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Innocent until proven guilty? Stable coexistence of alien rainbow trout and native marble trout in a Slovenian stream

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Abstract To understand the consequences of the invasion of the nonnative rainbow trout *Oncorhynchus mykiss* on the native marble trout *Salmo marmoratus*, we compared two distinct headwater sectors where marble trout occur in allopatry (MTa) or sympatry (MTs) with rainbow trout (RTs) in the Idrijca River (Slovenia). Using data from field surveys from 2002 to 2009, with biannual (June and September) sampling and tagging from June 2004 onwards, we analyzed body growth and survival probabilities of marble trout in each stream sector. Density of age-0 in September over the study period was greater for MTs than MTa and very similar between MTs and RTs, while density of trout \geq age-1 was similar for MTa and MTs and greater

than density of RTs. Monthly apparent survival probabilities were slightly higher in MTa than in MTs, while RTs showed a lower survival than MTs. Mean weight of marble and rainbow trout aged 0+ in September was negatively related to cohort density for both marble and rainbow trout, but the relationship was not significantly different between MTs and MTa. No clear depression of body growth of sympatric marble trout between sampling intervals was observed. Despite a later emergence, mean weight of RTs cohorts at age 0+ in September was significantly higher than weight of both MTs and MTa. The establishment of a self-sustaining population of rainbow trout does not have a significant impact on body growth and survival probabilities of sympatric marble trout. The numerical dominance of rainbow trout in streams at lower altitudes seem to suggest that while the low summer flow pattern of Slovenian streams is favorable for rainbow trout invasion, the adaptation of marble trout to headwater environments may limit the invasion success of rainbow trout in headwaters.

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Introduction

Invasions by alien species are a major threat to biodiversity and ecosystem functioning, leading to species extinctions and worldwide homogenization of the biota (e.g., Rahel et al. 2008; Olden 2006). The establishment of self-sustaining populations of alien species impact native communities at various levels and can alter fundamental ecological properties of the host ecosystems, such as species dominance, nutrient cycling and productivity (Simon and Townsend 2003) through competition, predation, and indirect cascade

effects (Crowl et al. 1992; Townsend 2003). The management and control of invasive species is one of the biggest challenges conservation biologists are facing (Allendorf and Lundquist 2003).

Marble trout *Salmo marmoratus* is a stream-living salmonid endemic to the Southern Alpine region and endangered in Switzerland, in the Po river basin in Italy and in the Adriatic basin of Slovenia (Povz 1995; Bulgarini et al. 1998; IUCN 2004), currently threatened by former introductions of foreign taxa into its habitat (Povz et al. 1996; Berrebi et al. 2000; Jug et al. 2005). Alien rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* have been introduced in the last 100 years in the distribution area of marble trout. The Adriatic and Danubian basins of Slovenia are among the few locations in Europe where rainbow trout established self-sustaining populations, despite the continuous stocking of rainbow trout in many European waters for more than one hundred years. Evidence of the negative impact of rainbow trout on native fish species have been frequently reported worldwide (e.g., Crowl et al. 1992; Weigel et al. 2003; Morita et al. 2004), but the importance of biotic competition for rainbow trout invasion success remains controversial (Fausch et al. 2001; Fausch 2008). Only seven pure populations of marble trout are presently viable in Slovenian streams, threatened by hybridization with brown trout, displacement by rainbow trout and episodes of massive mortality caused by exogenous events, such as floods and landslides (Vincenzi et al. 2008a). Given the threatened status of marble trout, understanding the population-level mechanisms (Peterson and Fausch 2003) of rainbow trout invasion is urgently needed to prioritize conservation efforts.

Results obtained in experimental settings are likely to be influenced by spatial constraints that may force the fish to interact at unnaturally small scales (Korsu et al. 2009). Therefore, it is necessary to study of interaction among native and introduced species in natural streams explicitly considering the space required by native and invading species to complete their life histories (Peterson and Fausch 2003). In addition, as stream salmonids have age-structured populations and reproduction may begin after their second or third year of life (McFadden 1961; Behnke 1992), repeated annual samplings are needed to detect changes in demographic rates and long-term data should be gathered in systems with fluctuating environmental conditions (Werner 1998; Peterson and Fausch 2003). For Korsu et al. (2007), both carefully designed experiments and long-term monitoring of both the invading and the native species are needed to clarify the mechanisms underlying patterns of invasion. Despite this, a surprisingly low number of studies have monitored natural populations for more than one generation (Peterson and Fausch 2003).

