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Competition, predation and flow rate as mediators of direct and indirect effects in a stream food chain

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Abstract Using semi-natural stream channels, we estimated the effects of competition and predation exerted by juvenile and adult exotic rainbow trout (*Oncorhynchus mykiss*) on the diel activity pattern of juvenile native Atlantic salmon (*Salmo salar*), a secondary consumer. We also evaluated the direct and indirect effects of competition, predation and abiotic factors (water depth and velocity) on the growth rate of salmon, the biomass of invertebrate grazers (primary consumers) and the biomass of periphytic algae (primary producers; chlorophyll *a*). The presence of chemical cues emanating from adult predatory trout reduced the daily activity of juvenile Atlantic salmon. In contrast, competition imposed by juvenile rainbow trout forced Atlantic salmon to be more active during the day, even if adult rainbow trout were also present. We found no effect of either competition or of predatory cues on the growth rate of Atlantic salmon, and no evidence of indirect effects on either the biomass of invertebrates or the biomass of chlorophyll *a*. In contrast, we demonstrated that this food chain (fish—invertebrate grazers—periphytic algae) was under the control of a critical abiotic factor, the water velocity, and of bottom-up processes. We concluded that the exotic species directly increases the risk of predation of the native Atlantic salmon, but behavioral compensation probably limits the effects on growth rate. The competition and predation imposed by the invaders had no indirect effects on lower trophic levels. Top-down effects may have been mitigated by the dominant influence of water velocity controlling all components of the food chain and by elevated levels of primary production.

Keywords Trait-mediated indirect effects · Invasive species · Trophic cascades · Bottom-up · Diel activity patterns

Introduction

Understanding the role of biotic and abiotic factors in regulating the functioning and the dynamic of ecosystems is a fundamental topic in ecology (Begon et al. 1996). Among biotic factors, predation affects population dynamics through direct consumption ("consumptive effect") or by stimulating costly defensive strategies in the prey population ("non-consumptive effect"; Abrams 1995, 2007). Such costs are generally mediated through behavioral, physiological or morphological changes in the prey population (Preisser et al. 2005). Interestingly, these plastic changes observed in prey can mediate indirect effects on other interacting species and hence influence the dynamic of entire food chains. Such effects are known as "trait-mediated indirect effects" (Abrams 1995, 2007) since they are mediated by a trait's plasticity. For instance, a prey may

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react behaviorally to a predator (e.g., reduce foraging activity and increase refuge use) and this predator effect can in turn mediate the impact of prey on its basal food resource (through top-down processes; Schmitz et al. 1997; Werner and Peacor 2003).

Competition is also expected to trigger indirect effects on lower trophic levels through trophic cascades (Peacor and Werner 1997; Abrams 2007). In such cases, the most parsimonious prediction would be that adding competitors in an ecosystem should strengthen trophic cascades, because of an increase in the density of consumers (Abrams 1995, 2007). It is worth noting, however, that the indirect effects of intraspecific competition and interspecific competition can be considered as equal only if the two competing species have an equal capacity to feed on the lower trophic level. However, if the two competing species differ in their capacity to exploit the lower trophic level (e.g., one species has a higher consumption rate than the other), the effect of interspecific competition should be different from a simple density-mediated effect. In this latter case, a species-specific effect may contribute to the indirect effects of competition. It is therefore relevant to distinguish between intra- and interspecific competition when attempting to understand the indirect effects initiated by competition [see Baxter et al. (2004) for further discussion]. Finally, evaluating the strength of indirect effects in natural ecosystems must also take into account a possible interaction between competition and predation risk (Werner and Peacor 2003) given that a prey's behavioral reaction to predators is dependent on the density and/or the type of competitors present in a given environment (Chase et al. 2002; Luttbeg et al. 2003; Teplitsky and Laurila 2007).

The abiotic properties of the environment have also been recognized as strong determinants of the trophic dynamic of ecosystems (Leonard et al. 1998). For instance, the strength of biotic interactions and of indirect effects can be dependent upon habitat characteristics (e.g., Griffen and Byers 2006; Trussell et al. 2006). Ecosystem productivity greatly influences the strength of trophic interactions within food chains and is itself strongly dependent upon abiotic characteristics (Chase 2003; Wojdak 2005; Elmhagen and Rushton 2007; Pringle et al. 2007). Finally, many neutral processes structuring communities such as dispersal, emigration or immigration are governed by abiotic characteristics and are also prone to influence the outcome of species interactions (Leibold et al. 2004; Thompson and Townsend 2006; Howeth and Leibold 2008).

In this study, we first evaluated the combined effect of predation and competition (both intra- and interspecific competition) on two phenotypic traits of a secondary consumer (the diel activity pattern and the growth rate). Secondly, we tested whether competition with, and predation on the secondary consumer contributed to indirect changes in biomass of two lower trophic levels, i.e., primary consumers and primary producers. Concomitantly, we evaluated how the physical characteristics of the environment influenced the interaction between species and the dynamic of the entire food chain.

To do this, we conducted a semi-natural stream channel experiment in a North American river using the native Atlantic salmon (*Salmo salar*, a secondary consumer) and the exotic rainbow trout (*Oncorhynchus mykiss*, a competitor at the juvenile stage and a predator at the adult stage) as models. Indirect effects induced by exotic species have already been demonstrated (e.g., Vázquez and Simberloff 2004; Baxter et al. 2004). Using exotic species as a potential "initiating" species of indirect effects has the advantage of providing both applied (does the introduction of non-native species have negative impacts on a given food chain?) and fundamental (what are the mechanisms underlying the structure of a given food chain?) issues of trophodynamics (White et al. 2006).

