N, 70°16′W). A self-sustaining population of rainbow trout coexists with Atlantic salmon in the lower 9 km of the river. Atlantic salmon were sampled in locations where rainbow trout are not present (i.e., above a human-controlled fish ladder) to avoid the effects of previous encounters between the two species. Atlantic salmon fry emerged from their nests earlier than rainbow trout fry and consequently maintained a size advantage until the end of their first summer of life (i.e., end of August; S. Blanchet, G. Loot, and J.J. Dodson, unpublished data). In our experiments, we selected juvenile salmon and trout of similar size to avoid confounding the effects of size and species identity (Connell 1983; see Table 1 for the size range of each species). Fish were maintained in several holding tanks (0.30 × 0.30 × 0.60 m) placed in the river for 10–15 days before the experiments began.

Experimental design

The same experiment was carried out in the summers of 2005 and 2006 to test for the temporal consistency of the results. The experiments were done in flow-through stream channels installed along the bank of the river. Experiments started on 1 August and lasted 24 days and 28 days for 2005 and 2006, respectively. Channels were constructed of 20 mm thick plywood, but their dimensions varied between years (Table 1). In 2005, they were 4.8 m long × 0.6 m wide × 0.6 m deep, and six Plexiglas windows (0.30 m × 0.30 m) were disposed along one side of each channel to allow direct underwater observations. Both the upstream and downstream ends of each channel were covered with

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Table 1. Characteristics of the two semi-natural experiments carried out in 2005 and 2006 designed to assess the effects of competition and selected abiotic factors on the diel activity of Atlantic salmon (*Salmo salar*).

	Experiments	
	2005	2006
Channel characteristics		
Channel length (m)	4.80	2.00
Water depth (cm)	11 (7–19)	17 (9–24)
Water velocity ($cm\cdot s^{-1}$)	8.34 (6.32–12.41)	17.56 (9.34–28.82)
Screen mesh size (mm)	3.00	4.50
Biological material characteristics		
Length, Atlantic salmon (mm)	42.27 (38–49)	42.76 (35–56)
Weight, Atlantic salmon (g)	0.73 (0.48–0.96)	0.74 (0.37–1.61)
Length, rainbow trout (mm)	41.65 (34–47)	41.93 (37–46)
Weight, rainbow trout (g)	0.69 (0.52–1.01)	0.70 (0.51–0.98)
Total density ($individuals\cdot m^{-2}$)	3.13, 6.26	3.33, 6.66
Environmental characteristics		
Daytime water temperature (°C)	18.5 (15.8–22.0)	18.0 (14.5–20.0)
Crepuscular water temperature (°C)	18.0 (15.0–22.0)	17.0 (14.0–19.0)
Cloud cover (%)	52 (0–100)	43 (0–100)
Discharge ($m^3\cdot s^{-1}$)	8.92 (7.31–11.48)	12.29 (8.43–18.58)
Daytime food availability*	0.73 (0.42–1.22)	1.68 (0.8–2.48)
Crepuscular food availability*	5.62 (1.83–12.45)	13.65 (2.18–35.07)

Note: Values are expressed as the mean with the range given in parentheses.

*Daytime and crepuscular food availability was expressed as number of invertebrates per minute drifting in a net.

3 mm mesh plastic screen to allow natural drift of invertebrates and prevent fish from escaping. To increase the statistical power, more channels of smaller size were used in 2006. They were 2 m long × 0.6 m wide × 0.6 m deep, and there were three Plexiglas windows (0.30 m × 0.30 m). Moreover, to ensure that the flow was as natural as possible, the mesh size of the plastic screen was increased to 4.5 mm (see Table 1). Each year, the screens were gently brushed twice a day to prevent the mesh from clogging and to limit sedimentation. The top of each channel was covered with transparent nylon monofilament (10 cm × 10 cm mesh size) to prevent predation from birds (i.e., gulls). The bottom of the channels was covered with river substratum (mainly sand, gravel, pebbles, and cobbles) to mimic the natural habitat of juvenile Atlantic salmon and rainbow trout and to allow rapid colonization of invertebrates. Water depth and water velocity were repeatedly measured in each channel. Water depth was measured at a single fixed point (directly downstream of the upstream plastic screen) in each channel (the water depth of each channel was homogeneous along its length). Water velocity was evaluated as the time needed for an inert object (a 8 cm^3 piece of wood) to cover the distance of a channel. Water depth and water velocity in the channels varied according to daily discharge and years. In 2005, depth was 11 cm on average and velocity was 8.34 $cm\cdot s^{-1}$ on average, whereas in 2006, both depth (17 cm on average) and velocity (17.56 $cm\cdot s^{-1}$ on average) were higher (Table 1). Depth and water velocity values were in the range used by Atlantic salmon and rainbow trout in the Malbaie River (Blanchet et al. 2007*b*).

