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PRIMARY RESEARCH PAPER

The effects of invasive rainbow trout on habitat use and diel locomotor activity in the South American Creole perch: an experimental approach

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Abstract The effects of the introduced rainbow trout (*Oncorhynchus mykiss*) on both habitat use and diel locomotor activity of the native Creole perch (*Percichthys trucha*) were assessed. Experiments were performed with juveniles of both species during a 24-h period. Habitat use was measured in channels with different habitat categories, and diel locomotor activity was registered with an infrared sensor. Both species used mainly cobbles. In the absence of *O. mykiss*, *P. trucha* used macrophytes and gravel secondarily, during dusk and midnight, respectively. *Oncorhynchus mykiss* used gravel and macrophytes secondarily, during midday. In the presence of *O. mykiss*, *P. trucha* increased its use of macrophytes and decreased its use of less structured habitats. *Percichthys trucha* juveniles were more active during night. This pattern did not change in the presence of *O. mykiss,* nor was the intensity of movement affected. These results reveal the importance of structured environments for juveniles of both species. In particular, substrates of large size with interstitial spaces in between serve as shelter and reduce visual detection between individuals. Both the association of *P. trucha* juveniles with structured habitats and their nocturnal activity reduce predation risk.

Keywords Interspecific interactions · Habitat use · Diel activity · Introduced salmonids · *Percichthys trucha* · *Oncorhynchus mykiss*

Introduction

Several factors influence the habitat use of freshwater fishes (Jackson et al., 2001). Among these, substrate type, particle size, competition, and predation are important (Chase et al., 2002; Van Liefferinge et al., 2005). In rivers, habitat heterogeneity and patches of different substrates influence the spatial distribution of the fishes (Petty & Grossman, 1996; Dixon & Vokoun, 2009). Biotic factors are more conspicuous in small-scale studies and often underestimated in large-scale studies (Grossman et al., 2006).

Competition with introduced fish can lead to a decline in native fish populations (e.g., Vander-Zanden et al., 1999). There is evidence of asymmetric competition where the outcome is the habitat displacement of native by non-native species (Jonsson et al., 2008; Amundsen et al., 2010; Grabowska et al., 2016). An example of this is the habitat shift of *Etheostoma olmstedi* Storer, 1842 in sympatry with

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the non-native *E. zonale* (Copp, 1868), where *E. olmstedi* is restricted to shallower pools or marginal zones of streams (Van Snik Gray et al., 2016). A more complex situation was reported by Hasegawa & Maekawa (2006), when *Oncorhynchus mykiss* (Walbaum, 1792) displaces the white-spotted charr, *Salvelinus leucomaenis* (Pallas, 1814) forcing it to compete with masu salmon *Oncorhynchus masou* (Brevoort, 1856), another native species. In any case, the displacement to a suboptimal habitat implies a reduction in fitness (e.g., Blanchet et al., 2007).

Competition impact can be reduced by temporal segregation (Schoener, 1974; Brännäs & Alanärä, 1997; Kronfeld-Schor & Dayan, 2003). That is, different individuals can use the same resources at different times of the day, thus lessening the time they interact. This shift in the temporal use of resources has been shown at both inter and intraspecific level. Alanärä et al. (2001) pointed out that *Salmo trutta* Linnaeus, 1758 dominant individuals foraged mainly at optimal times while subordinates of the same species fed in suboptimal periods. Competition between juvenile exotic rainbow trout and native *Salmo salar* Linnaeus, 1758 forced Atlantic salmon to be more active during the day, thereby increasing the risk of being depredated (Blanchet et al., 2008). Therefore, as biotic variables may differ between day and night (Schlosser, 1988; Copp et al., 2005), habitat use and interspecific interaction studies must be performed over a complete daily cycle (Copp, 2008).

Studies of the diel activity of coexisting species are relevant for the evaluation of the dynamics of competitive interactions. This activity can be synchronized by factors such as light, temperature (López-Olmeda et al., 2006), feeding (Landless, 1976) or social interactions. Since locomotor activity is related to the light–dark cycle (Thorpe, 1978), measuring swimming activity contributes to the understanding of the daily rhythm of a species.

Salmonids are the main invasive fish species in Patagonia. They were introduced at the beginning of the 20th century (Marini, 1936) and *O. mykiss* in particular has become widely dispersed since 1904 (García de Leaniz et al., 2010; Macchi & Vigliano, 2014). It has successfully invaded several environments outside its original distribution range and is considered to be amongst the 100 most invasive species (ISSG, 2012). Among native Patagonian species, the most ecologically similar to *O. mykiss* is the Creole perch, *Percichthys trucha* (Valenciennes, 1833). This species is widely distributed in Argentina and Chile, both in lentic and lotic environments (Menni, 2004; Ruzzante et al., 2006). It presents remarkable intraspecific phenotypic variation (Ruzzante et al., 1998, 2003), associated to differences in predation risk (Ruzzante et al., 2011) and trophic resource use (Crichigno et al., 2014).