The diel activity pattern of species can be influenced by competition and predation (reviewed in Kronfeld-Schor and Dayan 2003). Indeed, when the risk of predation is perceived by prey, they may reduce their daytime activity (a period considered to be profitable for prey to feed) to reduce the risk of being preyed upon. Furthermore, dominant competitors can induce a temporal shift in the feeding activity of subordinates through interference or exploitative competition (e.g., Kelt et al. 2004). Predation and competition can also alter the feeding rate and thus the growth rate of the secondary consumer (Chase et al. 2002). According to the indirect effects hypothesis (Werner and Peacor 2003; Abrams 2007), it is expected that predation and competition exerted on a secondary consumer will indirectly affect the biomass and the feeding activity of primary consumers (here benthic invertebrates) and hence the biomass of primary producers (here unicellular benthic algae). An alternative hypothesis is that abiotic factors such as water velocity and water depth could be the major determinants of the functioning of this food chain. This is particularly expected in open systems such as rivers or streams (Leonard et al. 1998) in which the dynamics of benthic communities (both invertebrates and algae) have been shown to depend upon physical factors and bottom-up processes (e.g., Biggs et al. 1998; Forrester et al. 1999). For instance, water velocity governs neutral processes structuring benthic communities of invertebrates (Thompson and Townsend 2006), and also nutrient delivery rates that govern primary productivity in these systems (Biggs et al. 1998). According to the view that open ecosystems are structured by several interacting processes (Leonard et al. 1998; Nyström et al. 2003; Pringle et al. 2007), we predicted that both abiotic factors and biotic interactions should simultaneously contribute to structuring this food chain.

Food chain system and study site

Atlantic salmon occurs naturally in the rivers of North Atlantic coastlines. They spend the first 2–5 years of life in their natal river before migrating to sea to feed and grow. After maturing, they return to their natal river to spawn. The rainbow trout is a salmonid from the north-western coast of North America and is one of the world's most widely introduced fish species. Both species compete by interference for resources when juveniles (Blanchet et al. 2007a). Adult rainbow trout are partially piscivorous and can feed on juvenile Atlantic salmon. When juvenile, both species feed on benthic invertebrates (either moving over the substrate or drifting in the water column) and have been shown to influence the density and/or the feeding behavior of invertebrates (i.e., primary consumers, McIntosh and Townsend 1996; Dahl and Greenberg 1999). Among these invertebrates, some are grazers that feed on periphytic algae (i.e., diatoms growing on solid substrate such as stones) that represent an important component of the primary production of many rivers. This food chain (competing juvenile salmonids—invertebrate grazers—periphyton) has been widely studied and thus appears particularly appropriate to evaluate the relative importance of biotic and abiotic factors on its functioning (McIntosh and Townsend 1996; Biggs et al. 1998; Nyström et al. 2003; Baxter et al. 2004).

The experiment was conducted from 10 July to 30 August 2006 in the first 7 km of the Malbaie river (Québec, Canada, 47°67′N; 70°16′W). In this area, the river is about 20–25 m wide and has a summer discharge of 15–35 $m^3 s^{-1}$. The substratum is mainly cobbles and boulders covered by periphyton. Terrestrial invertebrates represent a negligible source of food to secondary consumers due to the large size of the river and the low forest cover. A self-sustaining population of rainbow trout cohabits with juvenile Atlantic salmon in the study area. Both primary and secondary production in this part of the river are relatively large, in part due to the surrounding urban and agricultural development and summer water temperatures that vary from 13 to 22°C from early July to the end of September.

Materials and methods

Experimental apparatus and design

Juvenile [i.e., young-of-the-year (YOY)] Atlantic salmon and rainbow trout were sampled by electrofishing in the Malbaie river. In our experiments, a uniform size range of juvenile salmon and trout was selected to avoid confounding the effects of size and species identity (Blanchet et al. 2007a). We used hatchery-reared adult rainbow trout (mean body length ± SD, 27.6 ± 3.1 cm) to simulate the presence of an exotic top predator. We chose to use hatchery fish rather than wild rainbow trout because the confinement protocol employed during the experiment would have been too stressful for wild fish. We have previously demonstrated that YOY Atlantic salmon respond behaviorally to such hatchery fish (Blanchet et al. 2007b).

The experiments were done in flow-through in situ channels installed along 300 m of river. Twenty-eight channels were constructed of 20-mm plywood; they were 2.4 m long, 0.6 m wide and 0.6 m deep, and three Plexiglas windows (0.30 × 0.30 m) were situated along one side of each channel to allow direct underwater observations. Each channel was divided into two sections with a 4.5-mm mesh plastic screen. The upstream section measured 0.40 m (hereafter referred to as the "predator section") while the downstream section measured 2.00 m (hereafter referred to as the "competitive section"). This allowed the physical separation of the top predators from the secondary consumers. The upstream and downstream ends of each channel were covered with 6- and 4.5-mm-mesh plastic screens, respectively. The screens did not impede the natural drift of invertebrates while preventing fish from escaping. The screens were gently brushed twice a day to prevent the mesh from clogging and to limit sedimentation. The bottom of each channel was entirely covered with river substratum (mainly sand, gravel, cobbles and pebbles) to mimic the natural habitat of juvenile Atlantic salmon and rainbow trout and to allow the natural colonization of channels by invertebrates and periphytic algae.

To test for the effect of species interaction we ran a full-factorial experiment consisting of three competitive treatments (low intraspecific competition, high intraspecific competition and interspecific competition) crossed with two predatory treatments (absence or presence of predatory cues). The number of juveniles introduced in each channel was either four or eight according to the competitive treatment we considered (i.e., four salmon in the low intraspecific competition treatment, eight salmon in the high intraspecific competition treatment and four salmon plus four trout in the interspecific competition treatment, see Table S1 in the Electronic Supplementary Material). This corresponds to a density of 3–6 individuals m^{-2}, which is within the upper limits of density and biomass found in Malbaie river and in other Atlantic salmon streams (S. Blanchet et al., unpublished data). We simulated the risk of predation by adding one adult rainbow trout in the predator section of twelve channels. Juvenile salmonids are sensitive to chemical cues released by predators and/or by conspecifics attacked by a predator (Blanchet et al. 2007b). Because the predator section was upstream of the competitor section, water-borne chemical cues continuously flowed through these channels. To enhance the effects of chemical cues, the adult rainbow trout were fed with a freshly dead Atlantic salmon or rainbow trout fry 3 times a week. The channels with predatory cues were located in the stream section so that they could not contaminate channels without predatory cues. For comparison, we also included a control fishless treatment (no predator, no competitors). Each treatment (seven in total) was replicated 4 times. Given the width and flow rate of the river, we considered that water temperature and water chemistry was homogeneous among channels and treatments.

