BEHAVIORAL ECOLOGY

The disruption of dominance hierarchies by a non-native species: an individual-based analysis

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Abstract We studied the effects of the exotic rainbow trout (*Oncorhynchus mykiss*) on the performance and the dominance hierarchy of native Atlantic salmon (*Salmo salar*) at the group and individual level using laboratory and semi-natural experiments. At the group level, we compared the effects of interspecific and intraspecific competition (substitutive and additive design) on behavioural responses and growth of young-of-the-year Atlantic salmon. At the individual level, the same design was used to evaluate: (1) the temporal consistency of behavioural responses, dominance hierarchy and growth rate of Atlantic salmon; (2) the pattern of correlations between behaviours; and (3) the relationship between individual growth rate and behaviour. In the laboratory, group-level analyses revealed a weak but similar effect of rainbow trout and intraspecific competition on the behaviour and growth of Atlantic salmon. In contrast, individual-based analyses demonstrated that rainbow trout (but not intraspecific competition) strongly affected behavioural strategy, dominance hierarchy and growth trajectory of individual Atlantic salmon. Specifically, behaviours, dominance status and growth rate of salmon were temporally consistent in the intraspecific environment,

while these patterns were disrupted when rainbow trout were present. Similarly, we found that rainbow trout strongly affected behavioural correlations and the relationships between individual growth rate and behaviour. The semi-natural experiments confirmed these results as interspecific competition affected relationships between individual growth rate of salmon, initial weight and activity index. Overall, individual-based analyses highlighted important mechanisms that were concealed at the group level, and that may be crucial to understand ecological and evolutionary consequences of exotic species. Moreover, these results demonstrated that competition with an exotic species disrupts the hierarchical relationship among native individuals and may therefore represent a potential for a shift in selective pressure.

Keywords Behavioural correlations · Social hierarchy · Competition · Salmonids · Phenotypic plasticity

Introduction

The invasion of exotic species is greatly facilitated by human activities and is considered as one of the major threats to biodiversity conservation (Clavero and Garcia-Berthou 2005; Li and Wilcove 2005). Invaders can directly influence native population dynamics, abundance and persistence through biological interactions such as competition, predation and/or parasitism (e.g. Blackburn et al. 2004, Morita et al. 2004, Gozlan et al. 2005, Ortega et al. 2006). Numerous studies have also revealed the ecological effects of invaders on native species at higher levels of organization, such as at the community and/or the ecosystem level (e.g. Vázquez and Simberloff 2003; Baxter et al. 2004; Asner and Vitousek 2005; Gorokhova et al.

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2005). Moreover, recent works (Phillips and Shine 2004; Freeman and Byers 2006; Grant and Grant 2006) have demonstrated that these new combinations of species may also modify the strength and direction of selective pressure leading to evolutionary changes of heritable traits in native populations. All of these ecological and evolutionary consequences of exotic species may lead to important environmental and economical damages (Lodge 1993; Pimentel et al. 2000).

To assess the short-term effects (i.e. within weeks or months) that an exotic species may have on a native population, the traditional approach involves comparing the average performance (e.g. habitat use, growth, mortality) of a target species maintained in the presence and absence of an exotic species (e.g. Gurnell et al. 2004; Mills et al. 2004; Blanchet et al. 2007). However, an original approach integrating the performance of individuals has been recently proposed by Sih et al. (2004). They proposed following the change in the relative behaviour of a given individual (i.e. the behaviour relative to other members of a group) across several social contexts (e.g. competitive, predatory or mating contexts). They argued that explicitly considering inter-individual behavioural variation provided crucial information for understanding both ecological and evolutionary processes (Bolnick et al. 2003; Dall et al. 2004; Sih et al. 2004). This approach has rarely been used in the context of species' invasions, yet offers potential advantages in assessing interactions between native and exotic species (Sih et al 2004). For example, in the case of competition between native and exotic species, the individual-based approach may enable us to test if the fitness (or a trait related to fitness, such as growth) of a given native individual differs (relative to the fitness of others individuals) between settings characterised by the absence or presence of exotic competitors. Such kinds of information may be crucial to understanding the ecological and evolutionary consequences of competitive invaders (Sih et al. 2004; Grant and Grant 2006).

The objective of the present study was to quantify, at both the group and individual level, the impact of an exotic species on the ability of a native species to acquire energy, to defend profitable territories and to grow. By integrating individual characteristics of the native species, we also aimed to test the hypothesis that an exotic species may alter the dominance hierarchies prevailing within a native population.

To address these issues, we used the salmonid model system [native Atlantic salmon (*Salmo salar*)–invasive rainbow trout (*Oncorhynchus mykiss*)]. Juvenile salmonids are territorial predators living in streams and feeding on invertebrate drift (Keenleyside and Yammamoto 1962). They generally interact (both con- and heterospecifically) through interference competition mediated by direct aggression to defend profitable territory providing maximum

energy gain and refuges against predators (Fausch 1984). Dominance hierarchies are commonly observed in natural populations, with dominant fish defending the more profitable foraging space and territory against subordinate intruders (Nakano 1995). Atlantic salmon is a culturally and economically important salmonid naturally inhabiting rivers of the North Atlantic coastlines. Worldwide stocks are declining and, in this context, interaction with exotic species may represent an additional risk to such weakened populations (Fausch 1998). Rainbow trout is an anadromous salmonid from the north-western coast of North America and is one of the most widely introduced fish species (Fausch et al. 2001). This species now cohabits with Atlantic salmon in many rivers throughout the salmon's native range. The ecology of both species is well known and juveniles have been shown to display significant spatial overlap and to likely compete for resources (i.e. territory, refuges, food; Gibson 1981; Hearn and Kynard 1986; Volpe et al. 2001; Blanchet et al., unpublished data).