Experiments consisted of three competitive treatments (combined substitutive and additive design; Connell 1983); each was replicated three times in 2005 ($n = 9$ channels) and four times in 2006 ($n = 12$ channels). In the low intraspecific competition treatment, salmon were maintained at a density of 3 $fish\cdot m^{-2}$. In the high intraspecific competition treatment, salmon density was doubled to 6 $fish\cdot m^{-2}$. Finally, in the interspecific competition treatment, equal numbers of salmon and trout were maintained in sympatry for a total density of 6 $fish\cdot m^{-2}$. A density of 3 salmon or trout $fry\cdot m^{-2}$ is commonly observed in Malbaie River (S. Blanchet, G. Loot, and J.J. Dodson, unpublished data), whereas a density of 6 $fish\cdot m^{-2}$ is observed in highly productive areas of the Malbaie River (S. Blanchet, G. Loot, and J.J. Dodson, unpublished data). A density of 6 $fish\cdot m^{-2}$ is high enough to expect interference competition, but below the maximum predicted density of 15 $fish\cdot m^{-2}$ (Grant and Kramer 1990) for fish as small as 45 mm. Space competition and aggressive interference in Atlantic salmon have already been observed at a density of 6 $fish\cdot m^{-2}$ (Blanchet et al. 2006).

The length and weight of fish used in the experiments are detailed in Table 1. The size and the weight of both Atlantic salmon and rainbow trout did not differ between years (one-way analyses of variance, ANOVAs, $p > 0.05$). Moreover, there was no difference between the size and weight of Atlantic salmon and rainbow trout used within a year (one-way ANOVAs, $p > 0.05$). In each channel, Atlantic salmon were individually marked using Visible Implant Elastomer tags (VIE; Northwest Marine Technology, Shaw Island, Washington) to evaluate and compare growth rate of salmon among treatments.

The activity observations were conducted once every 3 days, and between two and four channels per treatment were observed during each observation (i.e., 6 to 12 channels per observation). Daytime observations were performed in the morning (0900 to 1100). Activity was quantified by

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observing fish through the Plexiglas windows from the downstream to the upstream end of the channel. Each window was scanned for a 5 min period (i.e., 30 and 15 min per channel in 2005 and 2006, respectively), and the total number of active fish observed was counted. A fish was considered as active when it was observed out of the substrate for at least 30 s over the 5 min observation and when it was facing into the current, propped up on its pectoral fins. Salmon that briefly left its refuge to chase a competitor or to catch a drifting prey was not counted as active. In addition, we recorded the number and direction of aggression acts (chases, nips, and displays) and feeding events initiated by each species. Crepuscular observations were conducted during the early part of the night (2030 to 2230, a foraging period considered as being profitable for salmonids; Alanärä et al. (2001)). In Malbaie River, the time of sunset was 2017 on 1 August and 1927 on 30 August, and the nautical twilight was 2138 on 1 August and 2037 on 30 August. Thus, our crepuscular observations took place mainly during twilight. At this time, the light intensity was inferior to 0.01 lx (S. Blanchet and G. Loot, personal observation). Fish were detected, identified, and counted by briefly scanning the water surface from the downstream to the upstream end of the channels using a flashlight with a red filter to avoid disturbing the fish (Harwood et al. 2001; Reebs 2002). To ensure species identification (based on body shape, patterns of body pigmentation, and swimming behaviour of each species), counts were repeated twice by two different observers (S. Blanchet and G. Loot), and the mean of these two observations was used to quantify the number of active fish during twilight. The visibility was, however, too low to quantify rates of aggression and feeding.

To account for possible effects of fish size on growth rate, the mass-specific growth rate (Ω) (Ostrovsky 1995; Flodmark et al. 2006) was calculated for each individual using the following formula:

$$(1)\qquad \Omega = \frac{M_t^b - M_0^b}{b \cdot t}$$

where M_t and M_0 are body mass (g) at the end and start of the experiment, respectively; b is the allometric mass exponent for the relation between specific growth rate and body mass, estimated at 0.31 for Atlantic salmon (Elliott and Hurley 1997), and t is the experimental period.

