Direct and indirect effects of environmental factors on dietary niches in size-structured populations of a wild salmonid

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Abstract. Dietary plasticity of populations can be associated to ontogenetic diet preferences and depends on the size-structure of populations. Dietary niche characterizes the functional role of organisms in a food web, as it reflects both resources' diversity used by a consumer and trophic interactions in the system. Dietary niches are controlled both by biotic and abiotic factors, but their interactions in natural systems remain poorly studied. Here, we investigated the variability of dietary niche in salmonid wild populations focusing both on inter-population and intra-population (through time) trophic changes, using marble trout (*Salmo marmoratus*) living in Slovenian headwater streams as a model system. Stable isotope analysis showed high variability of dietary niche and trophic diversity among six of the seven remnant marble trout populations. We observed substantial differences in dietary niche width among populations and within populations through time. Results of partial least square path modelling highlighted opposite effects of immature and mature trout on trophic niche structure. Direct effects of temperature and slope (stream and watershed) were opposite; temperature narrowed dietary niches while slope increased them. Environmental factors (e.g., temperature, stream and watershed slope) had indirect effects on trophic niches after accounting for fish density. Our results showed that size-distribution and sexual maturity are key determinants of the dietary niche width in a population. Increasing density of immature trout tended to widen the dietary niche while increasing density of mature trout tended to narrow it. Environmental factors had direct effects both on resources and consumers densities and indirect effects. Direct and indirect effects were often antagonistic.

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INTRODUCTION

Within- and among-populations variation in dietary strategies has been observed in several animal species (Eloranta et al. 2011, Lehmann et al. 2013). Dietary plasticity can increase populations' chances of colonizing a habitat (Agrawal 2001) and facilitate long-term stability for organisms in fluctuating environments (Szepanski et al. 1999, Killengreen et al. 2011).

Within species and populations, variation in feeding strategies depends both on the availability of resources and on organisms' resource preferences. Environmental and climatic factors affecting the availability of resources are among the determinants of feeding strategies (Layman et al. 2007b, Darimont et al. 2009), which also contribute to determining patterns of ecological interactions in communities, such as competition and predation (Franco-Trecu et al. 2012, Polačik et al. 2013). As for resource preferences, changes in resource use during ontogeny have been reported to occur in more than 80% of animal taxa and they are common in many aquatic systems (Werner and Gilliam 1984, Werner 1988). Ontogenetic trophic shifts can influence population dynamics and have substantial effects on food web structure and dynamics (Claessen et al. 2004). For instance, trophic interactions between prey and consumers can be altered by body size, which is one of the fundamental biological factor controlling interactions within food webs (Woodward et al. 2005, Brose et al. 2006). In addition, differences in body size between individuals may avoid direct overlap in resources use within populations (Werner and Gilliam 1984, Zhao et al. 2014).

In many species, body size is one of the main determinants of sexual maturity. Sexual maturity increases demands of energy for reproductive processes like gonad development and egg formation (Robbins 1993, King and Murphy 1985), thus a qualitative or quantitative change in diet often occurs with sexual maturity in order to satisfy increasing energy requirements (Fishelson et al. 1987). As size and ontogenetic stage represent the main factors altering functional variability within species (Rudolf and Rasmussen 2013), it is crucial to study dietary preferences and trophic roles of different ontogenetic and sexual stages of organisms in food webs and functional structure of populations.

Dietary niche characterizes the functional role of organisms in a food web, as it reflects both resources' diversity used by a consumer and trophic interactions in the system. In recent years, the study of stable isotope niche as a proxy of dietary niche has become more frequent (Newsome et al. 2007, Layman et al. 2012, Newsome and Yeakel 2012), and community-wide measures to characterize dietary niches have been developed (Layman et al. 2007a, Jackson et al. 2011). Isotopic niches have been used to investigate the consequences of ecological processes, such as habitat fragmentation (Layman et al. 2007b), landscape heterogeneity (Darimont et al. 2009), ecosystems' connectivity through ecotones (Nifong et al. 2015) and biological invasions (Olsson et al. 2009) on food webs. Other biotic interactions like species coexistence (Genner et al. 1999) and resource use throughout ontogeny (Thomson et al. 2012) have been studied with isotopic niche. However, consequences of environmental factors coupled with life-history traits remain poorly studied. Environmental factors may have direct effect on consumers' dietary niches and can also influence indirectly dietary niches through controlling consumers' densities. Therefore, it is essential to study organisms in their natural habitat to understand the direct and indirect mechanisms that drive trophic variability among animal species.

In this work, we used marble trout *Salmo marmoratus* (Berrebi et al. 2000, Fumagalli et al. 2002, Pustovrh et al. 2014) as a model system to study among-population variation and within-population temporal variation in stable isotope (δ^{13}C and δ^{15}N) niche diversity in size-structured populations. Today, only seven pure populations of marble trout are persisting in Slovenian headwater streams. Marble trout is the only fish species present in those streams. This allows studying a simplified food web in a natural environment. Our main goal was to understand the effects of population size-structure and environmental factors (e.g., temperature, habitat and watershed characteristics) on trophic niche variation in absence of inter-specific competition. More specifically, our goal was to provide answers to the following questions: (1) Is there substantial inter- and intra-population variability of dietary niche in marble trout? (2) Do changes

in the size distribution among populations and within populations through time contribute to determine differences in dietary niches? (3) How do the abiotic factors influence the dietary niche through direct and indirect effects?

MATERIALS AND METHODS

Biological model and field study

Marble trout is a resident freshwater salmonid species living in streams with summer temperature below 14°C and winter temperature ranging from 0°C to 5°C. Only seven remnant pure populations persist today in the Soča and Idrijca river basins, both belonging to the Adriatic basin of Slovenia (Fumagalli et al. 2002).