To test the hypothesis that exotic rainbow trout alter the relative individual performance of the native Atlantic salmon, we conducted both laboratory and semi-natural experiments with native fish placed in both intra- and interspecific competitive situations (combined substitutive and additive design; Connell 1983). In the laboratory, we examined the behavioural and growth responses of Atlantic salmon at the group level under several situations of competition. At the individual level, we evaluated: (1) the consistency of behavioural responses (aggression rate, number of movements and distance to a food source) and of dominance hierarchy; (2) the correlation between different behavioural responses; and (3) the relation between individual growth rate and these behavioural responses. The semi-natural experiments aimed to verify our laboratory results in a more variable and natural environment. We studied the effects of competitors on the growth of Atlantic salmon at the group level. We also compared, at the individual level, the relationships between growth rate, activity and initial weight.

Materials and methods

Biological materials

For both experiments we used young-of-the-year (YOY) Atlantic salmon and rainbow trout caught by electrofishing in the Malbaie River (Québec, Canada; 47°67′N, 70°16′W). A self-sustaining population of rainbow trout cohabits with Atlantic salmon in the downstream part 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. In the sympatric section of the river, both species occupied similar macro-habitats (i.e. principally the bank section of riffles; Blanchet et al., unpublished data) and micro-habitat overlap increased as fish grew. Indeed, in mid July YOY Atlantic salmon were found in habitat where depth was 21.80 cm on average (range 7–45 cm) and current velocity was 16.18 cm s^{-1} (range 0–60 cm s^{-1}). YOY rainbow trout used habitat where depth was 16.20 cm (range 7–30 cm) and current velocity was 8.11 cm s^{-1} (range 0–45 cm s^{-1}) [non-parametric overlap index (Mouillot et al. 2005) between species was 0.64 and 0.63 for depth and current velocity, respectively; Blanchet et al., unpublished data]. Later in the summer, at the end of August, Atlantic salmon were found in habitats where depth was 22.60 cm in average (range 5–35 cm) and current velocity was 23.40 cm s^{-1} (range 4–72 cm s^{-1}), and YOY rainbow trout used habitat where depth was 18.97 cm (range 10–35 cm) and current velocity was 21.99 cm s^{-1} (range 2–60 cm s^{-1}) [non-parametric overlap index (Mouillot et al. 2005) between species was 0.72 and 0.82 for depth and current velocity, respectively; Blanchet et al., unpublished data]. Atlantic salmon fry emerged from their nests earlier than rainbow trout fry and consequently they maintained a size advantage until the end of their first summer of life (i.e. end of August; Blanchet et al., 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).

Laboratory experiments

In September 2004, Atlantic salmon and rainbow trout were transferred from Malbaie River to the laboratory. They were reared in separate holding tanks and fed ad libitum with commercial fish food pellets for 1 month before experiments started.

Experiments were conducted simultaneously using 12 artificial channels fitted with a re-circulating water system. Each channel was made of transparent Plexiglas and was 1.90 m long, 0.30 m wide and 0.30 m deep. The water depth in each channel was 12 cm and average current velocity was 8 cm s^{-1} (see Table 1). These values were in the range of the habitat requirements of both species (see Biological materials). A single layer of river cobbles (2–3 cm in diameter) covered the entire surface of the arena, and four pebbles (10 cm in diameter) were added to serve as current refuges. They were arranged so that their distribution was identical among channels. We simulated day, dawn, dusk and night (7% of the available intensity) with light bulbs placed above each channel. Light:dark cycle was 9:14 h plus 30 min of dawn and dusk. Water temperature was maintained constant at 14 ± 1°C, which is similar to the water temperature of the river in mid September

(13.5 ± 3.3°C). Daily food ration (0.8 g artificial pellets) was dispensed at the upstream end of the channel by an automatic feeder at 15-min intervals. This ration was maintained constant over the course of the experiment and among treatments. It corresponded to between 2.5 and 8% of the total wet fish biomass in each channel, depending on the competitive treatment and on the moment of the experiment; 4% is considered as a normal food ration for juvenile salmonids (Höjesjö et al. 2004). The inner side of all channels was marked to define 15 equal zones (zone 1 being upstream, directly below the automatic feeder) to allow recording of horizontal distribution.

After 24 h of food deprivation, 72 Atlantic salmon were selected from the holding tank to constitute 12 groups of six fish of similar size (mean fork length ± SD, 55.76 mm ± 1.74) [ANOVA, $F(11, 60) = 0.17$, $P = 0.99$] and weight (1.64 g ± 0.17) [ANOVA, $F(11,60) = 0.33$, $P = 0.97$]. Before the experiment, each individual was marked using a unique Alcyan Blue dye mark (Sloman et al. 2002) to allow individual identification during the experiment.

The experiment was performed in two steps. During an initial 15-day period, marked Atlantic salmon were kept at a low density (six fish per channel). At the end of this initial period, they were anaesthetized and weighed after 24 h of food deprivation. Then, fish were reintroduced into their respective channels for a second 15-day period and exposed to three different competitive treatments. In four channels no additional fish were added (treatment 1, low intraspecific competition effect and time effect). In four other channels, six additional salmon were added (treatment 2, high intraspecific competition effect) and in the last four channels, six trout were added (treatment 3, interspecific competition effect). The additional competitors (both rainbow trout and Atlantic salmon) were selected from the holding tank to be similar in size with the experimental fish at this moment of the experiment [ANOVA, $F(2, 116) = 0.62$, $P = 0.54$].

