

Invasive brook trout disrupt the diel activity and aggregation patterns of native brown trout

Nicolas Larranaga, Magnus L. Wallerius, Haoyu Guo, Julien Cucherousset, and Jörgen I. Johnsson

Abstract: In European streams, native brown trout (*Salmo trutta*) feed primarily on aquatic prey but consume a higher proportion of terrestrial prey in sympatry with non-native brook trout (*Salvelinus fontinalis*). This is a rare example of diet convergence that may be associated with changes in diel activity or aggregation pattern by brown trout in sympatry. We recorded the activity and positions of brown trout from two origins and in two competition modes (allopatry versus sympatry, four combinations) placed in replicated stream enclosures for 29 days to test these hypotheses. Brown trout originating from or placed in sympatry were more diurnal and aggregated than those originating from or placed in allopatry. Changes in the diel activity of brown trout placed in a novel competition mode occurred progressively throughout the study. Thus, brown trout show strong behavioral flexibility in response to the non-native competitor and can revert to allopatric behavior when brook trout is removed from the system. These behavioral adjustments may have unsuspected effects on food webs and ecosystem functioning, which deserve further attention.

Résumé : Dans les cours d'eau européens, les truites brunes (*Salmo trutta*) indigènes se nourrissent principalement de proies aquatiques, mais consomment une plus forte proportion de proies terrestres quand elles sont en sympatrie avec des ombles de fontaine (*Salvelinus fontinalis*) non indigènes. Il s'agit d'un rare exemple de convergence de régimes alimentaires qui pourrait être associée à des changements de l'activité nyctémérale et du motif de regroupement par les truites brunes sympatriques. Nous avons enregistré l'activité et les emplacements de truites brunes de deux origines et pour deux modes de concurrence (allopatrie et sympatrie, quatre combinaisons) placées dans des enclos doublés en rivière pendant 29 jours pour vérifier ces hypothèses. Les truites brunes d'origine sympatrique ou placées en sympatrie étaient plus diurnes et regroupées que celles d'origine allopatricque ou placées en allopatrie. Des changements de l'activité nyctémérale des truites brunes mises dans un nouveau mode de concurrence se sont produits graduellement au fil de l'étude. Ainsi, les truites brunes présentent une forte souplesse comportementale en réaction au concurrent non indigène et peuvent reprendre un comportement allopatricque quand les ombles de fontaine sont retirés du système. Ces ajustements comportementaux pourraient avoir des effets insoupçonnés sur les réseaux trophiques et le fonctionnement d'écosystèmes, ce qui mérite plus d'attention. [Traduit par la Rédaction]

Introduction

Biological invasions have important ecological and evolutionary consequences on native biodiversity (Strayer et al. 2006; Ehrenfeld 2010; Lowry et al. 2013). One of the most common and pervasive effects of non-native species is competition for ecological resources (e.g., food and shelter), with native species displaying overlapping habitat and (or) trophic niches. This competition can have a number of impacts on native species, such as reduced growth rate, increased mortality and displacement (Didham et al. 2007). However, co-existence between native and non-native species can be facilitated by plastic phenotypic changes, such as behavioral adjustments allowing the partitioning in time and space of resources used commonly by native and non-native species. Those include shifts in diel activity patterns (Gerber et al. 2012), habitat use (Ayala et al. 2007), or prey selection (Strauss et al. 2006).

Because of competitive exclusion (Crowder and Snyder 2010), competition with non-native species is generally expected to result in diverging resource selection (Day and Young 2004). De-

pending on the relative competitive ability of non-native and native species, the former may change their diet in response to the latter (Harrington et al. 2009), or vice-versa (Gerber et al. 2012). Interestingly, co-existence between species using overlapping resources may also induce diet convergence (Cucherousset et al. 2007; Fox and Vasseur 2008). Several hypotheses have been put forward to explain this phenomenon. Convergence may occur when two species compete for several nutritionally essential resources that are limited in abundance (Fox and Vasseur 2008). It may also be caused by shifts in diel activity patterns (Gerber et al. 2012) or habitat use (Losos et al. 1993), whereby native species feed on an alternative prey type that is more abundant during their new window of activity or in their new habitat (Murdoch et al. 1975). Alternatively, diet selectivity of the native species may change following the introduction of the non-native species (e.g., via interspecific social learning; Seppänen and Forsman 2007). Identifying the mechanisms behind such a seemingly counterintuitive phenomenon as diet convergence is crucial to understand how native and non-native species interact. In particular, more

Received 20 March 2018. Accepted 11 August 2018.

N. Larranaga, M.L. Wallerius, and J.I. Johnsson. Department of Biological and Environmental Sciences, University of Gothenburg, Box 463, SE-405 30, Gothenburg, Sweden.

H. Guo. Department of Biological and Environmental Sciences, University of Gothenburg, Box 463, SE-405 30, Gothenburg, Sweden; The Key Laboratory of Mariculture, Ministry of Education, Ocean University of China, Qingdao 266003, China.

J. Cucherousset. Laboratoire Evolution et Diversité Biologique (EDB UMR 5174), Université de Toulouse, CNRS, ENFA, UPS, 118 route de Narbonne, F-31062 Toulouse, France.

Corresponding author: Nicolas Larranaga (email: nicolas.larranaga@bioenv.gu.se).

Copyright remains with the author(s) or their institution(s). Permission for reuse (free in most cases) can be obtained from [RightsLink](https://www.copyright.com).

empirical research is needed to evaluate to what extent the behavioral plasticity of native species allows them to respond rapidly to competition with invaders (Strauss et al. 2006; Berthon 2015) and also how rapidly they may recover when measures are taken to remove non-native species.

Salmonids have been introduced worldwide (Stanković et al. 2015) and represent an ideal model to study responses to invading competitors, as they demonstrate high behavioral plasticity (Dill 1983; Reeb 2002) and induce important ecological impacts on native salmonids (Buoro et al. 2016). Brook trout (*Salvelinus fontinalis*) in particular has been continuously introduced since the late 1800s in European streams, some of which were originally populated by native brown trout (*Salmo trutta*) (Hutchings 2014). Using stable isotope analyses, previous studies have compared the diet of brown trout in allopatry and sympatry with non-native brook trout (Cucherousset et al. 2007; Závorka et al. 2017) and demonstrated that while brook trout consumed primarily terrestrial invertebrates, the proportion of this food type in the diet of brown trout increased when they co-existed with brook trout (Cucherousset et al. 2007). However, the mechanisms leading to this trophic niche convergence remain unknown. Activity patterns may play an important role, because they mirror daily changes in food availability in streams. Allopatric brown trout are primarily active during dusk and early night (Alanärä et al. 2001; Závorka et al. 2016) and feed mostly on aquatic prey that drift at higher rate at night (Young et al. 1997; Giroux et al. 2000). In contrast, brook trout are predominantly diurnal (Allan 1981) and feed on terrestrial insects (Allan 1981; Závorka et al. 2017), whose activity is higher during daytime (Lewis and Taylor 1965). The diet of sympatric brown trout suggests that they may be more diurnal than allopatric brown trout. Such shifts have been reported previously (Blanchet et al. 2008) and may be due to behavioral plasticity, selection, or a combination of both.