For marble trout, the sexual maturation is size-dependent and spawning occurs usually when females reach 200 mm in length (Vincenzi et al. 2008a, b). Accordingly, in this work we assigned fish to one of two size-classes/sexual maturity status: (1) fish smaller than 200 mm were considered as immature, (2) fish bigger than 201 mm were considered as sexually mature (Vincenzi et al. 2008b). In marble trout, spawning typically occurs in November-December; eggs hatch in March and emerge in May–June (Vincenzi et al. 2007).

Six of the seven remnant marble trout populations were electrofished using a gasoline-powered, portable backpack electrofishing unit in June 2011, 2012 and 2013. Each fish was anaesthetized with phenoxy-ethanol and its length (mm) and weight (g) were recorded in situ. Fish pectoral fin samples were taken from fish and put in individual tube for isotopic analyses. Benthic invertebrates were sampled using a surber sampler for biomass quantification. Benthic invertebrates of different trophic group (decomposers, grazers, predators) were collected for isotopic analyses. Terrestrial invertebrates were collected by hand and nets along the riverbanks. Stream length and topographical features (pool surface, watershed area, land average slope and surface stream average slope) were acquired from surveyor field investigations and from available GIS (source: Surveying and Mapping Authority of the Republic of Slovenia). Mean annual daily water temperature was recorded by ONSET material for each stream and rainfall data was acquired from ARSO (Environmental Agency of Slovenia) data. Since water flow rates data were not available for the investigated streams, watershed area, land average slope and rainfall data were used as a proxy. Biotic and abiotic characteristics of every population and stream are fully described in Appendix A (Tables A1, A2).

Stable isotope metrics

Fin and invertebrate samples were oven-dried for 48 h 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 were analyzed in a Carlo Erba NC2500 elemental analyzer coupled to a Thermo Finnigan MAT Delta XP isotope ratio mass spectrometer. All stable isotope analyses were performed at the Cornell Isotope Laboratory, Cornell University, Ithaca, New York, USA.

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 baselines correction, as they are primary consumers. For $\delta^{15}N$ correction, the trophic position of fish was calculated following Anderson and Cabana (2007) and the $\delta^{13}C$ correction according to Olsson et al. (2009).

Then, different niche metrics were calculated to characterize dietary niche for each population and each sampling year from baseline-corrected values. We first computed Layman's niche metrics (Layman et al. 2007a). Each Layman's metric is a proxy of a trophic variable; $\delta^{15}N$ range (NR) represents the vertical structure of a food web and the diversity in trophic position, $\delta^{13}C$ range (CR) reflects the niche diversification at the base of the food web (i.e., diversity of resource use). Trophic area (TA) is the volume of the bi-dimensional space occupied by all individuals in a population within the isotopic space (i.e., convex hull area), and it is considered as a proxy trophic richness or niche width. The mean distance to centroid (CD) provides a measure of the average degree of trophic diversity in the food web. The mean nearest neighbour distance (NND) in the isotopic space characterizes trophic redundancy among individuals; a small NND

means trophic redundancy between two organisms. The standard deviation of nearest neighbour distance (SDNND) is a measure of the regularity of the distribution of individual in the isotopic space (i.e., trophic evenness). All Layman's metrics were bootstrapped ($n = 1\,000$) based on the common minimum number of samples ($n = 32$).

To compute niche overlap we used the standard ellipse area (SEA; Jackson et al. 2011). When niches overlap, the groups/populations are feeding partially or completely on the same resources; SEA is a proxy of trophic similarity between two group/populations. All metrics were calculated using the R package 'siar' (Parnell et al. 2010).

Statistical analyses

We compared trophic metrics and niche overlap among the six populations using data collected in June 2013. Within-population variation in dietary niche was investigated by comparing trophic metrics for the three consecutive years (2011, 2012 and 2013) in the populations of Huda Grapa, Studenc and Upper Idrijca and, for the two consecutive years (2012 and 2013) in the population of Lipovscek.

Following Turner et al. (2010), we tested for differences (among-populations and within-population through time) in location and dispersion of isotopic niche using a residual permutation procedure (RPP, $n = 10\,000$) on the centroid location of the isotopic niche and the two Layman's metrics CD and NDD. Significant results suggest potential differences in resources use and niche breadth.

We tested for significant differences in size distributions between and within populations using Kolmogorov-Smirnov tests, in which the null hypothesis is that the samples are drawn from the same distribution.

We used partial least squares path modelling (PLS-PM; Sanchez 2013) on Layman's metrics to understand the environmental factors and the mechanisms that affect directly and indirectly variations in trout dietary niche. PLS-PM is a robust form of structural equation modelling (Sanchez 2013) that is particularly useful when predictors (in our case, the environmental variables) are highly correlated. With PLS-PM, the first step of the analysis consists in pooling correlated observed variables in blocks. Each block can be summarized as a latent variable. We used manifest variables (indicators) that are observed or measured to create latent variables. These latent variables are connected to each other by links called "paths." A path coefficient represents a direct effect of a latent variable on another one, while an indirect effect describes the influence of one construct on another construct by taking an indirect path. Total effects are the sum of the direct and indirect effects. The full path model is composed by two sub-models: the inner model (i.e., the relationship between latent variables) and the outer model (i.e., the relationship between indicators and their own latent variable).