At the end of the second period, fish were anaesthetized and weighed after 24 h of food deprivation. 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 both periods and for each individual using the following formula:

$$\Omega = (M_t^b - M_0^b)/(b \cdot t) \qquad (1)$$

where M_t and M_0 are body mass (g) at the end and the beginning of each period respectively, b is the allometric mass exponent for the relation between specific growth rate and body mass, estimated at 0.31 for Atlantic salmon (Elliot and Hurley 1997), and t is the experimental period (i.e. 15 days).

Table 1 Environmental conditions [mean (range)] in the laboratory and in semi-natural experiments. *ind.* Individual

	Experiments	
	Laboratory	Semi-natural
Density (ind. m^{-2})	10.5–21	3.13–6.25
Daytime air temperature (°C)	15 (14.5–15.5)	20.9 (10.5–25)
Nighttime air temperature (°C)	15 (14.5–15.5)	15.6 (11.8–20)
Water temperature (°C)	14.2 (13.5–14.5)	18.5 (15.2–22)
Depth (cm)	12 (Constant)	11.13 (7–19)
Velocity (cm s^{-1})	8 (0–20)	8.34 (6.32–12.41)
Daytime food availability[a]	0.40 (Constant)	0.73 (0.42–1.22)
Nighttime food availability[a]	0.40 (Constant)	5.62 (1.83–10.23)

[a] Daytime and nighttime food availability are expressed in grams of artificial pellets per day in the laboratory experiments and in number of invertebrates per minute in the semi-natural experiments

For each experimental period, we observed fish for 5 days following 3 days of acclimatization. We randomly selected nine channels (three per treatment) and we filmed for 15 min (the observer was present for 5 min before filming to accustom the fish to his presence). We measured three behavioural variables: (1) the distance to the food source, (2) the number of aggressive interactions (chase, displays and nip; Keenleyside and Yamamoto 1962) initiated by each marked fish, and (3) the number of movements. A movement was scored only when a fish moved a distance superior to its body length and when this fish remained at its new site for at least 10 s in a fixed position. Displacements associated with aggression were not scored as movements.

To establish the dominance status of each fish, results from aggression, position and movements were combined into a single synthetic dominance score. Principal component analysis was used to reduce dimensionality and eliminate co-linearity in these three variables. The projected scores on the first principal component (PC1) were used as a synthetic independent variable reflecting the dominance status of each fish (described in Sloman et al. 2002). Thus, fish having a high PC1 score (i.e. strong positive values) are considered as being high dominance-status individuals (Solman et al. 2002).

In this experiment, total fish density varied from 10.5 to 21 fish m^{-2} according to treatments (Table 1). These densities were higher than natural density, and were 2–4 times higher than maximum density predicted by the model of Grant and Kramer (1990). Because such a high density may have altered the natural behaviour of salmon, we decided to verify our results in a semi-natural experiment where densities were closer to the natural situation and where environmental conditions were free to vary as in nature (see Table 1 for a summary of the main differences between the laboratory and the semi-natural experiments).

Semi-natural experiments

In mid July 2005, Atlantic salmon and rainbow trout were sampled in the Malbaie River and maintained in several holding tanks placed in the river for 10 days before experiments began.

The experiments were carried out simultaneously in 12 flow-through stream channels installed along the bank of the river. Channels were 4.8 m long, 0.6 m wide and 0.6 m deep and constructed of 20-mm plywood. 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 3-mm-mesh plastic screen to allow natural drift of invertebrates and prevent fish from escaping. The screens were brushed gently 2 times a day to prevent the mesh from clogging and to limit sedimentation. The bottom was covered with river substratum (mainly sand, gravel, cobbles and pebbles) to mimic the natural habitat of juvenile salmonids and to allow a rapid colonization of invertebrates. We positioned six artificial refuges (half tiles of 12 × 5 × 0.8 cm) in front of each Plexiglas window. Both depth and velocity changed daily following fluctuations in natural flow but were comparable to the conditions used in the laboratory experiment (see Table 1).

We selected 108 Atlantic salmon from the holding tanks to constitute 12 groups of nine fish. They were measured (mean fork length ± SD, 43.03 mm ± 2.41) and weighed (0.77 g ± 0.13). Fish were then individually marked using Visible Implant Elastomer tags (Northwest Marine Technology, Shaw Island, Wash.) to allow individual identification throughout the experiment.

In a first experiment, we verified the temporal consistency of individual growth rate of Atlantic salmon with three groups of fish in three different channels. Initial fish size [ANOVA, $F(2, 24) = 1.77$, $P = 0.191$] and weight [ANOVA, $F(2, 24) = 0.67$, $P = 0.521$] were similar among groups. After 15 days, fish were measured, weighed and then reintroduced for another 15-day period in their respective channels. The individual mass-specific growth rate was calculated using Eq. 1 and compared between both periods.