This diet convergence may be alternatively explained by other behavioral mechanisms. A recent laboratory experiment revealed that brown trout keep shorter distances to brook trout than to conspecifics at the fry stage (Lovén Wallerius et al. 2017). If valid also for other life stages in the wild, this could indicate that sympatric brown trout remain closer to hetero- than conspecifics. In turn, this may induce diet convergence in at least two ways. Sympatric brown trout may be foraging in habitats where terrestrial prey are relatively more abundant or may acquire a preference for terrestrial prey by copying brook trout (Seppänen and Forsman 2007). Determining whether sympatric brown trout forage closer to brook trout than to conspecifics would be an important first step towards measuring the spatial overlap between the two species, and ultimately, understanding the proximate factors behind diet convergence.

In the present study, we compared the behavior of juvenile brown trout (age 1+) originating either from a sympatric or an allopatric site in presence or absence of non-native brook trout. For this purpose, we performed a 29-day replicated mesocosm experiment using a 2 × 2 full-factorial design with Origin (allopatry versus sympatry) × Competition mode (allopatry versus sympatry). Based on the reported diet convergence (Cucherousset et al. 2007; Závorka et al. 2017), we predicted that brown trout will be more day active in sympatry than in allopatry, and that brown trout of sympatric origin will be more day active than those of allopatric origin. Based on previous laboratory studies on fry (Lovén Wallerius et al. 2017), we predicted that brown trout from allopatric origin and in allopatric competition mode should maintain longer distances to other individuals, and that in the sympatric competition mode brown trout should remain closer to brook trout than to conspecifics. Finally, we predicted that behavioral

responses would be plastic; that is, brown trout will adjust their diel activity and aggregation pattern rapidly (i.e., within a week) in response to the competition mode.

Materials and methods

Study site and fish sampling

The study was conducted in stream Ringsbäcken, Sweden (57°39'44.1"N, 12°58'58.6"E). Brown trout are present throughout the stream, and brook trout also occupy the upstream sections, separating the stream into an allopatric part and a sympatric part (Závorka et al. 2017). On 29 May 2017, 90 brown trout and 30 brook trout of age 1+ were captured in Ringsbäcken by electrofishing (Smith-Root LR-20B, Vancouver, Washington, USA). More specifically, we captured 45 brown trout in the allopatric section, 45 brown trout and 30 brook trout in the sympatric section. Fish were maintained in stream containers overnight, and brown trout were separated from brook trout. On 30 May 2017, all individuals were anesthetized with 2-phenoxyethanol (0.3 mL·L⁻¹), measured for fork length to the closest mm (measuring board) and body mass to the closest 0.01 g (Valor 3000 Xtreme). On average (± standard deviation, SD), brown trout were 9.6 (±1.8) cm and 9.61 (±5.66) g. Brook trout were 9.0 (±1.4) cm and 7.07 (±3.51) g. Fish were then tagged with visible implant elastomer (Northwest Marine Technology, Shaw Island, Washington, USA). Four colors were used (red, green, orange, and yellow), and two tags were injected in the dorsal fin to create unique individual combinations in each enclosure and facilitate identification during overhead observations. Upon recovery, fish were released into one of the 12 enclosures to match experimental treatments.

Experimental setup

Between 25 and 28 May 2017, six pairs of enclosures made of nylon mesh (2.4 and 0.8 m along the length and width of the stream, respectively, 75 cm high) were set up in the stream at the downstream limit of the distribution of brook trout. Enclosures were set up in pairs separated by 5–10 m, and enclosures within a pair were separated by 20–80 cm (see online Supplementary data¹). The mesh size was 6 mm, which is small enough to contain fish but large enough to allow the invertebrates that salmonids feed on to drift through (Zimmerman and Vondracek 2006). The bottom of all enclosures was filled with a mixture of rocks, pebbles, and gravel from the study stream to mimic its microhabitat heterogeneity. This provided ample opportunity for fish to hide (e.g., in the interstitial zones between the rocks). A grid made of bamboo sticks (80 cm long, 0.8 cm thick) was placed over the substrate to serve as an *x*-*y* coordinate grid. Three sticks were placed along the length of the stream (*y* = 40), and three were placed along the width (*x* = 40, *x* = 120, and *x* = 200). The sticks were taped every 10 cm so the position of fish within enclosures could be determined to the closest 5 cm.

Brown trout were studied in two competition modes: allopatry (10 brown trout per enclosure, six enclosures) or sympatry (five brown trout and five brook trout per enclosure, six enclosures). We also separated brown trout based on their origin (i.e., from the allopatric or sympatric section of the stream). The four experimental treatments (allopatric origin – allopatric competition mode; allopatric origin – sympatric competition mode; sympatric origin – allopatric competition mode; sympatric origin – sympatric competition mode) were replicated three times. The question of the impact of brook trout on native brown trout has yielded equivocal results, as some studies report negative impacts (Öhlund et al. 2008; Závorka et al. 2017) while others suggest that brook trout use mostly places unoccupied by brown trout (Korsu et al. 2009). In our study stream, total densities of fish were similar

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2018-0110>.

between allopatry and sympatry sites. Therefore, a substitutive design was used: total density of fish was constant, and the proportion of each species was changed according to the competition mode (Fausch 1988).

Only one of each pair of enclosures contained brook trout (i.e., sympatry), and its position was alternated between the left and right side of the pair. The distribution of the origin among all enclosures was selected randomly at the start of the study. There were significant differences in body size among treatments, reflecting the natural distribution of brown trout body size between the allopatric and sympatric sections of the stream. Specifically, enclosures with brown trout from sympatric origin had larger individuals than those from allopatric origin (ANOVA, $df = 1$, $P < 0.001$ for length and mass). This resulted in brown trout from sympatry, but not allopatry, being larger than brook trout in sympatric enclosures (ANOVA, $df = 1$, $P = 0.012$ and 0.868 , respectively, for body mass). However, there were no differences between brown trout in allopatry and sympatry (ANOVA, $df = 1$, $P = 0.325$ and 0.162 for length and mass, respectively).

After 17 days, a flooding event due to heavy rainfall led to the escape of 35 individuals from all treatments (six in the allopatric origin – allopatric competition, 12 in the allopatric origin – sympatric competition, 13 in the sympatric origin – allopatric competition, and four in the sympatric origin – sympatric competition). These individuals were replaced with new fish captured in the same locations as the escaped individuals, and subjected to the same handling procedure, except one that was recaptured in the sympatric origin – sympatric competition treatment. The experiment was terminated on 27 June 2017 when all but eight individuals were recaptured and measured for body length and mass. Stomach samples were also collected before fish were released into the stream. The eight missing individuals were assumed to be dead.