The use of lotic environments by juveniles of both *O. mykiss* and *P. trucha* (Barriga et al., 2007) would indicate that the probability of interspecific interactions is high in these habitats. Juvenile *O. mykiss* have been found from fast, shallower waters to slower, deeper habitats and also using the interstitial space between rocks (Johnson & Douglass, 2009). *Percichthys trucha* juveniles, in turn, have been registered in slow water habitats with aquatic vegetation in rivers with *O. mykiss* presence (Barriga et al., 2013). The diel activity of *P. trucha* juveniles is currently unknown. The main goals of this study were (1) to determine *P. trucha* and *O. mykiss* habitat use during a diel cycle and to evaluate whether *P. trucha* habitat use varies in the presence of *O. mykiss*; (2) to determine the diel locomotor activity of *P. trucha* and to evaluate whether it is affected by the presence of *O. mykiss*. The study hypotheses were as follows: (1) Juveniles of *P. trucha* use vegetated areas whereas juveniles of *O. mykiss* select habitats of coarse substrate. (2) A shift in *P. trucha* habitat use is evident when *O. mykiss* is present. (3) *Percichthys trucha* locomotor activity diel pattern is affected by the presence of *O. mykiss*.

Materials and methods

Fish collection

Fish were collected during the fall of 2013, in two locations on the Limay River Basin: Pichileufu River (41°05′S, 70°49′W, 926 m a.s.l.) and Piedra del Águila Reservoir (40°27′S, 70°39′W, 590 m a.s.l.). The ichthyofauna of the Basin includes native species: *Galaxias maculatus* (Jenyns, 1842), *G. platei* Steindachner, 1898, *P. trucha*, *Hatcheria macraei* (Girard, 1855), *Trichomycterus areolatus* Valenciennes, 1846, *Olivaichthys viedmensis* (MacDonagh, 1931) and *Odontesthes hatcheri* (Eigenmann, 1909), and introduced salmonids: *O. mykiss*, *S. trutta* and *Salvelinus fontinalis* (Mitchill, 1814). Fish were captured using a

24 V DC backpack electrofishing unit, model 12-B (Smith-Root, Inc., Vancouver, WA, USA) and a seine net (20-m-long, 1.6-m-deep, 12-mm mesh size, with a 10-m-long central section of 1-mm mesh size). A total of 100 *P. trucha* juveniles and 80 *O. mykiss* juveniles were captured and transported in heat insulated containers to the *Centro de Salmonicultura Bariloche* of the *Universidad Nacional del Comahue* in San Carlos de Bariloche city, Río Negro province, Argentina.

Habitat use experiment

Habitat use experiments were performed indoors in four flow-regulated channels (2.85 m long × 0.3 m wide × 0.27 m depth). Each channel was subdivided into four equal-sized sections, and different categories of habitat were placed in each one. Water was supplied from Gutierrez Stream, constituting an open system with an average flow of 90 ml/s, temperature: 11.2°C; pH: 7.43; O_2: 5.9 mg/l and conductivity: 70.5 µS/cm. The natural photoperiod was imitated artificially using an electronic device. Dawn was simulated by means of a progressive lineal increment of light intensity from 0 to 85 lx (or lumen m^{-2}) in one hour. The inverse situation was generated to simulate dusk, namely a lineal decrement from 85 to 0 lx in one hour. The beginning of each crepuscule was set to approximate the natural cycle; thus, the 24-h cycle was divided as follows: 1 h of dawn, 11 h of maximum light intensity (at 85 lx measured at water surface level), 1 h of dusk, and 11 h of darkness (at 0 lx). Lamps were placed in a position that ensured homogeneous distribution of light over the entire surface of the channel. Four habitat categories were used: sand (<4 mm in diameter), gravel (>4 and <64 mm), cobbles (>64 and <150 mm), and 20-cm-tall green artificial aquarium plants (Sunny Aquarium Company, Singapore) to mimic *Myriophyllum* sp., the dominant macrophyte species found in the river. Habitat categories were placed in each channel in different positions relative to the water inlet, so as to discern whether fish distribution was related to habitat or to position within the channel (Fig. 1). Channels were covered with black opaque plastic both above and at the sides, to prevent infiltration of external light and fish disturbance. Fish were not fed either during acclimation or experimental periods. In addition, macroinvertebrate colonization was prevented using mechanical filters placed under the inlet water tap of each channel, to exclude the possible effect of non-random distribution of prey on fish behavior.

