

Dietary niche expansion and niche shift in native marble trout (*Salmo marmoratus*) living in sympatry with introduced rainbow trout (*Oncorhynchus mykiss*)

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Abstract

The non-native rainbow trout (*Oncorhynchus mykiss*) has been introduced worldwide for angling purposes and has established self-reproducing populations in many parts of the world. Introduced rainbow trout often have negative effects on the native salmonid species, ranging from decrease abundance, growth and survival, to their local extinction. Assessing the effects of introduced rainbow trout on the native species is thus crucial to better set up conservation programmes. In this study, we investigated the effects of non-native rainbow trout on the diet of native marble trout (*Salmo marmoratus*) living in the Idrijca River (Slovenia). An impassable waterfall separates the stream in two sectors only a few hundred metres apart: a downstream sector (treatment) in which marble trout live in sympatry (MTs) with rainbow trout (RTs) and an upstream sector (control) in which marble trout live in allopatry (MTa). Specifically, we investigated using stable isotopes the effects of rainbow trout on dietary niche, diet composition, body condition, and lipid content of marble trout. We found dietary niche expansion and niche shift in marble trout living in sympatry with rainbow trout. Compared to MTa, MTs had higher piscivory rate and showed higher body condition and prereproduction lipid content. Our results indicate that the presence of rainbow trout did not have negative effects on marble trout diet and condition and that changes in dietary niche of marble trout are likely to be an adaptive response to the presence of rainbow trout, and further research is needed to better understand.

KEYWORDS

biological invasions, body condition, lipid content, niche segregation, stable isotope analysis, trophic niche breadth

1 | INTRODUCTION

Exotic species have been introduced worldwide, voluntarily or accidentally, leading to economical, ecological and evolutionary damages (Perrings et al., 2002). Biological invasions are now recognised as the second main cause of the current biodiversity decline after habitat degradation (Clavero & García-Berthou, 2005; Mack et al., 2000). Fishes are the most commonly introduced organisms outside their native ranges,

either by accidental release of ornamental species or by intentional stocking for recreational purposes (Gozlan, Britton, Cowx, & Copp, 2010). Their introduction can have deleterious effects on native populations by displacing them from their original niches (Bøhn, Amundsen, & Sparrow, 2008) and decreasing their fitness (Irons, Sass, McClelland, & Stafford, 2007), on native communities by modifying food-web structure (Eby, Roach, Crowder, & Stanford, 2006), and on recipient ecosystems by changing biochemical cycles (Schindler, Knapp, & Leavitt, 2001).

As many non-native fish species have established self-sustaining populations in European freshwaters after their introduction (Strayer, 2010), assessing the effects of their presence on native species is crucial to improve management and conservation programmes. Salmonids are among the most frequently introduced fish species (Cucherousset & Olden, 2011); they are often detrimental to native salmonid populations because of potential predation and competition for food and space (Morita, Tsuboi, & Matsuda, 2004) and are a serious threat to the persistence of native populations (Seiler & Keeley, 2009; Takami, Yoshihara, Miyakoshi, & Kuwabara, 2002). Invasions by non-native salmonids often lead to slow growth rate (Carlson, Hendry, & Letcher, 2007; van Zwol, Neff, & Wilson, 2012), reduced survival (Blanchet, Loot, Grenouillet, & Brosse, 2007; Houde, Wilson, & Neff, 2015) and decrease in abundance of the native species (Benjamin & Baxter, 2012). Nevertheless, some sympatric cases between native and non-native salmonids are reported without detrimental effect on native species, showing biotic resistance and pre-adapted habitat and/or dietary niche segregation to the invasion success (Hasegawa, Yamamoto, & Kitanishi, 2010; Inoue, Miyata, Tange, & Taniguchi, 2009; Korsu, Huusko, & Muotka, 2009).

Investigating the dietary niches of sympatric species and variation in physiological and life-history traits between allopatric and sympatric populations allow exploring the ecological effects of biological invasions on native populations and communities. In recent years, the study of stable isotope niche as a proxy of dietary niches has become more popular as they reflect both resources' diversity used by a consumer and trophic interactions in the system (Layman, Araújo, Boucek, Hammerschlag-Peyer, & Harrison, 2012; Newsome, Martinez del Rio, Bearhop, & Phillips, 2007). Stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) are powerful tools for investigating the flow of energy through food webs. $\delta^{13}\text{C}$ is the indicator of energy source, and $\delta^{15}\text{N}$ is the indicator of trophic level (Layman et al., 2012). Using $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ is common in fish diet analysis for quantifying the relative contribution of different types of prey in predator diet and for characterising species trophic niche variability as responses to abiotic and biotic factors (Musseau, Boulenger, et al., 2015; Musseau, Vincenzi, et al., 2015).

Rainbow trout (*Oncorhynchus mykiss*) has been introduced worldwide (Crawford & Muir, 2008) and has been listed among the worst invasive species by the International Union for Conservation of Nature (Lowe, Browne, Boudjelas, & De Poorter, 2000). Many studies have shown large negative effects (i.e. hybridisation, disease transmission, predation and competition) of non-native rainbow trout on native fish species across continents (Nomoto et al., 2010; Shelton, Bird, Samways, & Day, 2017), including Europe (Blanchet et al., 2007; Stanković, Crivelli, & Snoj, 2015). Rainbow trout have been introduced in Slovenia in the early 20th century for recreational purposes and have established numerous self-sustaining populations in Slovenian Adriatic basin (Stanković et al., 2015), threatening the viability of the endangered native salmonid species marble trout *Salmo marmoratus* Cuvier, 1829.

The marble trout is a stream-dwelling trout living in cold freshwater. Sexually mature trout (above 200 mm and 2 years old) spawn

in November–December and emergence typically occurs in May–June (Meldgaard et al., 2007; Vincenzi, Crivelli, Jesensek, Rossi, & De Leo, 2011). The species shows a high trophic plasticity between populations and larger individuals are cannibals (Musseau, Vincenzi, et al., 2015). Only eight small, isolated and genetically pure populations of marble trout remain in the pristine upper parts of Soča River basin in Slovenia (Fumagalli et al., 2002). Marble trout is threatened by biological invasions and the increasing frequency of flash floods and debris flows (Meldgaard et al., 2007; Vincenzi, Mangel, Jesensek, Garza, & Crivelli, 2017). Due to its high patrimonial value, a conservation and rehabilitating project was launched in 1993 (Crivelli, Poizat, Berrebi, Jesensek, & Rubin, 2000).