Habitat characteristics and food availability

Water depth and current velocity (OTT Compact Current Meter C20, Kempton, Germany) were measured at 20 random locations in each enclosure at the start of the study. On average, water depth was $17.02 (\pm 1.47)$ cm and current velocity was $17.62 (\pm 1.94)$ $\text{cm}\cdot\text{s}^{-1}$. Habitats were similar among treatments (ANOVA, $df = 3$, $P = 0.689$ and 0.179 for depth and current velocity, respectively). The flow varied during the study, but we ensured that it remained similar among enclosures. Water temperature and light intensity were recorded automatically using three data loggers (UA-002-08 HOBO Pendant Temp/Light, 8K) positioned in three different enclosures. On average, water temperature was 13.41 ± 1.47 °C and light intensity was 1.69 ± 5.09 klux.

To assess the diel patterns of food availability, we measured the relative abundance of terrestrial and aquatic food at different times of the day. The amount of terrestrial input was estimated using 15 pantraps (30 cm × 40 cm) disposed randomly around the stream and containing 2–3 cm of water with a drop of ecofriendly soap. Five traps were opened during the day (0600 to 1800), five during crepuscular hours (0300 to 0600 and 1800 to 2100) and five at night (2100 to 0300). The invertebrates captured in the traps were collected after two 24 h cycles, and we repeated the process once, yielding 30 samples in total. The abundance of aquatic invertebrates was determined using driftnets (30 cm wide, 15 cm deep) positioned approximately 10 m downstream from the enclosures to avoid limiting food availability for experimental fish. Nets were set up in 22–26 cm water depth and 8–15 $\text{cm}\cdot\text{s}^{-1}$ current velocity. The driftnet was maintained in the water for 40 min every three hours (starting at 0000) for three 24 h cycles distributed throughout the study, yielding a total of 24 samples. Too few invertebrates were counted in the samples to determine food abundance, potentially because of the high density of fish in the enclosures depleting the resource at a fast rate. Therefore, we decided to use the number of exuviae in the sample instead,

which has been reported to accurately estimate the abundance of larvae (Ruse 1995). Daytime samples were collected at 0900, 1200, and 1500, crepuscular samples at 0600 and 1800, and night samples at 2100, 0000, and 0300.

Behavioral observations

Observations started on 1 July 2017 and finished on 24 July 2017. Pairs of enclosures were visited from downstream to upstream or vice versa (alternatively) for 15 min by an observer that stood motionless and recorded the activity status (active or inactive) of all individuals and the position of active individuals. We recorded activity eight times per day (i.e., every 3 h) over six 24 h cycles (i.e., every 3 days on average), yielding a total of 576 measurements of activity rates. The activity status of a fish was determined by whether it was inside or outside a shelter. Such method (i.e., detectability of individuals) has been used as a proxy for activity level in previous studies using telemetry (Roy et al. 2013; Závorka et al. 2017) and direct observations (appearance rates in Larranaga and Steingrímsson 2015). In the majority of observations, fish remained immobile, which facilitated the determination of x - y coordinates. Because light intensity at night (0000 and 0300 observations) was too low to detect fish, we used a flashlight with an adjustable beam size. The light was turned on only for a few seconds every 2–3 min. The size was maximized so light intensity was low to minimize fish disturbance. Most individuals could be correctly identified at that stage, but on few occasions we increased light by focusing the beam only to the point when a tag could be identified. Fish movement was not more frequent under those conditions than during the day, which indicates that the use of a flashlight had a negligible effect on fish (Larranaga and Steingrímsson 2015). The sides of the enclosures were cleaned after each session of observations.

Data analyses

For each observation, and in each enclosure, we calculated the percentage of active brown trout, hereinafter referred to as “activity rates” (Larranaga and Steingrímsson 2015). Measurements obtained within the same enclosure, as well as subsequent measurements (3 h difference), were not considered as not being independent. Therefore, we analyzed all behavioral results with linear mixed models (LMM) using enclosure and day of observation as random factors. Differences in activity rates among brown trout of different origin (allopatry versus sympatry), competition mode (allopatry versus sympatry), and between times of day (day versus night) were tested using a LMM. We included these three variables and their interactions as fixed factors (model M1). Daytime observations corresponded to measurements made between 0600 and 1800 and night observations from 2100 and 0300. In this model, the day of observation was considered as a random factor nested within the variable time of day (i.e., day or night). A separate model (LMM) was run to compare the activity rates between species (brown trout versus brook trout), and times of day (day versus night) in the sympatric competition mode.

We separated our data set into two subsets to distinguish immediate behavioral responses to experimental conditions from slower responses. More specifically, we compared activity patterns during the first 7 days of the study (period 1) with all observations performed later (i.e., from day 8 to day 29; period 2). Fish from six enclosures escaped after the second 24 h cycle of observations and were replaced with new individuals. We reset the time for those six enclosures after fish replacement. To limit the number of variables in this analysis, we used a single variable treatment with four categories (allopatric origin – allopatric competition mode, allopatric origin – sympatric competition mode, etc.) that encompasses information from the variables origin and competition mode. Activity rates of brown trout were compared across treatments, times of day (day versus night) and periods (first versus second) using a LMM (M2). In this model, the day of observation

was a random factor nested within the variable period (first or second).

For all observations after the first 24 h cycle of measurements (five cycles in total), and when two or more individuals were active, we calculated the distance between each fish and its nearest neighbor. In the sympatric competition mode, we also measured the distance between a fish and the nearest brown trout and brook trout. Hence, we were able to calculate three pair types of distance: brown trout – brown trout, brown trout – brook trout, and brook trout – brook trout. Based on these data, we calculated an overall index of aggregation sensu Clark and Evans (1954), modified by Petreere (1985) to account for differences in number of active individuals among observations. High values of this index indicate overdispersion (i.e., individuals are more dispersed than expected by chance). We obtained 300 measurements of aggregation that we analyzed using a LMM to measure the effect of competition mode, origin of brown trout and their interaction (M3). A second analysis was used to test if, in the sympatric competition mode, brown trout and brook trout maintain different distances to hetero- and conspecifics (pair type, M4). In both models, enclosure and day of observation were considered as random factors. When interaction terms were significant, Tukey post hoc tests were run to detect significant pairwise differences (see Supplementary data¹). Finally, differences in the abundance of terrestrial and aquatic food were assessed with Wilcoxon's sign-ranked tests. The lme4 package (Bates et al. 2015) was used to examine the effects of explanatory variables in all models described above in R 3.4.3 (R Core Team 2015).

We calculated specific growth rate (SGR, sensu Ostrovsky 1995) for all individuals recaptured at the end of the study. Most brown trout lost weight during the study (SGR = $-0.38 \pm 0.64\% \cdot \text{day}^{-1}$ in allopatric origin – allopatric competition, $-0.30 \pm 0.74\% \cdot \text{day}^{-1}$ in the allopatric origin – sympatric competition, $-0.67 \pm 0.85\% \cdot \text{day}^{-1}$ in the sympatric origin – allopatric competition, and $-0.20 \pm 0.65\% \cdot \text{day}^{-1}$ in the sympatric origin – sympatric competition). No difference was detected between brown trout of different origin or in different competition modes, (ANOVA, $P > 0.05$ for both variables; see online Supplementary data¹).