For each observation, selected environmental variables were measured according to previous studies on the foraging activity of Atlantic salmon (five for daytime observations and six for crepuscular observations). First, before behavioral observations, water temperature was recorded (±0.5 °C), as it has been shown to influence diel activity patterns of Atlantic salmon (e.g., Johnston et al. 2004). The percentage of cloud cover (±5%) was also visually estimated as a surrogate of light intensity (see Girard et al. 2003). In addition, during the crepuscular observations, we evaluated the percentage of moon visible (based on calendar estimation) (see Imre and Boisclair 2005). Secondly, after behavioral observations, water depth (±1 cm) and water velocity (±1 $\text{cm}\cdot\text{s}^{-1}$) were measured to evaluate hydraulic variation in the habitat. Finally, during the behavioral observations, invertebrate drift (as a measure of food supply) was quantified at a fixed sampling point within the study section. Drift was sampled during a 30–60 min period during each activity observation using a drift net (mesh size 250 μm). We assumed that the quantity of invertebrates drifting at this sampling point was representative of the quantity of food available in each channel for a given observation session. This assumption seems realistic for two reasons. First, in 2005, two nets separated by a 200 m long transect were simultaneously used to estimate invertebrate drift. The correlation between the numbers of invertebrates drifting at the two sampling sites was strong and highly significant ($r = 0.83$, $n = 22$, $p < 0.001$). Secondly, in 2006, we found that the quantity of food drifting in seven channels monitored individually was relatively homogenous within an observation period. The variance in invertebrate drift was two times higher between sampling periods than between channels within a sampling period (the coefficients of variation were 59.01% and 33.58%, respectively; S. Blanchet, G. Loot, and J.J. Dodson, unpublished data). These two observations indicated that the drift of invertebrate was relatively spatially homogeneous and that sampling the invertebrate at single sampling site was representative of what was drifting in each channel. The mouth of the drift net was covered with 3 and 4.5 mm mesh plastic screen in 2005 and 2006, respectively, to insure that the drift net filtered the same size range of drift that was filtered at the entrance to the experimental channels in the two years. Given the gape size of Atlantic salmon and rainbow trout, all the invertebrates (mainly chironomid larvae) sampled in the drift net were potential prey for the fish. Invertebrates were preserved in 95% alcohol and counted under a binocular microscope. Food supply in each channel was expressed as the number of invertebrates caught at the fixed station per minute and per cubic metre per second by multiplying the number of invertebrates caught per minute in the drift net by the flow rate (width × depth × water velocity) of each channel.

Statistical analyses

Diel activity

Atlantic salmon activity was expressed as the number of fish active in a channel divided by the number of salmon present in this channel at the end of the experiment (mortality was low but occurred in some channels (mean = 0.24 $\text{individuals}\cdot\text{channel}^{-1}$) and was unrelated to the treatments). The proportion of active salmon was arcsin-transformed (Zar 1999) in all subsequent analyses to meet the assumptions of normality and homoscedasticity.

We first assessed the influence of year of the experiments (2005 or 2006), period of observation (daytime or twilight), and competitive treatments on the proportion of active salmon. In this analysis, the mean of each channel, for daytime and crepuscular observations, was used as the replicate unit. We used mixed linear models, which are a generalization of standard linear models; the generalization permits the data to exhibit dependency (Pinheiro and Bates 2000). Because the proportion of active fish observed during the day in a channel may be dependent on the proportion of fish active during twilight (repeated measures), channel was integrated as the random factor to deal with this potential temporal dependency (Pinheiro and Bates 2000). Year of the experi-

Table 2. Results of mixed-linear models used to evaluate the effect of the year of experiment (2005 or 2006), period of observation (daytime vs. crepuscular), and competitive treatment (low intraspecific, high intraspecific, and interspecific competition) and the resulting interactions on the proportion of active Atlantic salmon (*Salmo salar*).

