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Comparing dominance relationships and movement of native marble trout (*Salmo marmoratus*) and introduced rainbow trout (*Oncorhynchus mykiss*)

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Abstract

Behaviour observations of the endangered native marble trout (*Salmo marmoratus* Cuvier, 1829) and introduced rainbow trout (*Oncorhynchus mykiss* Walbaum, 1792) in the laboratory and in a tributary to the Idrijca River in Slovenia were combined to study the movements and dominance relationships between individuals of the two species in an open field test. Under laboratory conditions, no difference between the species was detected for neither time spent active or distance moved. In species paired tests, rainbow trout initiated more aggressive behaviours towards marble trout than *vice versa*, and rainbow trout were clearly the dominant individuals. After simultaneous release in the river, marble trout immediately left the release area and spent twice as long time as rainbow trout until they settled in an area of the river, hence, the release site was immediately occupied exclusively by rainbow trout. Thus, the dominant and aggressive behaviour of rainbow trout seen in the laboratory before release might have influenced marble trout's subsequent behaviour in the river, by marble trout leaving the areas occupied by rainbow trout and moving to locations further away from the release site. In

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the field, the marble trout occupied sites individually, while rainbow aggregated at a few locations. Rainbow trout showed higher movement activity in the morning compared to marble trout. There was a positive correlation between swimming speed in the laboratory and movement in the field for marble trout but not for rainbow trout. In conclusion, the results in this study support the need to end stocking of rainbow trout in rivers with native marble trout. To better understand the interaction between the species, and to develop efficient management plans to protect the native marble trout, reference behaviours should first be understood, and future research in sites where the two species do not co-exist is needed. This is especially important for marble trout for which behavioural research and data are lacking.

Keywords: activity, behaviour, dominance, movement, *Oncorhynchus mykiss*, radio telemetry, *Salmo marmoratus*

Introduction

Freshwater ecosystems are among the most endangered ecosystems in the world, and declines in biodiversity are far greater in fresh waters than in the most affected terrestrial ecosystems (Sala et al., 2000; Dudgeon et al., 2006). One of the greatest threats to global freshwater biodiversity is invasions by excotic species (Dudgeon et al. 2006). While some invasive species directly impact the native species with clearly visible consequences (hybridisation, population decline, etc.), most of the times the impacts are more subtile (poor fitness, behavioural changes etc.) and may remain unnoticed and poorly understood (Welcomme, 1992; COMM, 2016/1141; SCOM, 2001). Studies around the world confirm the negative impacts of rainbow trout introductions on native populations of for instance brown trout (*Salmo trutta*), white charr (*Salvelinus alpinus*) and Atlantic salmon (*Salmo salar*), mostly in the form of habitat shift and/or exclusion, but also lower growth rate and egg survival (Landergren, 1999; Scott and Irvine, 2001; Hasegawa et al., 2004; Hasegawa and Maekawa, 2006; Fausch, 2007; Musseau et al., 2017; Sahashi and Morita, 2016).

The marble trout (*Salmo marmoratus* Cuvier, 1829) is a freshwater fish species in a declining trend (IUCN, 2021). It is a stream-living Salmonid, popular among anglers as trophy fish, with a restricted geographical distribution in the Po basin in northern Italy and Adriatic basin of Slovenia, Croatia, Bosnia-Herzegovina and Albania (Figure 1). It is hypothesised that the species evolved from the more common brown trout (*Salmo trutta* Linnaeus, 1758) after the isolation during the last glaciation period (Bernatchez et al., 1992). Hybridization with brown trout stocked for angling, displacement by alien rainbow trout (*Oncorhynchus mykiss* Walbaum, 1792), habitat alterations (barriers, channelization, erosion control structures etc.), water extraction and pollution may be the major threats to marble trout (Razpet et al., 2007; Vincenzi et al., 2012; Torkar and Zwitter, 2015; Berrebi et al., 2016; IUCN, 2021). By the end of the 20th century, the marble trout was on the brink of extinction, with only a handful of genetically pure lineages remaining in small isolated streams (Povž, 1995; Berrebi et al., 2000). The ongoing gene flow leading to hybridization between brown and marble trout threatens the ongoing speciation process of marble trout in areas where brown trout has been artificially reintroduced (Meraner et al., 2007, Bajec et al., 2015). Conservation efforts are focused on habitat protection and repopulation from breeding and stocking the identified pure lineages (Vincenzi et al., 2012; Torkar and Zwitter, 2015; Berrebi et al., 2016). According to the latest monitoring report for Slovenia, the status of marble trout populations is unfavourable, but with signs of improvement (Pajk et al., 2014).