Results

Overall (mean \pm SD), 18.8% \pm 11.6% of brown trout were active during the observations. Brown trout from sympatric origin placed in allopatry were less active (14.58% \pm 13.32%) than brown trout from allopatric origin placed in allopatry (19.51% \pm 22.66%, post hoc test, $P = 0.009$) or in sympatry (19.72% \pm 17.70%, $P = 0.006$), and less active than brown trout from sympatric origin placed in sympatry (21.81% \pm 15.49%, $P < 0.001$; Table 1a; Fig. 1). Other pairwise comparisons were nonsignificant (Supplementary data¹). Brook trout were moderately but significantly less active than brown trout in sympatry (i.e., 18.1 (\pm 13.5) and 20.7 (\pm 16.6); $P = 0.034$).

Brown trout were more active during the night than during daytime (Table 1a; Fig. 1). Consistent with our predictions, brown trout were more diurnal in the sympatric than in the allopatric competition mode ($P < 0.001$), and those from sympatric origin were more diurnal than those from allopatric origin ($P < 0.001$). Brook trout distributed their activity more evenly throughout the day than brown trout, with no difference in activity rates between times of day (post hoc test, $P = 0.921$). Brown trout in the allopatric competition mode became more nocturnal during the second period ($P < 0.001$). In contrast, brown trout of allopatric origin placed in the sympatric competition mode became more diurnal over time ($P < 0.001$; Table 1a; Fig. 2). Brown trout of sympatric origin in the sympatric competition mode distributed their activity similarly throughout the day during the first and second period (see Supplementary data for more detailed pairwise comparisons of activity rates between times of day¹).

Table 1. Summary statistics (linear mixed model) on (a) activity rates of juvenile brown trout and (b) aggregation.

Model	Variable	df	Mean square	F value	P value
(a) Activity rate					
M1	Origin	1	1 334.4	9.459	0.014
	Competition mode	1	80.1	0.582	0.471
	Time of day	1	11 963.7	84.806	<0.001
	Origin \times competition mode	1	627	4.445	0.068
	Origin \times time of day	1	30 412.5	215.583	<0.001
	Competition mode \times time of day	1	12 931.1	91.66	<0.001
M2	Treatment	3	860.3	6.736	<0.001
	Time of day	1	429.9	3.366	0.067
	Period	1	539	4.221	0.204
	Treatment \times time of day	3	4 375.6	34.259	<0.001
	Treatment \times period	3	410.6	3.215	0.236
	Daytime \times period	1	1 637.8	12.824	0.023
	Treatment \times time of day \times period	3	2 466.2	19.310	<0.001
(b) Aggregation					
M3	Origin	1	94.16	25.116	<0.001
	Competition mode	1	24.25	7.535	0.021
	Origin \times competition mode	1	0.01	0.002	0.968
M4	Origin	1	5 617.7	24.208	0.060
	Pair type	2	281.38	1.922	0.174
	Origin \times pair type	2	279.26	2.171	0.141

Note: M1 and M2: the effects of origin (brown trout originating either from allopatry or sympatry), competition mode (allopatry and sympatry with brook trout), time of day (day and night), and period (week 1 versus rest of the study) on activity rates of juvenile brown trout. M3: the effects of brown trout origin and competition mode on aggregation (based on distance between individuals). M4: the effects of brown trout origin and pair type (brown trout – brown trout; brown trout – brook trout; brook trout – brook trout) on the distance to the nearest neighbor. Bold *P* values indicate significant effects.

During the study, aggregation (modified Clark–Evans index) was on average 1.27, suggesting that fish were more dispersed than expected by chance, with a standard deviation of 2.10 indicating large variation. Fish in the sympatric competition mode (both species) were more aggregated (1.01 ± 2.26 , average of brown trout and brook trout) than brown trout in the allopatric competition mode (1.74 ± 1.69 ; $P < 0.001$). In the allopatric competition mode, brown trout of sympatric origin (0.63 ± 1.88) were more aggregated than those of allopatric origin (2.04 ± 2.08 ; $P < 0.001$; Table 1b; Fig. 3A). An analysis of the distance between individuals showed that in the sympatric competition mode, both brown trout and brook trout maintained similar distance to hetero- and conspecifics (pair type; $P = 0.174$; Table 1b). This was true regardless of the origin of brown trout ($P > 0.05$ in all post hoc pairwise comparisons). Brown trout from allopatric origin tended to keep longer distances to both hetero- and conspecifics ($P = 0.060$; Table 1b) than those from sympatric origin (Fig. 3B). Finally, there was no significant difference in aggregation between the first and second period of the study ($P > 0.05$ in all four combinations of origin and competition mode).

On average, 4.44 (\pm 2.81) terrestrial invertebrates were captured in the pantraps per square metre per hour. This abundance was higher during the day (7.14 ± 2.18 items \cdot m⁻² \cdot h⁻¹) than during crepuscular hours (3.65 ± 2.25 items \cdot m⁻² \cdot h⁻¹) and during the night (2.53 ± 1.71 items \cdot m⁻² \cdot h⁻¹, Wilcoxon's sign-ranked test, $P < 0.05$ for all three pairwise comparisons). On average, 17.08 (\pm 8.03) exuviae drifted per square metre per minute in the stream. This abundance was greater at night (24.93 ± 4.92 items \cdot m⁻² \cdot min⁻¹) than during crepuscular hours (17.60 ± 2.83 items \cdot m⁻² \cdot min⁻¹) and daytime (8.89 ± 3.34 items \cdot m⁻² \cdot min⁻¹), and the differences were significant (Wilcoxon's sign-ranked test, $P < 0.05$) for all three pairwise comparisons.

Fig. 1. Activity rates (% of active individuals) of brown trout measured every 3 h over six 24 h cycles in experimental enclosures in allopatry (left) or in sympatry with brook trout (right). In sympatric conditions, the activity pattern of brown trout and brook trout are represented in black and green, respectively. Brown trout originated from either an allopatric (top) or sympatric (bottom) section of the study stream. Data are given as mean (solid line) \pm 95% confidence interval of the mean (dashed lines). [Color online.]