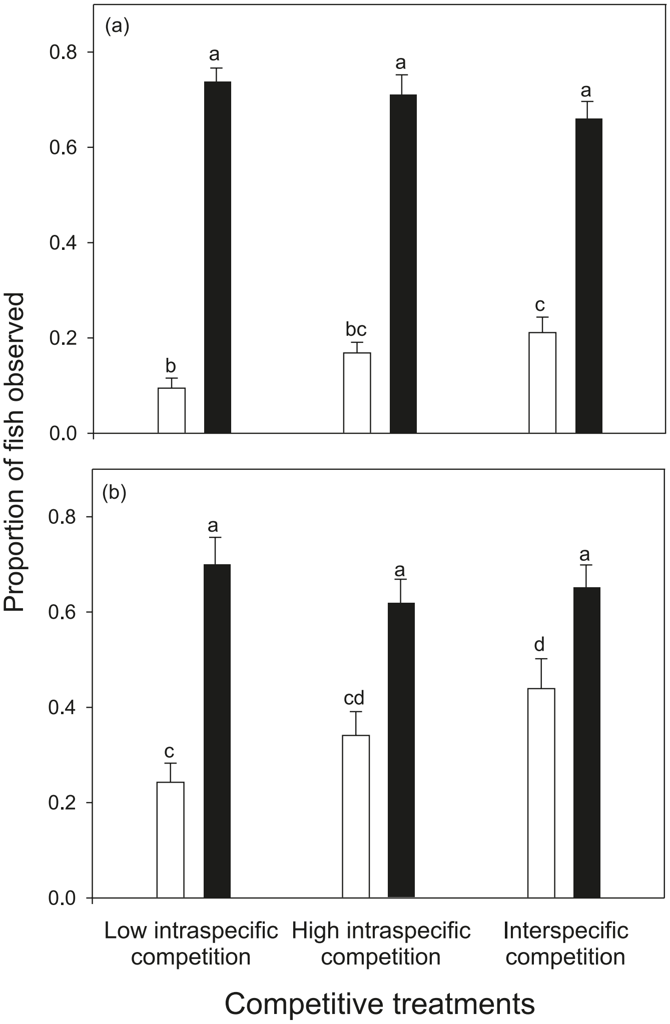
Source of variation	df	*F* value	*P* value
Year of experiment	1,19	3.76	0.067
Period of observation	1,12	124.49	**<0.001**
Competitive treatment	2,12	2.12	0.163
Year × period	1,12	13.19	**0.003**
Year × treatment	2,12	0.07	0.925
Period × treatment	2,12	4.64	**0.032**
Year × period × treatment	2,12	0.14	0.871

Note: Significant effects (p <0.05) are indicated in bold. df, degrees of freedom.

ments, period of observation, and competitive treatments were the fixed factors. Multiple comparisons were performed using contrast tests.

Secondly, we assessed the relative contribution of biotic (competitive treatments, expressed as a categorical factor) and abiotic variables (environmental factors, expressed as continuous factors). Recently, several statistical tools have been developed to evaluate the relative importance of each predictor in multiple linear regressions, particularly in the case of collinear predictors (for a review, see Grömping 2007). However, to our knowledge, no tool has been specifically published for models integrating both fixed and random factors (i.e., mixed models; U. Grömping, Department II — Mathematics, Physics and Chemistry, TFH Berlin, University of Applied Sciences, Berlin, Germany, personal communication). Here, to deal with mixed models, we used a simple technique developed online within the R project (R Development Core Team 2005). We calculated the contribution of a given predictor by comparing the percentage of variance explained by the fixed factors of a full model (i.e., all predictors included) with the variance explained by the fixed factors of the same model without the predictor of interest. The difference of variance explained between the two models gives the relative contribution of the given predictor. Because statistical interactions are difficult to test (and to interpret) with such an approach (Grömping 2007) and because environmental differences occurred between the two years of experiments (for a summary, see Table 1), 2005 and 2006 were analyzed separately. For each year, two full models were constructed: one for daytime and one for crepuscular observations. In this descriptive analysis, we used each observation as a replicate unit. The full model included competitive treatments and the five or six environmental variables (i.e., invertebrates drift, water temperature, cloud cover, water depth, water velocity, and moon phase for crepuscular observations) as fixed factors. Period of observation nested within channel was the random factor (Pinheiro and Bates 2000). The variance explained by the fixed portion of this model was compared with the variance explained by the fixed portion of simplified models that each included all but the predictor of interest. This relative contribution (or effect size) of each predictor was expressed as the percentage of the total variance explained by each variable itself.