We built a priori models with the following latent variables and their indicators. Geography: altitude (a.s.l., m), distance to the spring of the stream (km); habitat: pool surface (m^2), invertebrate biomass (dry weight in mg), canopy openness (two classes: $0 =$ no openness, $1 =$ openness); watershed: annual rainfall (mm), watershed area (km^2), land average slope (%), surface stream average slope (%); temperature: mean annual daily water temperature (ONSET material); immature fish density (N·ha^{-1}) or mature fish density of mature (N·ha^{-1}). Based on model assessment criteria, Goodness-of-Fit (GoF) score and the Average Variance Extracted (AVE), we modified a priori models to obtain a posteriori ones, as follows. An indicator was removed whether both the correlation with its latent variable (i.e., 'loadings') was smaller than 0.7 and the communality value (i.e., squares correlation) was smaller than 0.4 (Sanchez 2013). We used bootstrap calculation ($n = 200$) to estimate and validate the precision of the PLS-PM and the path coefficient (PC) estimates. PLS-PM was performed on the 2012 and 2013 data due to the lack of invertebrate biomass quantification in 2011.

All statistical analyses were performed using R (2.15.1 version, R Development Core Team 2012). The 'siar' (Parnell et al. 2010) and 'plspm' packages (Sanchez and Trinchera 2013, http://cran.r-project.org/web/packages/plspm/index.html) packages were used for stable isotope metrics analysis and partial least squares path modelling, respectively.

Results

Diversity of dietary niche between populations

In 2013, the broadest TA was in Upper Idrijca (0.20) while the narrowest was in Lipovscek (0.07). The CR increased by a factor two between the lowest (0.30, Lipovscek) and the highest (0.61, Trebuščica) measures and the NR ranged from 0.46 (Svenica) to 0.86 (Upper Idrijca; Appendix B: Table B1).

Pairwise niche overlap varied between 0% and 22%, with the greatest overlap occurring between Studenc and Trebuščica (Appendix: Table B2). Dietary niches of Upper Idrijca and Lipovscek were completely segregated from the other four populations (Fig. 1a; Appendix B: Table B2).

RPP results highlighted differences in centroid location in the isotopic space for all pairwise comparisons except for Svenica and Trebuščica ($p = 0.11$; Appendix C: Table C1). NND comparisons were non-significant except between Studenc and Upper Idrijca, and Upper Idrijca and Lipovscek ($p = 0.03$ and $p = 0.02$, respectively, Appendix C: Table C1). CDs of Studenc and Trebuščica were significantly different than those of all other populations, but Studenc and Trebuščica CDs were not significantly different ($p = 0.40$). All results of the RPP are reported in the Appendix C (Table C1).

For 2013, no difference was found between size distributions of trout living in Huda Grapa and Trebuščica ($D = 0.14$, $p = 0.40$) and size distributions of Svenica and Trebuščica ($D = 0.26$, $p = 0.06$). All the other pairwise comparisons gave significant results (Kolmogorov-Smirnov test, $p < 0.05$, Fig. 1b). Niche overlaps were not always consistent with the size distribution overlaps (Fig. 1a, b).

Temporal evolution of dietary niche

TA of Huda Grapa monotonically decreased through time (0.24, 0.15, 0.08 for 2011, 2012 and 2013, respectively) and CR was halved (from 0.63 to 0.32). In Upper Idrijca, TA was stable between 2012 and 2013 (0.19 and 0.20, respectively). In Studenc, we observed a significant increase of NR over time from 0.50 to 0.81.

There was a 4% overlap between the 2011 and 2013 niches in the Huda Grapa population (Fig. 2a). However, there was no overlap of dietary niches within population across sampling years

for the populations of Studenc, Upper Idrijca, and Lipovscek (Fig. 2b–d).

We observed a significant shift of the niche centroid location through time for each population ($p < 0.001$). In Huda Grapa, both CD and NND were different between 2011 and 2012 ($p < 0.001$ and $p < 0.05$, respectively) and between 2011 and 2013 ($p < 0.001$ and $p < 0.05$, respectively). Huda Grapa was the only population with NND differences through time. CD values were different in Upper Idrijca (2011–2012) and Lipovscek ($p < 0.05$, $p < 0.001$, respectively).

In Huda Grapa, size distribution of fish was significantly different between 2011 and 2012 (Kolmogorov-Smirnov test, $D = 0.28$, $p < 0.01$) and 2011 and 2013 (Kolmogorov-Smirnov test, $D = 0.45$, $p < 0.001$, Fig. 2e), while size distributions of 2012 and 2013 were not significantly different (Kolmogorov-Smirnov test, $D = 0.20$, $p = 0.06$, Fig. 2e). In Studenc, there was no significant difference between 2011 and 2012 (Kolmogorov-Smirnov test, $D = 0.27$, $p = 0.17$), but we found significant differences between 2012–2013 and 2011–2013 (Kolmogorov-Smirnov test, $D = 0.59$, $p < 0.001$ and $D = 0.69$, $p < 0.001$, respectively, Fig. 2f). In Upper Idrijca, there were no significant differences in fish size distribution between 2011 and 2012 and between 2012 and 2013 (Kolmogorov-Smirnov test, $D = 0.27$, $p = 0.06$ and $D = 0.15$, $p = 0.31$, respectively), but size distributions were different between 2011 and 2013 (Kolmogorov-Smirnov test, $D = 0.31$, $p < 0.01$, Fig. 2g). In Lipovscek, size distribution was different between the two years of the study (Kolmogorov-Smirnov test, $D = 0.74$, $p < 0.001$, Fig. 2h).