Two of the eight remaining genetically pure populations of marble trout are in the Idrijca River (Western Slovenia), where an impassable waterfall separates fish in upper Idrijca from a closely related group in lower Idrijca. Marble trout in lower Idrijca coexist with non-native rainbow trout, which were introduced only once in the 1960s and have been established since then, but they are absent in upper Idrijca (Stanković et al., 2015). As the environmental and habitat conditions for salmonids in lower and upper Idrijca are highly similar (Vincenzi, Mangel, Jesensek, Garza, & Crivelli, 2016), this unintended treatment-control experiment allows studying variation in vital rates, population dynamics and diet of the native species when competing with an invasive species of the same taxonomic Family. Vincenzi et al. (2011) found minor effects of rainbow trout on body growth and survival of marble trout living in sympatry with rainbow trout in lower Idrijca when comparing those vital rates to those of marble trout in allopatry in upper Idrijca and showed long-term coexistence of marble and rainbow trout. However, data to understand the impact of the rainbow trout on marble trout are still missing, particularly on trophic ecology and physiology of marble trout have not been examined yet.

In this work, we investigated the effects of the non-native rainbow trout (RTs) on trophic ecology and physiological conditions of marble trout living in sympatry (MTs), using an allopatric marble trout population as control (MTa). The Idrijca River provides a unique opportunity to investigate the potential effects that the non-native rainbow trout may have on the native and endangered marble trout. Although the uniqueness of the situation prevented sites replication, we followed these populations over 2 years. We aimed at quantifying the effects of the rainbow trout on marble trout (i) dietary niches, (ii) diet composition and (iii) two physiological traits: body condition and lipid content.

2 | MATERIAL AND METHODS

2.1 | Study area and sampling

Sampling was conducted in 2012 (June 19) and 2013 (June 20 and September 16) in the Idrijca River, a 60-km-long tributary of the Soča River (Slovenia). In its upper part, the Idrijca watershed is mainly covered by deciduous forests with the European beech (*Fagus sylvatica*) as the dominant species, with low human activity. An impassable waterfall in Idrijca prevents fish movement from downstream to upstream and provides two sectors of interest, Sector A and Sector S

(Fig. S1), which are separated by approximately 1 km. Marble trout live in allopatry in Sector A (Berrebi, Povz, Jesensek, Cattaneo-Berrebi, & Crivelli, 2000; Fumagalli et al., 2002) and in sympatry with non-native rainbow trout in Sector S (Vincenzi et al., 2011). Marble trout (Sectors A and S) and rainbow trout (Sector S only) are the only fish species living in those sectors. No sport fishing is allowed in the study areas, and poaching is absent. The altitude ranges are 718–720 m (Sector A) and 537–543 m (Sector S) above sea level. Pools (habitats deeper than the average sector depth and with water velocity slower than the average water velocity in the sector) occupy 65% of sector total surface of Sector A and 40% of the sector total surface of Sector S. Stream slopes are on average 1% and 2% in Sector A and Sector S respectively. Annual mean temperatures were similar in the two sectors in 2012 (Sector A: 7.42°C ± 3.14 and Sector S: 7.94°C ± 3.51) and in 2013 (Sector A: 7.87°C ± 3.11 and Sector S: 8.39°C ± 3.42). Sector A is 110.8 m long with a wet surface area of 888 m² and Sector S is 268.1 m long with a wet surface area of 1,513.1 m² and main substrate in both sectors are stones in riffles, litter in pools and blocks.

Sampling surveys were carried out on the whole length of each sector starting downstream using a gasoline-powered portable backpack electrofishing unit (Power goal: 500 Watts and ambient conductivity: 295 µS/cm). Each sector was electro-fished two times, allowing to produce a multiple-pass removal estimate of trout density using Microfish 3.0 (van Deventer & Platts, 1989). MTa, MTs and RTs populations have been surveyed biannually since June 2004 by local managers (Tolmin Angling Association) and scientists (A.J. Crivelli, Tour du Valat). Trout were individually tagged with Carlin tags when they reached 115 mm. Since the beginning of this survey, no trout tagged in Sector A has been found among the approximately 800 marble trout sampled in Sector S,

Each sampled trout was anaesthetised with phenoxyethanol and its length (mm) and weight (g) were recorded in situ. For each trout, we collected scales for age determination between the end of dorsal fin and the beginning of the tail (in the following analysis, we only used +1 year and older trout) and we clipped a small piece of the pelvic fin. Trout were released after data collection. Nonlethal sampling is mandatory due to the endangered status of marble trout, and fin tissues were allowed for stable carbon and nitrogen isotope and stoichiometry analysis (Busst, Bašić, & Britton, 2015; Curry, Gautreau, & Culp, 2014; Finlay, Khandwala, & Power, 2002; Jardine, Hunt, Pusey, & Bunn, 2011). We sampled benthic invertebrates using a surber net in three habitats (stones in riffles, litter in pools and blocks) within the two sectors for each sampling session. We collected aquatic invertebrates for baseline correction in the stable isotope analyses. Terrestrial invertebrates were collected by hand and net along the riverbanks.

2.2 | Stable isotope analysis

Fin samples and invertebrate samples were oven-dried for 48 hr at 60°C and ground into a fine homogenous powder using a mill (Spex Certiprep 6750 Freezer/Mill). Stable isotope ratios of carbon and nitrogen ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and content of both elements (C% and N%)

were analysed in a Carlo Erba NC2500 elemental analyser coupled to a Thermo Finnigan MAT Delta XP isotope ratio mass spectrometer. Stable isotope ratios are expressed in per mill (‰) delta values ($\delta^{13}\text{C}$ or $\delta^{15}\text{N}$) referring to the international standards for carbon (PeeDee Belemnite) and nitrogen (atmospheric nitrogen): $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ (‰) = $[(R_{\text{sam}} - R_{\text{std}})/R_{\text{std}}] \times 1,000$. Data were corrected using working standards (fish tissue, mink tissue and methionine SD < 0.2‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) that were previously calibrated according to International Atomic Energy Agency standards. All stable isotope and elemental content analyses were performed at the Cornell Isotope Laboratory, Cornell University, USA.

