

Within-individual trophic variability drives short-term intraspecific trait variation in natural populations

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Abstract

1. Intraspecific trait variability (ITV) maintains functional diversity in populations and communities, and plays a crucial role in ecological and evolutionary processes such as trophic cascades or speciation. Furthermore, functional variation within a species and its populations can help buffer against harmful environmental changes. Trait variability within species can be observed from differences among populations, and between- and within individuals. In animals, ITV can be driven by ontogeny, the environment in which populations live and by within-individual specialization or variation unrelated to growth. However, we still know little about the relative strength of these drivers in determining ITV variation in natural populations.
2. Here, we aimed to (a) measure the relative strength of between- and within-individual effects of body size on ITV over time, and (b) disentangle the trophic changes due to ontogeny from other sources of variability, such as the environment experienced by populations and individual preferences at varying temporal and spatial scales.
3. We used as a model system the endangered marble trout *Salmo marmoratus*, a freshwater fish living in a restricted geographical area (<900 km²) that shows marked changes in diet through ontogeny. We investigated two trophic traits, trophic position and resource use, with stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$), and followed over time 238 individually tagged marble trout from six populations to estimate the trophic changes between and within individuals through ontogeny at three different time-scales (short term: 3 months, medium term: 1 year and long term: 2 years).
4. We found that the relative strength of between- and within-individual effects of body size on trophic position and resource use change strongly over time. Both

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effects played a similar role in ITV over medium- and long-term time-scales, but within-individual effects were significantly driving trophic variability over short-term scales. Apart from ontogenetic shifts, individuals showed variability in trophic traits as big as the variability estimated between populations.

- Overall, our results show how the relative strengths of ITV drivers change over time. This study evidences the crucial importance of considering effects of time-scales on functional variability at individual, population and species levels.

KEYWORDS

between individual, individual trajectory, intraspecific trait variability, longitudinal survey, salmonid, stable isotope analysis, time-scales, within individual

1 | INTRODUCTION

Understanding the effects of trait variability on ecological mechanisms, such as species coexistence or food web structure, is among the fundamental goals of functional ecology. Functional differences among species have for a long time been considered the source of ecological variability in food webs and ecosystems. Yet, theoretical models and empirical studies both suggest that intraspecific trait variability (ITV) has a major role in maintaining functional diversity in populations, communities and ecosystems (Des Roches et al., 2018; Miller & Rudolf, 2011; Raffard, Santoul, Cucherousset, & Blanchet, 2018), but the extent of trait variability within species has been overlooked (Bolnick et al., 2011; Costa-Pereira, Rudolf, Souza, & Araújo, 2018).

Intraspecific trait variability can be partitioned into three main components: *population-level variability*, *between-individual variability* and *within-individual variability*, all potentially driven by genetic and environmental sources (Albert, Grassein, Schurr, Vieilledent, & Violle, 2011). The *population-level variability* describes trait (e.g. trophic position, body length) variation between populations of a single species (Musseau et al., 2015); the *between-individual variability* reflects the variation in traits among individuals of the same population (Darimont, Paquet, & Reimchen, 2009) and the *within-individual variability* is the variation in the traits of one individual over time (Vander Zanden, Bjorndal, Reich, & Bolten, 2010). Whether ITV is better explained by differences between individuals or changes within individuals is a central question in functional ecology (Bolnick et al., 2003; Lehmann, Mfune, Gewers, Brain, & Voigt, 2015). Additionally, the relative strength of the three components tends to vary over time. Since how much traits vary or are consistent over time has implications for ecological and evolutionary processes, it is crucial to determine the time-scale over which trait variations occur. Persistent between-individual differences in functional traits over time can be interpreted as evolutionarily fixed responses (i.e. genetically determined). On the other hand, differences observed over time within an individual represent trait variation emerging from environmental variability or biological processes, such as phenology or sexual maturity (van de Pol & Wright, 2009).

Between-individual variability in traits has been found across a wide range of species, including arthropods (Jackson et al., 2017), amphibians (Araújo, Bolnick, Martinelli, Giaretta, & Reis, 2009), reptiles (Vander Zanden, Bjorndal, & Bolten, 2013), birds (Cherel, Quillfeldt, Delord, Weimerskirch, & Inger, 2016), mammals (Novak & Tinker, 2015) and fish (Litz et al., 2017). However, little is known on the respective contribution and temporal consistency of between- and within-individual effects on the variability of trophic traits at the level of population and species (Novak & Tinker, 2015).

Within-individual variability—or specialization—is usually measured in homogeneous subgroups (i.e. sexual maturity, sexual, age, etc.) within populations. However, more than 80% of animal species show ontogenetic niche shifts during their development (Werner, 1988), and it is challenging, albeit crucial, to tease apart the role of ontogenetic processes from changes in the environment and individual plasticity when studying ITV in wild populations. Ontogeny involves the simultaneous changes in many biological and ecological traits, differences in energy and nutritional demands (Elliott & Hurley, 2000) and changes in individuals' interactions with their environment (Miller & Rudolf, 2011). Moreover, the range of suitable habitats (Ayllón, Almodóvar, Nicola, & Elvira, 2010), prey/predator interactions (Barnes, Maxwell, Reuman, & Jennings, 2010), inter- and intraspecific competition (Parra, Almodóvar, Ayllón, Nicola, & Elvira, 2011) and survival probability (Claessen, de Roos, & Persson, 2000) all depend on size. Ontogenetic niche shifts shape the functional changes in each individual, modulate the differences between individuals from the same population and lead to trait variation among and within size-structured populations. In taxa with growth continuing after sexual maturity like fishes, the more the time between sampling increases, the bigger should be the changes in body size and ontogenetic niche shifts. Theoretically, when time between samplings increases, between- and within-individual similarities in diet are expected to decrease; however, there has been little empirical support for this hypothesis (Novak & Tinker, 2015). Also, individuals can differ in their expressed phenotypes (between-individual variation) through ontogeny, but each individual can conserve their phenotype through time (specialization) or display plastic

ones (within-individual variability). Phenotypic plasticity often brings adaptive traits to individuals and populations in changing ecosystems (Reed, Schindler, & Waples, 2011). Teasing apart the relative importance of ontogeny from individual differences in maintaining intraspecific trait variation in natural populations can elucidate the processes leading to ITV.