In this work, we investigated the impact of introduced rainbow trout on a resident marble trout population living in Upper Idrijca (Slovenia). Our field study was of intermediate spatial scale (hundreds of meters) and temporal extent (8 years) (Peterson and Fausch 2003), with multiple sampling per year and fish individually tagged and recaptured. Specifically, we tested whether: (1) survival probabilities differed between marble trout living in sympatry with rainbow trout and marble trout living in allopatry in the same stream (Upper Idrijca) and rainbow trout survival probabilities differed from those of marble trout living in sympatry; (2) survival probabilities varied seasonally; and (3) body growth of marble trout living in sympatry with rainbow trout differed from body growth of marble trout living in allopatry in Upper Idrijca and of rainbow trout living in sympatry.

Materials and methods

Study area and species description

The Idrijca River is located in South-Western Slovenia. Its length from the spring to its outflow to the Soča River is approximately 60 km. The Idrijca basin presents a near-pristine environment with limited agricultural and industrial activities, absence of erosion due to deciduous forests, mainly *Fagus sylvatica*, and low human population density. Part of the Idrijca River is highly fragmented, with waterfalls precluding the upstream movement of fish.

Detailed description of the biology and ecology of marble trout can be found in Crivelli et al. (2000), Delling et al. (2000) and Vincenzi et al. (2008a, b, 2010). Rainbow trout (*O. mykiss*), a north Eastern Pacific species (Gall and Crandell 1992), was introduced in the Adriatic basin of Slovenia in the early twentieth century and here established self-sustaining stream-resident populations. Rainbow trout was stocked in the headwaters of the Idrijca River (Upper Idrijca) only once, in 1962. Since then, rainbow trout established a self-sustaining stream-resident population living in sympatry with genetically pure marble trout. No other fish species live in Upper Idrijca. Marble trout is a fall spawner (mid-November to mid-December), with emergence of juveniles in May-early June depending on water temperature, while rainbow trout is a spring spawner (April) with emergence in July in Upper Idrijca (Lee Tae Won and A.J. Crivelli, unpublished data). Marble trout is sexually mature at age 2 for males and 3 for females (Meldgaard et al. 2007), while rainbow trout males and females are sexually mature at age two (D. Jesensek and A.J. Crivelli, unpublished data). There are no other biological and ecological data for rainbow trout living in Slovenian streams.

Field data collection

Sampling surveys were carried out from September 2002 to September 2009 on the whole length of each station starting from downstream using a gasoline-powered, portable backpack electrofishing unit. Trout were sampled since 2002 in Station A1 and A2 of Sector A (Lat, 46°0'10.88" N; Long, 13°54'51.77" E), where marble trout live in allopatry (MTa) and in Station S of Sector S (Lat, 45°59'45.27" N; Long, 13°55'37.58" E), where marble trout live in sympatry (MTs) with rainbow trout (RTs) (Table 1). In 2002 and 2003, trout were sampled only in September and individuals were not tagged. Trout were individually tagged using Carlin tags since June 2004 with biannual sampling, in June and September. Each sampling session was carried out in the same day in all Stations. Each Station (A1, A2 and S) was electrofished two times to produce a multiple-pass removal estimate of trout abundance using Microfish 3.0 (Van Deventer and Platts 1989). In Sector A, density was estimated with data from both Station A1 and A2. Age designation follows standard terminology; marble trout in the first year of life were indicated as 0+ and in the second year, subsequent to winter annulus formation, as 1+. All captured fish aged $\geq 1+$ were anaesthetized with 2-phenoxyethanol, measured for total length (L_T , to the nearest mm) and weight (W , g) and if sampled for the first time the adipose fin was removed and scales were used for age determination. Sampled fish were tagged only in Stations A1 and S. Water temperature of the streams was recorded with temperature loggers (Optic StowAway model, Onset Corporation, USA) at hourly intervals. There was no evident difference in daily water temperature between Sector A and Sector S (see Appendix 1 of the Electronic supplementary material).