Fig. 1. Mean proportion (± standard error, SE) of Atlantic salmon (*Salmo salar*) active during daytime (open bars) and twilight (solid bars) when maintained at low intraspecific density (3 fish·m^{-2}) and high intraspecific density (6 fish·m^{-2}), and with rainbow trout (*Oncorhynchus mykiss*), respectively (3 + 3 fish·m^{-2}) for (*a*) 2005 and (*b*) 2006. Significantly different values (p < 0.05, contrasts tests) are identified with different letters.



Growth and behaviour

Growth rate of Atlantic salmon was compared among competitive treatments and years using a two-way ANOVA. Aggression rate and feeding rate (log($x+1$)-transformed) were tested across treatments and species using two-way ANOVAs (years and competitive treatments as main factors). In the latter analyses, the mean in each channel was used as the replicate unit. SNK tests (Zar 1999) were used for subsequent multiple comparisons analyses.

All statistical analyses were performed using R (version 2.2.1; R Development Core Team 2005).

Results

Diel activity

On average, there were no significant differences between the proportion of active Atlantic salmon observed in 2005 and 2006 (Table 2). We found that Atlantic salmon were

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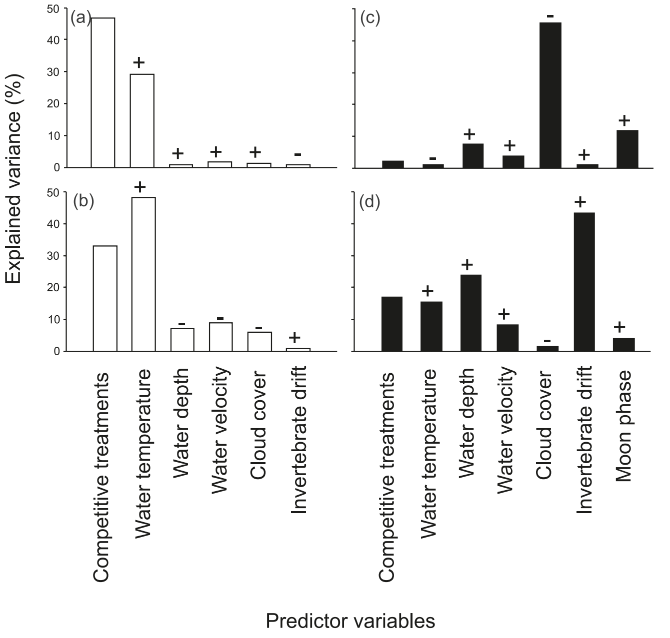
Fig. 2. The percentage of the total explained variance of the predictor variables from a mixed linear model explaining the activity of Atlantic salmon (*Salmo salar*), computed separately for daytime (open bars) and twilight (solid bars) in (*a* and *c*) 2005 and (*b* and *d*) 2006. The signs indicate the slope (+, positive slope; –, negative slope) for the relationship between each predictor and the proportion of active salmon.



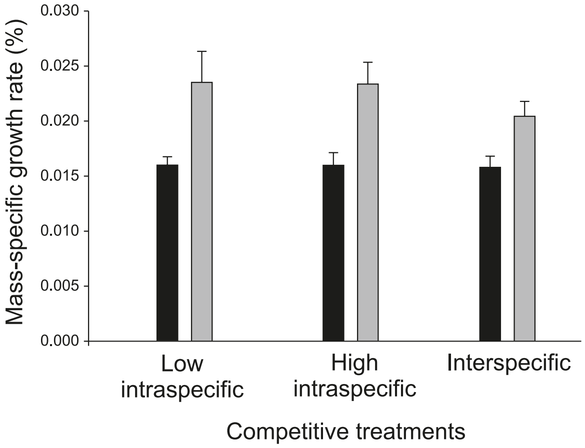
significantly more active during twilight (Fig. 1; Table 2). However, we detected a significant interaction between the year of experiment and the period of observation, indicating that the daytime activity of salmon was higher in 2006 than in 2005 (Table 2; Fig. 1). We found a significant interaction between periods of observation and competitive treatment (Table 2). Indeed, the proportion of salmon active during daytime was significantly higher when salmon occurred with rainbow trout than when salmon occurred at a low density (contrast test, both years pooled, $p = 0.01$; Fig. 1). During the day, there was no difference between either the low and high intraspecific treatments (contrast test, both years pooled, $p = 0.09$; Fig. 1) or between the high intraspecific and interspecific treatments (contrast test, both years pooled, $p = 0.21$; Fig. 1). In contrast, during twilight, competitive treatments did not affect the proportion of active salmon (Fig. 1). The nonsignificant three-term interaction indicated that these patterns were identical in 2005 and 2006 (see Fig. 1).