2.3 | Isotopic niches and diet composition

Stable isotopic signatures were baseline-corrected (France, 1995). Baseline correction is necessary because basal resources can be highly variable between sites. Mayflies' grazer larvae (Ephemeroptera) from Baetidae (*Baetis* sp.) and Heptageniidae (*Ecdyonurus* sp., *Epeorus* sp., *Rhitrogena* sp.) families were used for trophic position baselines correction, as they are primary consumers. For $\delta^{15}\text{N}$ correction, the trophic position of fish was calculated following Anderson and Cabana (2007):

$$\text{TP}_i = \frac{\delta^{15}\text{N}_i - \delta^{15}\text{N}_{\text{baseline}}}{\Delta^{15}\text{N}} + 2 \quad (1)$$

where TP_i is the trophic position for individual i , $\delta^{15}\text{N}_i$ is the nitrogen isotopic ratio for individual i , $\delta^{15}\text{N}_{\text{baseline}}$ is the nitrogen isotopic ratio of primary consumers, $\Delta^{15}\text{N}$ is the trophic enrichment factor and 2 is the trophic position of the organisms used as baseline.

Then, we corrected $\delta^{13}\text{C}$ values following Olsson, Stenroth, Nyström, and Granéli (2009):

$$\delta^{13}\text{C}_{\text{corr}_i} = \frac{\delta^{13}\text{C}_i - \delta^{13}\text{C}_{\text{meaninv}}}{\text{CR}_{\text{inv}}} \quad (2)$$

where $\delta^{13}\text{C}_{\text{corr}_i}$ is the corrected carbon isotopic ratio for individual i , $\delta^{13}\text{C}_i$ is the carbon isotopic ratio for individual i , $\delta^{13}\text{C}_{\text{meaninv}}$ is the average carbon isotope ratio of benthic invertebrates sampled for putative prey sources (see below) and CR_{inv} is the carbon range ($\delta^{13}\text{C}_{\text{max}} - \delta^{13}\text{C}_{\text{min}}$) of benthic invertebrates used for baseline correction of trophic position (i.e. primary consumers).

In our study, the isotopic niche is the area occupied by all sampled trout belonging to a population/species for a given sampling occasion in the biplot formed by two axes (TP and $\delta^{13}\text{C}_{\text{corr}}$). We estimated differences in niche centroid location (the mean of TP and $\delta^{13}\text{C}_{\text{corr}}$ of all individuals in the given group) with a residual permutation procedure ($n = 9,999$, Turner, Collyer, & Krabbenhoft, 2010) to test for niche shift, where significant results suggest differences in use of resources (Hotelling's T^2 statistical test, multivariate analogue of the t test). We combined niche centroid location analysis with overlap of standard ellipse area within a Bayesian framework (SEA_b , SIBER, Jackson, Inger, Parnell, & Bearhop, 2011, version 2.1.2). The standard ellipse area is a measure of niche breadth, while overlap between SEA_b is a proxy of trophic similarity between two groups. First, we assessed the potential competitive interaction between MTs and RTs by estimating SEA_b overlaps and niche centroid locations. Then, we investigated the

effects of rainbow trout on marble trout resource use by focusing on differences in niche centroid location and SEA_b overlaps between MTa and MTs. Finally, we compared position of MTa and RTs in the bivariate isotopic plot to evaluate a potential trophic niche replacement of marble trout by rainbow trout in the food web. We quantified niche breadth for each population by calculating SEA_b values, and we compared the relative size of ellipses between populations for each sampling period to assess niche expansion under sympatry. All of these comparisons in centroid locations and SEA_b overlaps were run for each sampling period (i.e. June 2012, June 2013 and September 2013) for the $\geq 1+$ trout.

To estimate proportion of each food resource to the diet of each trout, we ran mixing models for stable isotopic data (package SIAR, Parnell, Inger, Bearhop, & Jackson, 2010, version 4.2.2). This method uses Bayesian inference to estimate diet proportion from set of isotopic data of set of possible food sources and set of consumers. We ran a mixing model for each trout with three categories of prey: "freshwater invertebrates" composed by different macroinvertebrates taxa including grazers (*Baetis* sp., *Ecdyonurus* sp., *Electrogena* sp., *Limnius* sp.) and predators (*Perla* sp., *Isoperla* sp., *Rhyacophila* sp.) ($n = 4-10$), "terrestrial invertebrates" including phytophagous (Coleoptera or Acrididae) and predators (Formicidae and Araneae) ($n = 3-10$) and "fish." Freshwater and terrestrial invertebrates were maintained alive during 24 hr with no food to enable gut evacuation. Marble trout in allopatry was the only species included in the group "fish" (only cannibalism is possible). In Lower Idrijca, both rainbow and marble trout were included (i.e. cannibalism or/and piscivory). We used Caut, Angulo, and Courchamp's (2009) formula for $\delta^{15}N$ and $\delta^{13}C$:

$$\Delta^{15}N = -0.261 \delta^{15}N + 4.895 \quad (3)$$

$$\Delta^{13}C = -0.213 \delta^{13}C - 2.848 \quad (4)$$

to determine the trophic enrichment factors (Table 1). For later analyses, we used the median of 500,000 simulations for each trout.

2.4 | Body condition and lipid content

Variation in body condition and lipid content is helpful for assessing potential changes in condition of organisms after food shortage or the interspecific competition deleterious effects (Arismendi, Penaluna, & Soto, 2011; Irons et al., 2007).

The body condition of organisms is commonly used as a proxy of individual fitness (Dempster et al., 2011; Jakob, Marshall, & Uetz, 1996). We computed the body condition index (K_i) for each MTa and MTs as following:

$$K_i = \left(\frac{W_i}{L_i^3} \right) \times 100 \quad (5)$$

where W is the weight (g) and L the total length (cm) for each fish (Arismendi et al., 2011; Nash, Valencia, Geffen, & Meek, 2006).