Measuring the within-individual variability in trophic traits requires the collection of biological data and tissues from sampling schemes (ideally non-invasive) and the use of laboratory and statistical analyses that allow the estimation of the effects of time, space and individuality on trait variability. Longitudinal sampling schemes (Araújo et al., 2009) and the analysis of stable isotopes (Bearhop, Adams, Waldron, Fuller, & Macleod, 2004) fulfil those requirements. Individual variation in stable isotope values can be measured in different continuously growing tissues, which retain a chronological history of resources consumed (Newsome et al., 2010; Newsome, Etnier, Monson, & Fogel, 2009; Vander Zanden et al., 2013), or on tissues from individuals tagged and recaptured through time. However, capture–recapture sampling over seasons and years of mobile populations in their natural environment is challenging.

Here, we use marble trout individuals *Salmo marmoratus* in their natural habitat as a model system for quantifying the variation in trophic traits over time and across populations. First, we focus on the effects of ontogeny on ITV and we tease apart within- from between-individual effects of ontogeny at three time-scales (long term: 2-year survey; medium term: 1-year survey and short term: 3-month survey) on trophic position and resource use with stable isotopes analysis ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$). Then, we test and estimate whether and how intraspecific trophic plasticity in marble trout is driven by either individuals specialized on different resources or plastic individuals expressing variable trophic phenotypes throughout their lifetime.

2 | MATERIALS AND METHODS

2.1 | Biological model and study area

Marble trout is a stream-dwelling salmonid of great conservation concern with only seven remnant, genetically pure populations that persist today in allopatry (marble trout is the only fish species) in the streams of the Soča and Idrija River basins (the total surface of the basins is approximately 900 km²). A conservation programme for marble trout (Marble Trout Project) started in Western Slovenia in 1993 (Crivelli, Poizat, Berrebi, Jesenšek, & Rubin, 2000) due to increasing threats to marble trout survival from biological invasions (Meldgaard et al., 2007; Musseau et al., 2018), habitat fragmentation and more intense and frequent extreme events (i.e. floods) due to global climate change (Pujolar et al., 2011; Vincenzi, Crivelli, Satterthwaite, & Mangel, 2014; Vincenzi, Mangel, Jesensek, Garza, & Crivelli, 2017). Sexual maturation of marble trout is size dependent, with spawning occurring when male and female trout are at least

200 mm long. Spawning typically occurs in November–December, followed by the hatching of larvae in March and the emergence of juveniles in June.

2.2 | Field study

As part of the conservation programme, the seven marble trout populations were sampled twice a year (June and September) or once a year (September; Crivelli et al., 2000). When reaching 115 mm in total length, each trout received a Carlin tag. In the present study, six (Huda Grapa, Studenc, Upper Idrija, Lipovscek, Svenica and Trebuscica) of the seven remnant pure marble trout populations were electro-fished using a gasoline-powered, portable backpack electrofishing unit in June 2011, 2012 and 2013, and in September 2013, and sampled for stable isotope analyses. Trout were anaesthetized with phenoxyethanol and their length (mm) and weight (g) were recorded in situ. Part of the pectoral fin, a strong surrogate of fish muscle (Busst, Bašić, & Britton, 2015; Sanderson et al., 2009), was collected from anaesthetized trout and stored in individual tubes for isotopic analyses. Benthic invertebrates of different trophic groups (decomposers, grazers, predators) were used for baseline correction of trout isotopic values. Terrestrial arthropods (phytophagous: Cicadellidae, Noctulidae and Tetrigidae; predators: *Pardosa* spp. and Formicidae) were collected by hand and net along the streambanks for stable isotope analyses (mean values are provided in Appendix S1). All samples collected for stable isotope analyses were placed in a cooler during the transportation of samples from the field to the laboratory. There, fin samples were immediately dried, and invertebrate samples were dried after individuals were allowed to empty their guts for 36 hr in the buckets in which they were individually stored. Samples were dried for 48 hr at 60°C.

We defined three time-scales over which we estimated individual changes in diet: long term, when trout were sampled three times during the 2-year survey (June 2011, June 2012 and June 2013); medium term, when trout were sampled twice during the 1-year study (June 2011 and June 2012 or June 2012 and June 2013); short term, when trout were captured in June 2013 and recaptured in September 2013. We assigned each trout to one of two size classes, which we also considered as sexual maturity classes: trout with total length smaller than 200 mm were considered as sexually immature, trout with total length greater than 201 mm were considered as mature (Musseau et al., 2015; Vincenzi et al., 2008). We categorized as mature the few trout that were sampled for SIA for the first time when smaller than 200 mm and then reached 200 mm during the survey. In total, we collected 704 fin samples on 238 individuals coming from six marble trout populations: 16 individuals were sampled three times during the 2-year survey, 124 individuals during the 1-year survey (two different measures for 41 immature trout and 83 mature trout) and 196 individuals for the 3-month survey (two different measures for 88 immature trout and 108 mature trout). Huda Grapa,

Student and Upper Idrijca populations were sampled four times, Lipovsek three times (June 2012, June 2013, September 2013), and Svenica and Trebuscica were sampled twice (June 2013 and September 2013).

2.3 | Stable isotope analysis

Dried samples were 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 $\delta^{15}\text{N}$ respectively) were analysed in an elemental analyser (Carlo Erba NC2500a) coupled with an isotope ratio mass spectrometer (Thermo Finnigan MAT Delta XP). 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 $SD < 0.2\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) that were previously calibrated according to International Atomic Energy Agency standards. Stable isotope analyses were performed at the Cornell Isotope Laboratory, Cornell University, USA.