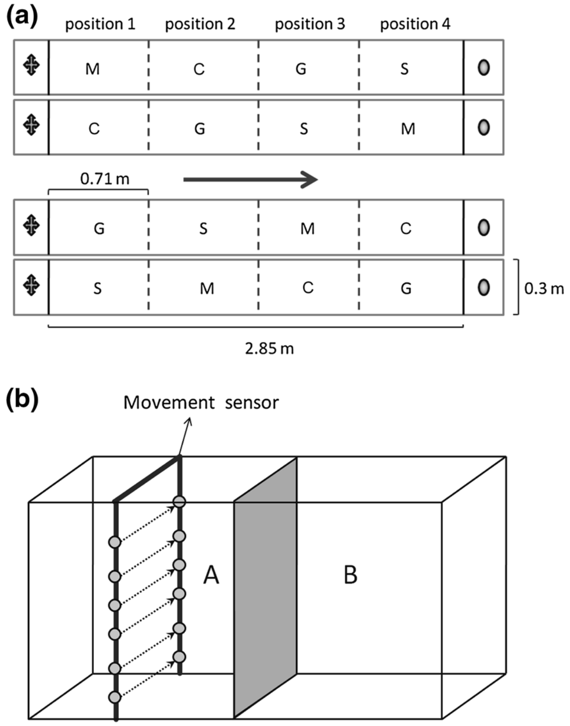


Fig. 1 **a** Scheme of experimental channels and distribution of habitats: *S* sand, *G* gravel, *C* cobbles, and *M* macrophytes. The *arrow* indicates water flow direction. *Left crosses* and *right circles* indicate water inlet and outlet, respectively. *Dotted lines* represent the sluices. **b** Scheme of experimental aquarium and movement sensor (*dotted arrows* represent infrared beams). *A* Compartment where locomotor activity of *P. trucha* juvenile was registered in both treatments. *B* compartment where *O. mykiss* was placed during the second treatment

Three series of habitat use experiments were performed, all following the same procedure. First, fish were acclimated for 24 h in the experimental channels, allowing them to swim freely through the four compartments. Following this, the location of individuals was recorded every 6 h (coinciding with dawn, dusk, midday, and midnight) for a period of 24 h. Before counting, each substrate was isolated using a mobile sluice that prevented fish moving from one section to another as a result of the presence of the observer. The first and second series of experiments were conducted with the presence of only one species per experiment (*P. trucha* or *O. mykiss*, respectively), using 4 individuals per channel, with 4 repetitions (series 1—*P. trucha*: $N = 64$, 4.45 ± 0.83 cm TL;

series 2—*O. mykiss*: $N = 64$, 7.98 ± 1.25 cm TL). The third series combined the presence of both species, with 4 individuals of each species per channel and 4 repetitions (64 *P. trucha* of 4.32 ± 0.79 cm TL and 64 *O. mykiss* 7.89 ± 1.28 cm TL).

Differences in habitat use were analyzed with Kruskal–Wallis test (KW), since data normality and homoscedasticity assumptions failed. Following this, a multiple comparison procedure (Tukey test) was used to detect differences between pairs of habitats. The same procedure was used to check for differences in the use of any position of the channel, with regard to water inlet. A Spearman correlation test was used to establish whether there was a correlation between *P. trucha* and *O. mykiss* presence in the third series of experiments.

Diel locomotor activity experiment

This experiment was performed in a 30-l aquarium, divided into two compartments by a transparent glass sheet that allowed visual fish detection without water exchange. One compartment (A) was equipped with a movement sensor to register *P. trucha* locomotor activity. The equipment comprised 6 vertically disposed infrared beams (with a distance of 1.5 cm between each one) which crossed the aquarium transversely (Fig. 1). The interruption of any of these beams was registered by a computer every second for 48 h (i.e., the duration of the experiment). The other compartment (B) was destined for the *O. mykiss* individual.

The aquarium was placed in an incubator (Ingelab, Modelo I.501 PF) to provide a stable temperature of 10°C. The natural photoperiod was imitated using the same device as in the habitat use experiment. Light intensity varied from 0 to 97 lx measured at water surface level. All fish were acclimated for a period of at least 10 days prior to experimentation, in two aquariums placed in the incubator, under identical experimental conditions (i.e., temperature and photoperiod). During this period fish were fed with *Tubifex* sp.

In the first treatment, one individual of *P. trucha* was placed in compartment A and acclimated for 24 h before its locomotor activity was registered for the following 24 h. For the second treatment, an individual of *O. mykiss* was placed in compartment B. After 24 h of measuring *P. trucha* activity in the presence of *O. mykiss*, both fish were removed from the aquarium. A total of 10 replicates were performed, using 10 *P. trucha* individuals of 5.02 ± 0.58 cm TL and the same individual of *O. mykiss* (10.53 cm TL).

Although *P. trucha* and *O. mykiss* had no contact (visual or olfactory) during night (0 lx period) in the second treatment, the rationale of this experiment included possible *P. trucha* stress due to the *O. mykiss* presence during the previous day, and its putative impact on *P. trucha* activity the following night.