Analysis of recapture probabilities and survival

As only trout aged 1+ or older were tagged, capture histories were generated for a fish only if it was sampled at age $\geq 1+$. Two probabilities can be estimated from a capture history matrix: ϕ , the apparent survival probability, and p ,

the capture probability (Lebreton et al. 1992). Apparent survival represents the probability that an individual survives from year t to year $t+1$ and does not leave the study area. As individuals that move outside the sampling area are not available for recapture, apparent survival is a deflated estimate of true survival. Capture probability represents the probability that an individual alive in the area at year t is captured at year t . Capture history matrices were used as input files for the Program MARK (White and Burnham 1999) to compute maximum likelihood estimates of the apparent survival (ϕ), the recapture probability (p), and their respective 95% CI. The Cormack–Jolly–Seber (CJS) model was used as a starting point for the analyses. This model allows both survival and recapture probabilities to vary with time for a single group of animals (Lebreton et al. 1992). The CJS model assumes that the fate of each individual is independent of the fates of all others and that all individuals have the same survival and capture probabilities. In order to reach these assumptions, individuals can be divided in groups to be included in the model. The global starting model, that is the model with the maximum parameterization, included for both ϕ and p a multiplicative interaction between year of birth, Distribution (MTa, MTs and RTs) and sampling occasion (Table 2). Previous studies on marble trout showed that survival is constant across age-classes (Vincenzi et al. 2008b), therefore age was not included as a group (i.e., categorical) variable.

The goodness-of-fit (GOF) test of the CJS model was performed using the program U-CARE 2.0 (Choquet et al. 2005). This was done to explore the fit of the CJS to the data, but also to identify if the global model fits the data from which to start model selection. U-CARE produces a global GOF test and two particular tests for transience (test 3.SR) and trap-dependency (test 2.CT). The CJS model fitted the data adequately for each study group ($p > 0.05$), with no evidence of transience effect and trap-dependency (test 3.SR and test 2.CT, $p > 0.05$). No adjustment to the AIC scores for over-dispersion (\hat{c}) (White and Burnham 1999) was required. Therefore, the global model was a good starting point to model survival and capture probabilities. All other survival models tested were simplified

Table 1 Stream characteristics of Sector A (marble trout *Salmo marmoratus* living in allopatry: Lat, 46°0'10.88" N; Long, 13°54'51.77" E) and Sector S (marble trout living in sympatry with rainbow trout *Oncorhynchus mykiss*: Lat, 45°59'45.27" N; Long, 13°55'37.58" E)

| | Length (m) | Surface area (m ²) | Gradient (%) | Number of pools | Total pool surface (m ²) | Elevation (a.s.l.) |
|------------|------------|--------------------------------|--------------|-----------------|--------------------------------------|--------------------|
| Sector A | 1,000 | | | | | |
| Station A1 | 110.8 | 888 | 0.009 | 2 | 603.6 | 718–719 |
| Station A2 | 110.8 | 775 | 0.009 | 5 | 510.4 | 719–720 |
| Sector S | 1,200 | | | | | |
| Station S | 268.2 | 1084 | 0.026 | 2 | 429.2 | 544–537 |

Trout were sampled in Station A1 and A2 of Sector A and Station S of Sector S. Trout were tagged only in Station A1 and S

Table 2 Model notation and explanation of model tested for the estimation of survival and capture probabilities for marble trout *Salmo marmoratus* living in allopatry (MTa) or sympatry (MTs) with rainbow trout *Oncorhynchus mykiss* (RTs)

| Model notation | Explanation |
|---|--|
| Time component | |
| (.) | Constant |
| (s) | Winter (September to June) vs summer (June to September) |
| (t) | Sampling occasion |
| Distribution component | |
| (.) | Constant |
| (Sector) | Effect of sector (S and A) |
| (Species) | Effect of species (MT and RT) |
| (Distr) | Effect of distribution (MTa, MTs, RTs) |
| Year of birth component | |
| (.) | Constant |
| (yob) | Effect of year of birth |
| <i>Global model</i> | |
| $\phi(yob \times t \times Distr)p(yob \times t \times Distr)$ | |

versions of this global starting model. Each model included a temporal component, a year of birth component and a Distribution component (Table 2). Only models with biological significance were tested (Table 3; see Appendix 2 of the Electronic supplementary material). A seasonal effect was modelled as a simplification of full-time variation, where each year is divided in two periods: the season from June to September (named “summer”), and the season covering the time period between September and June (“winter”). As length of sampling intervals (summer and winter) was different, we estimated a monthly survival via techniques within the Program MARK (White and Burnham 1999), thus making comparisons across intervals feasible. Therefore, ϕ will denote monthly apparent survival, where 1 month is defined as 30 days. Model selection among the candidate models was based on the corrected Akaike Information Criterion, AICc (Hurvich and Tsai 1989). Models within two AICc units of the best

model also have substantial support and should receive consideration in making inferences (Burnham and Anderson 1998). Normalized Akaike weights (AICc weights) represent the relative probability of a model being closest to the unknown reality that generated the data, among the candidate models (Burnham and Anderson 1998). From the global model, recapture probability was modelled first, by allowing the survival probability to vary among year of birth, Distribution and time components (Table 2). The recapture model with the lowest AICc was then used to model survival probabilities (McCallum 2000). Fixing the recapture probability component of the model allowed the survival component of the model to be compared, as any difference in AICc and AICc weight given to individual models would be due specifically to the survival component. Paired *t* tests were used to test for differences in monthly survival from 0+ in September to 1+ in June, between (1) marble trout and rainbow trout living in sympatry, and (2)