For comparison, the percentage of rainbow trout active was 59% ± 0.26% (standard deviation, SD) during the day compared with 68% ± 0.23% during twilight (paired t test, $t = 0.73$, $p = 0.45$).

Relative contributions of environmental variables

During daytime, the relative importance of the various environmental variables was generally consistent in 2005 and 2006, with competitive treatment and water temperature each contributing to 30%–45% of the total variance (Figs. 2*a* and 2*b*). Water temperature positively affected the proportion of fish observed during the day (Figs. 2*a* and 2*b*).

Fig. 3. Mass-specific growth rate (mean ± standard error, SE) calculated for Atlantic salmon (*Salmo salar*) in two years (2005, solid bars; 2006, shaded bars) for the three treatments: low intraspecific competition (3 fish·m^{-2}), high intraspecific competition (6 fish·m^{-2}), and interspecific competition (3 + 3 fish·m^{-2}).



During twilight, the relative importance of variables differed between years (Figs. 2*c* and 2*d*). In 2005, the percentage of cloud cover alone contributed to ~45% of the total variance (Fig. 2*c*). Greater cloud cover reduced the crepuscular activity of salmon (Fig. 2*c*), and the other predictors contributed relatively little to the total variance (<16% each). In 2006, invertebrate drift was positively related to activity during twilight, explaining about 40% of the variation in activity (Fig. 2*d*). Greater invertebrate drift increased the crepuscular activity of salmon (Fig. 2*d*). During both years, water depth in each channel was a relatively good predictor of activity (Figs. 2*c* and 2*d*), with greater water depth being associated with a higher proportion of salmon active during twilight (Figs. 2*c* and 2*d*). In contrast to daytime activity, we detected no strong effects of competitive treatment or water temperature in explaining crepuscular activity in either 2005 or 2006 (Figs. 2*a*–2*d*).

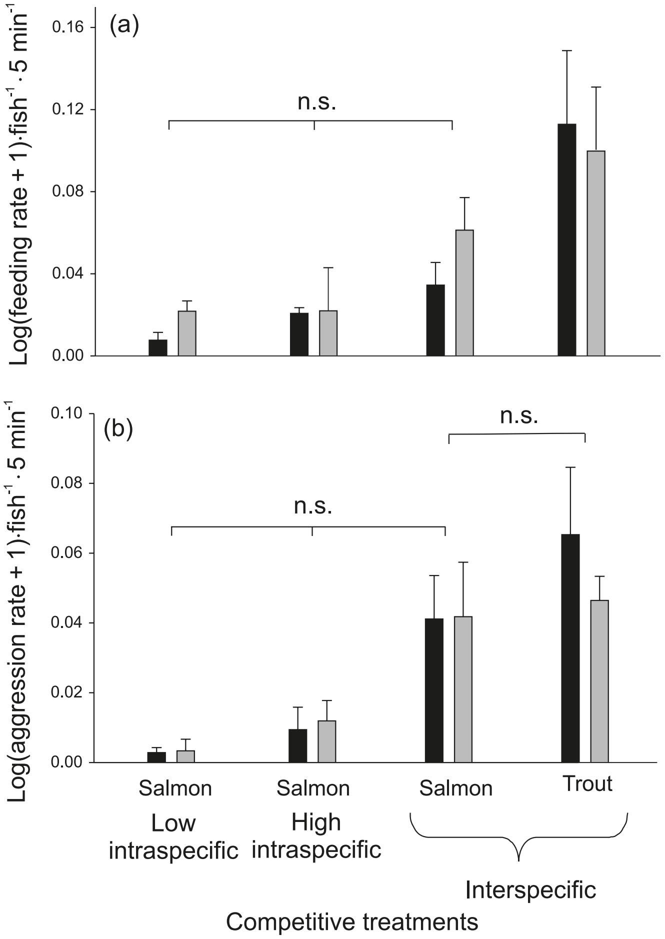
Growth and behaviour

Growth rate of Atlantic salmon was higher in 2006 than in 2005 (year effect, ANOVA, $F_{[1,15]} = 18.03$, $p = 0.001$; Fig. 3), but in both years, competitive treatments did not affect growth rate of salmon (competitive treatment effect, ANOVA, $F_{[2,15]} = 0.48$, $p = 0.63$; interaction term, ANOVA, $F_{[2,15]} = 0.37$, $p = 0.69$; Fig. 3). At the end of the experiment, the weight of the Atlantic salmon was increased by a factor of 1.35 in 2005 (all treatments pooled) and by a factor of 1.78 in 2006 (all treatments pooled).