To compare data of movement per individual between day, night and crepuscules, the relative percentage of movement was calculated as $M = R_{\mathrm{H}} \times R_{\mathrm{T}}^{-1}$. 100, where M is the percentage movement, R_{H} is the number of registers per hour and R_{T} is the total number of registers during the 24-h cycle. The movement of every individual was calculated separately for each treatment, then the average movement during day or night hours per individual (e.g., average of 11 h of the day for perch 1 = day % movement of perch 1) was used. Since data of each crepuscule corresponded only to one hour there was no need to obtain the average. Following this, a Rank Transformation (Conover & Iman, 1981) was applied to achieve normality and homoscedasticity before performing a two-way ANOVA. A multiple comparison procedure (Tukey test) was used to detect the factors that differed. To compare the intensity of movement between treatments (*P. trucha* alone vs. *P. trucha* with *O. mykiss*) the same procedure was followed, using the total data of movement (i.e., 11 h of day and 11 h of night, without averaging).

To detect any relationship between light intensity and *P. trucha* movement, data from crepuscules were analyzed. Percentage of crepuscular movement was calculated as $M_{\mathrm{c}} = R_{10\mathrm{m}} \times R_{\mathrm{c}}^{-1}$. 100, where M_{c} is the percentage movement during crepuscule, $R_{10\mathrm{m}}$ is the number of registers per 10 min and R_{c} is the total number of registers during that crepuscule (i.e., one hour). A Spearman Correlation test was used to check the relationship between $\mathrm{M_c}$ and light intensity.

Results

Habitat use

There was no clear use by fish of any particular position regarding water inlet in the experimental channels. *Percichthys trucha* showed differences during dusk (KW; $H = 8.97$; df = 3; $P = 0.030$) and midnight (KW; $H = 8.39$; df = 3; $P = 0.039$); however, this was only between the use of positions 1 and 3 (Tukey, $P > 0.05$) in the first treatment.

The general pattern using the total number of registers indicates that cobbles was the habitat most frequented by *P. trucha* when experimenting with this species alone (KW; $H = 103.54$; df = 3; $P < 0.001$) (Fig. 2). Use of cobbles was significantly higher from the other habitats during both dawn and midday (Tukey, $P < 0.05$), but no differences from macrophytes were presented during dusk, or with gravel during midnight (Tukey, $P > 0.05$). These results suggest that at these two moments, macrophytes and gravel, are used secondarily by *P. trucha* (Fig. 3).

Similar to *P. trucha*, *O. mykiss* preferred the cobbles habitat when it was alone (KW; $H = 116.65$; df = 3; $P < 0.001$). However, *O. mykiss* had a slightly different order of preference when analyzing the total number of registers; it used mostly cobbles, and secondarily, macrophytes and gravel, whereas sand was the least used (Tukey, $P < 0.05$) (Fig. 2). The same pattern was observed during the day (KW; $H = 46.78$; df = 3; $P < 0.001$), when sand was the least-used habitat (Tukey, $P < 0.05$). In addition, for all moments of the cycle *O. mykiss* juveniles preferred cobbles (Tukey, $P < 0.05$) as also registered in the first experiment for *P. trucha* (Fig. 3).

Differences were found in *P. trucha* habitat use when the two species were together (KW; $H = 115.40$; df = 3; $P < 0.001$), with a preference for cobbles and secondarily, macrophytes. The least-used habitats were sand and gravel. This differed from the general pattern observed when *P. trucha* was alone, when macrophytes were as infrequently used as sand and gravel (Fig. 2). In particular, when habitat use was analyzed by moment of the day, differences were found during dawn (KW; $H = 41.11$; df = 3; $P < 0.001$), midday (KW; $H = 39.29$; df = 3; $P < 0.001$), dusk (KW; $H = 32.93$; df = 3; $P < 0.001$), and midnight (KW; $H = 9.09$; df = 3; $P = 0.028$). However, at midnight no differences were found when applying an a posteriori test (Tukey, $P > 0.05$). Macrophytes and cobbles were the most used during midday and dusk, whereas sand and gravel were less used. The preference order during dawn was, from most to least used, cobbles, macrophytes, gravel, and sand (Fig. 3).

There was also a negative correlation between the presence of *O. mykiss* and the presence of *P. trucha* in sand or gravel (Spearman, $\rho = -0.\ 377$, $P = 0.00512$). In addition, the only habitat in which the 8 individuals (i.e., third treatment) were found together was cobbles. Finally, this habitat was more frequently used during midday, whereas sand and gravel were used more often during midnight.