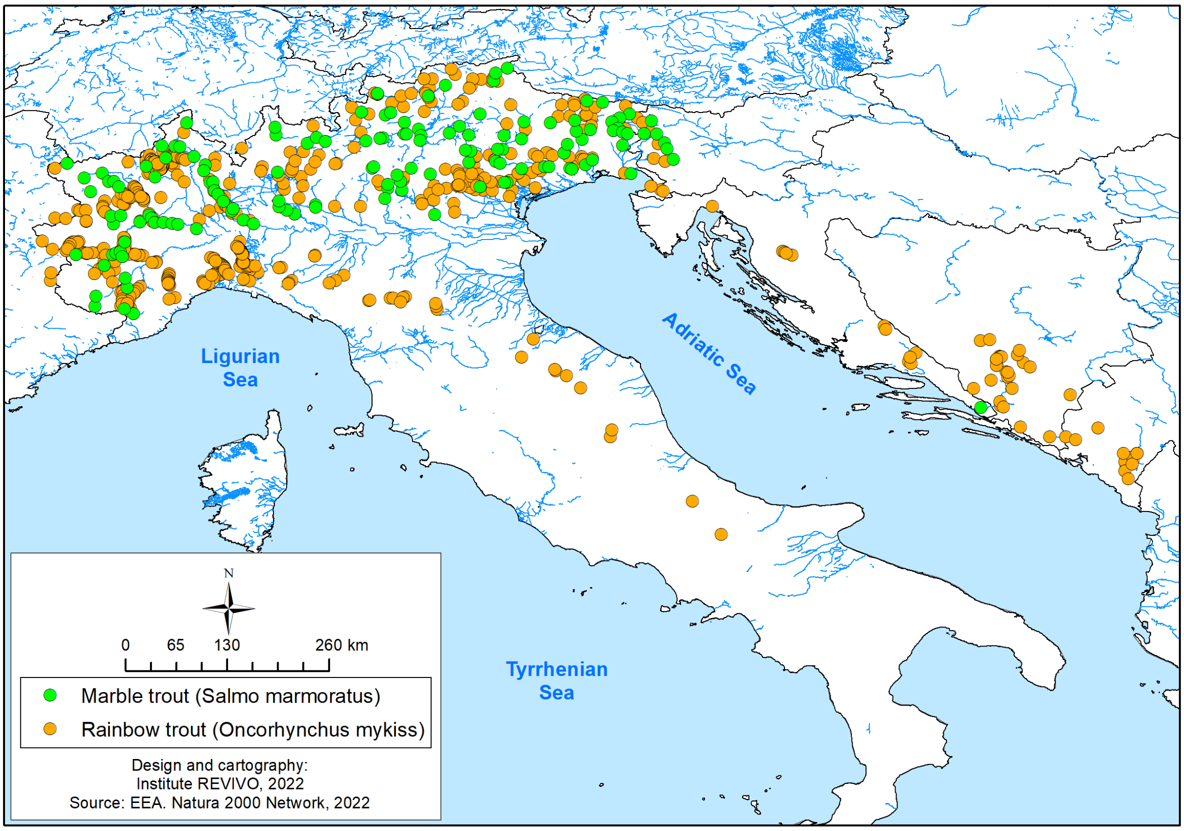

Figure 1: Distribution of endemic marble trout (Salmo marmoratus) and introduced rainbow trout (Oncorhynchus mykiss) in the Adriatic basin (Source: EEA. Natura 2000 Network, 2021; UICN, 2021). The information shown is based on the most recent EU wide Natura 2000 dataset that the European Environment Agency (EEA) has created on the basis of the data received from the EU Member States.

A number of genetic studies of marble trout have been performed during the last 25 years (Berrebi et al., 2000; Fumagalli et al., 2002; Meraner et al., 2007; Pujolar et al., 2011; Vincenzi et al., 2012; Bajec et al., 2015), but little is known about their habitat use, migration patterns, activity, diet, intra- and interspecific interactions and other aspects of their ecology. Information on habitat use, behaviour and interspecific interactions is particularly important for risk analyses and mitigation measures related to introduced species and other negative impact factors. Some inferences can likely also be drawn from its close and well-studied relative, the brown trout. For example, in the Pyrenean mountain stream, both laboratory and field results indicated that rainbow trout significantly affected native brown trout habitat selection and apparent survival (Blanchet et al., 2007). On the other hand, brown trout have been shown to be competitively superior to rainbow trout in areas where both species are exotic (Hasegawa, 2016).

Considering the lack of knowledge on movement behaviour and eology of marble trout, and the interactions with stocked rainbow trout, this study on the behavioral characteristics of marble trout and rainbow trout was performed in order to better understand the competitive and dominance relationships between the species. Studies in the laboratory and in nature have each their strengths and weaknesses, so the study was designed to obtain data under both controlled laboratory conditions and in a natural Slovenian river. The behaviour of individual fish and interactions between individuals of the two species were examined in the laboratory by video observations. Subsequently, the same individuals were radio tagged and released into the Kanomljica River, and their behaviour and habitat use were monitored by tracking their positions regularly during a two-month period. The specific aims of the study were to compare the activity level of the two species in the laboratory, examine relative dominance of individuals of the two species in the laboratory, and compare their movement patterns and distances, home range size and activity levels after release in the river. Finally, the correlation between the two sets of observations (laboratory and field) were used to draw conclusions on competitive interactions in the field.

Materials and Methods

The care and use of experimental animals complied with the Ministry of agriculture, forestry and food of the Republic of Slovenia animal welfare laws, guidelines and policies as approved by the Administration for Food Safety, Veterinary Sector and Plant Protection as per the permit U34401-19/2015/6.