Because of the variability in basal resources both between the different streams and within stream through time, stable isotope values were baseline corrected (France, 1995). Trophic positions (TP) were calculated following Anderson and Cabana (2007):

$$\text{TP}_i = \frac{\delta^{15}\text{N}_i - \delta^{15}\text{N}_{\text{baseline}}}{3.4} + 2, \quad (1)$$

where TP_i is the trophic position for individual i , $\delta^{15}\text{N}_i$ is the isotopic value for individual i , $\delta^{15}\text{N}_{\text{baseline}}$ is the nitrogen isotopic ratio of primary consumers, the number 3.4 is the trophic enrichment factor and the number 2 is the trophic position of the organisms used as baseline (Post, 2002). For baseline corrections, we used grazing larval mayflies (Ephemeroptera) of Baetidae (*Baetis fuscatus* and *Baetis melanonyx*), Ephemerellidae (*Seratella ignita*) and Heptageniidae (*Ecdyonurus venosus*, *Epeorus sylvicola* and *Electrogena lateralis*) as those taxa were present in the different streams.

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

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

where $\delta^{13}\text{C}_{\text{corri}}$ is the corrected carbon isotopic ratio for individual i , $\delta^{13}\text{C}_i$ is the carbon isotopic ratio for individual i , $\delta^{13}\text{C}_{\text{inv}}$ is the average carbon isotope ratio of the different trophic groups of benthic invertebrates sampled in the surber (decomposers: *Gammarus fossarum*, *Amphinemura triangularis*, *Leuctra* sp.; grazers: used for baseline correction of $\delta^{15}\text{N}$; predators: *Perla marginata*, *Perlodes microcephalus*) and CR_{inv} is the carbon range ($\delta^{13}\text{C}_{\text{max}} - \delta^{13}\text{C}_{\text{min}}$). Raw stable isotope values are provided in Appendix S1.

2.4 | Within- and between-individual effects of body size on trophic traits

We used the *within-subject centring* method, which uses linear mixed effects models (van de Pol & Wright, 2009) to tease apart within-individual (β_{W}) effects from between-individual (β_{B}) effects. Linear mixed effects models estimate how much of the total variance of the dependent variables (here, TP and $\delta^{13}\text{C}_{\text{corr}}$) is explained by between- and within-individual effect of ontogeny and temporal variability (fixed effects) and by individuals nested within populations (random effects). Herein, value and sign of β_{W} and β_{B} represent the strength and the direction of changes in diet (as described by TP and $\delta^{13}\text{C}_{\text{corr}}$) as the individual is growing (Figure 1). The value of β_{B} increases with the degree of difference in individual diets. The value of β_{W} increases with the difference in diet of an individual between sampling occasions. Low β_{W} values point to individuals with specialized diet.

Values of β_{W} and β_{B} indicate the strength of the diet shift while the sign of β_{B} and β_{W} indicate whether individuals shift to higher (+) or lower (-) trophic positions and to resources that are depleted (benthic invertebrates) or enriched (terrestrial arthropods or fish prey) in ^{13}C .

We estimated β_{W} and β_{B} using van de Pol and Wright's models:

$$Y_{ijkm} = \beta_0 + \beta_{\text{W}} (L_{ij} - \bar{L}_i) \theta_m + \beta_{\text{B}} \bar{L}_i \theta_m + v_{0k} + u_{0i(k)} + \varepsilon_{0ijkm}, \quad (3)$$

$$Y_{ijkm} = \beta_0 + \beta_{\text{W}} L_{ij} \theta_m + (\beta_{\text{B}} - \beta_{\text{W}}) \bar{L}_i \theta_m + v_{0k} + u_{0i(k)} + \varepsilon_{0ijkm}, \quad (4)$$

where Y_{ijkm} in our study is either TP or $\delta^{13}\text{C}_{\text{corr}}$ for individual i in population k measured at sampling time j , L_{ij} is the length of individual i at sampling time j , \bar{L}_i is the mean length L individual i over all measurements, θ_m is the temporal effect for temporal scale m (short-, medium- or long term), β_0 is the intercept of the regression equation, β_{W} is the within-individual effect of body size, β_{B} is between-individual effect of body size, $u_{0i(k)}$ is the random effect for the intercept for individual i nested in population k , v_{0k} is the random effect for the intercept for population k and ε_{0ijkm} the residual error for individual i nested in population k sampled at a time j for the temporal scale m . The sign of $(|\beta_{\text{B}}| - |\beta_{\text{W}}|)$ in Equation (2) indicates whether the strength of between-individual effect of body size is bigger (+) or smaller (-) than the strength of within-individual effect of body size. The estimate of $\beta_{\text{B}} - \beta_{\text{W}}$ goes to zero when both ITV components are similar, $|\beta_{\text{B}}| - |\beta_{\text{W}}| < 0$ when the between-individual effect of body size is bigger than the within-individual effect of body size and $|\beta_{\text{B}}| - |\beta_{\text{W}}| > 0$ when the between-individual effect of body size is smaller than the within-individual effect of body size. The two linear mixed models (Equations 3 and 4) were fitted on two different subsets of the whole dataset based on the sexual maturity of individuals (Table 1).

2.5 | Statistical analyses

We performed all statistical analyses using R software version 3.5.0 (R Development Core Team, 2016). We used nested linear mixed models (*lme* function, package 'nlme', Pinheiro, Bates, DebRoy, & Sarkar, 2019) to estimate β_{W} and β_{B} and their relative importance

through time (Equations 3 and 4). We selected the best models with the Akaike information criterion (AIC; *dredge* function, package 'MuMIn', Bartoń, 2019). The list of full models is provided in Table 1. For each full model, we kept the best candidate models with the lowest AIC score and highest model weight (AICw). The marginal R^2 (R^2_M) is the proportion of the total variance that is explained

by fixed factors (β_W , β_B , $\beta_W:\theta_m$ and $\beta_B:\theta_m$), and the conditional R^2 (R^2_C) is the proportion of the total variance explained by both random (v_{Ok} , $u_{O(i,k)}$) and the residual variance, Table 2) and fixed factors (Nakagawa & Schielzeth, 2013).