Diel locomotor activity

Percichthys trucha were more active during night in both treatments. In general, no differences were found

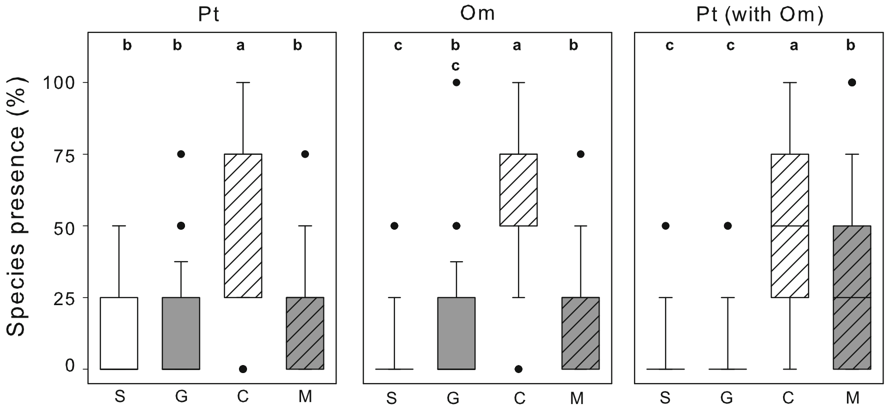


Fig. 2 General pattern of *P. trucha and O. mykiss* habitat selection as percentage of individuals present in each habitat. Pt: *P. trucha* alone (experiment 1). Om: *O. mykiss* alone (experiment 2). Pt (with Om): *P. trucha* in the presence of O. mykiss (experiment 3). Median, quartiles and data outside 10th and 90th percentiles are indicated for sand (S), gravel (G), cobbles (C) and macrophytes (M). Significant differences between substrates are indicated by different letters (Tukey, $P < 0.05$)

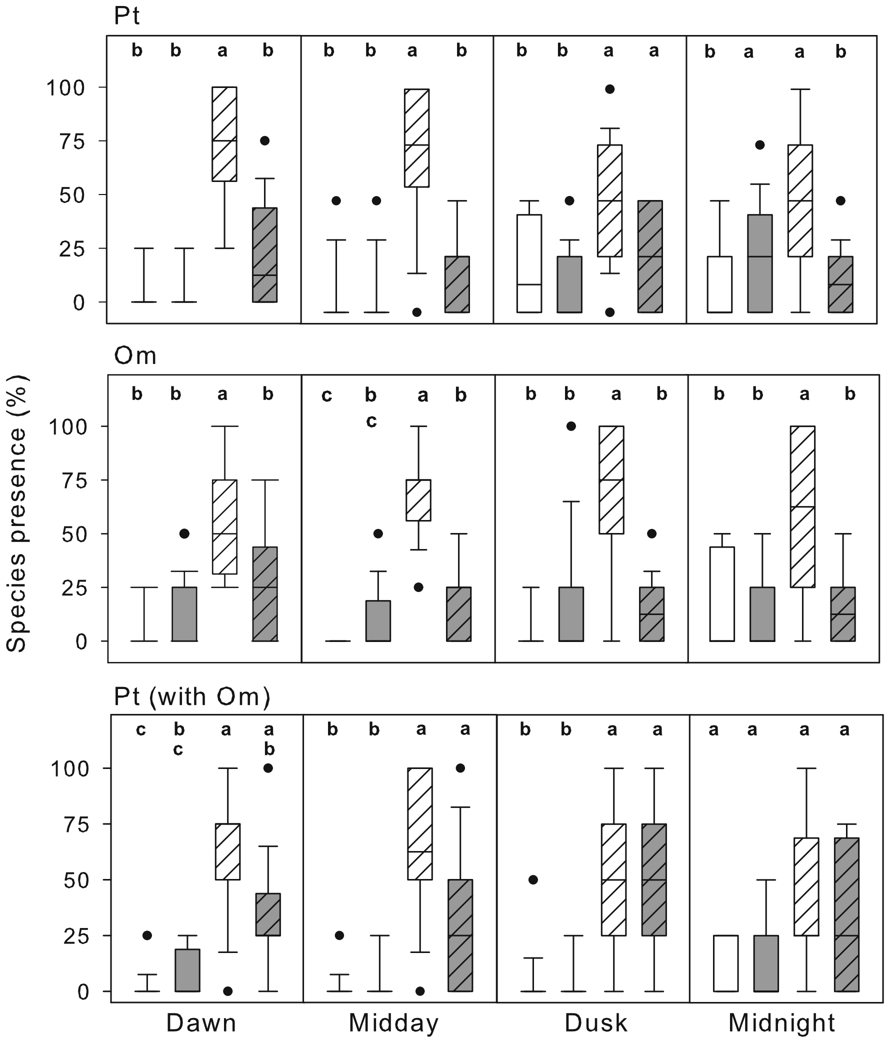


Fig. 3 Habitat selection of *P. trucha* and *O. mykiss* per moment of the cycle as percentage of individuals present in each habitat. Pt: *P. trucha* alone (experiment 1). Om: *O. mykiss* alone (experiment 2). Pt (with Om): *P. trucha* in the presence of O. mykiss (experiment 3). Median, quartiles, and data outside 10th and 90th percentiles are indicated for sand (*white*), gravel (*gray*), cobbles (*striped white*), and macrophytes (*striped gray*). Significant differences between substrates within each time of the day (dawn, midday, dusk, and midnight) are indicated by different letters (Tukey, $P < 0.05$)

between treatments in the activity of *P. trucha* per hour (KW; $H < 1.12$; $\mathrm{df} = 1$; $P > 0.23$). The ANOVA performed with the relative movement data showed differences between moments of the day ($F = 14.1; P < 0.001$), showing that *P. trucha* is more active during night (Tukey, $P < 0.05$) (Fig. 4).