Direct and indirect effects on dietary niches

We estimated the relationships between indicators and their own latent variable (i.e., outer model) using model selection criteria (both Goodness-of-Fit score and the Average Variance Extracted). Indicators that did not meet the required criteria were removed from the models. Accordingly, we removed distance to the spring, invertebrate biomass, canopy openness, annual rainfall and watershed area. A posteriori models included altitude, pool surface, average slope of the watershed and average slope of the surface stream, mean annual daily water temperature and mature fish density or immature fish density.
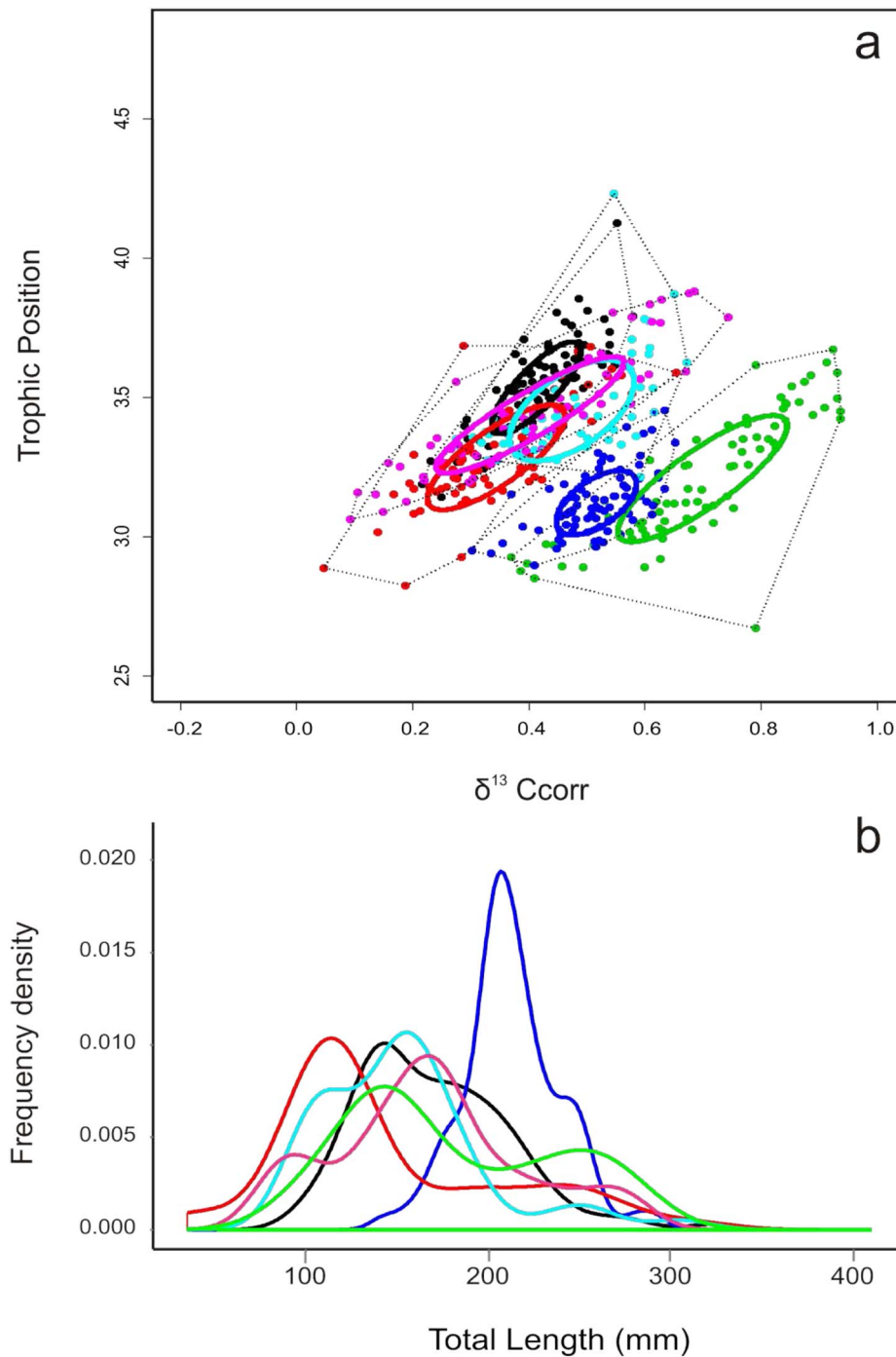
Fig. 1. Inter-population variation in (a) stable isotope niche and (b) size-distribution for each population for Huda Grapa (black), Lipovscek (dark blue), Studenc (light blue), Svenica (red), Trebuščica (pink) and Upper Idrijca (green). On the stable isotope space (a) with baseline corrected value for nitrogen (trophic position) and carbon ($\delta^{13}C$ corr) are represented total trophic areas (dashed lines) and standard ellipse areas (SEA, solid lines). The SEA overlaps between two populations' SEA ranged from 0 to 22% with the maximum overlap between Studenc and Trebuščica.
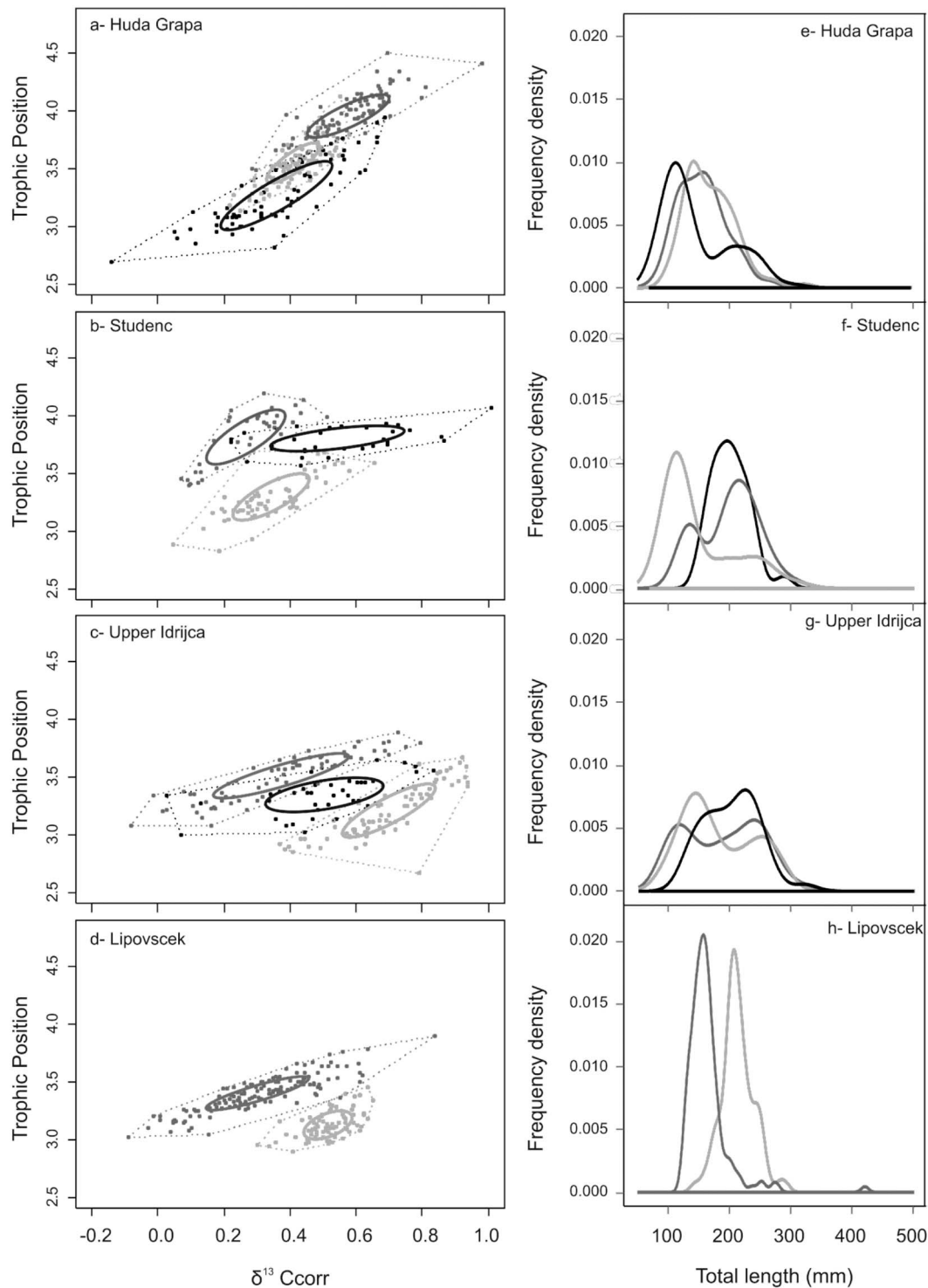
Fig. 2. Intra-population variations in (a–d) total trophic areas (dashed lines) and standard ellipse areas (SEA, solid lines) and (e–h) size-distribution for each population for Huda Grapa, Studenc, Upper Idrijca and Lipovscek in 2011 (black), 2012 (dark grey) and 2013 (light grey). The only observed SEA overlap was 4% in Huda Grapa (a) between 2011 and 2013.