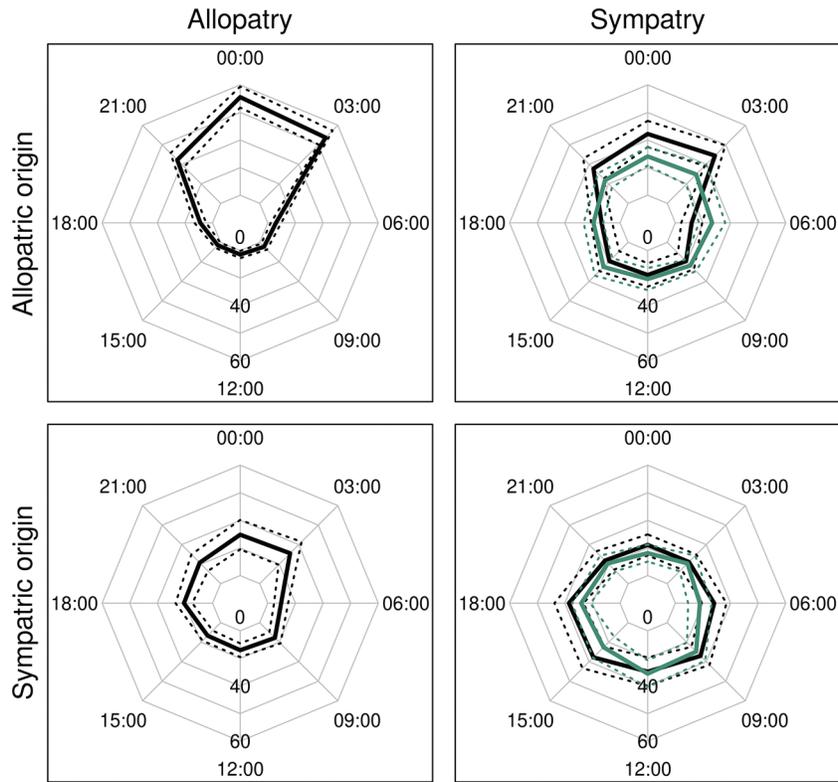
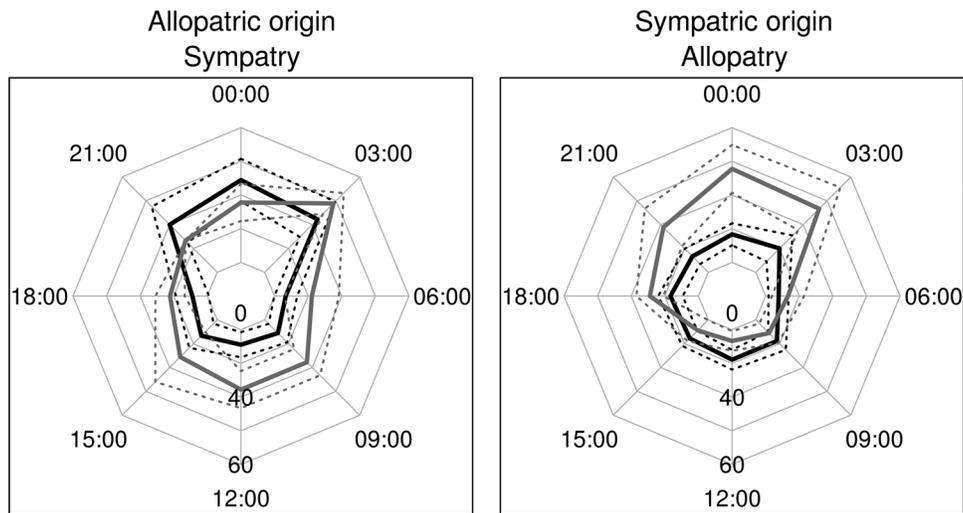


Fig. 2. Change in the timing of activity of brown trout (% of active individuals every 3 h during six 24 h cycles) from allopatric origin and placed in sympatry (left) or from sympatric origin and placed in allopatry (right), from the first period (week 1, black line) to the second period (rest of the study, grey line). Data are given as mean (solid line) \pm 95% confidence interval of the mean (dashed lines).



Discussion

This study demonstrated that native brown trout become more diurnal when brook trout are present. This effect was detected in less than 1 week and became stronger over the course of the study. When placed in allopatry, brown trout from the sympatric site were more diurnal than those from the allopatric site but gradually reverted to nocturnal activity. Sympatry also induces changes in aggregation, as brown trout from sympatric origin or in sym-

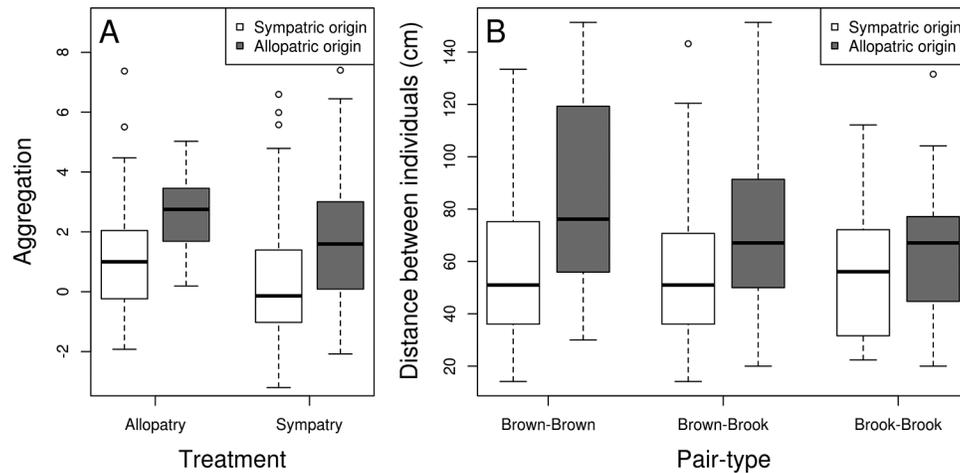
patric conditions were more aggregated than those from allopatric origin or in allopatric conditions.

Contrasting behavior in allopatry and sympatry

Consistent with previous studies, we found that allopatric brown trout were predominantly nocturnal (Young 1999; Závorka et al. 2016), and that brook trout were more diurnal than brown trout in sympatry (Allan 1981). Our results suggest that the longer

Can. J. Fish. Aquat. Sci. Downloaded from www.nrcresearchpress.com by GOTEBORGS UNIVERSITETSBIBL on 02/26/19 For personal use only.

Fig. 3. (A) Aggregation (modified Clark–Evans index) based on distance between individuals in enclosures containing fish from allopatric or sympatric origin and competition mode. Positive and negative values indicate situations when fish maintained longer and shorter distances than expected by chance, respectively. (B) Distance between individuals and the nearest brown trout and brook trout in enclosures containing both species.



brown trout are in sympatry with brook trout (origin versus competition mode), the more diurnal they become. Interspecific competition is generally expected to promote divergent diel activity patterns, which has been observed previously in a variety of organisms, including mammals (Gerber et al. 2012), reptiles (Pianka 1969), and insects (Caveney et al. 1995). Here, we present evidence for the opposite, convergent diel activity pattern, which to our knowledge has not been reported in the past. An earlier study suggested that native Atlantic salmon (*Salmo salar*) became more diurnal in presence of non-native rainbow trout (*Oncorhynchus mykiss*) (Blanchet et al. 2008) but did not report the activity patterns of the non-native species.

Several mechanisms may be responsible for these effects. One possibility is that they are mediated by interspecific social interactions, especially as the non-native brook trout is closely related to brown trout. During the day, stream-dwelling salmonids forage more efficiently (Rader et al. 2007) but are exposed to increased predation risk compared with night conditions (Metcalf et al. 1999). Competition for food with brook trout may encourage brown trout to engage in a riskier but more rewarding activity pattern (e.g., to secure optimal foraging positions and maintain fast growth during early life selective bottlenecks). Inversely, brown trout may have a preference for the more energetic terrestrial prey but adopt a risk-averse activity pattern with limited access to this prey type in allopatry. The presence of day-active brook trout may render diurnal activity safer, through a dilution of predation risk. This would also be supported by the higher aggregation in sympatric conditions. Brown trout have been found to use visual cues of brook trout to adjust their behavior at the fry stage (Lovén Wallerius et al. 2017). Similar adjustments may explain the present results and may be further strengthened if brown trout observe that brook trout activity patterns are rewarding and safe in our stream enclosures where predation risk is virtually null. Size differences between brown trout originating from sympatry and brook trout at the start of the study are unlikely to be a major driver of the observed results for two reasons. First, salmonids generally become more nocturnal as they grow (Imre and Boisclair 2004). In addition, activity timings became similar between brown trout originating from sympatry and allopatry at the end of the study, which also suggests that competition mode was a more important driver of behavior in this study.