Regarding the intensity of movement (total registers), there was no difference between treatments during crepuscules (ANOVA; $F = 0.040$, $P = 0.84$) or between dawn and dusk (ANOVA; $F = 0.150$, $P = 0.70$). Nor did the interaction between factors show differences (ANOVA; $F = 0.011$, $P = 0.92$). When nighttime and daytime were compared, the activity of *P. trucha* depended on time of day ($F = 19.170$, $P < 0.001$), movement levels being higher during night (Tukey, $P < 0.05$), without differences between treatments ($F = 0.066$, $P = 0.80$). That is, no differences were found regarding the intensity of activity of *P. trucha* with or without trout (Fig. 5).

Finally, *P. trucha* activity was correlated with light intensity during crepuscules (dawn treatment 1: Spearman; $\rho = -0.558$; $P < 0.001$; dusk treatment 1: $\rho = -0.433$; $P < 0.001$; dusk treatment 2: $\rho = 0.526$; $P < 0.001$), with the exception of dawn in the second treatment (Fig. 6).

Discussion

Fish distribution was related to habitat category rather than channel position. The habitat results highlight that *Percichhtys trucha* juveniles, in the absence of *Oncorhynchus mykiss*, mainly used environments that provide refuge: mostly cobbles, and secondarily macrophytes and gravel during dusk and midnight, respectively. Sand was the most exposed (i.e., least structured) habitat and least used by *P. trucha*, only during midnight or dusk. *Oncorhynchus mykiss* juveniles displayed a similar pattern to *P. trucha*: cobbles were preferred during all periods of the cycle and sand was the least used during midday. As predicted, *O. mykiss* used mainly coarse substrate. However, *P. trucha* juveniles were expected to use mainly macrophytes, but instead they were found to use mainly cobbles. Lapointe & Corkum (2007) pointed out that small-sized fish are strongly associated with habitat variables that reduce predation risk. Small fishes are important food items for adults of *P. trucha*, *O. mykiss* and *Odontesthes hatcheri* in Negro River (Alvear et al., 2007). In addition, the Neotropical Cormorant *Phalacrocorax brasilianus* (Gmelin, 1789) also preys on small fishes, as has been inferred by its diet (Alarcón et al., 2012). Structured environments like cobbles may provide low-risk areas, inaccessible to predators because of the formation of interstitial spaces that can be used by small fish. This substrate is commonly found in erosional zones of rivers, where high water velocity prevents the deposit of fine particles between larger rocks.

In the presence of *O. mykiss*, *P. trucha* increased the use of macrophytes and decreased the use of sand. This supports the second hypothesis of the study, since a shift in *P. trucha* habitat use was evident in the presence of *O. mykiss*. Moreover, the increased use of macrophytes agrees with field observations. Barriga et al. (2013) found a higher abundance of *P. trucha* juveniles associated with macrophytes in Pichileufu River, where the abundance of salmonids, mainly *O. mykiss* and *Salmo trutta*, was high. Other ecologically similar species of the northern hemisphere, such as *Perca fluviatilis* Linnaeus, 1758, also use vegetated areas as an antipredatory strategy during early life stages (Byström et al., 2003; Lewin et al., 2004;

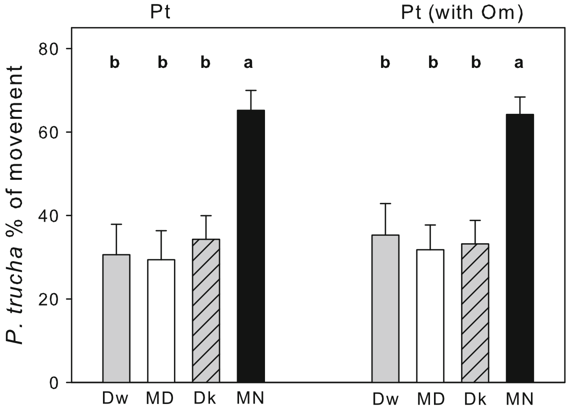
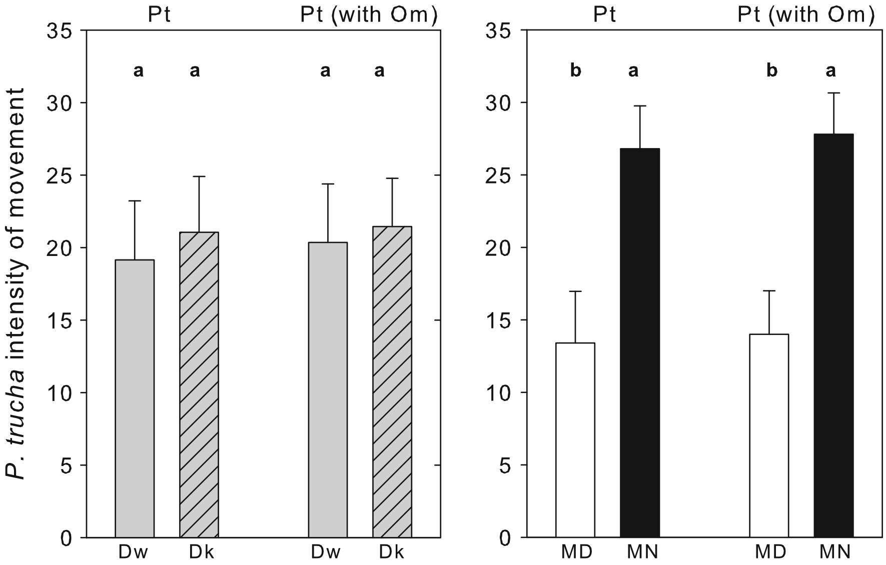