As "Watershed" latent variable was explained by two indicators, i.e., average slope of watershed and average slope of the surface stream, it was renamed "Slope" latent variable. All total effects were significant except the direct effect of the habitat variable on NND for immature trout.

Direct effects of immature and mature trout densities on trophic metrics were in opposite direction (Figs. 3 and 4). Immature trout density was positively related to every trophic metric except NR (Fig. 4a). The biggest path coefficient magnitude observed was for CR (1.1). On the contrary, trophic metrics were negatively related to mature fish density (Fig. 4a). In addition, trout densities were directly influenced by the three environmental factors included in the model (Fig. 4b). While the Habitat path coefficient values were mainly lower than Temperature or Slope path coefficients on trout density, Habitat had positive direct effects on both immature (path coefficient = 0.52) and mature trout densities (path coefficient = 0.04, Fig. 4b). Immature trout density was positively influenced by Temperature (1.3) and negatively by Slope (−1.3), whereas mature trout density was negatively correlated with Temperature (−0.9) and positively with Slope (0.8, Fig. 4b).

Direct and indirect effects of each environmental factor on trophic metrics were mainly opposite direction, with path values often larger for immature trout than for mature trout densities (Fig. 5a, b). NND (trophic redundancy) and SDNND (trophic evenness) were mostly under control of trout densities' direct effects (Fig. 5a, b and Appendix D: Table D1). Both for immature and mature trout, direct effects of Slope were positive on TA, CR and CD while indirect ones were negative. Temperature had opposite effects, with negative direct effects and positive indirect effects for both immature and mature on TA, CR and CD. All effects (direct, indirect and total) are detailed in Fig. 5 and Appendix D (Table D1).

DISCUSSION

Inter- and intra-population trophic variability

We found high variability of dietary niche and trophic diversity among natural populations of marble trout, a resident salmonid living in a narrow geographical range. Trophic niche width showed substantial differences among populations, with Huda Grapa and Lipovscek showing narrower trophic niches and Upper Idrijca, Studenc and Trebuščica showing broader trophic niches. Among-population differences in trophic location and dispersion suggested that populations strongly differed in trophic diversity and exhibited low trophic redundancy. The maximum overlap between two populations was 22%, which suggests a fairly low trophic similarity with respect to what has been found in other species and taxa (Forero et al. 2004, Jackson et al. 2012, Jackson and Britton 2013). Our 3-year and 2-year studies also showed that within the same populations dietary niches tend to change substantially through time. We observed overlaps among populations both for isotopic niches and size distributions for Huda Grapa and Trebuščica and for Svenica and Trebuščica. However, trophic niche overlaps were not always consistent with the size distribution overlaps. While Studenc isotopic niche was overlapping with those of Huda Grapa, Trebuščica and Svenica, the size distribution of Studenc in 2013 was substantially different from the size distributions of the other populations. Similarly, when investigating niche variation through time, we did not observed any niche overlap for Upper Idrijca and Studenc during the 3-years study, whereas size distributions were often very similar. These patterns were confirmed by the PLS-PM results, which revealed strong effects of mature trout density and immature trout density on the trophic metrics.