Table 3 Model selection for estimation of apparent monthly survival (ϕ) and recapture (*p*) probabilities for marble trout *Salmo marmoratus* and rainbow trout *Oncorhynchus mykiss* living in sympatry and for marble trout living in allopatry in Upper Idrija

| Model | | AICc | Delta AICc | AICc weight | ML | N par | Dev |
|-----------------------------------|---------------------|----------|------------|-------------|------|-------|--------|
| Modelling capture | | | | | | | |
| $\phi(t \times yob \times Distr)$ | <i>p</i> (Distr) | 1,837.00 | 0.00 | 0.65 | 1.00 | 68 | 404.91 |
| $\phi(t \times yob \times Distr)$ | <i>p</i> (sector) | 1,839.76 | 2.76 | 0.16 | 0.25 | 71 | 400.77 |
| $\phi(t \times yob \times Distr)$ | <i>p</i> (s+sector) | 1,841.49 | 4.49 | 0.07 | 0.11 | 72 | 400.18 |
| Modelling survival | | | | | | | |
| <i>p</i> (Distr) | ϕ (Distr) | 1,811.04 | 0 | 0.31 | 1.00 | 6 | 512.61 |
| <i>p</i> (Distr) | ϕ (s×Distr) | 1,812.64 | 1.60 | 0.14 | 0.45 | 9 | 508.11 |
| <i>p</i> (Distr) | ϕ (s+Distr) | 1,813.04 | 1.99 | 0.11 | 0.37 | 7 | 512.58 |

Firstly, we modelled probability of recapture *p* by keeping the global model of survival. Then, we used the best model for *p* to model survival probabilities ϕ . For each candidate model, we report the AICc, Delta AICc, AICc weight, and ML. Only the best three models are presented. Models with lower AIC are shown in Appendix 2 of the Electronic supplementary material

ML Model Likelihood, N par number of parameters, Dev deviance

marble trout in sympatry and marble trout in allopatry. As fish were not tagged when 0+, we computed monthly survival by simply dividing the estimated number of 0+ in September by the estimated number of 1+ in June and then dividing by nine months. Data for early survival span from September 2004 to June 2005 to September 2008 to June 2009.

Analysis of body growth

Differences in mean \ln -transformed weight ($\ln W$) of marble trout cohorts at age 0+ and 1+ (in September for 0+ and June for 1+) living in sympatry with rainbow trout and allopatry were tested using t tests. The same tests were also used to investigate if mean $\ln W$ differed between marble and rainbow trout living in sympatry. When variances were unequal according to Levene's test for equality of variances, means were compared using Welch's approximate t (Zar 1999).

Mean \ln -transformed weight of 0+ trout cohorts (marble and rainbow) in September ($\ln W_{0+}$) was tested for density dependence using three analysis of covariance (ANCOVA) models. The common covariate in the three models was \ln -transformed density of the cohort (continuous variable), while the grouping variable was either (1) the combination Sector/species (MTa, MTs, RTs), (2) Sector (Sector S, Sector A), (3) species (MT, RT). The interaction between density and the grouping variable was accordingly included in the model. As sympatric marble and rainbow trout cohorts overlap for only one month before sampling in September, we used separated species-specific density of cohorts as predictors. AIC was used for model selection.

Then, we tested with ANCOVAs if body growth between sampling intervals of allopatric and sympatric marble trout born in the same year was different. We chose as response variable the natural logarithm of weight at the end of an interval ($\ln W_2$), while the independent variables were the natural logarithm of weight at the beginning of the interval ($\ln W_1$) and the grouping factor allopatry/sympatry. We used only combination of cohorts and years with a minimum of three individuals. For each ANCOVA, we tested for the interaction term that is the heterogeneity in the slopes of lines relating final size to initial size. If the interaction term was not significant, the model was fitted again without the interaction term, thus allowing comparisons of line elevations (i.e., final sizes at a common initial size). These are standard procedures for statistically removing the effects of covariation with body size (Huitema 1980). If the interaction term was significant, this meant that the groups (allopatry/sympatry) differed in growth when the final sizes of the one group were consistently above or below final sizes of the other group (i.e., if the final sizes for one group fell above or below

those of the other group across the entire range of initial sizes). Unfortunately, due to the limited sample size (we never reached the minimum threshold of three individuals) we could not include rainbow trout in the ANCOVAs.