Variance component analysis is a powerful tool for partitioning variation in a trait among groups of interest (Harrison et al.,

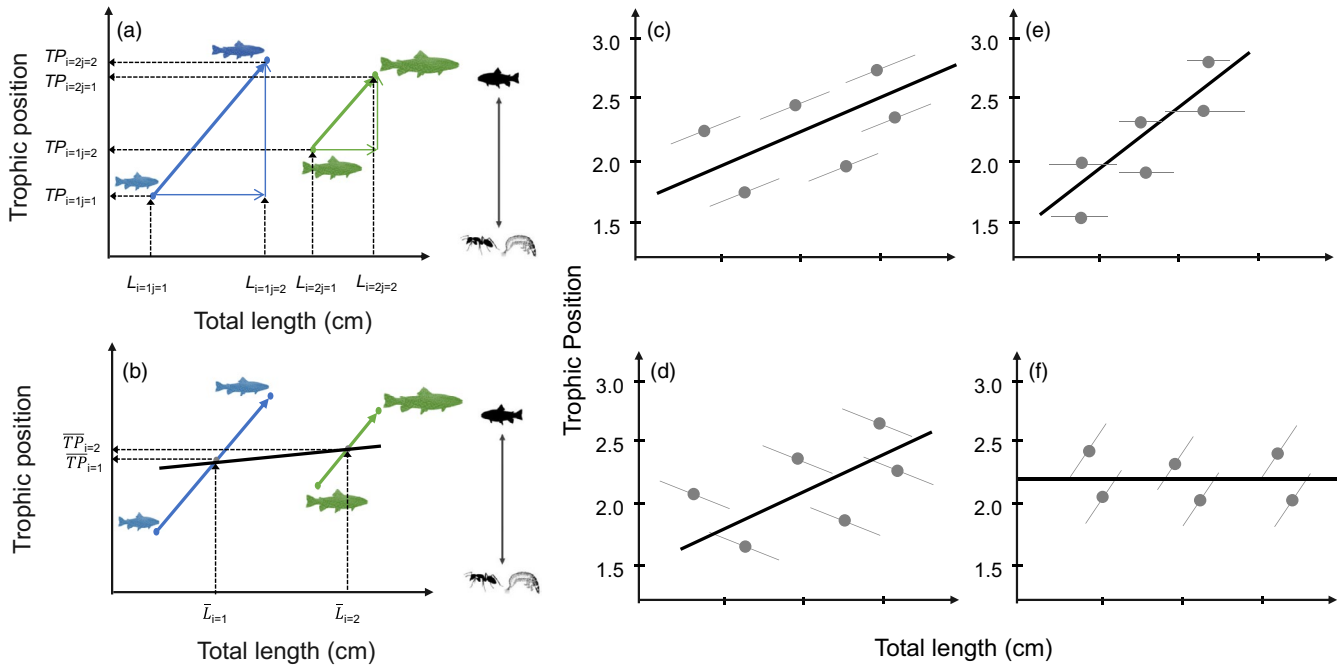


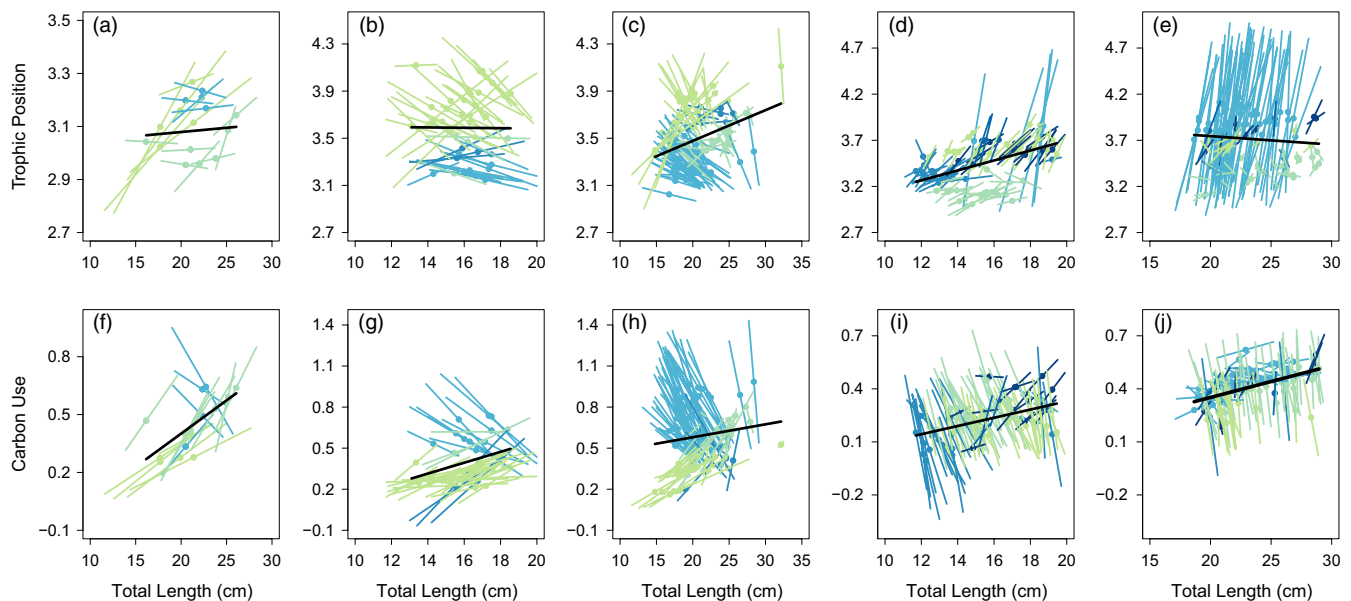
FIGURE 1 Measurements of the within-individual effect of growth on trophic position variation (a) and of the between-individual effects of growth on the same trait (b), example based on repeated samples from two individuals i (1 and 2) where L_{ij} is the total length (mm) of individual i sampled at time j , TP_{ij} is the trophic position of individual i sampled at time j , L_i is the average total length of individual i and \overline{TP}_i is the average trophic position of individual i . Different scenarios explaining how within- (β_W) and between-individual (β_B) effects of body size on individual diet (here, trophic position) differ with total length of individuals. (c) $\beta_W = \beta_B > 0$; trophic position is higher in large trout than small ones ($\beta_B > 0$) and individuals shift to higher trophic positions through ontogeny ($\beta_W > 0$). (d) $\beta_B > \beta_W$ and $\beta_W < 0$. Large trout show higher trophic position than small trout, but individuals shift to lower trophic position through time. (e) $\beta_B > \beta_W = 0$; trophic position is higher in large trout than small ones, but individuals keep the same trophic position through time. Individuals are specialized. (f) $\beta_W > \beta_B = 0$; individuals exhibit similar trophic position but each individual shift evenly to higher trophic positions through time. Modified from van de Pol and Wright (2009)