Lipid content (%) in individual is a measurement of energy storage in animal (Thompson, Bergersen, Carlson, & Kaeding, 1991). It was computed using Post et al. (2007)'s equation:

$$\% \text{ lipid}_i = -20.54 + 7.24 \times (C:N)_i \quad (6)$$

TABLE 1 Trophic enrichment factors of nitrogen ($\Delta^{15}N$) and carbon ($\Delta^{13}C$) for marble trout living in allopatry (MTa) and in sympatry (MTs) with the non-native rainbow trout (RTs) for the three sampling occasions

| Sampling | Treatment | $\Delta^{15}N$ (‰) | | $\Delta^{13}C$ (‰) | |
|----------------|-----------|--------------------|------|--------------------|------|
| | | Mean | SD | Mean | SD |
| June 2012 | MTa | 4.37 | 0.18 | 3.25 | 0.24 |
| | MTs | 4.22 | 0.28 | 3.14 | 0.26 |
| | RTs | 4.45 | 0.22 | 3.13 | 0.19 |
| June 2013 | MTa | 4.44 | 0.20 | 3.36 | 0.22 |
| | MTs | 4.44 | 0.28 | 3.22 | 0.22 |
| | RTs | 4.79 | 0.18 | 3.40 | 0.19 |
| September 2013 | MTa | 4.27 | 0.12 | 3.29 | 0.21 |
| | MTs | 4.28 | 0.19 | 3.05 | 0.23 |
| | RTs | 4.31 | 0.21 | 2.89 | 0.25 |

where $\% \text{ lipid}_i$ is lipid content for individual i and $(C:N)_i$ is C:N ratio for individual i . C:N molar ratios were computed from the C and N elemental composition of samples.

2.5 | Statistical analysis

We used generalised linear models (GLM, *quasibinomial* distribution with *logit* as link function) to test the effects of the rainbow trout on marble trout diet and the differences between MTs and RTs diets. We tested the effects of *Treatment* (allopatry or sympatry), total size of trout (*TL*), *Sampling* (June 2012, June 2013 and September 2013) and *Species* (MT or RT) on the contribution of each food item in trout diet. We tested the interactions between the different predictors, and they were removed when nonsignificant ($p > .05$, Engqvist, 2005; Crawley, 2012). The contribution of model terms and their significance were tested by calculating the change in deviance from a null model (i.e. intercept only) and comparing them to the chi-square distribution for the GLM.

We used multivariate linear regression models to estimate the effect of the rainbow trout on marble trout body condition and lipid content through ontogeny. Models were run for both response variables independently. For each response variable, we tested a combination of the additive and multiplicative interactions among predictors (*TL*, *Sampling*, *Treatment*). Nonsignificant interactions were removed from the final models (Crawley, 2012; Engqvist, 2005). Statistical analyses were performed using R software version 3.3.0 (R Development Core Team, 2014).

3 | RESULTS

Overall, we did not find negative effects of rainbow trout on native marble trout. Our results first showed that MTs displayed broader dietary niche than MTa and, then, that the body condition and preproduction lipid content of MTs were higher than in MTa.

3.1 | Trout densities and benthic invertebrates' communities

In total, we sampled fin tissue in 633 fish, 246 from marble trout in allopatry (MTa), 224 from marble trout in sympatry (MTs) and 163 from rainbow trout in sympatry (RTs). Estimated total densities and number of salmonids were 0.1076 ind/m² in Sector A and 0.1296 ind/m² (0.1124 MTs/0.0172 RTs) in Sector S in June 2012, 0.1298 ind/m² in Sector A and 0.0741 ind/m² (0.0648 MTs/0.0093 RTs) in Sector S in June 2013 and 0.1094 ind/m² in Sector A and 0.0781 ind/m² (0.0688 MTs/0.0093 RTs) in Sector S in September 2013. Dry weight biomass (mg/m²) was very similar between Sectors A and S, indicating no difference in resource availability between both sectors (Fig. S3). Indexes of evenness, diversity and similarity in benthic invertebrates' communities showed similar taxonomic compositions in Sectors A and S (Tables S1 and S2).

3.2 | Trophic niche breadth and overlap

Standard ellipse areas were significantly bigger for MTs than for MTa in June 2012 and 2013 (Figure 1), MTa SEA_b only represented 65% of the MTs total SEA_b in June 2012 ($p = .005$) and 74% in June

2013 ($p = .04$). Standard ellipse areas of MTa and MTs were similar in September 2013 ($p = .07$).

We found niche segregation between MTs and RTs for each sampling period with low niche overlap (0.1% in June 2012 and 2013 and 6.8% in September 2013, Figure 2) and significantly different centroid locations (Hotelling's $T^2 = 128.57$, $p < .001$, Hotelling's $T^2 = 89.03$ $p < .001$ and Hotelling's $T^2 = 61.01$, $p < .001$ in June 2012, June 2013 and September 2013 respectively). Marble trout displayed different niches between allopatry and sympatry with niche centroids significantly different in June 2012 and September 2013: (Hotelling's $T^2 = 165.01$, $p < .001$ and Hotelling's $T^2 = 197.55$, $p < .001$ respectively) but similar in June 2013 (June 2013: Hotelling's $T^2 = 5.13$, $p = .082$). 33.6% of niches overlapped in June 2013, but we found no overlap in June 2012 and September 2013 (Figure 2). The trophic niche breadth of MTa did not overlap that of RTs, and centroids were significantly different in June 2013 and September 2013 (Hotelling's $T^2 = 290.99$, $p < .001$ and Hotelling's $T^2 = 537.30$, $p < .001$ respectively). In June 2012, niches were more similar with a 29.4% overlap but different centroid locations (Hotelling's $T^2 = 12.29$, $p = .003$).

3.3 | Trout diet composition

The estimated proportion of benthic and terrestrial invertebrates and fish in MTs and MTa changed through ontogeny and between