In a second experiment we compared the effect of interspecific and intraspecific competition on the individual performance of Atlantic salmon. Underwater individual identification was difficult due to substrate heterogeneity and water turbidity. For this reason, the design was different from the laboratory experiment. In an initial 6-day period, we introduced nine groups of Atlantic salmon in different channels. Initial fish size [ANOVA, $F(8, 78) = 0.99$, $P = 0.445$] and weight [ANOVA, $F(8, 78) = 0.858$, $P = 0.556$] were similar between groups. Fish were confined to the first upstream metre of the channels with a 3-mm-plastic-mesh partition. The substrate was sand to facilitate individual

identification of the fish. Each channel was observed for 5 min twice a day during 4 days. We measured an activity index for each individual: zero points were given to fish not visible, one point to fish present on the bottom and immobile, two points to fish on the bottom but mobile at least once during the 5-min observation and three points to fish swimming in the water column. One supplementary point was given each time a fish initiated an aggression. These scores were summed over the eight observations to produce one activity index for each fish; overall, the activity index ranged between 0 and 31 and did not vary among groups [mean ($\pm$SD) = 10.80 ($\pm$8.48), ANOVA, $F(8, 66) = 0.89$, $P = 0.527$].

The 3-mm-plastic-mesh partition was removed and fish were set free to occupy the entire channel for a 24-day period. No additional fish were added in three channels (treatment 1, low intraspecific competition effect), nine additional salmon were added to three others (treatment 2, high intraspecific competition effect) and nine trout were added to the last three channels (treatment 3, interspecific competition effect). Within channels, we found no statistical differences between the size of the competitors we added and the initial size of the marked salmon [two-way ANOVA with Channel and Type of fish (i.e. competitors or marked salmon) as fixed factors; effect of Type of fish, $F(1, 96) = 2.72$, $P = 0.104$; interaction between Channel and Type of fish, $F(5, 96) = 0.45$, $P = 0.811$]. Moreover, the size of rainbow trout and Atlantic salmon we added did not differ significantly [ANOVA, $F(1, 52) = 2.12$, $P = 0.151$]. Total fish density in channels varied from 3.13 to 6.26 fish m^{-2} (Table 1). A density of 6 fish m^{-2} is observed in highly productive areas of the Malbaie river and of other Canadian rivers (Blanchet et al., unpublished data), and corresponds to a territory size of 0.16 m^2 individuals (ind.)$^{-1}$, which is higher than the territorial area calculated by Grant and Kramer (1990) for individuals as small as 45 mm (0.066 m^2 ind.$^{-1}$).

At the end of the experiment fish were anaesthetized, measured and weighed. The relationships between individual mass-specific growth rate (Eq. 1), initial weight and activity index were compared between treatments.

Statistical analyses

Group level

For group-level analyses, channel means were used as the replicate unit. In the laboratory, the effects of competitive treatment and time on the growth rate, the number of given aggressions, the number of movements and the distance from the food source were tested using four independent repeated measures ANOVA (ANOVAR). The number of given aggressions and the number of movements were log($x + 1$) transformed to meet the assumptions of homoscedasticity

and normality. To be robust, ANOVAR also requires that the variances and covariances of the different repeated measures are homogeneous (compound symmetry assumption) and that the within-subject ''model'' consists of independent components (sphericity assumption) (Baron and Li 2000). However these two assumptions do not apply to our models as compound symmetry and sphericity assumptions do not hold for a repeated measures design with only two levels (Baron and Li 2000). In the field experiment, we compared the effect of competitive treatments on the growth rate of Atlantic salmon using one-way ANOVA.

Individual level

For individual level analyses, individual means were used as the replicate unit. In the laboratory, Pearson correlations were used to assess consistency between behavioural responses (number of given aggressions, number of movements and distance to the feeding source) and between dominance status measured during the first and the second observational period. Significant correlations indicated that the relative status of a given fish was maintained over time. Growth rate consistency was evaluated using Spearman's rank correlations as preliminary analyses revealed that the correlations in the three treatments were strongly driven by a few outliers (results not shown).

Behavioral correlations were assessed using Pearson correlations between pairs of behavioural responses independently for the two periods. For each treatment, we also evaluated the relationship between individual growth rate (during the second period) and behavioural responses using mixed-model analyses (Pinheiro and Bates 2000). Individual growth was the dependent variable; number of given aggressions, number of movements and distance to food source were the independent variables and channel was a random factor. We compared the models to evaluate the effects of interspecific and intraspecific competition on the relationship between growth rate and behavioural responses. Slope coefficients were estimated for each variable and compared among treatments. The significance of a given behavioural response on the dependent variable was tested using F-statistics. Overall goodness of fit of each model was assessed calculating the determination coefficient for the correlation between the growth values predicted by the models and the observed values.

In the field, the temporal consistency of individual growth was assessed using Spearman's rank correlation. The relationships between individual growth rate and initial weight and between individual growth rate and activity were assessed and compared between competitive treatments using Pearson correlations. All statistical analyses were performed using R version 2.2.1. (R Development Core Team 2005).

Results

Laboratory experiment

Group level

Growth rate significantly decreased over time but the absence of a significant interaction between growth period and social treatment indicated that growth was not affected by intra- and interspecific competitors (Fig. 1a; Table 2). In contrast, the interaction between social treatment and growth period indicated that the presence of competitors significantly increased the number of aggressions initiated by Atlantic salmon (Fig 1b; Table 2). Both intra- and interspecific competitors had a similar effect [comparison of the number of given aggressions between the first and the second period for the high intraspecific and the interspecific treatment; Student Newman Keuls (SNK) test, $P = 0.009$ and $P = 0.008$, respectively] while time had no significant effect (comparison of the number of given aggression between the first and the second period for the low intraspecific treatment; SNK test, $P = 0.675$). Concerning the distance to the food source and the number of movements, no significant effect of time and competitive treatment was observed (Fig. 1c, d; Table 2).