Study area

Rainbow trout have been introduced to several sites in rivers draining to the Adriatic basin in the Mediteranean Sea, and now occur in sympatry with endemic native marble trout populations (Figure 1; Candiotto et al., 2011; Stanković et al., 2015). This study was carried out in Kanomljica, a small tributary to the Idrijca River upstream of the village of Spodnja Idrija in Slovenia. Most of the Idrijca River basin is dominated by native marble trout, introduced brown trout, their hybrids *Salmo* sp. and rainbow trout, but several other fish species also occur (Torkar and Zwitter, 2015).

The 4.7 km study area is situated near the source of the Kanomljica River between two large dams. The upstream dam (1.7 m height) serves the local aquaculture facilities and is located 5.8 km from the confluence with the Idrijca River. The downstream dam (1.8 m height) serves a small hydropower plant and is located 0.9 km from the confluence with the Idrijca River. No fish passage facilities exist at either of the two dams, so no upstream passage is possible, while downstream passage is considerably obstructed.

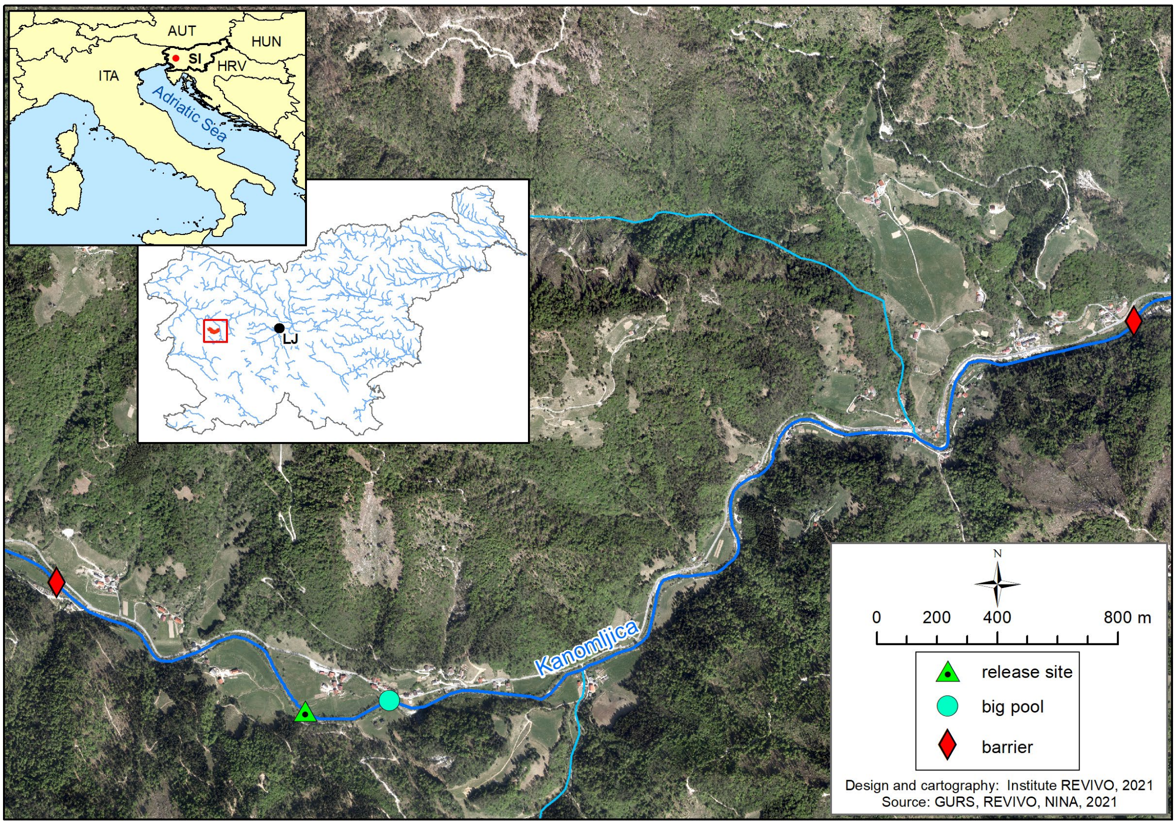

Figure 2: The study site in the Kanomljica River in Slovenia indicating the two dams, the release site and a big pool downstream of the release site (the direction of the river flow is from the left to the right in the map). Inlet map 1: the location of Slovenia by the Adriatic Sea. Inlet map 2: Location of Kanomljica river within Slovenia (LJ – Ljubljana, the capital city)

The in-stream habitat is mostly natural throughout the study area, with regular pool-riffle sequences, but with some local bank erosion protection measures. The water discharge is not regulated but natural. Tagged fish were released in a small pool 1.1 km from the upstream dam, in an area little disturbed by human activities (Figure 2 and 3). A bridge over a large river pool about 300 m downstream from the release site allowed for visual observation of tagged fish within the pool (Figure 3), which allowed us to observe the different micro-habitat selection of the two species within this pool.

Figure 3: The site where radio tagged fish were released (left) and a large pool downstream of the release site (right).