To test for the effect of abiotic factors (water depth and water velocity), we assigned each treatment to a wide array of water depths and velocities (see Table S1 in the Electronic Supplementary Material) which were in the range typically exploited by juvenile Atlantic salmon and rainbow trout in the Malbaie river (Blanchet et al. 2007a). Water depth and current speed were measured on five different occasions during the experiment to extract an average value for each channel. Water velocity was evaluated as the time needed for an inert object (a 8-cm^3 piece of wood) to cover the length of a channel, so that this measurement reflected the integrated water velocity through a channel. Overall, water depth was 16.8 ± 2.3 cm (mean ± SD) and surface water velocity was 30.7 ± 7.4 cm s^{-1} (mean ± SD). We arranged the channels so that neither average water depths nor water velocity varied among treatments [one-way ANOVAs: $F(6, 21) = 1.14$, $P = 0.38$ and $F(6, 21) = 0.82$, $P = 0.56$ for depth and water velocity, respectively]. Moreover, each treatment was represented by at least one channel with a low water velocity [23.42 ± 2.82 cm s^{-1} (mean ± SD)], a high water velocity [40.28 ± 2.05 cm s^{-1} (mean ± SD)], a low water depth [15.07 ± 1.16 cm (mean ± SD)] and a high water depth [19.93 ± 1.28 cm (mean ± SD)], respectively (Table S1). During the experiment water discharge varied during the course of the experiment between 9 and 20 $\text{m}^3\ \text{s}^{-1}$ and no storm or flood events occurred during this period.

In each of the 24 experimental units that contained fish, four Atlantic salmon were individually marked using Visible Implant Elastomer tags (Northwest Marine Technology, Shaw Island, Wash.). Marked Atlantic salmon measured 43.33 mm (±4.89 SD) and weighed 0.77 g (±0.29 SD) on average. Additional Atlantic salmon used in the high intraspecific competition treatment measured 42.64 mm (±2.30 SD) and weighed 0.75 g (±0.12 SD) on average. Additional rainbow trout used in the interspecific competition treatment were 41.63 mm (±2.82 SD) long and weighed 0.70 g (±0.17 SD) on average. Average length and weight of the fish did not vary among treatments and/or species (results not detailed).

Experimental timing and data collection

Salmon diel activity

The channels were left undisturbed for 20 days before adding both the competing secondary consumers and the top predators. The experiment lasted an additional 28 days. The activity was recorded every 3 days. Between two and four replicated channels per treatment were observed during each observation. A fish was considered as active when it was observed out of the substrate. Daytime observations were performed in the morning between 0900 and 1100 hours. Activity was quantified by 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., 15 min per channel), and the total number of active fish observed was counted. Nighttime observations were conducted during the early part of the night between 2030 and 2230 hours using a flashlight with a red filter to avoid disturbing the fish (Reebs 2002). Fish were detected, identified and counted by briefly scanning the water surface from the downstream to the upstream end of the channels. Counts were repeated twice by two different observers (S. B. and G. L.) and the mean of these two observations was used to quantify the number of active fish during the night.

Salmon growth rate

Marked Atlantic salmon were measured (±1 mm) and weighed (±0.01 g) both at the beginning and at the end of the experiment. Individual instantaneous growth rate (G) was calculated using the following formula:

$$G_{ij} = \frac{\ln(W_{i_{t2}}) - \ln(W_{i_{t1}})}{\text{t2} - \text{t1}}$$

where G_{ij} is the daily growth rate of individual i in the channel j, $W_{i_{t1}}$ is the weight of fish i at the beginning of the considered growth period, $W_{i_{t2}}$ is the weight of fish i at the end of the experiment and ($t2 - t1$) equals 28 days.

Invertebrate biomass change

We sampled five spherical cobbles of equal size (12–13 cm in diameter) in each channel on two occasions: (1) just before adding the fish (after the 20-day incubation period), and (2) at the end of the experiment (after the additional 28 days). Benthic invertebrates were sampled by placing a frame with a net (mesh size 250 μm) directly downstream of a stone, which was then lifted and scraped into the net. Invertebrates dislodged from the stone and caught by the net were preserved in 95% ethanol and all individuals were identified, counted and separated according to family, as trophic status is relatively homogeneous within a given family (Merritt and Cummins 1996). Most of the invertebrates we collected belonged to families of small-size invertebrates (Chironomidae, Baetidae, Hydropsychidae, Psychomiidae, Glossosomatidae) and most of them were potential prey for juvenile salmonids (Keeley and Grant 1997). In our samples, grazers were mainly represented by two Trichoptera families (Glossosomatidae and Psychomiidae) and one Ephemera family (Baetidae). Specimens were dried at 60°C for 24 h before being weighed by family (±0.00001 g). We calculated the total biomass of grazers for each period by summing the dry biomass of all these families. Glossosomatidae were not included in this total biomass for two reasons. First they were abundant during the first sampling occasion but absent at the end of the experiment. This suggests that they had emerged during the experiment and were therefore not prone to have contributed substantially to the grazing activity (the final biomass of chlorophyll *a* was not significantly related to the initial biomass of Glossosomatidae, $r = -0.11$, $P = 0.54$). Secondly, these larvae are enclosed in cases composed of sand grains cemented with silk that makes them less available to fish predation (Ruetz et al. 2004; Zimmerman and Vondracek 2007), particularly for YOY salmonids that are gape-size limited (Keeley and Grant 1997). At the beginning of the experiment, the average biomass of invertebrates was 1.52 ± 0.62 g m^{-2} (mean ± SD) and did not differ among treatments [$F(6, 21) = 1.25$, $P = 0.32$]. To evaluate the effect of secondary consumers on primary consumers, we calculated the change in biomass of grazers from the first sampling occasion to the last sampling occasion.