Individual level

Temporal consistency

At the individual level (Table 3), growth was temporally consistent in Atlantic salmon in the low intraspecific treatment (Table 3). Indeed, an individual which exhibited a relatively high growth rate during the first period also did so during the second period. Similar patterns were found for the three behaviours (number of given aggressions, number of movements and distance to the food source) and the dominance score. In the presence of intraspecific competitors, correlations between periods were significant for most traits and marginally non-significant ($P = 0.067$; Table 3) for the rate of given aggressions. In contrast, rainbow trout had a strong effect on growth, behaviour and dominance status, which resulted in the absence of correlations between periods (Table 3). These effects were particularly important for the distance to the food source, the number of movements and the dominance status.

Behavioural correlations

During the first observation period, Atlantic salmon that were aggressive toward conspecifics also generated many movements (Table 4). We found no significant relationships either between the distance to the food source and the

number of aggressions, or between the distance to the food source and the number of movements. Time had no effect on the pattern of correlations (see low intraspecific treatment in Table 4; comparison period 1 vs. period 2 corresponds to a control treatment). When intraspecific competitors were added in the second growth period, the relationship between the distance to the food source and the number of aggressions as well as the relationship between the distance to the food source and the number of movements became negative and significant (Table 4). That is, the closer a fish was to the food source, the more aggressive it was and the more it displayed movements. The presence of rainbow trout disrupted the relationship between the number of aggressions and the number of movements while the positive correlation between the distance to the food source and the number of movements became marginally significant.

Growth performance

When Atlantic salmon were maintained at either low or high intraspecific densities, individual growth rate was significantly predicted by the behavioural traits we measured (Table 5). In these latter cases, the models predicted 57.9% and 52.2% of the observed growth for the low and high intraspecific treatments, respectively. For both treatments the effect of the number of movements was positive and significant (Table 5). For the high intraspecific treatment, the effect of the number of given aggressions was significant (Table 5). On the contrary, when in sympatry with rainbow trout, only 6.1% of the variability was explained by the model and none of the measured behavioural traits significantly explained such variability (Table 5).

Semi-natural experiments

Group level

Growth rate did not differ between treatments [ANOVA, $F(2, 6) = 0.01$, $P = 0.988$] and was (mean ± SD); 0.0161 ± 0.0013, 0.0159 ± 0.0012 and 0.0158 ± 0.0010 for the low intraspecific, the high intraspecific and the interspecific competition treatments, respectively.

Individual level

Temporal consistency

At the individual level, there was no evidence that growth was temporally consistent because the individual growth of Atlantic salmon maintained at a low intraspecific competition during the first period was not correlated to growth
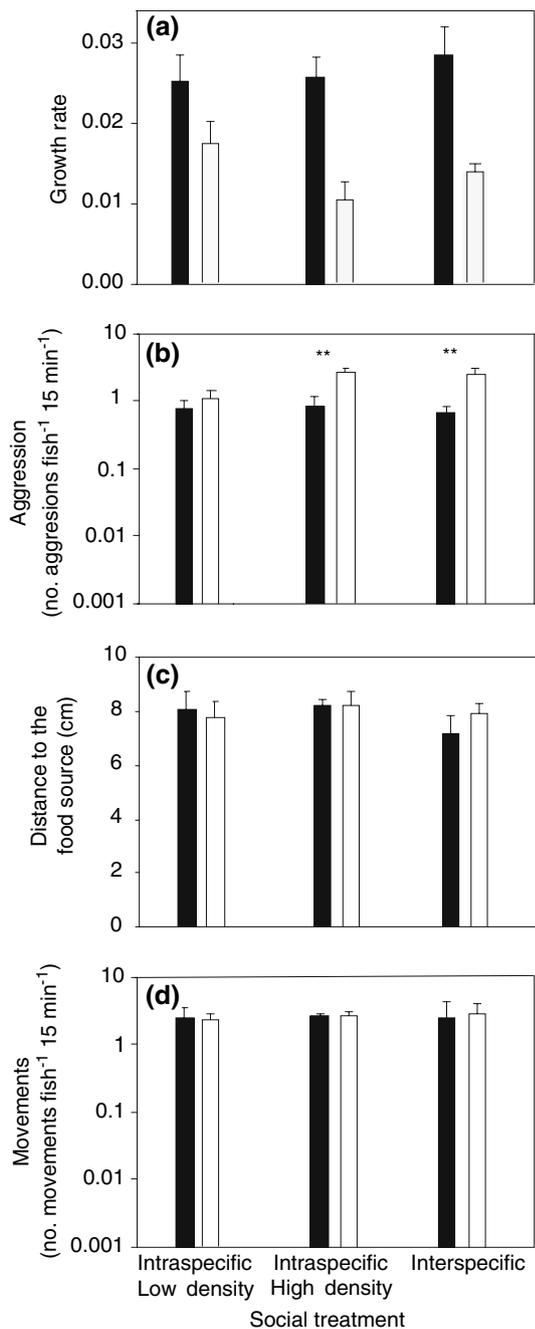
Fig. 1 a Growth rate, **b** aggression (number of aggression per fish per 15 min), **c** distance to the food source and **d** movements (number of movements per fish per 15 min) calculated at the group level for Atlantic salmon (*Salmo salar*) in the laboratory during the first period (*black bars* no competitors were added) and the second period (*white bars* competitors were added) for the three social treatments: low intraspecific density, high intraspecific density and interspecific competition. Multiple comparison (Student Newman Keuls) tests among treatments were performed when the interaction between Period and Social treatment was significant (see Table 2) (*******P* < 0.01). **b, d** Log scales are used. *Errors bars* are mean + SE