Antagonistic effects of immature and mature on trophic niche structure

Although we observed clear effects of both immature and mature trout density on trophic structure, the signs of the effects were often opposite. Whereas the density of immature trout led to an increase of all community-wide metrics except nitrogen range, the increase in mature trout density caused the decrease of all community-wide isotopic metrics. The strong positive path coefficient from immature trout density to carbon range suggests that immature trout establish a new basal resource in the food web. Terrestrial inputs may represent a high proportion in diet for opportunistic predators such as salmonids (Baxter et al. 2004, Evangelista et al.
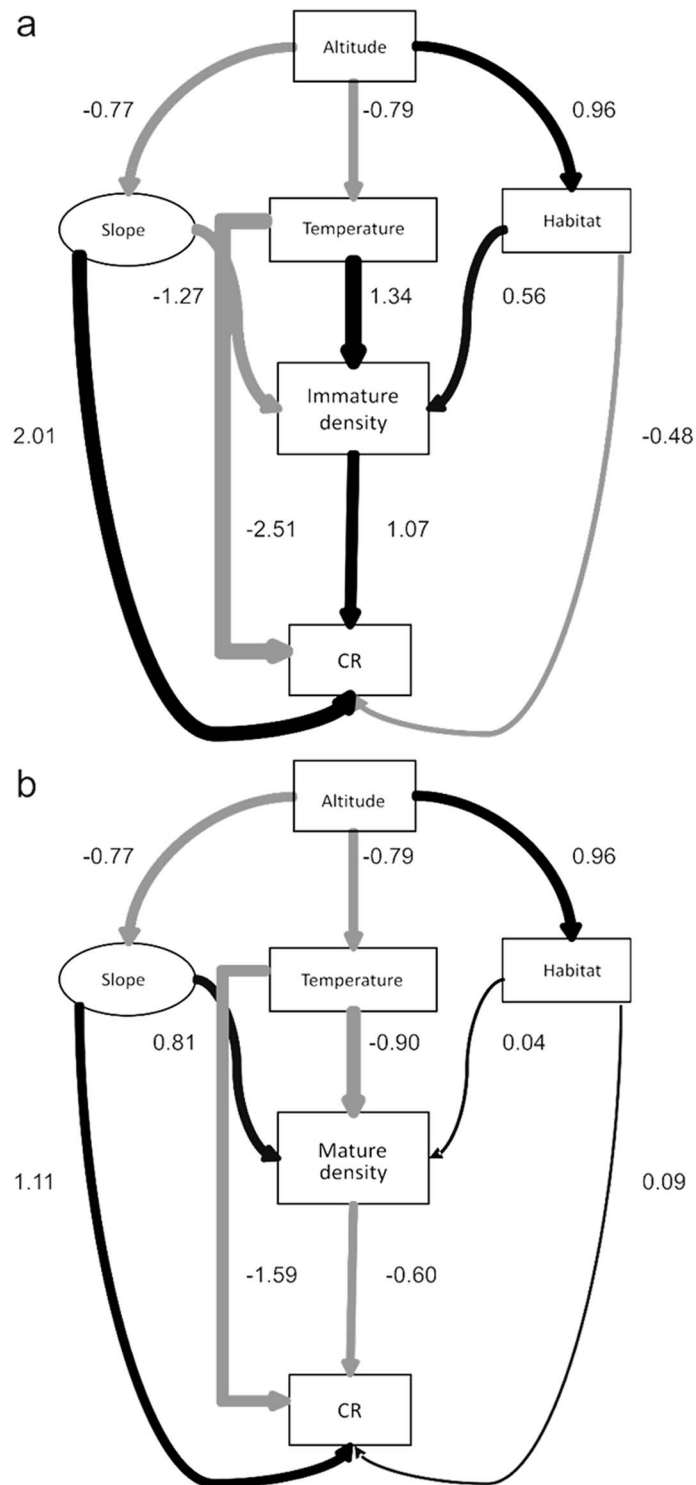
Fig. 3. Path diagrams and path coefficients (i.e., direct effects) between latent variables from the PLSPM for immature fish density (a) and mature fish density (b) populations for carbon range (CR) as response variable. Arrow widths are proportional to the path coefficient magnitudes. Positive and negative path coefficients are represented by black and grey arrows, respectively.
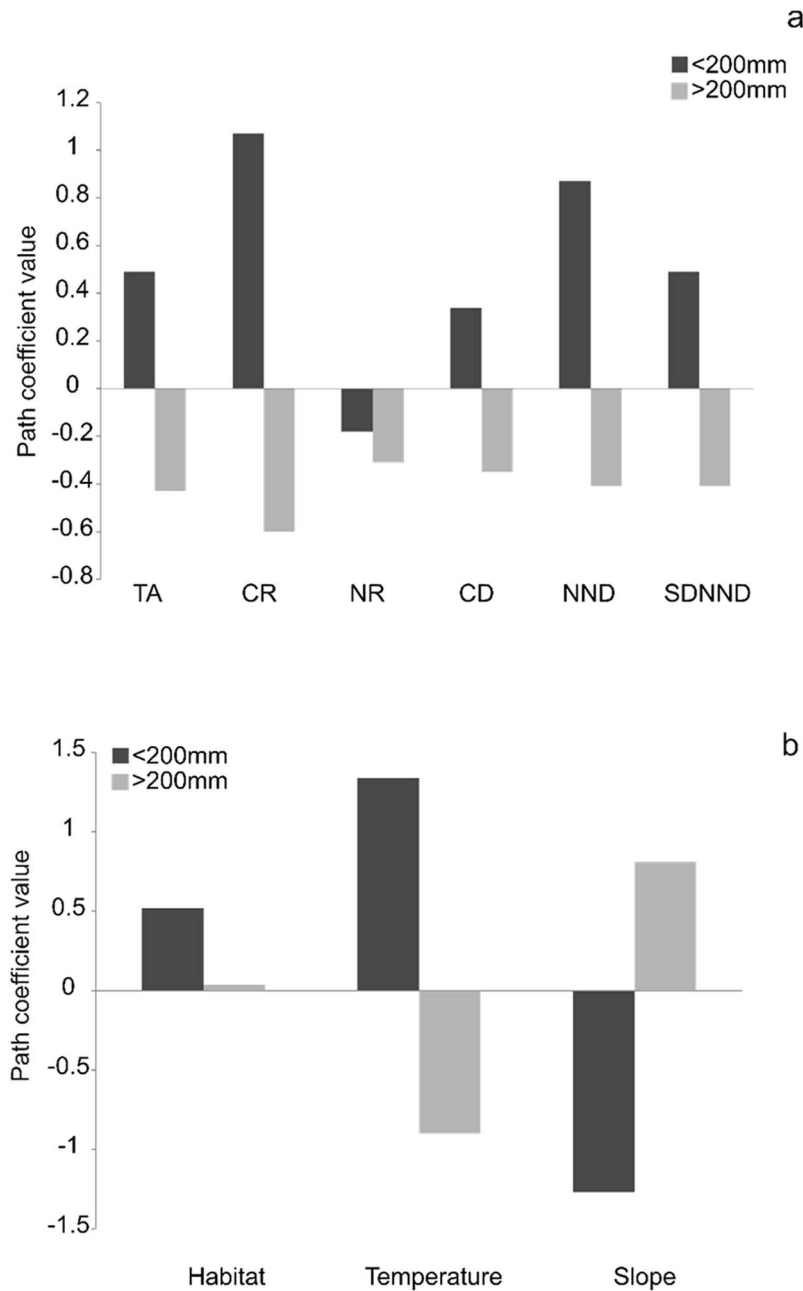
Fig. 4. Path coefficients (i.e., direct effects) from the PLSPM of immature trout density (dark grey) and mature trout density (light grey) on trophic metrics (a) and of environmental factors (habitat, temperature and slope) on immature and mature trout densities (b).