Brown trout introduced to a novel competition mode, compared with their origin, showed contrasting activity patterns compared with brown trout remaining in their original condition.

These changes occurred rapidly (i.e., within 1 week after introducing fish in our experimental mesocosms), indicating strong behavioral plasticity in brown trout. This is in line with previous studies that suggest that salmonids adjust the timing of their activity rapidly in response to novel environmental conditions like rare shelters or high density (Larranaga and Steingrímsson 2015; Fingerle et al. 2016). Brown trout activity patterns in our study continued to change after the first week, which may be in part caused by seasonal changes (e.g., salmonids become progressively more nocturnal as light intensity and water temperature decrease over the summer; Fraser et al. 1993). However, this alone cannot explain our results, as brown trout from allopatric origin placed in the sympatric competition mode became more diurnal, even during the second phase of the study. This suggests instead that long-term exposure to non-native brook trout can influence the behavior of brown trout over several weeks.

Fish in sympatry were more aggregated, which was in part caused by brown trout remaining closer to brook trout. This is consistent with previous findings by Lovén Wallerius et al. (2017) and suggests that positive association between brown trout and brook trout may remain past the fry stage. Interestingly, brown trout from sympatric origin also reduced their distance to conspecifics, which may indicate a generally relaxed competition for space when brook trout is present. Aggregation in the sympatric competition mode may alternatively be a consequence of fish being more diurnal. Indeed, schooling can be elicited as an anti-predatory response during the day when predation risk is higher (Metcalf et al. 1999), as was suggested by Larranaga and Steingrímsson (2015).

Linking behavior and diet convergence

The present study suggests that activity patterns play an important role in the diet convergence observed in brown trout. Terrestrial prey were comparatively more abundant during the day than at night. All else being equal, if brown trout attack prey indiscriminately, terrestrial prey should constitute a larger proportion of their diet, compared with allopatric trout. Importantly, the pattern we describe may not be ubiquitous. For instance, co-existing related lizard species have been found to display diverging activity patterns but have similar diets (Rouag et al. 2007). Conversely, competing species of geckos displayed the least dietary overlap when their temporal activity overlap was high (Cole and Harris 2011). The outcome may depend on a series of factors (e.g., food selectivity, the relative competitive ability of native and non-

native species, and whether one of the species significantly decreases access to a specific food type for the other species; Cole and Harris 2011).

Other mechanisms not tested in the present study may also contribute to the diet shift observed in sympatric brown trout. First, brook trout may usurp a significant fraction of the available aquatic prey (Benjamin et al. 2013), forcing brown trout to feed more actively on the alternative prey (i.e., terrestrial food). Brown trout placed in sympatry were also generally more exposed to brook trout than expected by chance, by being active at similar periods and remaining closer to them. Thus, diet preferences may be socially transmitted from brook trout to brown trout because of these frequent interactions (Camacho-Cervantes et al. 2015). Another possibility is that foraging mode, and not diet preference, is socially acquired. Brook trout attack prey at the surface more often (46% in McLaughlin and Grant 1994) than brown trout (5.8% in Tunney and Steingrímsson 2012), where terrestrial insects should be more abundant. These potential causes require that social information be transmitted to and used by brown trout in sympatry. Determining the likeliness and adaptive nature of such information use is not easy, because exposure to brook trout represents an evolutionary novelty (i.e., less than 200 years), and selection may not have had enough time to select against it (Laland and Williams 1998). On the other hand, changes in behavior based on the novel information provided by brook trout may be neutral or even adaptive for young stages of brown trout if they lead to higher food intake (e.g., to survive early life selective bottlenecks; Elliott 1994). Higher aggregation in response to the presence of brook trout may also have positive effects on survival (Wrona 1991).

Perspectives

The novel biotic interactions induced by the invasive species could cascade across levels of biological organization (Buoro et al. 2016). For instance, the presence of brook trout may affect insect emergence (Benjamin et al. 2013), which in turn may impact riparian communities and stream ecosystem functioning (Baxter et al. 2004). Brook trout consume fewer aquatic prey items in our study stream (Závorka et al. 2017), with potential consequences for primary productivity and insect emergence. The shift in activity pattern and diet convergence of brown trout induced by co-existence with brook trout should reinforce these effects. Co-existence between brown trout and brook trout may thus provide an interesting and rare example of converging behavior and diet, with potentially important consequences across levels of biological organization (Cucherousset and Olden 2011), which deserves further attention.

Acknowledgements

The authors thank Niklas Wengström, Johan Höjesjö, James Hinchcliffe, Leona Millec, and several Master students who helped setting up the mesocosms. Niklas Wengström, Johan Höjesjö, and Libor Závorka gave insightful comments on the study design. We are grateful to two anonymous reviewers who greatly helped in improving this paper. We also thank the residents of Björnåsen for kindly accepting that this experiment was run in Ringsbäcken. The study was approved by the Ethical Committee for Animal Research in Gothenburg (license No. 15-2014) and complies with current laws in Sweden. This work was supported by the Tryggers foundation (CT 16:221). Jörgen Johnsson was also supported by the Inter-reg project MarGen. Jörgen Johnsson and Julien Cucherousset have been supported by the French Laboratory of Excellence project TULIP (ANR-10-LABX.41; ANR-11-IDEX-002-02).

References

Alanärä, A., Burns, M., and Metcalfe, N. 2001. Intraspecific resource partitioning in brown trout: the temporal distribution of foraging is determined by social rank. *J. Anim. Ecol.* **70**(6): 980–986. doi:10.1046/j.0021-8790.2001.00550.x.

Allan, J.D. 1981. Determinants of diet of brook trout (*Salvelinus fontinalis*) in a mountain stream. *Can. J. Fish. Aquat. Sci.* **38**(2): 184–192. doi:10.1139/f81-024.

Ayala, J.R., Rader, R.B., Belk, M.C., and Schaalje, G.B. 2007. Ground-truthing the impact of invasive species: spatio-temporal overlap between native least chub and introduced western mosquitofish. *Biol. Invasions*, **9**(7): 857–869. doi:10.1007/s10530-006-9087-4.

Bates, D., Maechler, B., Bolker, B., and Walker, S. 2015. lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-10 [online]. Retrieved from <http://CRAN.R-project.org>.

Baxter, C.V., Fausch, K.D., Murakami, M., and Chapman, P.L. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology*, **85**(10): 2656–2663. doi:10.1890/04-138.

Benjamin, J.R., Lepori, F., Baxter, C.V., and Fausch, K.D. 2013. Can replacement of native by non-native trout alter stream-riparian food webs? *Freshw. Biol.* **58**(8): 1694–1709. doi:10.1111/fwb.12160.