Feeding rate did not differ between years (year effect, ANOVA, $F_{[1,20]} = 0.34$, $p = 0.57$; Fig. 4*a*), and trends were similar between years (interaction term, ANOVA, $F_{[3,20]} = 0.19$, $p = 0.89$; Fig. 4*a*). In 2005 and 2006, rainbow trout fed at a rate significantly higher than Atlantic salmon (competitive treatment and species effects, ANOVA, $F_{[3,20]} = 4.49$, $p = 0.01$; SNK tests, $p < 0.05$ for all comparisons; Fig. 4*a*), but the feeding rate of salmon did not differ between competitive treatments (SNK tests, $p > 0.05$ for all comparisons; Fig. 4*a*).

Aggression rate did not differ between years (year effect,

Fig. 4. (*a*) Mean (± standard error, SE) feeding rate ($\log(x+1)$) per fish per 5 min observation and (*b*) mean aggression rate ($\log(x+1)$) per fish per 5 min observation calculated for Atlantic salmon (*Salmo salar*, "Salmon") and rainbow trout (*Oncorhynchus mykiss*, "Trout") in two years (2005, solid bars; 2006, shaded bars) for the three treatments: low intraspecific competition (3 fish·m^{-2}), high intraspecific competition (6 fish·m^{-2}), and interspecific competition (3 + 3 fish·m^{-2}). Nonsignificant differences between species and (or) treatments are indicated (n.s.).



ANOVA, $F_{[1,20]} = 0.73$, $p = 0.40$; Fig. 4*b*), and trends were similar in both years (interaction term, ANOVA, $F_{[3,20]} = 0.91$, $p = 0.45$; Fig. 4*b*). The aggression rate of rainbow trout was higher than that of Atlantic salmon (competitive treatment and species effects, ANOVA, $F_{[3,20]} = 4.27$, $p = 0.02$; SNK tests, $p < 0.05$ for all comparisons; Fig. 4*b*). Moreover, the aggression rate of Atlantic salmon tended to be greater when maintained with rainbow trout than when in allopatry (salmon with rainbow trout compared with salmon in low intraspecific density, SNK test, $p = 0.08$; salmon with rainbow trout compared with salmon in high intraspecific density, SNK test, $p = 0.08$; Fig. 4*b*). Rainbow trout and Atlantic salmon displayed a similar rate of aggression when they were in sympatry (SNK test, $p = 0.53$; Fig. 4*b*). A finer analysis of the sympatric situation that integrated the direction of each aggressive act revealed that Atlantic salmon and rainbow trout directed a similar amount of aggression toward heterospecifics and toward conspecifics (paired *t* tests, $t = -0.68$, $p = 0.51$ for Atlantic salmon and $t = 0.28$, $p = 0.78$ for rainbow trout).

Discussion

Because our experimental design differed slightly between 2005 and 2006, it was difficult to disentangle the factors explaining some differences that we observed between years. For instance, larger screen mesh, greater depth and water velocity, and higher discharge could explain why invertebrate drift was higher in 2006 and therefore why daytime activity and growth rate of Atlantic salmon were also higher (for a study on the effects of changing screen mesh size in outdoor channels, see Dahl and Greenberg 1999). Nevertheless, some trends were consistent in both years, which will be the focus of our discussion.

Our study confirmed previous field observations reporting that Atlantic salmon fry were predominantly active during twilight at high summer temperatures (Gries et al. 1997; Johnston et al. 2004; but see Breau et al. 2007). More interestingly, we highlighted the importance of interspecific competition on diel activity patterns. Neither intraspecific nor interspecific competition influenced the crepuscular activity of Atlantic salmon. However, during the day, interspecific competition had a significant effect on the activity of Atlantic salmon fry. The effect of doubling the density of Atlantic salmon was half the effect of interspecific competition at the same total density. Moreover, we found no significant differences between the low and high intraspecific treatments and the high intra- and inter-specific treatments. These observations indicated that the effect of competition with rainbow trout was probably mediated by both the effect of increasing density and the identity of the competitors (Connell 1983; Blanchet et al. 2007*b*). The temporal partitioning (sensu stricto) of Atlantic salmon was not strongly affected by rainbow trout, as salmon remained mainly crepuscular, even in the presence of interspecific competitor. However, because fish increased their risk of predation when they are active during the day (Martel and Dill 1995; Fraser et al. 2004), Atlantic salmon used a more risky tactic when maintained in sympatry with rainbow trout than when maintained at a low intraspecific density.