2014). A positive relationship between terrestrial input and juvenile density for brown trout was previously shown (Evangelista et al. 2014). At higher density, the stronger competition between immature individuals may lead to resource partitioning and therefore to an increase in diet variation within population (Araújo et al. 2011). On the other hand, negative effects of mature trout density on dietary niche structure pointed to a restricted use in basal resources diversity and
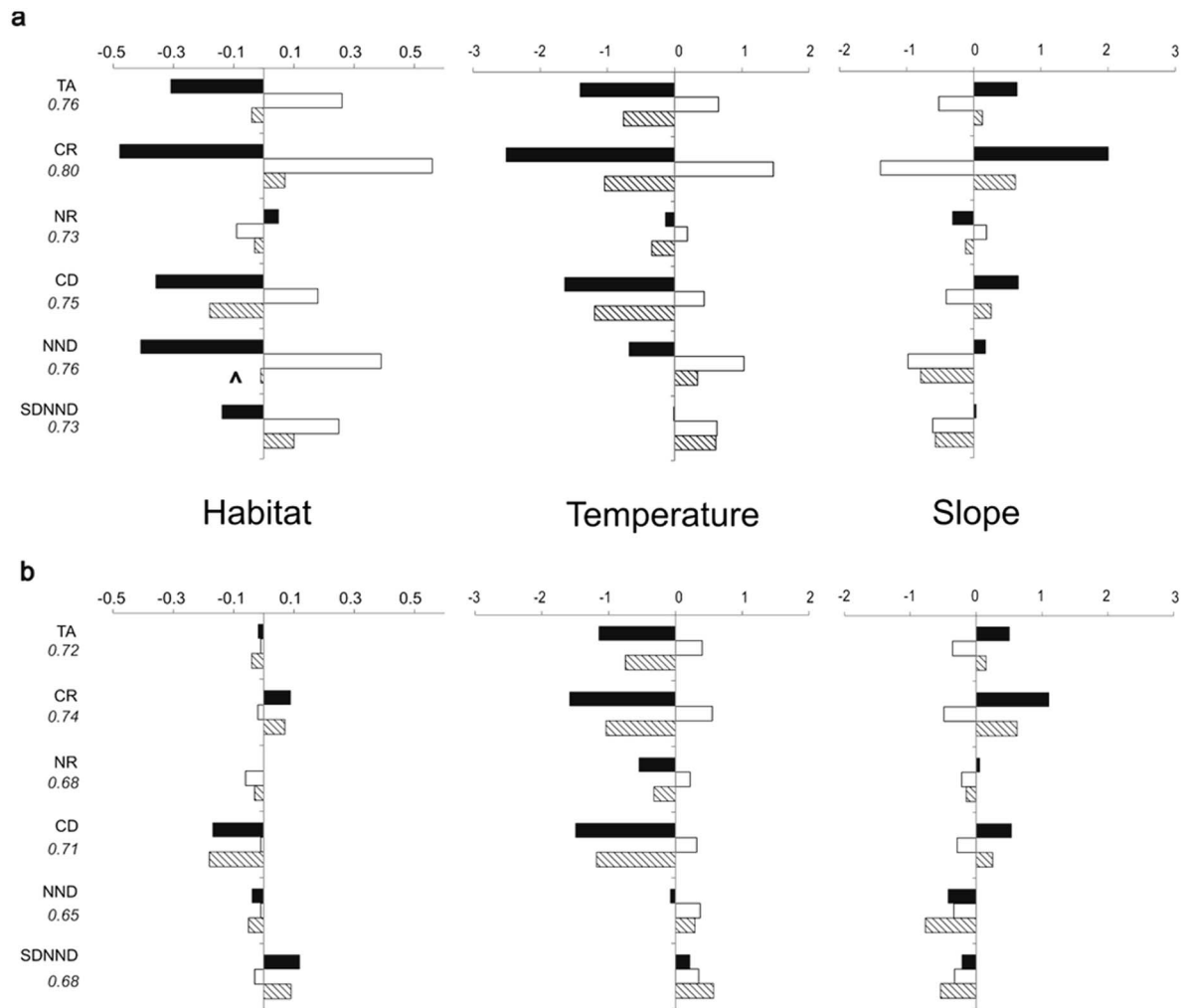
Fig. 5. Direct (black), indirect (white) and total (hatched) effects of habitat, temperature and slope on the trophic metrics for immature (a) and mature (b). The number below the trophic name is the associated GOF score; ^ indicates a non-significant effect ($p > 0.05$).

