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

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**Abstract**

1. Intra-specific 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 (1) measure the relative strength of between- and within-individual effects of body size on ITV over time, and (2) 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 (<900km²) that shows marked changes in diet through ontogeny. We investigated two trophic traits, trophic position and resource use, with stable isotopes ($\delta^{15}N$ and $\delta^{13}C$), 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 timescales (short-term: three months, medium-term: one year, and long-term: two 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 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.
5. Overall, our results show how the relative strengths of ITV drivers change over time. This study evidences the crucial importance of considering effects of timescales on functional variability at individual, population, and species levels.

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**Keywords**

Longitudinal survey; between-individual; within-individual; stable isotope analysis; intra-specific trait variability; individual trajectory; salmonid; timescales

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## 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 (Miller & Rudolf 2011; Raffard *et al.* 2018; Des Roches *et al.* 2018), but the extent of trait variability within species has been overlooked (Bolnick *et al.* 2011; Costa-Pereira *et al.* 2018).

ITV 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 *et al.* 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 *et al.* 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 *et al.* 2015). Additionally, the relative strength of the three components tend 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 timescale 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 *et al.* 2009), reptiles (Vander Zanden, Bjorndal & Bolten 2013), birds (Cherel *et al.* 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).

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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 of 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 *et al.* 2010), prey/predator interactions (Barnes *et al.* 2010), inter- and intra-specific competition (Parra *et al.* 2011), and survival probability (Claessen, de Roos & Persson 2000) all depend on size. Ontogenetic niche shifts shape the functional changes of 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 intra-specific 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 *et al.* 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.* 2009, 2010; Vander Zanden *et al.* 2013), or on tissues from

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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 of trophic traits over time and across populations and testing. First, we focus on the effects of ontogeny on ITV and we tease apart within- from between-individual effects of ontogeny at three timescales ( long-term: 2-years survey; medium-term: 1-year survey; and short-term: 3-months survey) on trophic position and resource use with stable isotopes analysis ($\delta^{15}N$ and $\delta^{13}C$). 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.

## Material and Methods

*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 Idrijca River basins (the total surface of the basins is approximately 900 km²). A conservation program for marble trout (Marble Trout Project) started in Western Slovenia in 1993 (Crivelli *et al.* 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 *et al.* 2014; Vincenzi *et al.* 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.

*Field study*

As part of the conservation program, 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

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mm in total length, each trout received a Carlin tag. In the present study, six (Huda Grapa, Studenc, Upper Idrijca, 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 phenoxy-ethanol and their length (mm) and weight (g) were recorded *in situ*. Part of the pectoral fin, a strong surrogate of fish muscle (Sanderson *et al.* 2009; Busst, Bašic & Britton 2015), 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 (phytophageous: 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 lab. There, fin samples were immediately dried, and invertebrate samples were dried after individuals were allowed to empty their guts for 36 hours in the buckets in which they were individually stored. Samples were dried for 48h 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 two-year survey (June 2011, June 2012 and June 2013); medium-term, when trout were sampled twice during the one-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 (Vincenzi *et al.* 2008; Musseau *et al.* 2015). 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 3 times during the two-year survey, 124 individuals during the one-year survey (2 different measures for 41 immature trout and 83 mature trout) and 196 individuals for the 3-month survey (2 different measures for 88 immature trout and 108 mature trout). Huda Grapa, Studenc and Upper Idrijca populations were sampled four times,

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Lipovscek three times (June 2012, June 2013, September 2013), and Svenica and Trebuscica were sampled twice (June 2013 and September 2013).

*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 ($\delta^{13}C$ and $\delta^{15}N$, respectively) were analysed in an elemental analyser (Carlo Erba NC2500a) coupled to an isotope ratio mass spectrometer (Thermo Finnigan MAT Delta XP). Stable isotope ratios are expressed in per mill (‰) delta values ($\delta^{13}C$ or $\delta^{15}N$) referring to the international standards for carbon (PeeDee Belemnite) and nitrogen (atmospheric nitrogen): $\delta^{13}C$ or $\delta^{15}N$ (‰) = $[(R_{sam} - R_{std})/R_{std}]$ x 1000. Data were corrected using working standards (fish tissue, mink tissue and methionine SD < 0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$) 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 of 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):

$$TP_i = \frac{\delta^{15}N_i - \delta^{15}N_{baseline}}{3.4} + 2 \qquad \textbf{(Eq. 1)}$$

where $TP_i$ is the trophic position for individual i, $\delta^{15}N_i$ is the isotopic value for individual i, $\delta^{15}N_{baseline}$ 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 $\delta^{13}C$ values ($\delta^{13}C_{corr}$) following Olsson et al. (2009):

$$\delta^{13}Ccorr_i = \frac{\delta^{13}C_i - \delta^{13}C_{inv}}{CR_{inv}} \qquad \textbf{(Eq. 2)}$$

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where $\delta^{13}Ccorr_i$ is the corrected carbon isotopic ratio for individual *i*, $\delta^{13}C_i$ is the carbon isotopic ratio for individual *i*, $\delta^{13}C_{inv}$ 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 $\delta^{15}N$; predators: *Perla marginata, Perlodes microcephalus*) and $CR_{inv}$ is the carbon range ($\delta^{13}C_{max}$ - $\delta^{13}C_{min}$). Raw stable isotope values are provided in Appendix S1.