Study approach

Marble trout were provided by the Idrija Fishing Club rearing facility on the Kanomljica River and rainbow trout by a hatchery at the Rižana River. The growth rate of rainbow trout both in the rearing facilities and nature by far exceeds that of marble trout. Vincenzi et al. (2011) found that despite a later emergence, mean weight of rainbow trout at age 0+ in September in headwaters of the Idrijca River was significantly higher than that of marble trout. Because of the growth differences between the two species, the body size difference of the same age class was too large to provide relevant comparisons. Therefore, age 1+ rainbow trout and age 2+ marble trout were compared to achieve the smallest size difference possible. These size differences account for the actual situation in the rivers of the Adriatic Basin, because these are the fish sizes regularly being stocked.

Testing activity patterns and dominance relationship in the laboratory

Hatchery-reared marble trout (n = 25, age 2+) and rainbow trout (n = 25, age 1+) were tagged with PIT-tags (size: 12 mm; HDX ISO 11784/11785, OREGON RFID, Portland, OR U.S.A.) on 9 August 2017, The rainbow trout were longer (TL 305 mm ± 16 SD vs TL 270 mm ± 14 SD, t-test $p < 0.00$, $t = 1.68$) and heavier (358 g ± 50 SD vs 241 g ± 40 SD, $p < 0.00$, $t = 1.68$)

than the marble trout. The activity pattern of four marble trout and four rainbow trout were tested simultaneously, in eight separate barren rectangular plastic tanks 50×74 cm with water level 15 cm, and filmed using a Sony camera HDR-XR155. These Open-field trials have been used widely when assessing acticvty patterns in animals, and are all based on placing an animal into a novel open space and monitoring subsequent behaviour (Walsh & Cummins, 1976). Fish were scanned for individual PIT- number, gently netted from the holding tanks and allowed to acclimatise for 15 minutes before being filmed for 20 minutes. After the filming, all fish were returned to the holding tank. The water in the trial tanks was taken from the hatchery facility (14 °C) to facilitate acclimatization and exchanged before a new batch of fish was scored. Two activity variables were analyzed using automated tracking software (LoliTrack v. 4; Loligo Systems, Denmark): (1) time spent actively swimming (movements of individual had to exceed velocity threshold of 3.5 cm/s to be classified as active swimming), and (2) total distance moved (measured to the nearest cm). Relative dominance in size-matched pairs of marble and rainbow trout was then assessed using larger tanks (40×60 cm), where the dyadic contest was observed and filmed during 20 min. As stated above rainbow trout were on averege larger than the marble trout so each species were ranked based on size in which the largest rainbow always faced the largest marble and vice verse. The relative dominance ranks were assessed according to Keenleyside and Yamamoto (1962) and Höjesjö et al. (1998) based on position in the tank, colour and initiated interactions (display, chase and bite). Dominant fish were generally more bright in their colouration, held a more central position in the tank and initiated more aggressions.

Radio tagging and riverine tracking surveys

Among the fish tested for boldness and dominance relationships in the laboratory, 20 individuals of each species were randomly selected for radio tagging (marble trout: mean 271 mm/243 g, range 255-314 mm/202-377 g, SD 15/44, rainbow trout: 304 mm/356 g, range 273-337 mm/261-463 g, SD 17/54) and released into the river the same day as they were tagged (17 August, release time 18:57 h, water temperature at release site 15 °C). Cutts et al. (1999) provide evidence that prior residence affects the outcome of intraspecific interactions, so resident fish were relocated from the release site prior to release of the tagged fish. The behaviour of the tagged fish was monitored by determining their location in the river during regular tracking surveys over a 9-week period (18 August-19 October 2017, Table 1).

Radio transmitters were surgically implanted into the body cavity according to methods described by Finstad et al. (2005). Prior to surgery, the fish were anaesthetized by immersion in an aqueous solution of 2-phenoxyethanol (EC No 204–589–7, SIGMA Chemical Co., St Louis, MI, U.S.A., 0.70 ml l^{-1}) for 1.3-1.6 min. During surgery, a 0.35 ml l^{-1} solution of 2-phenoxyethanol was circulated on the surgical table. Surgical incisions were closed with two independent sutures (Ethilon*II, 3–0 polyamid, Johnson & Johnson Services Inc., New Brunswick, NJ, USA). The radio transmitters (model F1530 from Advanced Telemetry Systems, Isanti, MN, USA, outline dimensions 9 × 20 x 5 mm, mass in air 1.8 g) produced signals within the 142.103-142.292 MHz range. Individual fish were recognised based on unique combinations of transmitter frequencies and pulse rates (35 or 54 pulses per minute). After tagging, the fish were brought to a 1 x 2 m large cage in the river (10 min transport time), where they were kept for 3-7 hours before all fish were released simultaneously.