TABLE 1 List of full models used as starting point for model selection for immature and mature trout and both trophic traits

Class	Trait	Model
Immature	Trophic position	$TP_{ijkm} = \beta_0 + \beta_W (L_{ij} - \overline{L}_i) \theta_m + \beta_B \overline{L}_i \theta_m + v_{Ok} + u_{O(i,k)} + \epsilon_{Oijkm}$
Immature	Trophic position	$TP_{ijkm} = \beta_0 + \beta_W L_{ij} \theta_m + (\beta_B - \beta_W) \overline{L}_i \theta_m + v_{Ok} + u_{O(i,k)} + \epsilon_{Oijkm}$
Mature	Trophic position	$TP_{ijkm} = \beta_0 + \beta_W (L_{ij} - \overline{L}_i) \theta_m + \beta_B \overline{L}_i \theta_m + v_{Ok} + u_{O(i,k)} + \epsilon_{Oijkm}$
Mature	Trophic position	$TP_{ijkm} = \beta_0 + \beta_W L_{ij} \theta_m + (\beta_B - \beta_W) \overline{L}_i \theta_m + v_{Ok} + u_{O(i,k)} + \epsilon_{Oijkm}$
Immature	Carbon use	$\delta^{13}C_{corr ijk m} = \beta_0 + \beta_W (L_{ij} - \overline{L}_i) \theta_m + \beta_B \overline{L}_i \theta_m + v_{Ok} + u_{O(i,k)} + \epsilon_{Oijkm}$
Immature	Carbon use	$\delta^{13}C_{corr ijk m} = \beta_0 + \beta_W L_{ij} \theta_m + (\beta_B - \beta_W) \overline{L}_i \theta_m + v_{Ok} + u_{O(i,k)} + \epsilon_{Oijkm}$
Mature	Carbon use	$\delta^{13}C_{corr ijk m} = \beta_0 + \beta_W (L_{ij} - \overline{L}_i) \theta_m + \beta_B \overline{L}_i \theta_m + v_{Ok} + u_{O(i,k)} + \epsilon_{Oijkm}$
Mature	Carbon use	$\delta^{13}C_{corr ijk m} = \beta_0 + \beta_W L_{ij} \theta_m + (\beta_B - \beta_W) \overline{L}_i \theta_m + v_{Ok} + u_{O(i,k)} + \epsilon_{Oijkm}$

TABLE 2 Statistical description and biological meaning of model parameters estimated in the models, variance of random effects and total variance explained in the models used in Equations (1 and 2)

Parameter	Statistical description	Biological description	References
β_0	Model intercept		van de Pol and Wright (2009)
β_W	Within-individual effect of size	Trophic shift (TP or $\delta^{13}C_{corr}$) of a given individual during ontogeny	van de Pol and Wright (2009)
β_B	Between-individual effect of size	Trophic shift (TP or $\delta^{13}C_{corr}$) between individuals based on their average size	van de Pol and Wright (2009)
$\beta_B - \beta_W$	Difference between between- and within-individual effects, statistical method to assess the statistical differences among intraspecific variation components	If $\beta_W - \beta_B = 0$, strength of trophic shifts is similar both within individuals during ontogeny and between individuals If $\beta_W - \beta_B > 0$, trophic shifts in TP or $\delta^{13}C_{corr}$ is driven by ontogenetic changes within individuals If $\beta_W - \beta_B < 0$, trophic shifts in TP or $\delta^{13}C_{corr}$ is driven by the differences among individuals	van de Pol and Wright (2009)
V_{pop}	Variance for phenotype for y depending on the population	Average between-population plasticity in response variable based on stimulus that are unaccounted in the model (e.g. genetic distance, environmental conditions)	Dingemans and Dochtermann (2013)
V_{ind}	Within-individual (residual) variance for phenotype for y	Average within-individual plasticity in response variable towards stimulus that is statistically unaccounted in the model (e.g. morphology, behaviour, personality, sex, etc.)	Dingemans and Dochtermann (2013)

**FIGURE 2** Individual ontogenetic trajectories of trophic position (upper line) and carbon use (lower line) for the 238 marble trout sampled across the long-time survey (a, f), medium-term survey for immature (b, g) and mature trout (c, h) and short-term survey for immature (d, i) and mature trout (e, j). Each dot represents a trout and the associated thin line is the individual trajectory (within-individual shift). Black lines represent the between-individual effect of body size in marble trout. Each colour represents a marble trout population

2018). The variance of response variables (TP and $\delta^{13}C_{corr}$) explained by time and ontogeny (fixed factors) shows how much of ITV is explained by the two processes. The variance of random factors (population, between individuals and within individuals, Table 2) is the amount of phenotypic variance not explained by

the fixed factors that can be attributed to differences in phenotype between populations, between individuals and within individuals (Dingemans & Dochtermann, 2013). Because of our nested design (individuals nested within populations), it was not possible to separate the main effect (*between individual*) from the

interaction (*population:between individual*) variance for the random effect $u_{oi(k)}$ (Schielzeth & Nakagawa, 2013). Therefore, we focused on the within-individual variance (V_{ind} , that is, the residual variance of the models, Table 2) and on the variance of the random effect 'population' (V_{pop} , Table 2). We computed confidence intervals (95%) of random effects using bootstrap ($n = 1,000$). When the 95% CIs of two variance estimates did not overlap, we concluded that the variance estimates were significantly different from each other.