Results

Age, size and population densities

Mean weight is reported for each species-age combination across samples in Appendix 3 of the Electronic supplementary material. Maximum age was 4+ for sympatric rainbow trout (with very few individuals older than 1+), 10+ for sympatric marble trout and 8+ for allopatric marble trout. In both sympatric and allopatric marble trout very few individuals were older than 6+ (see Appendix 3 of the Electronic supplementary material). Densities in ind. m^{-2} (for marble and rainbow trout aged 0+ and $\geq 1+$) estimated in September of each year from 2002 to 2009 are reported in Fig. 1. Density of marble trout aged $\geq 1+$ living in sympatry with rainbow trout were similar to density of marble trout in allopatry over the whole study period and they were both higher than density of rainbow trout by a factor ranging between 5 and 30 (Fig. 1a). On the other hand, density of 0+ in September was similar in rainbow trout and marble trout living in sympatry (Fig. 1b) and greater than density of marble trout living in allopatry in almost all years.

Recapture and survival probabilities

Marble trout living in sympatry and allopatry were sampled twelve times (June 2004–September 2009) allowing a potential comparison of apparent survival for eleven sampling intervals. Areas above and below the sampling sections were sampled in each sampling occasion to gain a qualitative impression of emigration. No tagged trout were recaptured outside the sampling sections. The best model of recapture and apparent survival probabilities included only the component Distribution (MTa, MTs and RTs). Models of apparent survival including also season as temporal component, either multiplicative or additive, in addition to Distribution, had very close AICc values (Table 3). Using the best model for inference, apparent survival varied by distribution, with the highest survival probability for MTa and the lowest for RTs, with a slight overlap of 95% confidence intervals for MTa and MTs (Fig. 2). In models including the seasonal component, survival was higher in summer for marble trout in allopatry, and higher in winter for marble and rainbow trout living in sympatry, although there was a substantial overlap of confidence intervals (Fig. 2).

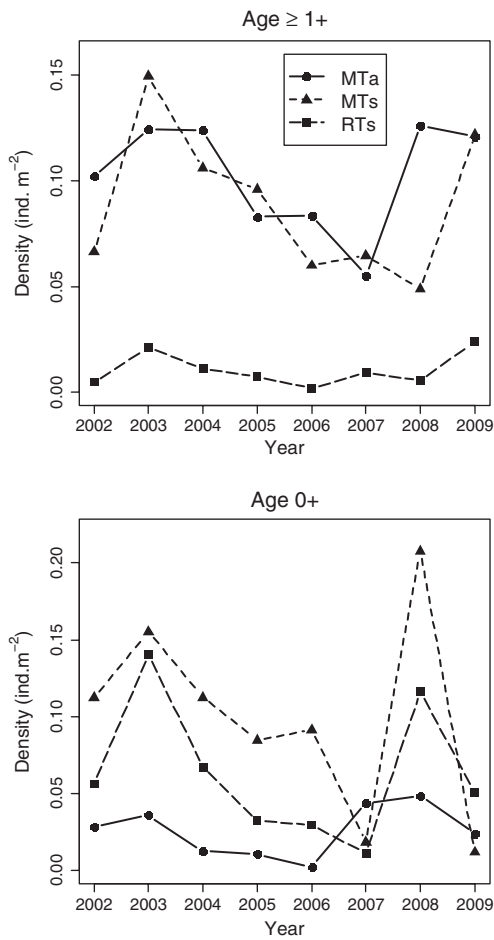


Fig. 1 Densities of rainbow trout *Oncorhynchus mykiss* and of marble trout *Salmo marmoratus* (in ind. m⁻²) estimated in September from 2002 to 2009 in Sector S and Sector A. In Sector S, marble trout (MTs) live in sympatry with rainbow trout (RTs), while in Sector A marble trout live in allopatry (MTa). For trout aged $\geq 1+$ (mean \pm SD): MTa, 0.10 \pm 0.03 ind. m⁻²; MTs, 0.09 \pm 0.03; RTs, 0.01 \pm 0.08. For trout age 0+: MTa, 0.03 \pm 0.02; MTs, 0.1 \pm 0.06; RTs, 0.07 \pm 0.04

Paired *t* tests revealed no significant differences ($p=0.13$) in monthly September to June survival of juveniles for marble trout in sympatry (mean \pm SD of survival=0.93 \pm 0.05) vs marble trout in allopatry (0.96 \pm 0.04). Differences in mean survival between sympatric marble trout and rainbow trout (0.82 \pm 0.09) were significant ($p<0.01$). The lower survival of rainbow trout appeared to be consistent across life-stages. As different techniques were used to estimate survival probabilities for age-0 fish and older fish, monthly survival probabilities should be compared with great caution.