Rainbow trout are generally considered to be more aggressive than Atlantic salmon (Volpe et al. 2001). Territorial interference competition imposed by trout may thus force salmon to leave their refuge during the day. Indeed, when in sympatry with rainbow trout, Atlantic salmon tended to be more aggressive than when in allopatry, and they directed half of their aggression toward rainbow trout and received the same amount of aggression from trout. Moreover, rainbow trout were highly active during both the day and twilight. Therefore, we propose that rainbow trout (which cruise more than Atlantic salmon; Volpe et al. 2001) frequently penetrated Atlantic salmon territories, resulting in greater daytime activity associated with territory defence in the presence of rainbow trout. During twilight, the effect of competition was lower, probably because aggressive interactions have been shown to be less frequent at this time or during low light intensity (Fraser et al. 1993; Blanchet et al. 2007*c*). Alternatively, Atlantic salmon may be more active

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during the day to compensate for strong exploitative competition imposed by rainbow trout.

In addition, we found that the growth rate of Atlantic salmon was not influenced by the presence of competitors, at least at the densities we studied. It is possible that even if the feeding rate of Atlantic salmon was constant across treatments, they maintained their growth rate by being active during a longer period of time during the day, thereby increasing feeding opportunities and compensating for the energy spent when in the presence of the rainbow trout. The weak effect of competition on the growth rate of Atlantic salmon suggested that the tactic adopted by the Atlantic salmon when in sympatry with the rainbow trout was not energetically costly but may nevertheless increase the probability of encountering predators. Such “growth compensation” is consistent with recent studies emphasizing the fact that animals adjust their behaviour in a manner to follow a maximal growth trajectory, even if they expose themselves to a higher predation risk (Biro et al. 2003; Imre et al. 2005).

We demonstrated that during the day, water temperature was another important factor to consider in explaining activity of Atlantic salmon. This positive effect of water temperature on the daytime activity pattern of Atlantic salmon was consistent with the results of previous studies (e.g., Gries et al. 1997; Johnston et al. 2004; Breau et al. 2007). During twilight, the effect of water temperature was weak relative to the effects of other environmental cues (invertebrate drift, cloud cover), at least within the range of temperatures found in this study. Fraser et al. (1993) also demonstrated in laboratory experiments that nocturnal foraging rate was independent of water temperature. By shifting from the use of thermal cues to other environmental cues during twilight, Atlantic salmon may acquire more accurate information about whether or not to be active. For instance, during twilight, the information provided by the level of light intensity (i.e., cloud cover and moon phase) is considered to be of high quality for use in predicting predation risk (Fraser et al. 1993) and food intake (Fraser and Metcalfe 1997). This result suggests that the sensitivity of Atlantic salmon to environmental cues might vary over a 24 h cycle, perhaps to maximize the ratio between energy gain and the risk of being detected by a predator.

To summarize, we demonstrated that interspecific competition acted as an important factor in shaping the daytime activity of Atlantic salmon. Moreover, we demonstrated that this effect was the result of both the competitor’s identity and the effect of increasing density. The effect of interspecific competition was strongest during the day and was probably the result of territorial interference between species. During twilight, no effect of competition was detected and the influence of the other environmental factors was different from the patterns observed during the day. Overall, these results suggest interplay between biotic and abiotic factors in determining fish activity (Reebs 2002; Kronfeld-Schor and Dayan 2003). Moreover, these results suggest that fish were highly plastic at the daily time scale in their responses to biotic and abiotic changes, probably to maximize the ratio between net energy gain and the risk of being eaten by predators.

The effect of competition imposed by rainbow trout did not seem to influence the growth rate of Atlantic salmon. However, by increasing activity during the day, Atlantic salmon increase the probability of being detected by a predator (Martel and Dill 1995), and in that context, the exotic species may indirectly alter the fitness of the native species by reducing survival probability. As such, our results illustrate how plasticity for foraging activity can occur along a temporal axis and how it may play a pivotal role in the outcome of interactions between native and exotic species.

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