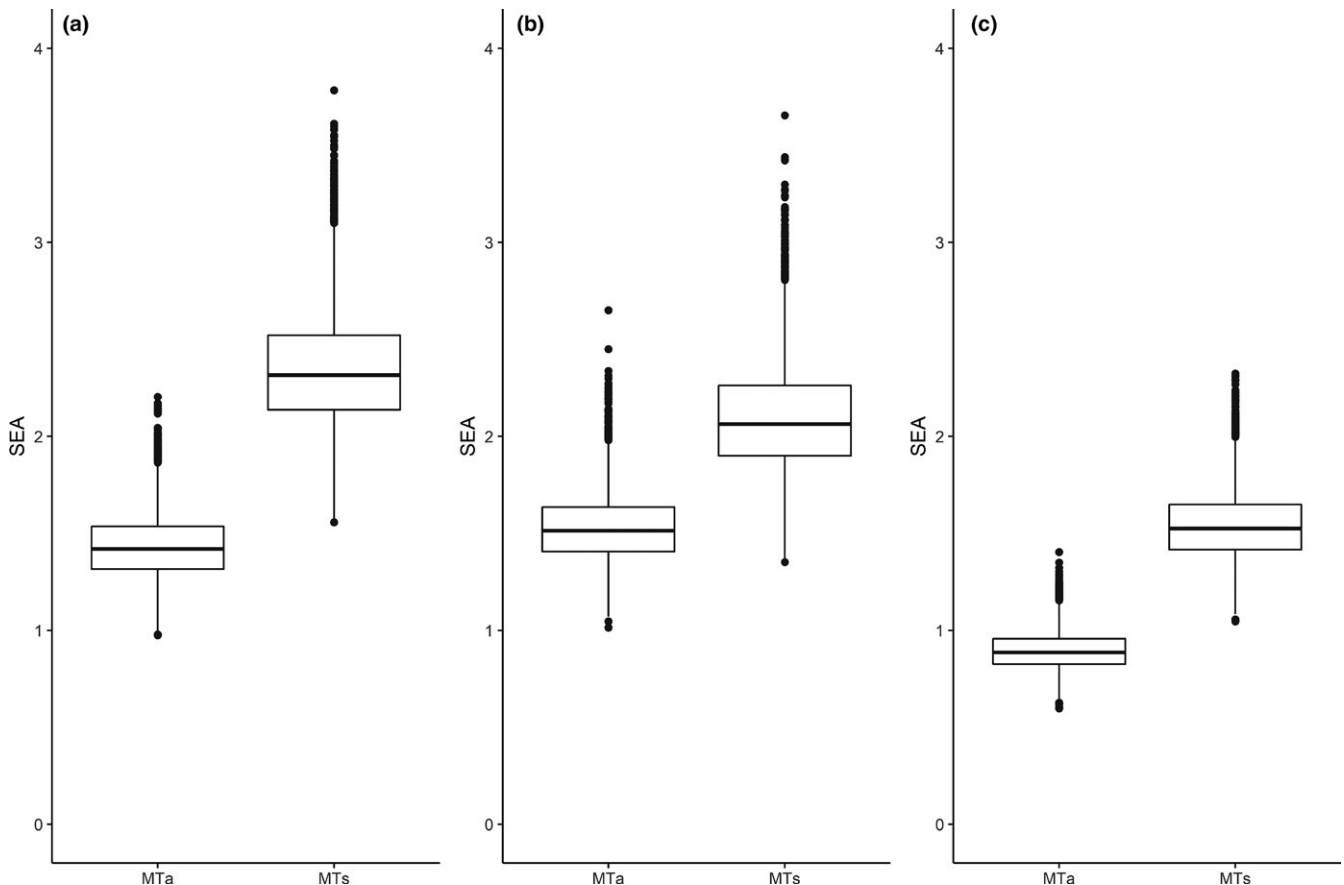


FIGURE 1 Distributions of the 10,000 simulations of Standard Ellipse Areas of marble trout living in allopatry (MTa) and in sympatry with the non-native rainbow trout (MTs) for each sampling occasion (a—June 2012, b—June 2013, c—September 2013). The horizontal line is the median value, box outlines upper and lower quartiles and outliers are black circles

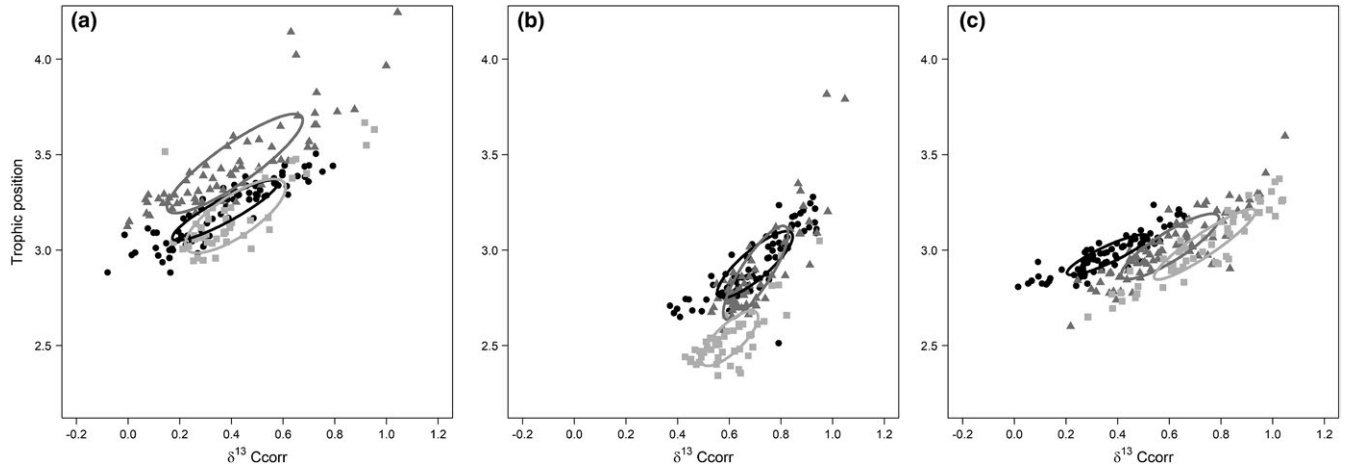


FIGURE 2 Stable isotope biplots of *Salmo marmoratus* in allopatry (MTa, black circles), in sympatry (MTs, dark grey triangles) and *Oncorhynchus mykiss* in sympatry (RTs, light grey squares) in June 2012 (a), June 2013 (b) and September 2013 (c). Standard ellipses areas (dietary niche breadth) are represented with a solid black line for MTa, dark grey line for MTs and solid light grey for RTs

| Prey categories | Predictors | df | Explained deviance | p (chi) | R ² |
|---------------------------|---------------------------|-----|--------------------|-----------------|----------------|
| MTa–MTs | | | | | |
| Benthic invertebrates | TL | 1 | 37.1 | <.001 | 0.76 |
| | Treatment | 1 | 0.8 | <.001 | |
| | Sampling | 2 | 3.5 | <.001 | |
| | Treatment:Sampling | 2 | 1.1 | <.001 | |
| Terrestrial invertebrates | TL | 1 | 1.3 | <.001 | 0.35 |
| | Treatment | 1 | 0.03 | .312 | |
| | Sampling | 2 | 3.1 | <.001 | |
| | TL:Treatment | 1 | 0.4 | <.001 | |
| | TL:Sampling | 2 | 0.15 | .06 | |
| | Treatment:Sampling | 2 | 1.2 | <.001 | |
| TL:Treatment:Sampling | 2 | 0.2 | <.01 | | |
| Fish | TL | 1 | 56.3 | <.001 | 0.67 |
| | Treatment | 1 | 0.2 | .088 | |
| | Sampling | 2 | 1.9 | <.001 | |
| | TL:Treatment | 1 | 1.1 | <.001 | |
| | Treatment:Sampling | 2 | 0.5 | .039 | |
| MTs–RTs | | | | | |
| Benthic invertebrates | TL | 1 | 32.6 | <.001 | 0.76 |
| | Species | 1 | 0.9 | <.001 | |
| | Sampling | 2 | 1.5 | <.001 | |
| Terrestrial invertebrates | TL | 1 | 13.7 | <.001 | 0.36 |
| | Species | 1 | 13.6 | .016 | |
| | Sampling | 2 | 10.6 | <.001 | |
| | TL:Species | 1 | 9.7 | <.001 | |
| Fish | TL | 1 | 44.2 | <.001 | 0.64 |
| | Sampling | 2 | 0.15 | .399 | |
| | Species | 1 | 0.8 | .001 | |
| | TL:Sampling | 2 | 1.4 | <.001 | |