Growth and size variation

Mean weight of 0+ cohorts of marble trout in September was significantly greater in MTa in 2004, 2005 and 2007 (*t* tests, $p<0.01$) and not significantly different in the

remaining years. Mean weight of 0+ cohorts of RTs in September was significantly greater than mean weight of 0+ cohorts of MTs in 2004, 2005, 2006 and 2008 (*t* tests, $p<0.01$) and not significantly different in 2007 and 2009. As for marble trout cohorts aged 1+ in June, mean weight of MTa was significantly greater in all years ($p<0.05$) except 2008, when mean weight of MTs was greater. Mean weight of RTs cohorts aged 1+ in June was greater ($p<0.01$) than mean weight of MTs for all years (for 2006, we did not have enough observations).

The model with the best AIC had trout species (MT and RT) as a grouping variable. In W_{0+} decreased with increasing cohort density (Fig. 3). The interaction term was significant, thus revealing different slopes for marble and rainbow trout. Mean weight of 0+ cohorts at equal cohort densities in the range of densities observed was higher for rainbow trout (Fig. 3).

The number of individuals for which growth between sampling intervals could be measured was a subset of the total, because growth rate estimation required that an individual be captured in both the starting and ending sample of an interval. For 16 combinations of age and cohort, we had the necessary sample size for comparison of growth of MTa and MTs (see Appendix 4 of the Electronic supplementary material). The interaction term between initial size (ln W_1) and Sector was never significant in the ANCOVAs. Removal of the interaction term revealed that marble trout cohorts grew equally in allopatry and in sympatry with rainbow trout (see Appendix 4 of the Electronic supplementary material). Only in one case, fish born in 2007, growth from September 2008 to June 2009 was greater for MTa. In Fig. 4, we show the growth

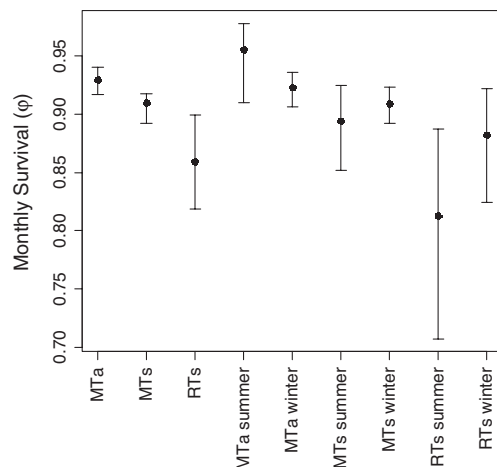


Fig. 2 Apparent survival estimates \pm 95% CI for the overall best model $\phi(\text{Distr})p(\text{Distr})$ and the best model with a time component $\phi(s \times \text{Distr})p(\text{Distr})$, where *s* represents season (summer and winter) and *Distr* represents trout populations: MTa marble trout *Salmo marmoratus* in allopatry; MTs marble trout in sympatry; RTs rainbow trout *Oncorhynchus mykiss* in sympatry

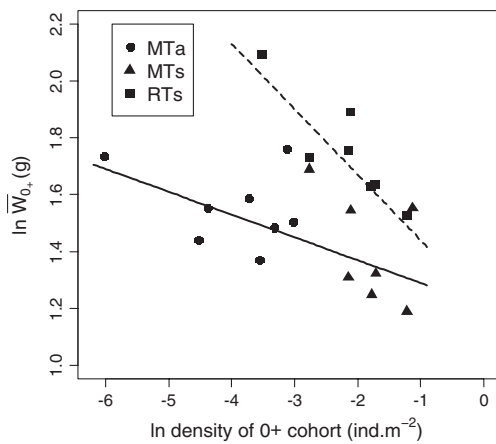


Fig. 3 Relationship between density of cohort aged 0+ (D) and mean weight of cohort (W), in the form $\ln W = \alpha + \beta_1 \ln D + \beta_2 \ln D \times TS$, where TS is trout species (rainbow trout *Oncorhynchus mykiss*, $RT=1$; marble trout *Salmo marmoratus*, $MT=0$). $\beta_1 = -0.08 \pm 0.03$; α , $RT = 1.02 \pm 0.21$, $MT = 1.21 \pm 0.09$; $\beta_2 = -0.14 \pm 0.07$. $p < 0.01$, $R^2 = 0.65$. Regression lines are shown for rainbow trout (dashed line) and marble trout (continuous line)