Chlorophyll *a* biomass change

At the beginning of the experiment, we homogeneously distributed 12 ceramic tiles (20.2 cm^2 each) in each channel. In each experimental unit, we sampled six ceramic tiles on each of two occasions: just before adding the fish (after the 20-day incubation period), and at the end of the experiment (after the additional 28 days of the experiment). After collection, all ceramic tiles were placed in aluminum foil and rapidly frozen (−80°C) before chlorophyll *a* concentrations were measured in the laboratory (see Dahl and Greenberg 1999). In the laboratory, pigments were extracted with 95% ethanol and chlorophyll *a* was measured using a spectrophotometer (Cary 300 Bio UV–Visible). At the beginning of the experiment, the average biomass of chlorophyll *a* was 1.65 ± 0.42 μg cm^{-2} (mean ± SD) and did not differ among treatments [$F(6, 21) = 1.24$, $P = 0.32$]. To evaluate the effect of primary consumers on primary producers, we calculated the change in chlorophyll *a* biomass from the first sampling occasion to the last sampling occasion.

Statistical analyses

In all subsequent analyses, we used the mean value of each parameter per channel as the replicate unit. Data obtained from the control treatment (fishless) were not included in the analyses but are only presented for the purpose of comparison.

Fish 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 relatively low: ~0.25 individuals channel^{-1}). We assessed the influence of period of observation (daytime and nighttime), competitive treatments (low intraspecific, high intraspecific and interspecific) and predatory treatments (presence or absence of predatory cues) on the proportion of active salmon. We used mixed linear models with channel as the random factor (to account for repeated measures and thus for non-independence between the replicate units; Faraway 2006). Period of observation, competitive treatments and predation treatments were the fixed categorical predictors. Multiple comparisons were performed using contrast tests. The proportion of active salmon was arcsine transformed to meet the assumptions of normality and homoscedasticity.

Fish growth rate, invertebrate biomass change and chlorophyll *a* biomass change

To explore the influence of competition, predation and abiotic factors on the biomass of each food chain component, we fit three independent generalized linear models (GLMs) with fish growth rate, invertebrate biomass change and chlorophyll *a* biomass change as response variables, respectively. Competition treatments and predation treatments were the categorical predictors. Water velocity and the water depth in each channel were the fixed continuous predictors. Because the strength of top-down effects can depend upon the initial resource level (Chase 2003), we included the initial resource level for the invertebrate biomass change and the chlorophyll *a* biomass change as possible covariates (i.e., the biomass of invertebrates and of chlorophyll *a* present at the beginning of the experiment, respectively). Because ecological processes are often non-linear (Begon et al. 1996), we included quadratic term(s) to test for possible non-linear relationships. The inclusion of quadratic terms provides an opportunity to reveal both U-shaped and inverted U-shaped curves which are commonly encountered in the theory of optimality (Begon et al. 1996). With U-shaped relationships, the main term is expected to be negative while the quadratic term is expected to be positive. In contrast, with inverted U-shaped relationships the main term is expected to be positive while the quadratic term is expected to be negative (Faraway 2006). Non-significant quadratic terms were excluded from the final models (Faraway 2006). The possible interactions between abiotic predictors and the categorical predictors were evaluated but deleted from the models as none of them were significant. Gaussian error distributions were assumed for all the traits.

Disentangling competing hypotheses

Finally, we combined path analyses (Shipley 2000) and a model selection procedure (Johnson and Omland 2004) to explore causal relationships among variables in this food chain and particularly to disentangle the role of competition, predation and abiotic factors in shaping such a food chain. Path analysis is a statistical method in which the paths between variables are relationships (expressed as equations) where the response variables are driven by predictor(s). The response variables in one equation may form predictors in others, thereby forming sequences of causal relationships (Shipley 2000). A model selection procedure is used to compare a particular set of a priori hypotheses, each expressed by a model (see Johnson and Omland 2004). Here we compared nine different competing models. Models were based on the different processes hypothesized to control a food chain in natural ecosystems (illustrated in Fig. S2 in the Electronic Supplementary Material). Each model has in common the inclusion of three response variables (i.e., salmon growth rate, invertebrate biomass change and chlorophyll *a* biomass change). We hypothesized that this food chain can be structured by competition and predation exerted on fish and/or by abiotic factors. Furthermore, we hypothesized that the three response variables can be linked together by either top-down or bottom-up links, or both. These terms stipulate that the biomass of one component causes a change in the biomass of a lower level (top-down link) or a change in biomass of a superior one (bottom-up link). Thus, the first three models included competition and predation as possible initiators of direct and indirect effects, and bottom-up links, top-down links or both as possible causal links between response variables (model 1–3, Fig. S2). Three others models included the effects of abiotic factors, bottom-up links, top-down links or both (model 4–6, Fig. S2; we integrated only water velocity in these analyses as water depth had no effect in preliminary analyses; see also the Results). Finally we built three models that integrated the effects of competition, predation and abiotic factors plus bottom-up links, top-down links or both (model 7–9, Fig. S2).

In path analyses, a model is judged as being interpretable when the covariance structure of the model does not differ from that of the data (tested with maximum likelihood χ^2 statistic; a non-significant χ^2 identifies a good fit between predicted and observed covariance matrices). Then, model comparisons were achieved using the Akaike information criterion (AIC). In model comparisons using AIC, the model with the lower AIC value is considered to be the one which is best supported by the data (Johnson and Omland 2004). In addition, we calculated the Akaike weight (W_i) which can be interpreted as the probability that a given model i is the best model for the observed data, given the candidate set of models (see Johnson and Omland 2004 for calculation of W_i).