Berthon, K. 2015. How do native species respond to invaders? Mechanistic and trait-based perspectives. *Biol. Invasions*, **17**(8): 2199–2211. doi:10.1007/s10530-015-0874-7.

Blanchet, S., Loot, G., Bernatchez, L., and Dodson, J.J. 2008. The effects of abiotic factors and intraspecific versus interspecific competition on the diel activity patterns of Atlantic salmon (*Salmo salar*) fry. *Can. J. Fish. Aquat. Sci.* **65**(8): 1545–1553. doi:10.1139/F08-079.

Buoro, M., Olden, J.D., and Cucherousset, J. 2016. Global Salmonidae introductions reveal stronger ecological effects of changing intraspecific compared to interspecific diversity. *Ecol. Lett.* **19**(11): 1363–1371. doi:10.1111/ele.12673. PMID:27654124.

Camacho-Cervantes, M., Ojanguren, A.F., and Magurran, A.E. 2015. Exploratory behaviour and transmission of information between the invasive guppy and native Mexican topminnows. *Anim. Behav.* **106**: 115–120. doi:10.1016/j.anbehav.2015.05.012.

Caveney, S., Scholtz, C.H., and McIntyre, P. 1995. Patterns of daily flight activity in onitine dung beetles (Scarabaeinae: Onitini). *Oecologia*, **103**(4): 444–452. doi:10.1007/BF00328682. PMID:28306992.

Clark, P.J., and Evans, F.C. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology*, **35**(4): 445–453. doi:10.2307/1931034.

Cole, N.C., and Harris, S. 2011. Environmentally-induced shifts in behavior intensify indirect competition by an invasive gecko in Mauritius. *Biol. Invasions*, **13**(9): 2063–2075. doi:10.1007/s10530-011-0025-8.

Crowder, D.W., and Snyder, W.E. 2010. Eating their way to the top? Mechanisms underlying the success of invasive insect generalist predators. *Biol. Invasions*, **12**(9): 2857–2876. doi:10.1007/s10530-010-9733-8.

Cucherousset, J., and Olden, J.D. 2011. Ecological impacts of nonnative freshwater fishes. *Fisheries*, **36**(5): 215–230. doi:10.1080/03632415.2011.574578.

Cucherousset, J., Aymes, J.C., Santoul, F., and Céréghino, R. 2007. Stable isotope evidence of trophic interactions between introduced brook trout *Salvelinus fontinalis* and native brown trout *Salmo trutta* in a mountain stream of south-west France. *J. Fish Biol.* **71**: 210–223. doi:10.1111/j.1095-8649.2007.01675.x.

Day, T., and Young, K.A. 2004. Competitive and facilitative evolutionary diversification. *BioScience*, **54**(2): 101–109. doi:10.1641/0006-3568(2004)054[0101:CAFED]2.0.CO;2.

Didham, R.K., Tylianakis, J.M., Gemmill, N.J., Rand, T.A., and Ewers, R.M. 2007. Interactive effects of habitat modification and species invasion on native species decline. *Trends Ecol. Evol.* **22**(9): 489–496. doi:10.1016/j.tree.2007.07.001. PMID:17673330.

Dill, L.M. 1983. Adaptive flexibility in the foraging behavior of fishes. *Can. J. Fish. Aquat. Sci.* **40**(4): 398–408. doi:10.1139/f83-058.

Ehrenfeld, J.G. 2010. Ecosystem consequences of biological invasions. *Annu. Rev. Ecol. Syst.* **41**(1): 59–80. doi:10.1146/annurev-ecolsys-102209-144650.

Elliott, J.M. 1994. Quantitative ecology and the brown trout. Oxford University Press, USA.

Fausch, K.D. 1988. Tests of competition between native and introduced salmonids in streams: what have we learned? *Can. J. Fish. Aquat. Sci.* **45**(12): 2238–2246. doi:10.1139/f88-260.

Fingerle, A., Larranaga, N., and Steingrímsson, S.Ó. 2016. Density-dependent diel activity in stream-dwelling Arctic charr *Salvelinus alpinus*. *Ecol. Evol.* **6**(12): 3965–3976. doi:10.1002/ece3.2177. PMID:27247761.

Fox, J.W., and Vasseur, D.A. 2008. Character convergence under competition for nutritionally essential resources. *Am. Nat.* **172**(5): 667–680. doi:10.1086/591689. PMID:18808302.

Fraser, N.H.C., Metcalfe, N.B., and Thorpe, J.E. 1993. Temperature-dependent switch between diurnal and nocturnal foraging in salmon. *Proc. R. Soc. B Biol. Sci.* **252**(1334): 135–139. doi:10.1098/rspb.1993.0057.

Gerber, B.D., Karpanty, S.M., and Randrianantenaina, J. 2012. Activity patterns of carnivores in the rain forests of Madagascar: implications for species coexistence. *J. Mammal.* **93**(3): 667–676. doi:10.1644/11-MAMM-A-265.1.

Giroux, F., Ovidio, M., Phillippart, J.-C., and Baras, E. 2000. Relationship between the drift of macroinvertebrates and the activity of brown trout in a small stream. *J. Fish Biol.* **56**(5): 1248–1257. doi:10.1111/j.1095-8649.2000.tb02137.x.

Harrington, L.A., Harrington, A.L., Yamaguchi, N., Thom, M.D., Ferreras, P., Windham, T.R., and Macdonald, D.W. 2009. The impact of native competitors on an alien invasive: temporal niche shifts to avoid interspecific aggression. *Ecology*, **90**(5): 1207–1216. doi:10.1890/08-0302.1. PMID:19537542.