3 | RESULTS

Individual marble trout trajectories in TP and $\delta^{13}C_{corr}$ showed high variability depending on the populations, time-scales and sexual maturity of trout (Figure 2).

3.1 | Variability in trophic traits

All models selected included β_W , β_B , θ_m and $\beta_W:\theta_m$ as fixed effects (Table 3). The interaction between the between-individual effect of body size and temporal scale ($\beta_B:\theta_m$) was not included in the best models. Most of the variance—from 44.4% to 65.3%—in trophic traits of immature and mature trout was explained by the random effects (i.e. individuals nested in populations) and the fixed effects (β_W , β_B , $\beta_W:\theta_m$) together (Table 3). Variance explained by fixed effects (R^2_M) explained between 15.6% and 56.4% of the variance over the different trophic traits and maturity categories (Table 3).

3.2 | Time-scale effects on between- and within-individual effects of body size

Both β_W and the interaction between β_W and θ_m accounted for the largest part of TP variability accounting for 84.0% and 72.1% of the variance of this trait in immature and mature trout, respectively, while the β_B —remaining similar through time—accounted for 15.7% (immature trout) and 2.6% (mature trout) of TP variability. For carbon use, we observed similar patterns with up to 74.3% and 41.7% of the total variance explained by β_W and $\beta_W:\theta_m$ in immature and mature trout respectively. β_B accounted for 4.6% and 13.9% of the carbon use variance in immature and mature trout respectively.

We found no differences between β_W and β_B during the long-term survey of mature trout and neither for the medium-term survey in immature trout (Figure 3). The value of β_B was positive during the long- and medium-term surveys (Figure 3), with larger trout of each sexual class having on average higher TP and higher $\delta^{13}C_{corr}$ in tissues (Figure 2). Short-term β_W was higher than long- and medium-term β_W in both immature and mature trout for both trophic position and carbon use (Figure 3). Individual immature marble trout shifted towards

TABLE 3 Variance decomposition of best linear mixed models fixed effects for immature and mature trout and trophic traits

Size	Predictor	Trophic position					$\delta^{13}C_{corr}$						
		df	S.Sq	Var. Exp. (%)	F-value	$R^2_M - R^2_C$	AICw	df	S.Sq	Var. Exp. (%)	F-value	$R^2_M - R^2_C$	AICw
Immature	β_W	1,138	0.096	2.56	1.74	0.15–0.44	0.712	1,138	0.428	9.29	17.19	0.39–0.51	0.659
	β_B	1,138	0.592	15.69	10.69			1,138	0.210	4.57	8.45		
	θ_m	1,138	0.011	0.29	0.19			1,138	0.974	21.15	39.12		
	$\beta_W:\theta_m$	1,138	3.071	81.45	55.49			1,138	2.993	64.98	120.20		
Mature	β_W	1,325	3.450	5.14	38.52	0.56–0.65	0.622	1,325	1.097	11.79	30.27	0.34–0.49	0.885
	β_B	1,325	1.725	2.57	19.26			1,325	1.297	13.89	35.66		
	θ_m	2,325	16.995	25.32	94.89			2,325	4.133	44.43	57.01		
	$\beta_W:\theta_m$	2,325	44.933	66.96	250.89			2,325	2.779	29.87	38.33		

Note: Percentage of variance explained (Var. Exp.) was calculated from the sum of square (S.Sq) and represent the respective part of variance explained by each fixed factor in the total variance explained by fixed factors (R^2_M). R^2_C is the total variance explained by both fixed and random factors.