Table 2 Results of one-way ANOVA with repeated measure used to compare salmon growth, aggression rate, number of movements and distance to the food source between periods and competition treatments

Source of variation	df	F	P-value[a]
Growth			
Growth period	1, 9	56.49	0.000
Social treatment	2, 9	0.73	0.508
Growth period × Social treatment	2, 9	2.04	0.186
Aggression rate			
Growth period	1, 9	43.62	0.000
Social treatment	2, 9	1.24	0.334
Growth period × Social treatment	2, 9	5.74	0.025
Distance to the food source			
Growth period	1, 90	0.024	0.881
Social treatment	2, 9	0.41	0.681
Growth period × Social treatment	2, 9	1.968	0.195
Number of movements			
Growth period	1, 9	0.68	0.432
Social treatment	2, 9	0.11	0.901
Growth period × Social treatment	2, 9	1.79	0.221

[a] $P < 0.05$ indicates a significant effect

we measured during the second period (Spearman's rank correlation, $n = 22$, $r = -0.012$, $P = 0.954$).

Growth performance

When Atlantic salmon were maintained at a low or at a high intraspecific density, individual growth rate was negatively correlated to initial weight but not to the index of activity (Fig. 2). On the contrary, when maintained with rainbow trout, individual growth rate of Atlantic salmon was positively correlated to the index of activity and was not related to the initial weight (Fig. 2).

Discussion

This study demonstrated that the exotic rainbow trout had strong effects on the behavioural strategies, the dominance status and individual growth of the native endangered Atlantic salmon in both laboratory and semi-natural conditions. A unique aspect of our experiments was to consider the effects of the exotic species at the group and the individual level. At the group level, results showed that interspecific and intraspecific competitions induced similar changes of Atlantic salmon behaviours in terms of

Table 3 Spearman's rank correlation coefficient applied to establish the strength and direction of individual growth rate relationships of salmon between the first and the second period. Pearson's correlation applied to establish the relationships of salmon's individual behavioural responses (aggression rate, distance to the food source and number of movements) and dominance score between the first and the second period. Coefficients were calculated for the three treatments: low intraspecific, high intraspecific and interspecific competition

	Treatments		
	Low intraspecific	High intraspecific	Interspecific
Growth rate			
Spearman's rank correlations (R)	**0.49**[a]	**0.49**	0.38
P-value	**0.017**	**0.017**	0.076
Aggression rate			
Pearson's correlation (R)	**0.43**	0.39	0.27
P-value	**0.039**	0.067	0.237
Distance to the food source			
Pearson's correlation (R)	**0.60**	**0.58**	0.25
P-value	**0.002**	**0.004**	0.252
Number of movements			
Pearson's correlation (R)	**0.63**	**0.53**	0.17
P- value	**0.001**	**0.010**	0.143
Dominance score			
Pearson's correlation (R)	**0.62**	**0.63**	0.21
P-value	**0.001**	**0.001**	0.193

[a] Significant correlations (P < 0.05) in *bold*

aggression rate but had no effect on the growth rate. However, results were very different when considering individuals, and revealed important modifications of salmon behavioural responses and growth performance induced by rainbow trout. In the same way, Forseth et al. (2003) analysed competition between Arctic charr (*Salvelinus*

alpinus) and brown trout (*Salmo trutta*), two morphologically and behaviourally comparable salmonids naturally co-occurring in northern European lakes. At the group level, they found that growth and feeding rates did not differ significantly between allopatric and sympatric treatments, indicating that inter- and intraspecific competition were of similar strength. They also observed that the two species occupied distinct niches and did not compete. However, at the individual level, they demonstrated a strong directional selection against Arctic charr. They concluded that Arctic charr may have evolved through ecological character displacement in response to a past interspecific competition imposed by the dominant brown trout. In our study, the issue of past competition was irrelevant since rainbow trout is a recent invader in eastern North America (Fausch et al. 2001). On the contrary, our results indicated ongoing events where rainbow trout induced changes in the behavioural strategy of Atlantic salmon which were not perceptible at the group level, but which were strong enough to modify the natural growth trajectory and relative individual competitive ability of salmon.

Behavioural consistency

Our study also revealed the importance of the competitor's identity on individual behavioural consistency and dominance status. Indeed, when the competitive environment was maintained constant, the individual behaviours as well as the individual dominance status of Atlantic salmon were temporally consistent indicating a stable hierarchical structure over time. Behavioural and dominance consistency over ontogeny and/or over long periods of time has been shown in several vertebrates including fish (e.g. Bell and Stamps 2004; Cutts et al. 2001), birds (e.g. Carere et al. 2005; Cresswell 2001) and mammals (e.g. Côté 2000; Réale et al. 2000). Moreover, we found

Table 4 Correlations between salmon behaviours observed during the first and the second period for the three treatments: low intraspecific, high intraspecific and interspecific competition