a reduction of vertical niche leading to a decrease of niche width. As mature trout strongly defend hides inside pools, they move less for foraging activity when density increases. Furthermore, smaller trout may also reduce predation risk being less active. Mature trout can reduce trophic diversity within a population also by consuming small trout.

Direct effects of environmental variables on trout densities

Trout density was affected by pool surface, mean water temperature and stream slope, but the direction of the response (higher or lower density with increasing values of the environmental variables) differed among immature and mature individuals. Habitat (i.e., pool surface) had a significant positive effect on the density of immature trout and a small effect on the density of mature trout. Large salmonids preferentially live in pools, while younger ones are more likely to live in riffles, since they provide a safer habitat against predation. Thus, it might be worthwhile exploring the underlying explanations for this mechanism in marble trout.

Warmer temperatures had a positive effect on density of immature trout, as fingerlings are more vulnerable to energy loss during cold

season and thus warmer temperatures may contribute to increase their survival (Berg and Bremset 1998). The negative relationship between temperature and density of mature trout might be due to metabolic reasons, as already observed in other salmonid populations; activity increases when temperature rises, which implies a substantial energetic cost for the individual (Beakes et al. 2014). Opposite effects of Slope on immature and mature trout densities are likely to be associated to flood events. The probability of occurrence of severe floods increases with watershed and stream steepness. Previous work has shown that severe floods can cause population collapses (Vincenzi et al. 2010, Pujolar et al. 2011); fish are killed or displaced by water or debris, spawning grounds are destroyed, which leads to low juveniles density and in the following years to low density of immature trout (Vincenzi et al. 2010). Since growth is density-dependent in marble trout, low population density following a flood event increases growth rates for fish born after the flood. As sexual maturity is size-dependent, faster-growing fish are able to reach sexual maturity at younger age.

Indirect effects of environmental variables

Our results showed that watershed and stream slope tended to increase basal resources pool in the trophic system and, consequently, trophic richness for both immature and mature trout. Steeper streams are also characterized by high canopy cover and the ecological importance of trophic subsidies between riparian forest and aquatic systems is now well known (Kawaguchi and Nakano 2001, Carpenter et al. 2005, Evangelista et al. 2014). Terrestrial resources inputs in streams provide a new basal resource in the streams for fish populations by increasing the carbon range of predators' trophic niches. Salmonids are important species in the flux of resources between terrestrial and freshwater systems (Nakano and Murakami 2001, Baxter et al. 2004). On the contrary, an increase in water temperature could lead to a higher production of freshwater invertebrates' biomass and thus may limit the need to expand the range of resources toward terrestrial invertebrates. The reduction of carbon range by warmer temperatures involved a reduction of trophic richness. Trophic redundancy was essentially controlled by immature trout

density; this suggested that trophic redundancy was better explained by biological interactions such as inter- or intra-cohort competition or predation than by environmental conditions. Although trophic redundancy of mature organisms was also altered by mature trout density, the effects were smaller than those observed in immature trout. Indirect effect of environmental conditions on trophic redundancy strengthened the biotic effect of this pattern. We showed that the trophic evenness for immature and mature trout was determined by indirect effects of environmental factors (i.e., slope and temperature) through trout density and direct effect of trout density, which supported the hypothesis that trophic evenness was under biotic control.

Biotic and abiotic factors did not affect nitrogen range as they did for other trophic metrics. Two complementary hypotheses may explain the observed pattern: (1) inputs of terrestrial resources bring numerous terrestrial prey into the system; trout focus then on insectivory instead of piscivory with prey easier to catch; (2) when watersheds are steeper, floods with a larger impact on ecosystems are more likely to occur and size structure and trout density of the population are highly affected by strong flood (spawning grounds destroyed, fish killed by flood debris, etc.) and less fish prey are therefore available in streams. Further investigations are needed to understand the consequences of cannibalism on population dynamics and dietary niche of marble trout.

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Supplemental Material

Ecological Archives

Appendices A–D are available online: http://dx.doi.org/10.1890/ES15-00109.1.sm