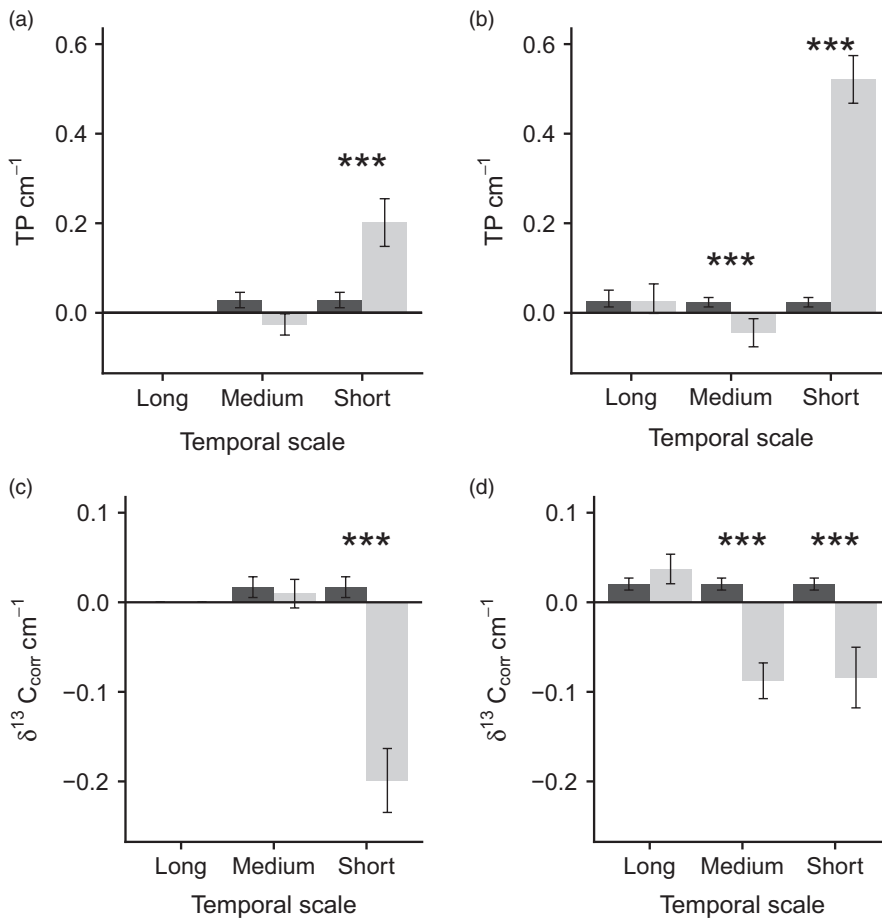


FIGURE 3 Averaged estimates and corresponding 95% CI of between- (β_B) and within-individual (β_W) effects of body size for the three considered time-scales (long-, medium- and short term), estimated from the linear mixed models (Equation 1) for TP in immature trout (a) and mature trout (c), and $\delta^{13}C_{corr}$ for immature trout (b) and mature trout (d). Significant differences between β_B and β_W are displayed by *** and were calculated using Equation (2), indicated by the sign of $|\beta_B| - |\beta_W|$ (see Section 2)

TABLE 4 Estimation of variance components (mean [95% CI]) of the random effects in Equation (1) for both trophic traits (TP, trophic position and $\delta^{13}C_{corr}$) and trout maturity classes

Trait	Class	V_{pop}	V_{ind}
TP	Immature	0.028 [0.010–0.109]	0.055 [0.046–0.066]
	Mature	0.023 [0.008–0.087]	0.089 [0.079–0.102]
$\delta^{13}C_{corr}$	Immature	0.006 [0.002–0.026]	0.025 [0.021–0.029]
	Mature	0.011 [0.004–0.039]	0.036 [0.032–0.041]

Note: V_{pop} is the variance of population random effect and V_{ind} is the residual variance, that is, the within-individual variance.

a higher trophic position through the summer and less negative $\delta^{13}C_{corr}$ resources (Figure 3). Individual trajectories strongly differed among populations (Figure 2).

3.3 | Variance of population and individual random effects

The within-individual variance of trophic traits (V_{ind}) is lower in immature trout than in mature ones (Table 4). V_{ind} is higher in

trophic position than in carbon use for both mature and immature trout. Except for the trophic position of mature trout, V_{ind} and V_{pop} are similar within a sexual maturity class for a given trophic trait (Table 4). V_{pop} displays a large range of values and it is similar between sexual maturity classes for both trophic position and carbon use (Table 4).

4 | DISCUSSION

We found that the degree of difference in individual diets of marble trout was consistent over time while the extent of trophic shifts within individuals changed significantly with time elapsing between sampling occasions. While the relative strength of between- and within-individual ontogenetic shifts was acting similarly on the intraspecific variability of trophic position and resource use at medium- and long-term scales, we found that the within-individual component was the main driver of trophic variability in marble trout populations during the short-term survey. Furthermore, we found a strong effect of population on trophic variability, and that the trophic plasticity displayed by individuals—apart from ontogenetic shifts—can be as large as the variability observed between marble trout populations. Our results show that marble trout show trophic phenotypes that vary through their lifetime and can be unrelated to the ontogenetic shifts.

4.1 | Temporal mismatch for between- and within-individual effects of body size

In gape size-limited consumers like fishes, the range of potential prey widens as the consumer grows in body size, and the increase in size tends to be larger when the time-scale between two samplings increases, especially when samplings occur before individuals have reached sexual maturity. We found that between-individual variability was constant over time-scales while within-individual variability significantly increased at short temporal scale, thus supporting the hypothesis of higher trophic position of large trout than small ones and individuals shift to higher trophic positions through ontogeny. These results do not support the hypothesis that both inter- and intra-individual similarities in diet are more likely to decrease with increasing time between two repeated samplings of the same individual (Novak & Tinker, 2015).

The very low variability in between-individual effects over time shows that larger trout have higher trophic positions compared to smaller ones, which is consistent with previous findings on the trophic ecology of marble trout (Musseau et al., 2015, 2018) and fish trophic ecology in general (Smith & Reay, 1991). High trophic positions in marble trout populations are caused by a sizeable proportion of fish prey in predators' diet (Musseau et al., 2018). The marble populations investigated in the present study are living in allopatry, therefore, the higher trophic positions are due to cannibalism, which has been directly observed several times during sampling campaigns (A. J. Crivelli, pers. comm.). This is consistent with optimal foraging theory, which states that individuals should feed on the most valuable resources, that is, the resources with the best energy-based trade-off between capturability, handling time, cost for digestion and gross energy intake (Araújo, Bolnick, & Layman, 2011; Werner & Hall, 1974). Fish prey represent a better trade-off between energy intake and capturability for salmonids with respect to invertebrates (Elliott & Hurley, 2000). Persistent patterns of differences between individuals can emerge during their early life or considered as evolutionarily fixed responses (van de Pol & Wright, 2009); understanding which one of these two phenomena maintains cannibalism in marble trout populations would help to better know the role of intraspecific predation in small populations.

The within-individual effect of body size on changes in diet differed with time-scale and was the main component of ITV at the seasonal level for the two ontogenetic classes and both trophic traits. The within-individual effect of body size was similar at long- and medium time-scales, showing that foraging activity and resources used by individuals were consistent over the years. Comparing the same season—spring in our study—over different years implies close ecological conditions across years in abiotic (temperature and habitat) and some biotic factors such as the absence of young-of-the-year as available prey. However, the within-individual effect of body size was much higher at the short-term scale—in our study, over the summer. European ecosystems are highly productive in the summer, with higher stream temperatures, and increased benthic biomass production and terrestrial subsidies. Quantifying individual trophic

trajectories in natural populations relative to the changes in biotic and abiotic environments over a season would help understand both the adaptive responses of individuals and the biological mechanisms underlying trophic plasticity in changing environments (Evangelista, Boiché, Lecerf, & Cucherousset, 2014).