- Hutchings, J.A. 2014. Unintentional selection, unanticipated insights: introductions, stocking and the evolutionary ecology of fishes. *J. Fish Biol.* **85**(6): 1907–1926. doi:10.1111/jfb.12545. PMID:25469951.
- Imre, I., and Boisclair, D. 2004. Age effects on diel activity patterns of juvenile Atlantic salmon: parr are more nocturnal than young-of-the-year. *J. Fish Biol.* **64**(6): 1731–1736. doi:10.1111/j.0022-1112.2004.00417.x.
- Korsu, K., Huusko, A., and Muotka, T. 2009. Does the introduced brook trout (*Salvelinus fontinalis*) affect growth of the native brown trout (*Salmo trutta*)? *Naturwissenschaften*, **96**(3): 347–353. doi:10.1007/s00114-008-0482-9. PMID:19050841.
- Laland, K.N., and Williams, K. 1998. Social transmission of maladaptive information in the guppy. *Behav. Ecol.* **9**(5): 493–499. doi:10.1093/beheco/9.5.493.
- Larranaga, N., and Steingrímsson, S.Ó. 2015. Shelter availability alters diel activity and space use in a stream fish. *Behav. Ecol.* **26**(2): 578–586. doi:10.1093/beheco/aru234.
- Lewis, T., and Taylor, L.R. 1965. Diurnal periodicity of flight by insects. *Trans. R. Entomol. Soc. Lond.* **116**(15): 393–435. doi:10.1111/j.1365-2311.1965.tb02304.x.
- Losos, J.B., Marks, J.C., and Schoener, T.W. 1993. Habitat use and ecological interactions of an introduced and a native species of Anolis lizard on Grand Cayman, with a review of the outcomes of anole introductions. *Oecologia*, **95**(4): 525–532. doi:10.1007/BF00317437. PMID:28313293.
- Lövén Wallerius, M., Näslund, J., Koeck, B., and Johnsson, J.I. 2017. Interspecific association of brown trout (*Salmo trutta*) with non-native brook trout (*Salvelinus fontinalis*) at the fry stage. *Ethology*, **123**(12): 933–941. doi:10.1111/eth.12692.
- Lowry, E., Rollinson, E.J., Laybourn, A.J., Scott, T.E., Aiello-Lammens, M.E., Gray, S.M., Mickle, J., and Gurevitch, J. 2013. Biological invasions: a field synopsis, systematic review, and database of the literature. *Ecol. Evol.* **3**(1): 182–196. doi:10.1002/ece3.431. PMID:23404636.
- McLaughlin, R.L., and Grant, J.W.A. 1994. Morphological and behavioural differences among recently-emerged brook charr, *Salvelinus fontinalis*, foraging in slow- vs. fast-running water. *Environ. Biol. Fishes*, **39**(3): 289–300. doi:10.1007/BF00005130.
- Metcalfe, N.B., Fraser, N.H.C., and Burns, M.D. 1999. Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. *J. Anim. Ecol.* **68**(2): 371–381. doi:10.1046/j.1365-2656.1999.00289.x.
- Murdoch, W.W., Avery, S., and Smyth, M.E.B. 1975. Switching in predatory fish. *Ecology*, **56**(5): 1094–1105. doi:10.2307/1936149.
- Öhlund, G., Nordwall, F., Degerman, E., and Eriksson, T. 2008. Life history and large-scale habitat use of brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*) — implications for species replacement patterns. *Can. J. Fish. Aquat. Sci.* **65**(4): 633–644. doi:10.1139/f08-003.
- Ostrovsky, I. 1995. The parabolic pattern of animal growth: determination of equation parameters and their temperature dependencies. *Freshw. Biol.* **33**(3): 357–371. doi:10.1111/j.1365-2427.1995.tb00398.x.
- Petere, M.J. 1985. The variance of the index (R) of aggregation of Clark and Evans. *Oecologia*, **68**(1): 158–159. doi:10.1007/BF00379489.
- Pianka, E.R. 1969. Sympatry of desert lizards (*Ctenotus*) in western Australia. *Ecology*, **50**(6): 1012–1030. doi:10.2307/1936893.
- R Core Team. 2015. R: a language and environment for statistical computing [online]. R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.R-project.org>.
- Rader, R.B., Belish, T., Young, M.K., and Rothlisberger, J. 2007. The scotopic visual sensitivity of four species of trout: a comparative study. *West. N. Am. Nat.* **67**(4): 524–537. doi:10.3398/1527-0904(2007)67[524:TSVSOF]2.0.CO;2.
- Reeb, S. 2002. Plasticity of diel and circadian activity rhythms in fishes. *Rev. Fish Biol. Fish.* **12**(4): 349–371. doi:10.1023/A:1025371804611.
- Rouag, R., Djilali, H., Gueraiche, H., and Luiselli, L. 2007. Resource partitioning patterns between two sympatric lizard species from Algeria. *J. Arid Environ.* **69**(1): 158–168. doi:10.1016/j.jaridenv.2006.08.008.
- Roy, M.L., Roy, A.G., Grant, J.W.A., and Bergeron, N.E. 2013. Individual variability of wild juvenile Atlantic salmon activity patterns: effect of flow stage, temperature, and habitat use. *Can. J. Fish. Aquat. Sci.* **70**(7): 1082–1091. doi:10.1139/cjfas-2012-0274.
- Ruse, L.P. 1995. Chironomid community structure deduced from larvae and pupal exuviae of a chalk stream. *Hydrobiologia*, **315**(2): 135–142. doi:10.1007/BF00033625.
- Seppänen, J.-T., and Forsman, J.T. 2007. Interspecific social learning: novel preference can be acquired from a competing species. *Curr. Biol.* **17**(14): 1248–1252. doi:10.1016/j.cub.2007.06.034. PMID:17614285.
- Stanković, D., Crivelli, A.J., and Snoj, A. 2015. Rainbow trout in Europe: introduction, naturalization, and impacts. *Rev. Fish. Sci. Aquacult.* **23**(1): 39–71. doi:10.1080/23308249.2015.1024825.
- Strauss, S.Y., Lau, J.A., and Carroll, S.P. 2006. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? *Ecol. Lett.* **9**(3): 357–374. doi:10.1111/j.1461-0248.2005.00874.x. PMID:16958902.
- Strayer, D.L., Eviner, V.T., Jeschke, J.M., and Pace, M.L. 2006. Understanding the long-term effects of species invasions. *Trends Ecol. Evol.* **21**(11): 645–651. doi:10.1016/j.tree.2006.07.007. PMID:16859805.
- Tunney, T.D., and Steingrímsson, S.Ó. 2012. Foraging mode variation in three stream-dwelling salmonid fishes. *Ecol. Freshw. Fish.* **21**(4): 570–580. doi:10.1111/j.1600-0633.2012.00577.x.
- Wrona, F.J. 1991. Group size and predation risk: a field analysis of encounter and dilution effects. *Am. Nat.* **137**(2): 186–201. doi:10.1086/285153.
- Young, M.K. 1999. Summer diel activity and movement of adult brown trout in high-elevation streams in Wyoming, U.S.A. *J. Fish Biol.* **54**(1): 181–189. doi:10.1111/j.1095-8649.1999.tb00621.x.
- Young, M.K., Rader, R.B., and Belish, T.A. 1997. Influence of macroinvertebrate drift and light on the activity and movement of Colorado river cutthroat trout. *Trans. Am. Fish. Soc.* **126**(3): 428–437. doi:10.1577/1548-8659(1997)126<0428:IOMDAL>2.3.CO;2.
- Závorka, L., Aldvén, D., Näslund, J., Höjesjö, J., and Johnsson, J.I. 2016. Inactive trout come out at night: behavioral variation, circadian activity, and fitness in the wild. *Ecology*, **97**(9): 2223–2231. doi:10.1002/ecy.1475. PMID:27859082.
- Závorka, L., Koeck, B., Cucherousset, J., Brijs, J., Näslund, J., Aldvén, D., Höjesjö, J., Fleming, I.A., and Johnsson, J.I. 2017. Co-existence with non-native brook trout breaks down the integration of phenotypic traits in brown trout parr. *Funct. Ecol.* **31**(8): 1582–1591. doi:10.1111/1365-2435.12862.
- Zimmerman, J.K.H., and Vondracek, B. 2006. Effects of stream enclosures on drifting invertebrates and fish growth. *J. N. Am. Benthol. Soc.* **25**(2): 453–464. doi:10.1899/0887-3593(2006)25[453:EOSEOD]2.0.CO;2.