Manual tracking surveys were performed using a radio receiver (model R4520CD, ATS) connected to a four-element Yagi antenna. During each survey, all tagged fish were located with ±1.3 m precision. Precision was determinded by performing a blind test for all four researchers involved in the tracking. Each researcher located three tags in the river, which were placed by other researchers in three different habitats, representative of the main habitats. The average precision was then calculated for each researcher and overall. For fish staying within the area between 450 m downstream to 50 m upstream of the release site, the fish location was noted to the nearest 1 m by using a system of numbered sticks placed along the river bank every 10 m. For fish outside this area, the fish location was recorded by using a handheld GPS unit. All location data were later transformed to meters from the release site, measured along the river. The frequency of tracking surveys varied according to the purpose of data collection during different time periods, ranging from one to four times per day (Table 1).

Table 1. Overview of manual tracking of radio tagged fish. The acclimation period was used to record the time until the fish settled, while the movement range and diel movement data were used to understand movement patterns and home range.

Tracking purpose	Tracking frequency	Period
Acclimation	Once a day	18-25 August
Movement range	Once a day	26 August-1 September
Diel movement	2-4 times a day	2-11 September
Movement range	Once a day	12-16 September

The day after release, two marble trout were predated on by grey heron *Ardea cinerea*. In addition, two marble trout and one rainbow trout were predated on by grey heron on 28-30 August. Predation was confirmed by retrieving fish tags from herons' nests. Data from these individuals were removed from the analyses. The first and second day after release, eight of the rainbow trout were visually observed in the pool downstream from the release site. They were actively feeding, and their behaviour resembled untagged rainbow trout in the same pool.

One rainbow trout showed an exceptional behaviour with a long-distant movement on the night between 2 and 3 September, coinciding with a high and increasing water discharge. The individual's behaviour after this relocation resembled its previous behaviour, so it is presumed this was a one-time event as a response to the change in water discharge, with no long-term effects. Data from this individual did not impact the majority of the test results, so this individual is included in all analyses, except where indicated.

Data analyses

Data were analysed using the SYSTAT 13.0 software from Systat Software, Inc., San Jose California USA, "www.sigmaplot.com". Nonparametric tests were used when assumptions for parametric tests were not met. Home range was determined as the length of the river stretch between the 1st and the 3rd quartiles of all the recorded fish locations during 26 August-16 September. The first occurance of the fish within the home range area was considered as the day of settlement. The absolute movement was defined as the distance between two consecutive locations for individual fish. The absolute movement for a specific day is the distance between the location of the individual on that day and the location of the same individual in the same time period on the next day, regardless of the movement direction. It should be noted that this is a minimum distance moved, because the fish might have moved undiscovered between tracking surveys. Tracking to determine movement range commenced each day at 12.00. Intensive tracking to examine diel variation in movements lasted for 10 days. During the first and last three days, tracking commenced at 12.00 and 24.00 (two surveys per day). During the he middle four days, tracking commenced at 6.00, 12.00, 18.00 and 24.00 (four surveys per day). All tracking surveys lasted about 2 hours. Morning absolute movement is the distance between the location of the individual on that day at 6.00 and the location of the same individual on the same day at 12.00. When analysing the relative movement, the direction of movemenet (upstream/downstream) was taken into account. Finally, a Pearsson correlation test was performed to test the relationship between swimming speed/ time spent active in the laboratory and absolute movement in the field.

There were exactly 3000 observations recorded between 26th August and 31st October. First, 450 records were removed from the pool belonging to the fish that were eaten. The first transmitter stopped working on 15th September in rainbow and the second on 30th September in marble. The 16th September was chosen as the final date for the analysis, so additional 1122 records were omitted from the pool, resulting in 1428 records from 34 individuals, each located 42 times.

Results

Behavioural scoring in the laboratory

In the laboratory trials, there was no difference in neither time spent active (General Linear Model; $p = 0.11$, $F_{1,43} = 2.65$) or distance moved between the species (General Linear Model; $p = 0.94$, $F_{1,43} = 0.05$). In the dyadic contest, rainbow trout initiated aggressive interactions in 24 of the 25 trials and was clearly the dominant individual in 18 of these trials. In the other 7 trials, no clear hierachy could be determined. Marble trout only initiated aggressive behaviour in one pair (one push and two displays). On average, the rainbow trout initiated 8 displays (± 5 SD), 3 pushes (± 2 SD), 7 chasees (± 10 SD), 2 circles (± 1 SD) and 16 bites (± 16 SD) towards the marble trout. When not engaged in any aggressive interaction, the rainbow trout also spend more time (on averegae 72%) patrolling the central part of the arena, whereas the marble trout were generally holding position in the corner. There was no correlation between the size differences in the pair and number of bites ($p = 0.24$; $t = -1.3$) nor displays ($p = 0.87$, $t = -0.016$).

Time until settlement in the river and home range

Most individuals of both species moved downstream from the release site (71% of all tagged individuals, Figure 4). The time from release until settlement was longer in marble trout (mean 7.2 days ± 3.5 SD) than in rainbow trout (mean 4.1 days ± 3.6 SD; t test $t = 1.69$ $p = 0.01$). Marble trout settled further from the release site than rainbow trout, in both up- and downstream directions (Table 2). Four rainbow trout remained at the release site, and five marble trout and one rainbow trout settled upstream of the release site. The four rainbow trout that settled at the release site later moved downstream during a high discharge period towards the end of the study. The minimum dispersal distance (the distance between release and settlement site) in marble trout was recorded for two individuals that settled 200 m upstream and one individual that settled 200 m downstream of the release site (Figure 4).