Many studies do not consider the direct consequences of individual growth on the intraspecific variation in trophic traits when quantifying the inter- and intra-individual components. However, our results on the role of intra- and inter-individual effects on the intrapopulation variation differ from previous results for other vertebrate species. In marble trout, the between-individual effect of ontogeny explained 15.7% and 3.0% of trophic position and 4.3% and 13.8% of carbon resources, for immature and mature trout respectively. Previous studies show that intrapopulation variation on trophic traits is mostly driven by differences between individuals: 93% for $\delta^{15}\text{N}$ and 98% for $\delta^{13}\text{C}$ in loggerhead sea turtles (Vander Zanden et al., 2010), 59% for $\delta^{13}\text{C}$ and 67% for $\delta^{15}\text{N}$ in coyotes (Newsome, Garbe, Wilson, & Gehrt, 2015) and 60% for $\delta^{13}\text{C}$ and 64% for $\delta^{15}\text{N}$ in the southern elephant seal (Hückstädt et al., 2012). These studies focused on large organisms with migratory behaviour and/or a large range of available habitats and available resources, allowing high inter-individual differences and showing the individual specialization in habitat and resource use. Lehmann et al. (2015) showed that in coexisting grazing ungulate populations, within-individual variation is the main cause of isotopic niche variation in gemsbok while inter- and intra-individual variations contributed similarly to trophic variation in springbok populations. Overall, these results show that the extent of trophic variation can vary widely between species and that the causes of ITV may differ among taxa.

4.2 | Causes and consequences of individual inconsistency

Marble trout showed a high remaining within-individual variance for both sexual maturity classes and trophic traits after accounting for ontogeny, time-scales and sources of plasticity in the different populations. The strength of trophic plasticity of individual marble trout is similar to the strength of trophic plasticity estimated between populations. Our results showed that individual trophic plasticity is higher in mature than immature trout. In fish, behavioural traits may contribute to within-individual variation in diet, for example, shyness/boldness, exploration/avoidance, activity, aggression and sociability (Conrad, Weinersmith, Brodin, Saltz, & Sih, 2011). Sex of individuals can affect their phenotypic variability through time, since in salmonids the adaptations and responses to changing conditions may vary with sex (Øverli, Sørensen, & Nilsson, 2006). However, in this study, we did not assign sex to marble trout, as males and females can be distinguished morphologically only just before or during the reproductive season, which for most marble trout populations occur in November or December.

Plasticity in key traits gives individuals the possibility to adapt to changing environments (Reed et al., 2011). Marble trout live in small streams affected by flash floods, whose intensity and frequency are

increasing owing to global climate change (Pujolar et al., 2011). While trait variability and phenotypic adaptations are unlikely to increase marble trout survival chances during flash floods (Vincenzi et al., 2014, 2017; Vincenzi, Jesenšek, Garza, & Crivelli, 2018), trophic plasticity may allow marble trout to more quickly adapt to changes in resources available to those individuals that survive flash floods. Faster somatic growth and younger mean age at reproduction, that is, faster life histories, are often observed in the years that follow flash floods (Vincenzi et al., 2017). Higher prevalence of faster life histories after extreme events is most likely caused by lower competition for food and space for individuals born after flash flood (Vincenzi et al., 2017). Our results showed high individual plasticity of individual marble trout and therefore support this hypothesis. By being highly plastic in their diet, marble trout can adapt to the availability of their preferred resources (i.e. type of invertebrates or small conspecific) and switch to alternative resources. Individual trophic plasticity could be one of the main factors explaining the resilience of marble trout populations observed during the last decade after massive mortality events.

4.3 | Trophic variation at population levels

Population as a random factor was a major determinant of the variation in trophic plasticity of marble trout. Causes of variation in functional traits between populations can have genetic and/or environmental sources (Albert et al., 2011). In our study, both environment and genetic structure are quite different among populations (Fumagalli et al., 2002; Musseau et al., 2015). Previous studies on the same marble trout populations showed a strong genetic differentiation among populations despite a very restricted geographical range, much greater than for other fish species living in larger areas (Fumagalli et al., 2002). From an evolutionary perspective, within-individual niche variation is either a fixed (Roughgarden, 1972) or a heritable (Ackermann & Doebeli, 2004) trait, contrary to the phenotypically flexible trait supported by optimal foraging theory, and between-individual diet variation comes from heritable phenotypic variance of resource use (Araújo et al., 2011). We argue that more studies on the heritability of trophic traits (i.e. genetic component of niche variation) are needed, particularly in species of conservation interest like marble trout. Environment can also be a major driver of trophic variability in populations (Darimont et al., 2009). Previous findings have shown how much habitat, temperature and terrestrial surroundings affect marble trout dietary niche (Musseau et al., 2015). However, little is known about how the changing environmental and ecological features are affecting individual trophic shifts in wild populations.

5 | CONCLUSIONS

Overall, our results show the crucial importance of considering effects of time-scales on functional variability at the individual, population and species level. The present study provides empirical evidence that (a) time-scale affects the relative strength of between- and

within-individual effects of ontogeny; (b) intra-individual variation on a short term is higher than medium- and long-term scales; and (c) the trophic trait variability displayed by individuals was similar to the variability measured between populations.

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AUTHORS' CONTRIBUTIONS

A.J.C., D.J. and C.M. designed the study and conducted field work; C.M. analysed the data and wrote the manuscript. All authors participated in the improvement of the manuscript and provided editorial advice.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.j0zpc8695> (Musseau et al., 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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