Analyses were performed using R version 2.2.1. (R Development Core Team 2005), except path analyses which were performed using the software program AMOS 5 (Arbuckle 2003).

Results

Fish diel activity

Overall, the proportion of juvenile Atlantic salmon that were active was not influenced by either water velocity or by water depth (see Table S3 in the Supplementary Electronic Material for the full table of *P*-values). The proportion of active salmon was significantly higher during the night than during the day (Fig. 1, Table S3). We detected significant interactions between periods of observation and competitive treatment and between periods of observation and predation treatment (Table S3). The first interaction indicated that the proportion of salmon active during daytime was significantly higher when salmon occurred with rainbow trout than when salmon occurred at a low density (Fig. 1). In contrast, during nighttime, competitive treatments did not affect the proportion of salmon that were active (Fig. 1). The second interaction indicated that during the day, but not during the night, the proportion of salmon active was significantly lower when predator cues were present (Fig. 1). The non-significant three-term interaction indicated that juvenile Atlantic salmon were more active during the day when together with rainbow trout, and that this trend was independent of whether predatory cues were absent or present (Fig. 1, Table S3).

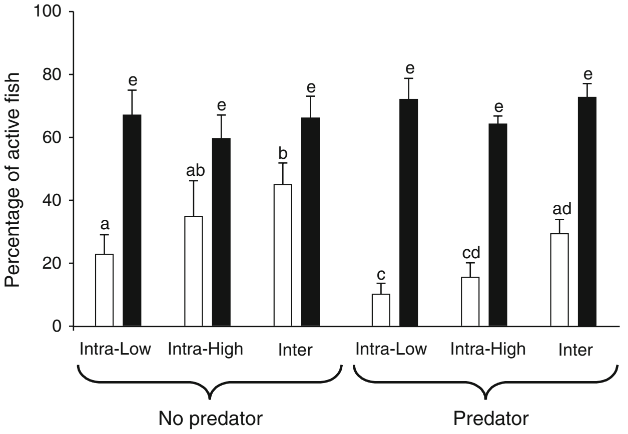

Fig. 1 Percentage (+SE) of juvenile Atlantic salmon (*Salmo salar*) that were active during the day (*white bars*) and night (*black bars*) under three competitive treatments (*Intra-Low* low intraspecific competition, *Intra-High* high intraspecific competition, *Inter* interspecific competition with juvenile rainbow trout) and two predation treatments (absence or presence of predatory cues emitted by adult rainbow trout). Statistically identical results ($P > 0.05$, contrast tests) are identified by the *same letter*

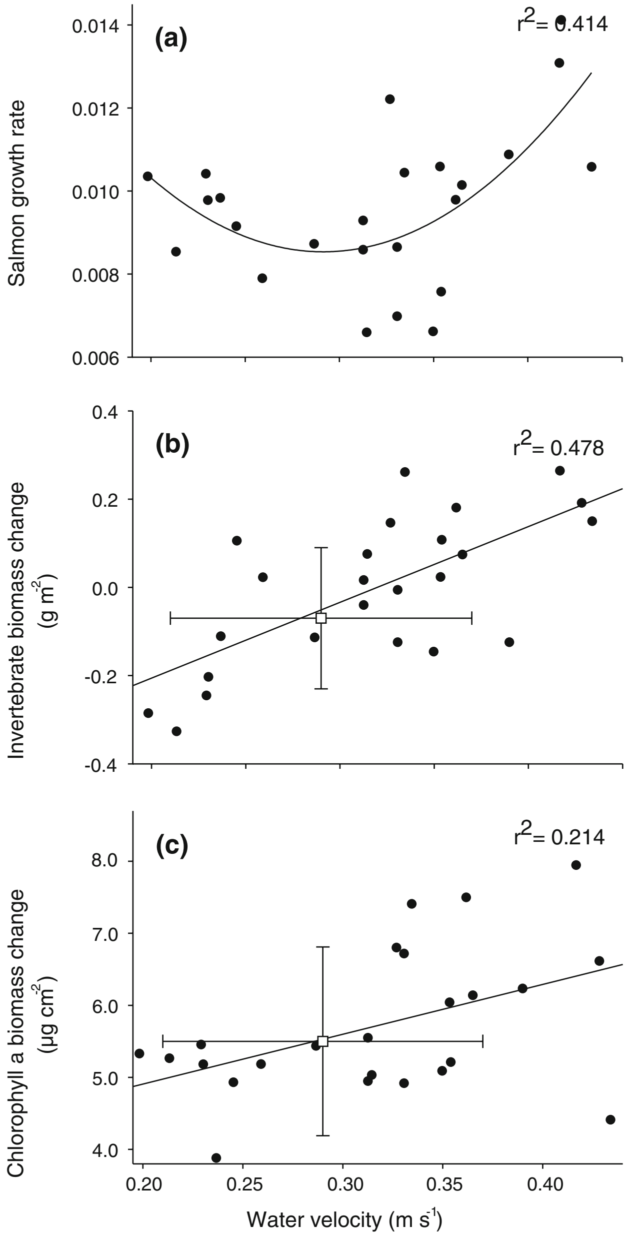

Fig. 2 Univariate relationships between the surface water velocity in each channel and **a** salmon growth rate, **b** invertebrate biomass change and **c** chlorophyll *a* biomass change. The coefficient of determination (r^2) of each relationship is indicated. For comparison, control data (the fishless treatment) are added to **b** and **c** with water surface velocity (mean ± SE) and average change in biomass (*square*, ±SE) of invertebrates **b** and chlorophyll *a* **c**. The data points from the fishless treatments were not included when calculating the linear predicted response