Behavioural correlations	Low intraspecific		High intraspecific		Interspecific	
	Period 1	Period 2	Period 1	Period 2	Period 1	Period 2
Number of aggressions–number of movements						
R	**0.65**[a]	**0.52**	**0.69**	**0.66**	**0.48**	0.17
P-value	**0.001**	**0.012**	**0.000**	**0.001**	**0.019**	0.437
Distance to the food source–number of aggressions						
R	0.10	0.27	0.14	**−0.50**	0.23	0.30
P-value	0.655	0.206	0.519	**0.015**	0.278	0.159
Distance to the food source–number of movements						
R	0.07	0.02	0.08	**−0.50**	0.17	**0.42**
P-value	0.754	0.941	0.733	**0.015**	0.437	**0.049**

[a] Significant correlations (P < 0.05) in *bold*

Table 5 Results of mixed-models analyses[a] used to evaluate the relationship between salmon's individual growth rate and behaviour for the three treatments: low intraspecific, high intraspecific and interspecific competition. *Slope coefficients* Direction of the relationship between the growth rate and the given behaviour, where b_1, b_2 and b_3 are the slope coefficients for the number of aggressions, the distance to the food source and the number of movements, respectively; *Fit/Obs.* value of the coefficient of determination calculated for the correlation between the growth values predicted by the models and the observed values

| Full models	Competitive treatments	Slope coefficients			Fit/Obs.
		b_1	b_2	b_3	
	Low intraspecific	0.0091	−0.0016	0.0336	**0.579**[b]
	High intraspecific	0.0004	−0.0008	0.027	**0.522**
	Interspecific	−0.0001	−0.0004	0.0065	0.060

Fixed effects	Low intraspecific		High intraspecific		Interspecific	
	F-value[c]	*P*-value[c]	*F*-value	*P*-value	*F*-value	*P*-value
Number of aggressions	0.57	0.461	10.27	**0.006**	0.02	0.902
Distance to the food source	2.25	0.153	1.90	0.187	0.14	0.712
Number of movements	23.18	**0.000**	9.08	**0.008**	1.06	0.317

[a] Aggression rate, distance to the food source and number of movements are the fixed factors, and channel the random factor

[b] Coefficients in *bold* are significant ($P < 0.05$)

[c] *F*-values and associated *P*-values indicate variables that significantly predict individual growth rate

Fig. 2 Correlation of activity index (**a**, **c**, **e**) and initial weight (**b**, **d**, **f**) with individual mass-specific growth rate of Atlantic salmon in the three treatments: low intraspecific density, high intraspecific density and interspecific competition. Pearson's correlation coefficient (*R*) is indicated for each graph and the associated *P*-value ($P < 0.05$ indicates significant relationships)
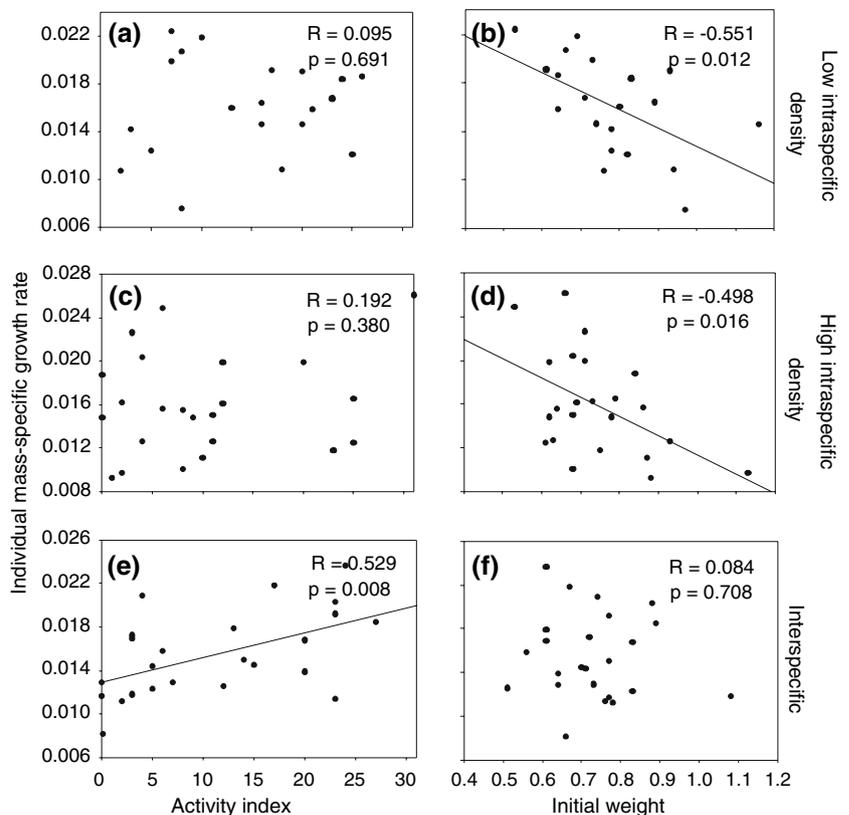
that intraspecific competition had little effect on such a hierarchical structure. This result differs from studies conducted in other species, which showed that intraspecific density modified relative competitive ability (Adams and Huntingford 1996; Cresswell 1998; Tregenza and Thompson 1998; but see Humphries et al. 1999). Such a discrepancy could be explained by the salmon's prior experience of the physical environment relative to the

introduced competitors. Nevertheless, despite the prior environmental experience of salmon, rainbow trout affected these temporal consistencies as correlations between periods of observation became non-significant, clearly illustrating that rainbow trout disrupted the pre-established dominance hierarchy. Because competitors were size matched among species and because general behaviour differed among species (Volpe et al. 2001; Blanchet et al., unpublished data) we hypothesize that different competitors may differentially influence the dominance structure classically observed in salmonids. Salmonids generally interact through interference competition to defend profitable territory (Fausch 1984; Nakano 1995). In complementary analyses, we showed that when together with rainbow trout, Atlantic salmon directed most of their aggression toward rainbow trout and they experienced 3 times more aggression from trout than from conspecifics (Blanchet et al., unpublished data; see also Volpe et al. 2001). Moreover, rainbow trout cruise more than Atlantic salmon (Volpe et al. 2001; Blanchet et al., unpublished data) and frequently penetrate the territories defended by Atlantic salmon. Therefore, we speculate that Atlantic salmon modified their behaviour in response to interference competition and intrusion of rainbow trout, which ultimately altered the natural dominance structure.