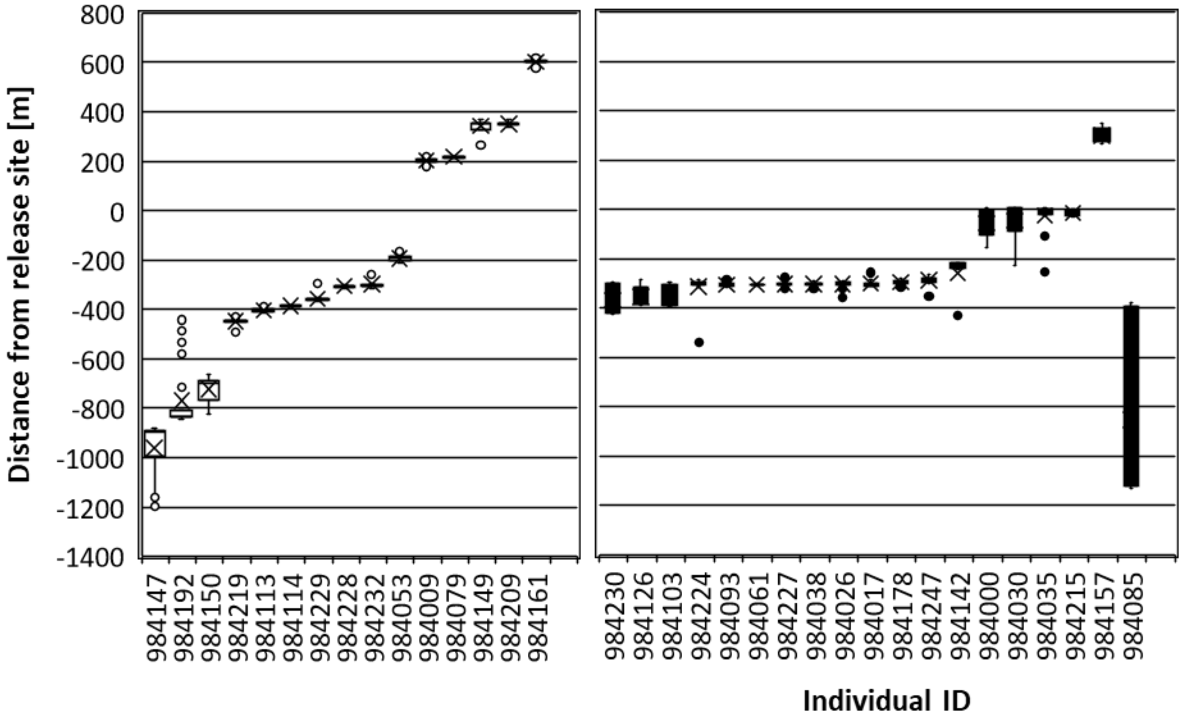

Figure 4: Settlement locations and home range sizes for marble trout (Salmo marmoratus; left panel) and rainbow trout (Oncorhynchus mykiss; right panel). Mean (x), 1st and 3rd quartile (box indicating the home range), 1.5 x the Interquartile Range (whiskers) and outliers (circles).

The difference in mean home range size between marble trout (20 m ± 31 SD) and rainbow trout (71 m ± 162 SD) was not significant (t test $t_{\text{one-tail assuming unequal variances}} = 1.7$ p = 0.09, Figure 4). The total length of river stretch used by marble trout (96 m ± 114 SD) and rainbow trout (142 m ± 168 SD) also did not differ (t test $t_{\text{one-tail assuming unequal variances}} = 1.69$ p = 0.19). Individuals of marble trout dispersed and distributed themselves more evenly along the river stretch used, while rainbow trout tended to aggregate at two locations (Table 2, Figure 4). A large pool (Figure 3) situated 290-330 m downstream from the release site attracted half (47%) of the tagged rainbow trout (Figure 4).

Table 2. Distribution metrics (distance settled from the release site) for marble trout (*Salmo marmoratust*) and rainbow trout (*Oncorhynchus mykiss*). Positive values indicate

positions upstream of the release site and negative values downstream. T tests were used to test if there were differences in any of the distribution parameters between the two species.

Parameter	Marble trout [m]	Rainbow trout [m]	t value; one tail, assuming unequal variances	p-value
Maximum value	603	298	1.71	< 0.001
Standard deviation	444	230	1.69	< 0.001
Mean	-208	-250	1.70	< 0.001

Absolute and relative movement distances

Total absolute movement did not differ between the species (Table 3). However, marble trout moved longer than rainbow in the morning, but no difference was found for day, evening or night movements. Relative movement also did not differ between the species (Table 3). Hence, overall the results indicated that marble trout were more active within their home range in the morning compared to rainbow trout.

Table 3: Absolute and relative movement with comparative statistics (analysis of variance) between marble (*Salmo marmoratus*) and rainbow trout (*Oncorhynchus mykiss*; m +/- SE).