trajectories of 2004 and 2005 cohorts for marble trout and rainbow trout living in sympatry (Sector S) and marble trout in allopatry (Sector A). While it was not possible to use the same approach to compare body growth between sympatric rainbow and marble trout living in Sector S, body growth of rainbow trout is remarkably higher than that of both MTa and MTs (see Appendix 4 of the Electronic supplementary material).

Discussion

The self-reproducing rainbow trout population of Upper Idrijca does not have a noticeable impact on body growth and survival of sympatric marble trout. This was quite surprising, as most of the studies dealing with the potential impact of rainbow trout on native salmonids showed reductions of populations size or extinction of native species due to redd superimposition, predation and competition for food (Peter et al. 1998; Scott and Irvine 2000; Taniguchi et al. 2000; Kitano 2004; Baxter et al. 2007; Blanchet et al. 2007; Fausch 2007; Nomoto et al. 2010). The pattern of coexistence after almost 50 years can be considered stable and not a transient phase in the invasion process.

Where two species of stream salmonids exhibit complementary distributions in abundances, interference competition often plays an important role (Fausch et al. 1994; Taniguchi and Nakano 2000; Rieman et al. 2006). As noted by Carlson et al. (2007), differences in the density of conspecifics and heterospecifics might influence growth rate differences and it was therefore expected that sympatric

marble trout were more growth limited than rainbow trout. Sectors A and S are very similar in terms of water temperature and physical features, and this might rule out alternative explanations sector related about the similarity in body growth of fish $\geq 1+$ between marble trout in allopatry and sympatry (for instance, warmer water temperatures in Sector S leading to greater body growth despite the presence of rainbow trout). Intra-specific mechanisms seem more important in influencing growth rates than inter-specific dynamics. This may suggest that resource limitation is different for the two species or the presence of habitat segregation, with rainbow trout occupying an unoccupied or underutilized niche space.

Differences in densities of juveniles between marble trout in sympatry and in allopatry could be related to the different availability of suitable micro-habitat for juveniles in sector S and sector A; in Sector S the stream surface not occupied by large pools, generally preferred by larger and older fish, is greater than in Sector A.

Other studies have shown that depending on several factors, such as overlap of habitat and diet (e.g., Hilderbrand and Kershner 2004; Höjesjö et al. 2005), reproductive success (e.g., Thériault et al. 2007) and redd superimposition (e.g., Essington et al. 1998), sympatric salmonids may show differences in survival. Our analysis was carried out on data gathered between 2002 and 2009 and more years of data are certainly necessary to assess whether the patterns observed here are consistent. On the contrary, the analysis of replicate streams and/or analysis of growth and survival of marble

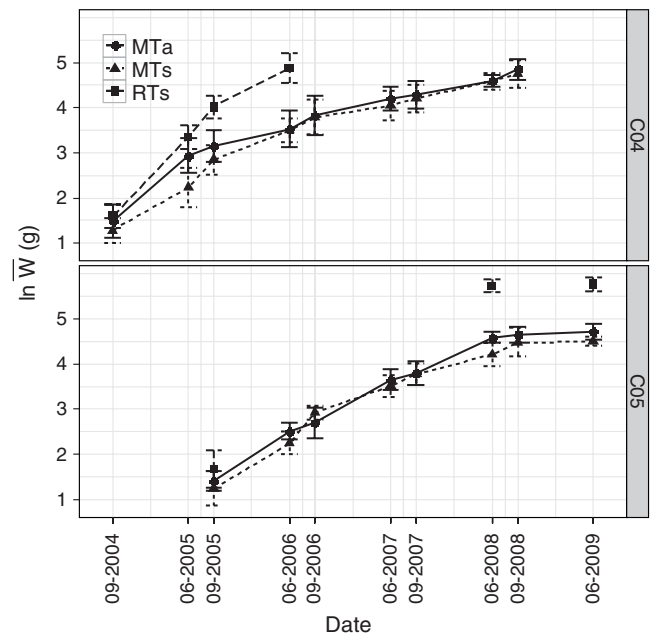


Fig. 4 Mean logarithm of weight \pm SD for marble trout *Salmo marmoratus* in sympatry (MTs), rainbow trout *Oncorhynchus mykiss* in sympatry (RTs) and marble trout in allopatry (MTa) for the 2004 (C04) and 2005 (C05) cohorts

trout after the removal of rainbow trout from Sector S could help clarify whether the slightly lower survival of sympatric marble trout is caused by competition with rainbow trout or by other environmental factors, such as differences in habitat availability between Sector A and Sector S.