Fig. 4 *P. trucha* percentage of movement (in ranks) per moment of the 24-h cycle. Significant differences between pairs are indicated by *different letters* (Tukey, $P < 0.05$). Dw: dawn, MD: midday, Dk: dusk, MN: midnight

Fig. 5 *P. trucha* intensity of movement (N° of registers, in ranks) per moment of the 24-h cycle. *Left* Crepuscules. *Right* Day and Night. Significant differences between pairs in each *panel* are indicated by *different letters* (Tukey, $P < 0.05$). *Dw* dawn, *MD* midday, *Dk* dusk, *MN* midnight



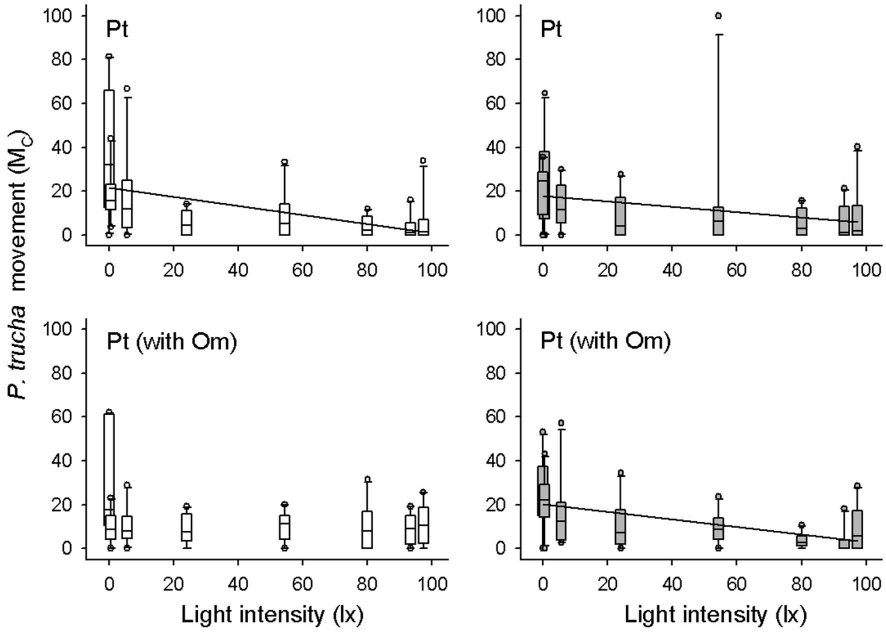


Fig. 6 Crepuscular movement of *P. trucha* (M_C) in relation to light intensity (lx) with and without *O. mykiss* presence. Median, quartiles and data outside 10th and 90th percentiles are indicated for dawn (*white*) and dusk (*gray*). Lines indicate negative correlations (Spearman, $P < 0.001$)

Snickars et al., 2004). Similar results were shown by Fullerton & Lamberti (2006), in habitat use experiments performed with the native *Perca flavescens* (Mitchill, 1814) and the introduced *Gymnocephalus cernua* (Linnaeus, 1758) in North America. Both species used macrophytes and secondarily cobbles over mud during day. During night, *G. cernua* used mud more often whereas *P. flavescens* showed the same pattern as during day. Differences between *P. trucha* and *P. flavescens* in the order of preference of the two structured habitats (macrophytes and cobbles) might be related to the fact that Fullerton & Lamberti (2006) employed a higher density of macrophytes. Regardless, their results also indicate that other juveniles of this family use structured habitats during day, while risky zones are used during nighttime.

Fine substrates constitute areas of high predation risk because fish cannot use shelters. These risky zones were used more often by *P. trucha* juveniles during midnight. The response of an individual to predation risk is shaped by the trade-off between the need to avoid predators and benefits of foraging in appropriate places (Barbosa & Castellanos, 2005). *Perca* juveniles undergo starvation during winter, which causes high mortality (Huss et al., 2008). Therefore, the use of risky habitats might be related to food search since feeding efficiency is diminished in complex environments (Crowder & Cooper, 1982; Starry et al., 1998; Kolar et al., 2002).