Parameter	Rainbow trout	Marble trout	$F_{1,31}$ value	p-value
Absolute movement	666 (± 106)	822 (±167)	0.66	0.42
Relative movement	-96 (± 42)	-55 (±32)	0.58	0.45
Absolute movement (morning)	23 (± 6)	52 (±13)	4.72	**0.038**
Absolute movement (day)	372 (± 77)	403 (±120)	2.0	0.16
Absolute movement (evening)	34 (± 7)	69 (±26)	2.05	0.16
Absolute movement (night)	217 (± 52)	199 (±60)	0.054	0.82
Relative movement (morning)	5 (± 3)	4 (±5)	0.018	0.90
Relative movement (day)	-96 (± 42)	-55 (±32)	0.57	0.46
Relative movemet (evening)	5 (± 8)	32 (±24)	1.3	0.26
Relative movement (night)	-36 (± 44)	-10 (±12)	0.28	0.60

Correlation between behaviour in the laboratory and field

there was an almost significant correlation between swimming speed in the laboratory and absolute movement in the field (Pearsson correlation, p=0,055, r=0,55) . However, there was a difference between the species, reflected in a significant correlation between swimming speed in the laboratory and absolute movement in the field for marble trout but not for rainbow trout (Figure 5).

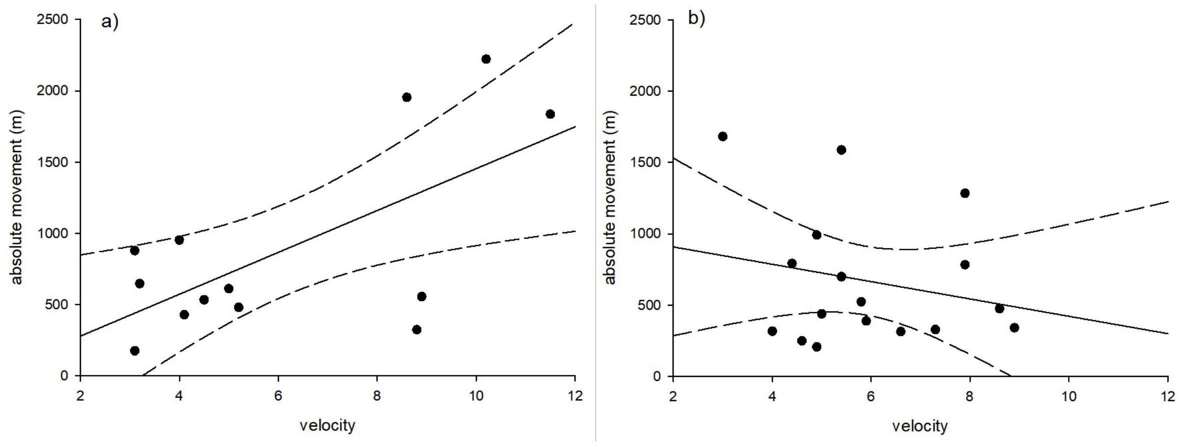

Figure 5: The Pearson correlation between swimming speed in the laboratory and absolute movement in the field for marble trout (Salmo marmoratus; a); p = 0.015, r=0.65) and rainbow trout (Oncorhynchus mykiss; b); p = 0.223, r=0.34).

Discussion

Individual rainbow trout frequently initiated agressive behaviours towards marble trout, which could lead to competitive inferiority and negative outcomes for marble trout in rivers where the two species co-occur. The rainbow trout were dominant in most of the laboratory trials, and patrolled the central part of the experimental arena most of the time, while the marble trout were generally holding position in the corner. This dominant and aggressive behaviour of rainbow trout might also be the reason marble trout dispersed further away and spent a longer time before they settled after simultaneous release in the river, while rainbow trout gathered in two nearby, big pools. The combined use of laboratory trials and field studies thus provided new insigths into the interactions between the two species, and also provided new information on the riverine behaviour of the little studied marble trout.

The dominance of rainbow trout concur with previous studies on behavioural relationships between rainbow trout and other native salmonid species, where rainbow trout is often recognised as the dominant species that can cause changes in native fish communities, and for instance lead to decreased density (Sahashi and Morita, 2016), increased downstream displacement of parr (Landergren et al., 1999), and altered habitat selection and apparent survival (Blanchet et al., 2007). The few studies of the impact of rainbow trout on marble trout somewhat differ in their results. A study by Musseau et al. (2018) in the Idrijca River showed a dietary niche expansion and niche shift in marble trout while living in sympatry with rainbow trout. While Vincenzi et al. (2011) concluded that the self-reproducing rainbow trout population of the headwaters of the Upper Idrijca does not have a noticeable impact on body growth and survival of sympatric marble trout, the same study also found a slightly lower survival of marble trout living in sympatry with rainbow compared with those that did not.