TABLE 2 GLM results for MTa/MTs and MTs/RTs diet comparisons for each prey category with TL, Treatment and Sampling effects with explained deviance. Significant results are displayed in bold

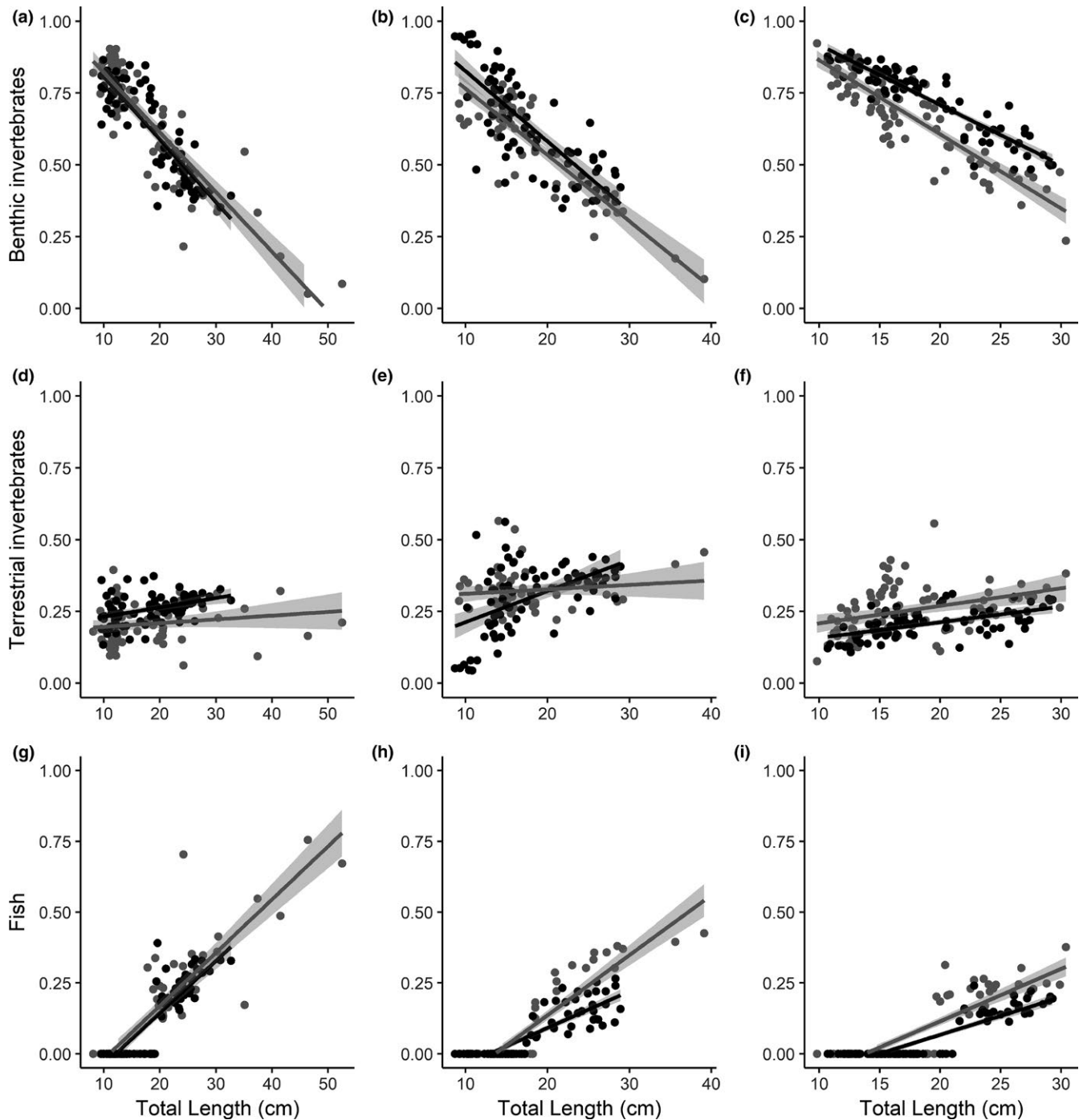


FIGURE 3 Bayesian mixing model estimated proportions of benthic invertebrates (a, b, c), terrestrial invertebrates (d, e, f) and fish (g, h, i) in diets of trout in June 2012 (a, d, g), June 2013 (b, e, h) and September 2013 (c, f, i) for the native marble trout living in allopatry (black circles) and in sympatry (grey circles). Solid lines correspond to the predictions from each generalised linear model for MTa (black) and MTs (grey) with associated 95% intervals

treatments and sampling occasions (Table 2). The estimated proportion of benthic invertebrates was negatively correlated with TL ($t = -32.8$, $p < .001$, Figure 3) while estimated proportions of terrestrial invertebrates and fish were positively correlated with TL in both MTa and MTs (Figure 3). Diet composition of MTs and MTa mostly diverged in June 2012 and September 2013 with significantly higher piscivory rate for MTs ($t = 3.4$, $p < .001$ and $t = 2.5$, $p < .05$

respectively) while the estimated proportion of fish in marble trout diet was similar between MTa and MTs in June 2013 ($t = 1.2$, $p = .22$, Figure 3). Estimated proportion of benthic invertebrates was similar between MTs and MTa in June 2012 ($t = 1.2$, $p = .23$) but significantly lower in MTs's diet in both June and September 2013 ($t = -3.5$, $p < .001$ and $t = -5.8$, $p < .001$ respectively). The estimated proportions of terrestrial invertebrates in fish diet were similar in MTa and

MTs in June 2012 and September 2013 ($t = -0.7$, $p = .50$ and $t = 1.6$, $p = .11$ respectively) but higher in MTs's diet in June 2013 ($t = 3.9$, $p < .001$).