Fish growth rate, invertebrate biomass change and chlorophyll *a* biomass change

We found a significant U-shaped relationship between the growth of juvenile Atlantic salmon and the water velocity (Table 1, Fig. 2a). The growth of Atlantic salmon was higher for either lower or higher water velocity (Fig. 2a). It is worth noting that these tendencies cannot be extrapolated beyond the range of observed current velocities as growth rate cannot be expected to rise indefinitely with increasingly faster or slower currents. Water depth did not influence the growth of salmon (Table 1). The presence of fish competitors (either intra- or interspecific) and/or the presence of predatory cues did not influence the growth of salmon (Table 1). For the invertebrate component, we found that the biomass increase of invertebrate grazers was positively correlated with the current velocity (Table 1, Fig. 2b). We found no effect of water depth but the initial biomass of grazers negatively influenced the biomass increase (Table 1). Neither the presence of competitors (intra- or interspecific) nor the presence of predatory cues influenced the biomass increase of invertebrate grazers (Table 1). The presence of fish had no influence on families of non-grazer invertebrates (mainly Chironomidae and Hydropsychidae; results not shown). Finally, we found that the increase in chlorophyll *a* biomass was positively correlated with water velocity (Table 1, Fig. 2c). Neither water depth nor the initial biomass of chlorophyll *a* influenced the biomass increase of chlorophyll *a* (Table 1). Visually, it seems that the presence of fish (whatever the species composition and/or the density) did not influence the biomass of invertebrates and chlorophyll *a*, as the average values of the invertebrate biomass change and the chlorophyll *a* biomass change for the fishless treatment were similar to those of the fish treatments (Fig. 2b, c). To test this, we computed GLMs that integrated treatment (with 7 categories), water depth and water velocity as fixed

Table 1 Result of generalized linear models used to evaluate the effects of competition and predation risk imposed by the exotic rainbow trout, water velocity and water depth on the growth rate of Atlantic salmon, the biomass change of invertebrates and the biomass change of chlorophyll *a*, respectively. The initial resource biomasses (only for the invertebrates and the chorophyll *a* components) calculated for each channel were included as covariates. Quadratic terms were included when necessary (see the text). Significant *P*-values ($P < 0.05$) are in *bold*

Source of variation	Salmon growth rate			Invertebrate biomass change			Chlorophyll *a* biomass change		
	df	*F*-value	*P*-value	*df*	*F*-value	*P*-value	*df*	*F*-value	*P*-value
Water velocity	1, 22	4.63	**0.048**	1, 22	28.77	**0.000**	1, 22	5.66	**0.031**
Water velocity^2	1, 21	10.83	**0.005**	–	–	–	–	–	–
Water depth	1, 20	1.13	0.304	1, 21	0.92	0.351	1, 21	0.05	0.833
Initial resource biomass[a]	–	–	–	1, 20	7.73	**0.013**	1, 20	3.57	0.078
Competition treatment	2, 18	2.57	0.109	2, 18	1.71	0.214	2, 18	0.24	0.790
Predation treatment	1, 17	0.27	0.609	1, 17	1.96	0.181	1, 17	0.21	0.652
Competition × Predation	2, 15	0.18	0.839	2, 15	1.15	0.341	2, 15	0.52	0.606

[a] Initial resource biomass was, for the invertebrates and the chorophyll a components respectively, the biomass of invertebrate and the biomass of chlorophyll a present in each experimental unit before introducing the fish

factors. We did not find any significant treatment effects for invertebrate biomass change [GLM, treatment effect, $F(1, 19) = 2.15$, $P = 0.095$] or chlorophyll *a* biomass change [GLM, treatment effect, $F(1, 19) = 0.38$, $P = 0.882$].

Disentangling competing hypotheses

Among the nine models we tested, model 4 had the lowest AIC value (Table 2, Fig. 3) and was therefore considered as the best model for fitting our dataset. This model also had the highest probability (53%, Table 2) of being the best model for the observed data. This model had a non-significant χ^2 statistic, and all standardized regression weights were significant (Fig. 3). The percentage of variance explained was 53, 59 and 21% for the growth rate of Atlantic salmon, the change in biomass of invertebrates and the biomass change of chlorophyll *a*, respectively (Table S4 in the Supplementary Electronic Material). In this model, water velocity had a direct effect on all three trophic levels (Fig. 3, Table S4). This effect was particularly strong for the growth rate of salmon, with a significant curvilinear effect (Table S4, see also Fig. 2a). The effect of water velocity was linear and positive for both the change in biomass of invertebrates and of chlorophyll *a* (Fig. 3, Table S4). We also found an indirect positive effect of water velocity for both the growth of Atlantic salmon and the change in biomass of invertebrates (Table S4). These indirect effects were the result of bottom-up links from the chlorophyll *a* to salmon. Indeed, the water velocity positively affected the biomass of chlorophyll *a*, which in turn positively contributed to the biomass increase of invertebrates, which itself favoured the growth of juvenile Atlantic salmon (Fig. 3, Table S4).

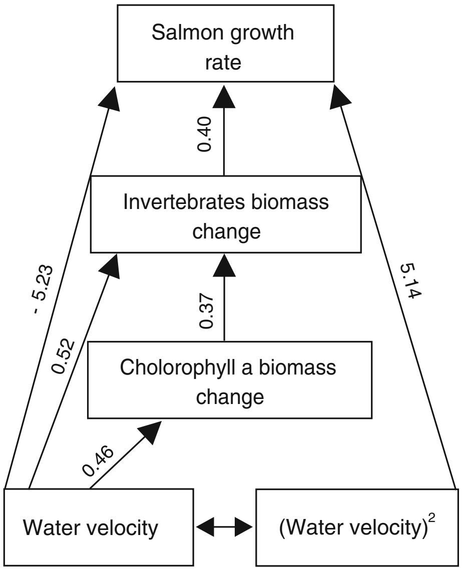

Fig. 3 Structure of the best model retained to explain the functioning of the food chain under study. Eight other competing models were tested (see Table 2, Fig. S2). In this model, there is a strong influence of surface water velocity on the different food web components, and each component was linked by bottom-up processes. *Single-headed arrows* indicate causal relationships and their path coefficients. *Double-headed arrow* indicates two variables that covary. Path coefficients for each relationship are indicated; they were all significant ($P < 0.05$)

For comparison, we recalculated these models while integrating the total biomass increase of both fish species together instead of the growth of the four marked Atlantic salmon. The main results remained unchanged (results not shown), indicating that conclusions about trophic relationships did not change when including the two competitive species at the same consumer level.