The dynamics of invasion of two trout species outside their native range in western and southeastern USA can help understand the dynamics of invasion of rainbow trout in Slovenian streams. Fausch (2008) formulated a novel hypothesis to explain why brook trout are able to displace native cutthroat trout (*Oncorhynchus clarkia Richardson*) in the western United States, but are themselves displaced by alien rainbow trout in the southeastern US. Fausch (2008) highlighted the importance of the adaptation of species to natural disturbance regimes in their native ranges. Invasions occur where the nonnative species are, by chance, better adapted than the native species to the natural disturbance regime of the system being invaded. As a consequence, brook trout is an effective invader in regions with floods in spring and low flows in winter (southern Rocky Mountains) while rainbow trout are better adapted to the winter flood—summer low flow regime (southern Appalachians). Inoue et al. (2009) found that in Hokkaido streams (Northern Japan) the occurrence of introduced rainbow trout was limited to streams with stable flows and suggested that biotic resistance from the native salmonid (masu salmon *Oncorhynchus masou*) plays no role or a lesser role in controlling rainbow trout invasion.

Most of Slovenian streams are spring-fed, with floods seldom occur in spring and early summer, when rainbow trout emerge. Floods occur mainly in autumn, about 3–4 months after emergence of rainbow trout and this may be favorable for the establishment of self-sustaining populations of rainbow trout. In other streams at lower altitudes we investigated in the Adriatic basin of Slovenia where pure and hybrid marble trout live in sympatry with rainbow trout, we found much higher densities of rainbow trout (0.026 to 0.11 trout m⁻²) with a ratio marble/rainbow lower than 1 (D. Jesensek and A.J. Crivelli, unpublished data). A similar spatial pattern was found for alien brook trout and native brown trout in North European streams, with alien brook trout—an headwater specialist—found mainly in small tributary streams characterized by harsh and variable environmental conditions whereas brown trout is prevalent in larger, more benign downstream sites (Korsu et al. 2007). Interestingly, the pattern is reversed in North America, where brown trout occupies headwater streams and brook trout lower altitude streams.

Meldgaard et al. (2007) performed an in-stream experiment by mixing marble trout and brown trout in two Slovenian streams (Driselpoh and Stopnikarca) and used capture-recapture data to estimate body growth and survival rates of fish. Hybridization took place in both streams, thus

suggesting the absence of reproductive isolation marble and brown trout, but marble trout seemed to grow and survive better in Stopnikarca, which is three times steeper and more fragmented than Driselpoh. Meldgaard et al. (2007) hypothesized that habitat features such as stream slope and fragmentation as well as density are determining factors for the higher relative success of marble trout in Stopnikarca. They suggested for conservation purposes to stock marble trout in steep fragmented streams because they seem to reside much better in those streams than brown and hybrid trout and thus may experience higher growth and survival rates due to lower levels of stress from other trout.

Although further evidence is needed, it seems that marble trout is better adapted to the harsh and more variable conditions of headwater streams than alien salmonids and thus offer a high biotic resistance to invasion, although we cannot exclude that the lower biotic resistance offered by hybrid marble trout in streams at lower altitudes could explain the numerical dominance of rainbow trout. Our results provide further support for the management action suggested by Meldgaard et al. (2007) for the conservation of marble trout.

Habitat and resource partitioning between marble and rainbow trout deserve further investigations and our study needs to be integrated with lab and enclosure experiments (Peterson and Fausch 2003; Korsu et al. 2009). The study of dietary habits of sympatric rainbow and marble trout can give substantial insight into the relative role of competitive and/or predatory interactions in native-fish decline or dominance. In any case, as also recently discussed by Korsu et al. (2010), understanding the key environmental filters that determine the distributions of invasive species, the scales at which these filters operate, and the population-level mechanisms determining the outcome of invasions is a difficult, but necessary step toward effective management of invasive species and conservation of native species.

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