In sympatry, MTs was significantly more piscivorous than RTs in each sampling occasion ($t = -3.7$, $p < .001$). On the other hand, the dietary contribution of benthic invertebrates was significantly higher in RTs than in MTs in each sampling period ($t = 5.4$, $p < .001$). The proportion of terrestrial invertebrates increased more through ontogeny in RTs than in MTs' diet ($t = 5.4$, $p < .001$).

3.4 | Body condition index and lipids contents

Body condition (K) in marble trout changed between treatments ($F = 4.7$, $p = .03$), and the relationships between TL and K varied across the different sampling occasions ($F = 4.6$, $p = .01$, Figure 4). K was on average higher in MTs than in MTa when pooling together data from all sampling occasions ($t = 2.3$, $p = .02$, Figure 4).

The relationship between TL and lipids content varied with Treatment and Sampling ($F = 3.9$, $p = .02$, Figure 4). Lipid contents were similar between MTa and MTs in June 2012 and June 2013 ($t = -0.1$, $p = .90$ and $t = 0.7$, $p = .48$ respectively) but significantly higher in MTs in September 2013 ($t = 3.1$, $p < .001$, Figure 4).

4 | DISCUSSION

A better understanding of the effects of introduced salmonids on the native species is crucial to better set up conservation programmes and protect biodiversity. Among the few populations of marble trout persisting in the Adriatic basin, one of them is living in sympatry with an exotic rainbow trout population that has been introduced 1960s. Here, we assessed the effects of the rainbow trout on trophic ecology and physiology of the marble trout using an allopatric marble trout population as control. Our results show dietary niche partitioning between two sympatric salmonid species and that rainbow trout lead to a dietary niche expansion and niche shift in marble trout population living in sympatry. Marble trout living in sympatry with the non-native rainbow trout showed a higher piscivory rate, a higher body condition and a higher prereproduction lipid content than marble trout living in allopatry.

The native marble trout and the non-native rainbow trout showed dietary segregation and niche overlaps ranged from 0% to 7%. Trophic niche segregation between native and non-native salmonids has been often observed in lakes with pelagic and littoral feeding areas (Eloranta, Nieminen, & Kahilainen, 2015; Langeland, L'Abée-Lund, Jonsson, & Jonsson, 1991). In streams, the two different feeding areas

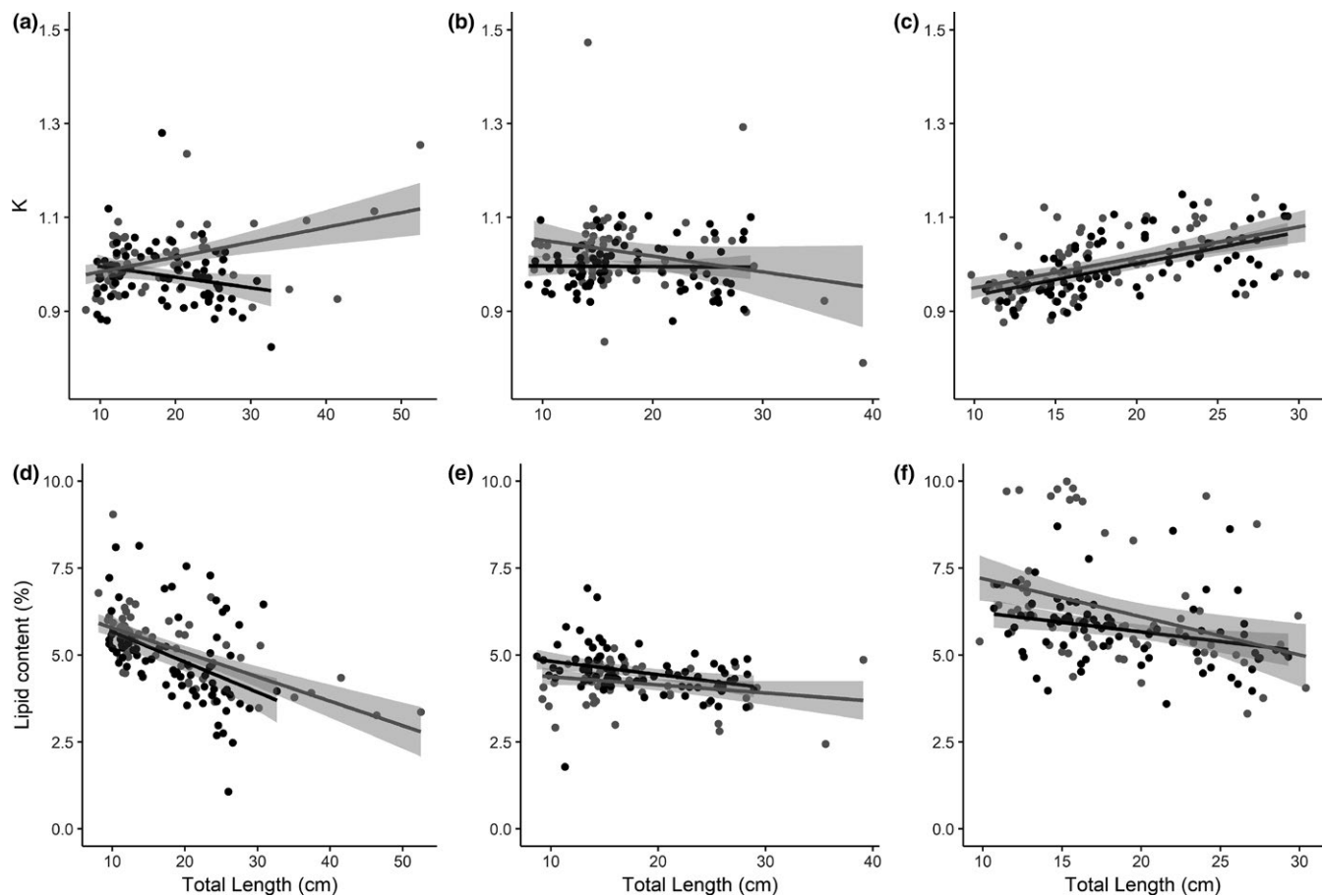


FIGURE 4 Body condition (a, b, c) and lipid content (%) (d, e, f) in June 2012 (a, d), June 2013 (b, e) and September 2013 (c, f) of the native marble trout living in allopatry (MTa, black circles) and in sympatry (MTs, grey circles). Solid lines correspond to the predictions from each generalised linear model for MTa (black) and MTs (grey) with associated 95% intervals