Table 2 Summary of the nine competing models built to disentangle the role of competition, predation risk, water velocity, top-down links and bottom-up links in shaping the studied food chain (see also Fig. S2)

Model[a]	Water velocity	Competition + Predation	Bottom-up link	Top-down link	χ^2 statistic	*df*	*P*-value	AIC value	W_i value
M1		X		X	11.02	6	0.088	29.03	0.102
M2		X	X		14.10	6	0.028	32.14	0.022
M3		X	X	X	13.56	4	0.034	31.88	0.025
M4	X		X		1.74	3	0.628	**25.74**	**0.532**
M5	X			X	4.30	3	0.233	28.27	0.150
M6	X		X	X	0.25	1	0.875	28.03	0.169
M7	X	X	X		18.84	12	0.093	50.84	<0.001
M8	X	X		X	18.66	12	0.097	50.66	<0.001
M9	X	X	X	X	17.08	10	0.073	53.08	<0.001

[a] Models M1–M3 included competition and predation as possible initiators of direct and indirect effects, and bottom-up processes, top-down processes or both as possible links between responses variables. Models M4–M6 included the direct and indirect effects of water velocity, bottom-up links, top-down links or both. Models M7–M9 included the effects of competition, predation risk, water velocity plus bottom-up links, top-down links or both. For a given model, a non-significant χ^2 statistic indicates a good fit between predicted and observed covariance matrices. The best model (highlighted in *bold*) for fitting the data has the lowest Akaike information criteria (*AIC*) value and the higher Akaike weight (W_i) probability

Discussion

Our study demonstrated that an exotic species that can be both a competitor and a predator strongly modified the diel activity pattern of a native species. However, we found no evidence that either fish density or the presence of exotic species affected the growth rate of the native species. Furthermore, neither competition nor predation mediated indirect effects on lower trophic levels. In contrast, we found strong evidence that the system was controlled by an abiotic factor, the water velocity, and that bottom-up processes linked the trophic components of this food chain.

We demonstrated that both competition and predation imposed by the exotic rainbow trout modulated the diel activity, and specifically the daytime activity of juvenile Atlantic salmon. The impact of competition and predation on diel activity patterns has been recognized as important in influencing community structure (Kronfeld-Schor and Dayan 2003; Kelt et al. 2004). However, the simultaneous effects of both forces on species activity have yet to be considered. In the study system analyzed here, these two forces had opposite effects. Indeed, juvenile Atlantic salmon were, on average, more active during the day when in the presence of the competitive rainbow trout. This trend probably resulted from both density-dependent and species-specific effects. Indeed, the effect of doubling the density of Atlantic salmon was intermediate to the effect of adding interspecific competitors, indicating that the effect of rainbow trout was not solely species-specific (see also Blanchet et al. 2007a). In contrast, the presence of predator cues decreased the daytime activity of juvenile Atlantic salmon, as already demonstrated in other animals (Kelt et al. 2004). In general, when animals are confronted with the trade-off between the necessity of escaping predators and of acquiring resources, theoretical models predict that for behavioral traits, the effect of predators should be strongest when competition is weak (Luttbeg et al. 2003; Teplitsky and Laurila 2007). Our results do not support this prediction since the effect of predation was not lower when the density of fish was presumably high (i.e., high intra- or interspecific competition treatments). Instead, the effect of predation was constant for all the competitive treatments.

Predation and competition had, however, no effects on the growth rate of Atlantic salmon. During the day, we also evaluated how the feeding rate varied among treatments (results detailed in Table and Fig. S5 in the Electronic Supplementary Material). We observed that the feeding rate of Atlantic salmon was on average lower in the presence of predatory cues and higher in the presence of competing rainbow trout (Table and Fig. S5). This indicated that daytime activity was a good surrogate of the feeding rate of Atlantic salmon. We thus suggest that Atlantic salmon modulated their daytime activity according to the treatments, and were able to maximize the energy gain afforded by feeding rate and discounted by activity costs (such as swimming against the current). This result is consistent with recent field studies emphasizing the fact that animals compensate their behavior to maximize growth, even if this strategy is risky in terms of predation risk (Biro et al. 2003).

Given the theoretical background on indirect effects, we expected that competition and predation would have initiated significant indirect effects on lower trophic levels (Abrams 1995; Werner and Peacor 2003; Abrams 2007). However, we found no such evidence as there was not any effect of competition and predation on either the biomass of grazers (i.e., primary consumers) or on the biomass of periphytic algae (i.e., primary producers). The absence of a top-down effect of secondary consumers in the study system was also supported by the observation that the biomass of primary producers and primary consumers was identical between the fishless treatment and the fish treatments. This absence of a trophic cascade contrasted with previous studies in similar ecosystems (e.g., McIntosh and Townsend 1996; Dahl and Greenberg 1999; Baxter et al. 2004) and in others ecosystems (e.g., Schmitz et al. 1997; Pringle et al. 2007). Two non-exclusive hypotheses might explain this discrepancy. First, Atlantic salmon may feed on invertebrate groups other than grazers (e.g., filterers such as Chironomidae) which were excluded from the food chain analyzed in this paper. Secondly, YOY salmonids are gape-size-limited predators that may feed preferentially on the smallest prey, and may thus not be able to significantly reduce the biomass and/or the behavior (including grazing and emigration) of grazers. However, the analyses of gut contents of the fish at the end of the experiment demonstrated that Atlantic salmon (and rainbow trout) fed on all invertebrate groups and fed over the entire invertebrate size range observed in the benthic and drift samples (S. Blanchet, personal observation). Furthermore, rainbow trout were highly active during the day (48% of the juveniles were active on average during the day) and had a higher feeding rate than that of Atlantic salmon (results not shown). Thus, the addition of juvenile rainbow trout should have resulted in a stronger trophic cascade (resulting in a higher biomass of chlorophyll *a*). Given that the biomass of invertebrates and chlorophyll *a* did not change between the fishless treatment and the interspecific competition treatment, this suggests that even the addition of an additional secondary consumer did not induce trophic cascades. Finally, it could be argued that increasing fish densities in our stream channels would eventually lead to a significant top-down effect. However, one must keep in mind that the densities we used were in the upper range of what is found in nature for most salmonid species (see for instance Bilby et al. 1998 for Pacific salmon, Hendry et al. 2004 for brown trout, Imre et al. 2005 for Atlantic salmon). Increasing fish densities beyond those encountered in nature to trigger top-down effects would thus be of limited interest to understanding trophic dynamics in nature.