The comparisons in the present study represent the behaviour of similarly aged hatchery-reared fish of the marble trout and rainbow trout. Dominance relationships and aggressive bahaviour may depend on hatchery versus wild origin (Rhodes and Quinn, 1998; Sundström et al., 2014), but in this study, individuals of both species were of hatchery origin and therefore comparable. Prior residency may also be a factor that influence dominance relationships (Beaugrand et al., 1996; Cutts et al., 1999; Wallerius et al., 2022). However, since the rainbow trout and marble trout were released simultaneously both into the laboratory arenas and at the riverine release site, and resident fish were relocated from the riverine release site prior to release of the tagged fish, it was not expected that the benefit of prior residency would influence the initial behaviour of the fish. When the fish spread out over larger river stretches later in the study, their behaviour might have been influenced by other fish being present in the river, but the densities of rainbow trout and marble trout in the river are not known, except that prior resident rainbow trout were visually observed in one of the big pools where many of the tagged rainbow trout established a home range. Fish body size may also impact dominance relationships (Beaugrand et al., 1996; Rhodes and Quinn, 1998; Alonso et al., 2012; Reddon et al., 2019), and the results may have been impacted by the rainbow trout being larger (average

30.5 cm) than the marble trout (average 27.5 cm). A study by Hayes (1989) showed that as fry, rainbow trout were dominant over brown trout in the shallow, faster water nearest the incoming food supply, while in fingerlings, brown trout dominated over rainbow trout. This suggests that dominance relationships may be more impacted by other factors than relatively small body size difference (Beaugrand et al., 1996), and in Brazilian streams, it has even been shown that subordinate species are often bigger than the dominant species (Oliveira et al., 2022). The dominance of rainbow trout over marble trout in the present study may therefore be related to a more generally aggressive behaviour of rainbow trout than the size difference per se, adding to the many arguments against rainbow stocking. Nevertheless, the comparison performed in the present study is relevant for many rivers with marble trout, because the size and age of the hatchery-fish in the study resemble rainbow trout released for angling purposes and marble trout released to support wild populations.

Since settlement often requires the newcomers to overcome the aggressive superiority of several residents in order to remain there (Jenkins, 1969), bigger and more robust-set individuals are more likely to settle closer to the release site than smaller and more elongated fish (Sánchez-González & Nicieza, 2021) and the costs of searching for the best territory may overwehight the benefits of obtaining an optimal territorry (Cutts et al., 1999), the dominant fish are expected to settle faster and closer to the release site. This was found in our study for rainbow trout, despite the fact that all fish were released simultaneously. The marble trout immediately left the release area and spent twice as long time until they settled in an area of the river, while the release site was immediately occupied exclusively by rainbow trout. Thus, it seems like the dominant and aggressive behaviour of rainbow trout seen in the laboratory before release might have influenced marble trout's subsequent behaviour in the river, by marble trout leaving the areas occupied by rainbow trout and moving to locations further away from the release site. Potential differences in habitat preference between rainbow trout and marble trout might also have contributed to their different behaviour after release, and further studies of the specific habitat preferences by marble trout are needed.

After release, only a small fraction of fish (15%) moved upstream, consistent with previous research (Sanchez & Nicieza, 2021). Throughout the study, individuals of the two species occupied different locations, because the rainbow trout remained in pools and marble trout spread more out, which is a behaviour that may contribute to reduce competitive encounters between the species in the river enviroment. The marble trout occupied sites individually, with non-overlapping home ranges among the tagged fish, whereas rainbow trout aggregated at a few locations, and home ranges of tagged fish overlapped to a large extent. A home range size (20.1 ± 6.8 m) for brown trout was found by Höjesjö et al. (2007), which was similar to that of marble trout in the present study, but the 43% of overlap in territories for brown trout in their study is closer to the territorial overlap for rainbow trout (85%) than marble trout in the present study. However, they also found that during the summer period dominant individuals generally moved more than subordinate fish.

The results in the present study may indicte a lower tendency of territoriallity in rainbow trout than marble trout, but with the reservation that the density of other non-tagged fish on these river stretches is not known.

The results on morning absolute movement indicate a larger movement activity in rainbow than in marble trout, which concur with their different behaviour in the laboratory trials. A further relationship between laboratory and field observations is evident because individuals of marble trout that exhibited higher swimming speeds in the laboratory also displayed higher absolute movement in the field. The same correlation, although not significant, was reversed in rainbow trout and might be connected to a smaller home range for this species. While the considerable difference in home range sizes for the two species was not significant, this could be due to the low number of individuals.

The results in this study suggest possible negative impacts of introduced rainbow trout on native marble trout based on the dominant status of the rainbow trout over marble trout, with important implications for future management of these two species. In conclusion, the results in this study support the need to end stocking of rainbow trout in rivers with native marble trout. The outcome in river areas where both species occur may depend on the densities of fish of both species in the different habitats, and the extent to which marble trout are displaced to suboptimal habitats. More detailed studies of the habitat use of marble trout are needed, and studies at several life stages. This study was conducted at a site where both rainbow trout and marble trout occur along the same river stretches, which is the case for most of the rivers and streams of the Adriatic Basin in Slovenia. To better understand the interaction between the species, and to develop efficient management plans to protect the native marble trout, reference behaviours should first be understood, and future research in sites where the two species do not co-exist is needed. This is especially important for marble trout, for which behavioural research and data are lacking.

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Contributions

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