for salmonids are pools and riffles; unfortunately, stable isotope signatures of benthic invertebrates living in these two places were too similar to explore the preferences of feeding areas of the two trout species. However, dietary niche segregation is known to facilitate coexistence between native and introduced fish species. By making use of minimal niche overlap, two competitive species avoid the interspecific competition allowing them to coexist within the same system (Eloranta et al., 2015; Juncos, Milano, Macchi, & Vigliano, 2015). We postulate that the observed niche segregation between the marble trout and the rainbow trout is a main factor explaining the stable coexistence between the two salmonids in Lower Idrijca since the beginning of the monitoring in 2002 (Vincenzi et al., 2011).

Furthermore, our study provides evidence of invasion from non-native rainbow trout results in shift and expansion—up to 35% during springtime—of native marble trout dietary niche. Niche expansion in wild populations can be caused by different abiotic and biotic drivers such as individual specialisation (Bolnick et al., 2003), interindividual niche variation (Araújo, Langerhans, Giery, & Layman, 2014), intraspecific competition (Musseau, Vincenzi, et al., 2015; Svanbäck & Bolnick, 2007), ecological release from interspecific competition (Bolnick et al., 2010), predation pressure (Sharpe & Chapman, 2014) and ecological opportunity (Layman, Quattrochi, Peyer, & Allgeier, 2007). The uniqueness of the sympatric situation prevented us to test the effect of environmental features on interspecific trophic interactions, but a study on intraspecific dietary niche variation in marble trout highlighted that temperature, slope and habitat are drivers of trophic variation (Musseau, Vincenzi, et al., 2015). However, temperature was basically the same in the two sectors of Idrijca River and both stream slope and riparian forest are very similar. In our study, the dietary niche shift and niche expansion in marble trout are concurrent with a substantial increase in the relative contribution of fish prey to its diet when living in sympatry with the rainbow trout. Although pool surface tended to increase piscivory rate in allopatric marble trout populations (Musseau, Vincenzi, et al., 2015), the highest piscivory rate in the present study was in Lower Idrijca, the sector with the lower pool surface. Therefore, pool surface is unlikely to affect piscivory in marble trout. In Lower Idrijca, both species showed ontogenetic dietary shifts from terrestrial and benthic invertebrates to fish preys but the piscivory rate in rainbow trout was much lower. The rainbow trout relied more on benthic invertebrates, and the relative contribution of terrestrial invertebrates increased with size.

Although niche segregation between native and non-native salmonids usually results from competitive exclusion of the native species in profitable feeding territories and so tend to decrease somatic growth in the native species (Seiler & Keeley, 2007, 2009), marble trout shifted to more valuable prey when occurring in sympatry with the rainbow trout. The relative high contribution to marble trout in Lower Idrijca diet of fish preys is consistent with the higher body condition of marble trout living in sympatry with the non-native rainbow trout compared to the trout living in allopatry. Fish represent an excellent food resource for predator fish, as they provide large calories, and their composition in terms of proteins, lipids, minerals and vitamins is close to that of the predator (Elliott & Hurley, 2000). While individual growth increased in piscivorous trout (Jensen, Amundsen,

Elliott, Bøhn, & Aspholm, 2006; Jonsson, Naesje, Jonsson, Saksgard, & Sandlund, 1999), individual growth of marble trout does not differ in sympatry from allopatry (Vincenzi et al., 2011). The temporal variability in lipid content in marble trout with a higher lipid content in September 2013 is consistent with the temporal variability in energy reserve in somatic tissues found in salmonid species (Jonsson & Jonsson, 2009). The increase in energy reserves in late summer is considered as an adaptation to seasonality in response to higher accessibility to food and longer daily feeding activity in summer (Taylor, North, Porter, Bromage, & Migaud, 2006). The prewinter lipid storage may play a substantial role in survival strategy for salmonids (Berg, Rød, Solem, & Finstad, 2011). Hence, energy in marble trout living in sympatry with the non-native marble trout is unlikely allocated to somatic growth but for energy storage that becomes available for reproductive investment later in the year—spawning takes place in November–December in marble trout—that could lead to an increase in the annual fecundity and egg size, and to an earlier age at maturity (Mcbride et al., 2015). A recent study showed that marble trout reproducers are younger when living in sympatry with the non-native rainbow trout (Vincenzi, Crivelli, Jesensek, Campbell, & Garza, in press). The main hypothesis for a higher lipid content in sympatric marble trout population at the end of the summer may be an adaptive foraging strategy facing to interspecific interaction.

It is not possible, using stable isotope analysis, to distinguish the proportion of cannibalism (i.e. strict intraspecific predation, Fox, 1975) from predation on rainbow trout. Therefore, further study is needed to estimate the predation of marble trout on the non-native species using adapted method (e.g. DNA barcoding on faeces, Valentini, Pompanon, & Taberlet, 2009). In Lower Idrijca, the density of non-native rainbow trout is stable and low (0.0143 ± 0.0091 ind/m² between 2002 and 2014, Vincenzi et al., 2011) compared to other self-sustaining populations living in Slovenia in allopatry in the Soča basin (Godiča: 0.1732 ± 0.1134 ind/m² between 2010 and 2016 and Upper Brinta: 0.3048 ± 0.0025 ind/m² between 2014 and 2016). Although studies demonstrated that most piscivorous fish species showed preference for cannibalism instead of interspecific predation (Byström, Ask, Andersson, & Persson, 2013; Grey, Thackeray, Jones, & Shine, 2002), our hypothesis is that the marble trout preferably prey upon non-native rainbow trout and act as a main regulator of rainbow trout populations.

To conclude, this study shows that the presence of non-native rainbow trout in the Idrijca River did not involve negative effects either on marble trout trophic ecology or on marble trout physiology. Nevertheless, exotic rainbow trout had a noticeable impact on the native marble trout, as found in dietary niche shift, higher piscivory rate and an increase in body condition and lipid content before the reproduction season. Further investigations are needed to explore the mechanisms behind the observed response from marble trout to the invasion of rainbow trout.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

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