Behavioural correlations

Our results indicated that rainbow trout affected the pattern of correlations between behaviours. Namely, the positive correlation between the number of aggressions initiated by each fish and the number of movements they displayed was strongly significant and persistent over time when Atlantic salmon were maintained at a low or at a high intraspecific density, whereas the presence of rainbow trout eroded such a correlation. Moreover, we found that, as intraspecific density increased, Atlantic salmon located directly downstream of the food source, were more aggressive toward conspecifics and moved more than others. Distance to the food source is an important variable in predicting individual growth rate (Fausch 1984; Fausch and White 1986), and we therefore hypothesize that Atlantic salmon increased aggression and territorial vigilance to defend high-quality territories against intruders. However, this process was not observed when intruders were the exotic species, indicating a change in behavioural strategy induced by the identity of the competitor. This result adds weight to the recent finding of Bell (2005) who proposed that invasive species could be a key selective factor that shapes the evolution of behavioural differences between populations by uncoupling correlations between behaviours (see also Dall et al. 2004).

Individual growth trajectories

We have shown that changes in behavioural strategies and dominance hierarchies significantly altered growth trajectories of Atlantic salmon. Thus, results in the laboratory showed that the presence of rainbow trout cancelled the growth consistency observed over time when Atlantic salmon were held in allopatry at a low or a high density. Moreover, in these latter situations, individual growth rate was significantly explained by behavioural traits. In contrast, when rainbow trout were introduced, individual growth rate of salmon became unpredictable when the same behavioural traits were analysed. The change in behavioural strategy we observed when rainbow trout were present probably explained the absence of relationships between the growth rate and behaviour of Atlantic salmon. These changes may result from particular behavioural strategies such as sneaky or cryptic feeding (Höjesjö et al. 2005; Blanchet et al. 2006). These strategies are likely to modify relationships between behaviours (i.e. aggression, number of movements) and feeding acts at the individual level, while maintaining a constant food intake (and therefore growth) at the group level (Höjesjö et al. 2005). However, no growth consistency was observed when Atlantic salmon were maintained at a low level of intraspecific competition in the first semi-natural experiment. Such a difference between the laboratory and the semi-natural experiment was in accordance with studies highlighting the role of environmental variability (invertebrate drift, water temperature, discharge, etc.) on the relationship between dominance and growth rate in other salmonids (Harwood et al. 2002; Martin-Smith and Armstrong 2002). In our case, discrepancy between laboratory and semi-natural experiments may also result from subtle differences between experiments. Indeed, Atlantic salmon were smaller, at a lower density and water temperature was higher in the semi-natural experiment. Changes in environmental conditions have been shown to alter dominance hierarchies (Sloman et al. 2002). Yet, despite this effect of environmental variability and the variations among experiments, a pronounced difference between intraspecific and interspecific competition was observed at the individual level. Indeed, the individual growth rate of Atlantic salmon was related to the initial weight of the fish and correlation coefficients were significantly lower in allopatric treatments, whereas it was related to the activity index in the sympatric treatment. Overall, these results corroborated the laboratory experiment, and demonstrated that the effect of competition predominated over the effect of environmental variability in shaping individual growth trajectories. The relative importance of biotic interactions and environmental variability in population and community ecology has been intensely discussed (see, for example, Chesson

1994; Saetre et al. 1999; Hansen et al. 1999) and our results provide evidence that competition with an exotic species may counteract environmental effects.

Conclusions

This study highlighted the importance of including the individual-based approach in future investigations. Indeed, investigations at the individual level provide insights into mechanisms and processes concealed at the group level that may be relevant for the conservation and management of native species facing the invasion of their habitat by exotic species. In this study, an exotic species modified the behavioural strategies and the dominance status of the native species, which in turn altered the growth pattern of individuals. In many taxa, growth and body size are important fitness-related traits (Roff 2002; Wilson et al. 2005). For instance, size-selective survival following extreme climate events (i.e. floods, winter, etc.), or size-selective mortality related to predation or parasitism are common observations in nature (e.g. Sparrevik and Leonardsson 1999; Coltman et al. 2001; Hipkiss et al. 2002; Aubin Horth et al. 2005; Kalisaewicz et al. 2005; Johnsson and Bohlin 2006). Moreover, numerous authors have suggested that growth performance and social status play a significant role in shaping individual life history, and particularly reproductive tactics (Gross 1996; Hoffman et al. 1999; Burmeister et al. 2005; Kraus et al. 2005; Shine and Mason 2005). Thus, exotic species, by modifying individual growth patterns, may directly (i.e. through mortality) or indirectly (i.e. through the adoption of a given reproductive tactic) alter individual fitness and therefore potentially change patterns of selection in native populations.

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