According to the trophic cascade hypothesis, top-down links between food chain components were expected. Instead, we found that food chain components were linked together through bottom-up processes operating from primary producers to secondary consumers. Using pond ecosystems, Chase (2003) and Wojdak (2005) demonstrated that the strength of top-down effects decreased as the productivity of the ponds increased. Bottom-up effects prevailed in high-productivity ponds. In light of these results, we speculate that the prevalence of bottom-up processes in our study system probably reflects the high primary productivity of the Malbaie river. Indeed, the biomass of periphytic algae (primary producers) was up to 2 times higher in our study system than in other salmonid streams where top-down effects have been detected (e.g., McIntosh and Townsend 1996; Dahl and Greenberg 1999; Baxter et al. 2004). Concomitantly, we cannot exclude the possibility that the processes of emigration, immigration and colonization are principally responsible for structuring the community of invertebrate grazers and thus, might have masked the top-down effect of secondary consumers on invertebrate biomass and hence on periphyton biomass. This latter hypothesis is consistent with recent theories and experimental work that emphasize the role of dispersal in structuring communities and ecosystems in space and time (Leibold et al. 2004; Howeth and Leibold 2008).

Furthermore, we demonstrated that the biomass of the trophic components was highly dependent on water velocity. Effects of abiotic parameters (such as light, nutrients, habitat characteristics) along food chains have been demonstrated in several ecosystems (e.g., Leonard et al. 1998; Vucetich and Peterson 2004; Mallory and Richardson 2005). We observed that water velocity increased the biomass of chlorophyll *a*. This was already observed by Biggs et al. (1998) and the relationship seems to be strongly dependent upon the community growth form of the periphytic algae. Indeed, dense and coherent growth forms are less sensitive to shear stress induced by high water velocity, and higher water velocity may enhance nutrient delivery rates (Biggs et al. 1998). As a result, increased water velocity indirectly favored the biomass of primary and secondary consumers via bottom-up processes.

In addition, we demonstrated that water velocity also had strong direct effects on the biomass of both primary and secondary consumers. Indeed, it has been demonstrated that water velocity affects grazer efficiency and patterns of emigration and colonization in benthic invertebrates (reviewed in Hart and Finelli 1999). For instance, *Baetis sp.* (the dominant grazer group in our experiment) had a higher grazing efficiency at higher water velocity (Poff et al. 2003). Although other abiotic factors no doubt influence the biomass of primary producers, we hypothesize that channels with higher water velocity supported a higher biomass of grazers because: (1) resource biomass was higher (the indirect effect of water velocity through the enhancement of the biomass of primary producers), (2) grazing efficiency was better (the direct effect of water velocity), and (3) the colonization rate was higher. The growth rate of Atlantic salmon was higher for both high and low current velocities. At low current speeds, minor swimming costs may counteract the low delivery rate of prey. In high current speeds, the high rate of prey delivery may counteract increased activity costs and thus complex trade-offs between physiological demands and the availability of drifting prey could explain such a pattern (Girard et al. 2004).

Conclusions and implications

A growing number of studies have identified the importance of temporal partitioning in structuring communities and facilitating species coexistence (reviewed in Kronfeld-Schor and Dayan 2003). Our study revealed that competition and predation exerted by an exotic species modified the daytime activity pattern of a native species. This finding highlights the importance of behavioral plasticity in dealing with environmental variability and with the trade-off between growth and mortality. This result has also strong implications for the conservation of native species as it highlights a pervasive effect of exotic species. Indeed, the increased daytime activity of Atlantic salmon observed when together with the rainbow trout was maintained even when the exotic predator was present. Hence, because daytime is a period recognized to increase the risk of predation (Reebs 2002; Kronfeld-Schor and Dayan 2003), the competitive effect of rainbow trout may be detrimental to the survival of Atlantic salmon.

Our results also showed that, contrary to most previously published studies, indirect effects initiated by either predation, competition or both were not detectable. Indeed, competition and predation imposed by the exotic species had no cascading effect on lower trophic levels. We believe this result is important, particularly for ecologists working on open systems in which neutral processes such as dispersal might play an important role in structuring communities and species interactions. The absence of top-down processes may also be the result of the masking effect of the high productivity of the system (Chase 2003; Wojdak 2005). This result is important as it suggests that high productivity might, in certain cases, buffer the cascading ecosystem impacts of invading species (White et al. 2006).

Finally, the strong direct effect of water velocity we identified underlines the importance of simultaneously considering abiotic as well as biotic factors to understand food chain mechanisms and ecosystem functioning. Such an integrated approach is essential for managers and conservationists interested in preserving biodiversity at the ecosystem level, as it should help identify factors that could limit the impacts of the many anthropogenic perturbations in ecosystems (Franklin 1993).

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