In the absence of refuge, *P. trucha* and *O. mykiss* juveniles segregate spatially. This is supported by the negative correlation found between the presence of the two species in the less structured habitats. The only habitat in which the total number of fish was found at the same moment was cobbles. Hence, the size of the interstitial space is key in providing shelter for small fish. Similarly, Heggenes et al. (2013) found that Atlantic salmon could easily move within the substrate and that fish size and substrate harshness were the parameters that limited their movement. As *P. trucha* and *O. mykiss* juveniles share structured habitats in nature, and considering their similar diets (Cussac et al., 1998; Ruzzante et al., 1998; Macchi et al., 1999; Lattuca et al., 2008), the potential for competition is very high if one of these resources is limited (Fullerton & Lamberti, 2006). In this context, the ability of *P. trucha* to increase the use of macrophytes could represent an advantage, allowing niche segregation to avoid competition with *O. mykiss* juveniles.

Concerning diel activity, *P. trucha* juveniles exhibited a nocturnal movement pattern, showing that photoperiod is an important synchronizer of activity in this species. Fullerton & Lamberti (2006) found a similar pattern for *G. cernua,* which was very active during nighttime but remained almost still during daytime. Barriga et al. (2016) also registered the same diel pattern in the small stream catfish *Hatcheria macraei*. Moreover, the negative correlation between the activity of *P. trucha* and light intensity during crepuscules is consistent with a nocturnal habit.

Contrary to the last hypothesis, the presence of *O. mykiss* did not affect the movement pattern of *P. trucha*. Neither was movement intensity affected. At this point it is important to note that although *P. trucha* was unable to detect *O mykiss* during night, *P trucha* behavior could have been affected during nighttime by the previous exposition to *O. mykiss* presence during the light period. However, this was not the case, ruling out a possible stress effect generated previously by the presence of *O. mykiss*. Nonetheless, it was confirmed that *P. trucha* did detect the presence of *O. mykiss* during the light period, since defensive responses were repeatedly observed. This behavior entailed an erection of the dorsal fin spines and an unusual opening of the operculum (Otturi, personal observation). This response was also observed by Ylönen et al. (2007) in *P. fluviatilis* and *G. cernua*, while they evaluated response to predator odor. Furthermore, predation pressure effects can be so important that they can even induce morphological changes in prey, such as enlargement of defensive structures. For example, Ruzzante et al. (2011) found a direct relationship between the dorsal spine length of *P. trucha* and the density of potential predators.

The introduction of exotic species in an ecosystem entails a potential ecological risk (Gozlan & Newton, 2009), resulting in possible detrimental effects for native species or ecosystem function (Gozlan et al., 2010). Both the habitat use and diel activity registered in this study suggest that predation is a key factor in early life stages of *P. trucha*. This factor is likely to have increased in importance since the introduction of salmonids in Patagonia, although this is difficult to prove due to lack of data prior to introduction (Macchi et al., 2007). However, there is consistent evidence of the deleterious effects that salmonids have had on native populations in other countries (Tilzey, 1976; McDowall, 1990, 2006; Glova et al., 1992; McIntosh et al., 1992). For example, competition for space and food has been proposed as the cause of decline in the *Galaxias vulgaris* Stokell, 1949 population in New Zealand streams (McIntosh et al., 1992). In addition, introduced salmonids resulted in a 26% decline in Galaxiidae populations in Chile (Habit et al., 2010), and Young et al. (2010) showed a decline in the growth rate of *Aplochiton zebra* Jenyns, 1842 in artificial enclosures. Elgueta et al. (2013) suggested that the absence of *A. zebra* in rivers invaded with *S. trutta* may reflect competitive exclusion in trophic resource use. Penaluna et al. (2009) registered a shift in the mesohabitat use of three native species when salmonids were removed from a river section.

In conclusion, the trade-off between feeding in appropriate but dangerous areas and sheltering in areas with less food (Ydenberg & Dill, 1986) is directly related to diel cycle. Light intensity appears to be the variable that regulates this balance in order to minimize the risk of being preyed upon. Most animals experience a certain degree of predation risk associated with most of their activities (Abrahams, 2005). *P. trucha* juveniles minimize this risk by sheltering in structured areas during daytime and exploring less structured areas during nighttime, when this species is more active. However, sharing the same habitat with other individuals, such as *O. mykiss* juveniles, could entail resource competition during shelter use periods. The ability of *P. trucha* to use macrophytes could solve this problem for juveniles of this species. In any case, the use of structured habitats is crucial for juvenile fish. In this sense, the removal of substratum from a riverbed or the construction of channels or dams could have a severe impact on river fish communities. Therefore, the structural factors of a river must be considered when developing management strategies to improve the conservation status of native fish species.

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