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

We used the *within-subject centering* method, which uses linear mixed-effects models (van de Pol & Wright 2009) to tease apart within-individual ($\beta_W$) effects from between-individual ($\beta_B$) effects. Linear mixed-effects models estimate how much of the total variance of the dependent variables (here, TP and $\delta^{13}C_{corr}$) 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 $\beta_W$ and $\beta_B$ represent the strength and the direction of changes in diet (as described by TP and $\delta^{13}C_{corr}$) as the individual is growing (Fig. 1). The value of $\beta_B$ increases with the degree of difference in individual diets. The value of $\beta_W$ increases with the difference in diet of an individual between sampling occasions. Low $\beta_W$ values point to individuals with specialized diet.

Values of $\beta_W$ and $\beta_B$ indicate the strength of the diet shift while the sign of $\beta_B$ and $\beta_W$ 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 $\beta_W$ and $\beta_B$ using van de Pol and Wright's models:

$$Y_{ijkm} = \beta_0 + \beta_W (L_{ij} - \bar{L}_i)\, \theta_m + \beta_B\, \bar{L}_i\, \theta_m + v_{0k} + u_{0i(k)} + \varepsilon_{0ijkm} \quad \textbf{(Eq. 3)}$$

$$Y_{ijkm} = \beta_0 + \beta_W L_{ij}\, \theta_m + (\beta_B - \beta_W)\, \bar{L}_i\, \theta_m + v_{0k} + u_{0i(k)} + \varepsilon_{0ijkm} \quad \textbf{(Eq. 4)}$$

where $Y_{ijkm}$ in our study is either *TP* or $\delta^{13}C_{corr}$ 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, $\theta_m$ is the temporal effect for temporal scale *m* (short-, medium-, or long-term), $\beta_0$ is the intercept of the regression equation, $\beta_W$ is the within-individual effect of body size, $\beta_B$ is between-individual effect of body size, $u_{0i(k)}$ is the random effect for the intercept

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for individual $i$ nested in population $k$, $v_{0k}$ is the random effect for the intercept for population $k$, and $\varepsilon_{0ijkm}$ the residual error for individual $i$ nested in population $k$ sampled at a time $j$ for the temporal scale $m$. The sign of ($|\beta_B| - |\beta_W|$) in Eq. 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 $\beta_B - \beta_W$ goes to zero when both ITV components are similar, $|\beta_B| - |\beta_W| < 0$ when the between-individual effect of body size is bigger than the within-individual effect of body size, and $|\beta_B| - |\beta_W| > 0$ 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).

*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 et al. 2019) to estimate $\beta_W$ and $\beta_B$ and their relative importance through time (Eq. 3 and 4). We selected the best models with the Akaike Information Criterion (AIC) (*dredge* function, package 'MuMIn', Bartoń 2017). 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 (AIC*w*). The marginal $R^2$ ($R^2_M$) is the proportion of the total variance that is explained by fixed factors ($\beta_W$ , $\beta_B$, $\beta_W$:$\theta_m$, and $\beta_B$:$\theta_m$), and the conditional $R^2$ ($R^2_C$) is the proportion of the total variance explained by both random ($v_{0k}$, $u_{0i(k)}$ and the residual variance, Table 2) and fixed factors (Nakagawa & Schielzeth 2013).

Variance components analysis is a powerful tool for partitioning variation in a trait among groups of interest (Harrison *et al.* 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 (Dingemanse & Dochtermann 2013). Because of our nested design (individuals nested within populations), it was not possible to separate the main effect (*between-individual*) from the

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interaction (*population:between-individual*) variance for the random effect $u_{0i(k)}$ (Schielzeth & Nakagawa 2013). Therefore, we focused on the within-individual variance ($V_{ind}$, i.e. 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 ($n = 1000$). When the 95% CIs of two variance estimates did not overlap, we concluded that the variance estimates were significantly different from each other.

## 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 (Fig. 2).

*Variability in trophic traits*

All models selected included $\beta_W$, $\beta_B$, $\theta_m$ 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 ($\beta_W$, $\beta_B$, $\beta_W$:$\theta_m$) 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).

*Timescale effects on between- and within-individual effects of body size*

Both $\beta_W$ and the interaction between $\beta_W$ and $\theta_m$ 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 $\beta_B$ – 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 $\beta_W$ and $\beta_W$:$\theta_m$ in immature and mature trout, respectively. $\beta_B$ accounted for 4.6% and 13.9% of the carbon use variance in immature and mature trout, respectively.

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We found no differences between $\beta_W$ and $\beta_B$ during the long-term survey of mature trout neither for the medium-term survey in immature trout (Fig. 3). The value of $\beta_B$ was positive during the long- and medium-term surveys (Fig. 3), with larger trout of each sexual class having on average higher TP and higher $\delta^{13}C_{corr}$ in tissues (Fig. 2). Short-term $\beta_W$ was higher than long- and medium-term $\beta_W$ in both immature and mature trout for both trophic position and carbon use (Fig. 3). Individual immature marble trout shifted toward higher trophic position through the summer and less negative $\delta^{13}C_{corr}$ resources (Fig. 3). Individual trajectories strongly differed among populations (Fig. 2).

*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 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 large range of values and it is similar between sexual maturity classes for both trophic position and carbon use (Table 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 intra-specific 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.

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*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 timescale 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 of 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 (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 (Werner & Hall 1974; Araújo, Bolnick & Layman 2011). 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 intra-specific predation in small populations.

The within-individual effect of body size on changes in diet differed with timescale 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- timescales, 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

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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 *et al.* 2014).

Many studies do not consider the direct consequences of individual growth on the intraspecific variation of 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, 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 $\delta^{15}N$ and 98% for $\delta^{13}C$ in loggerhead sea turtles (Vander Zanden *et al.* 2010), 59% for $\delta^{13}C$ and 67% for $\delta^{15}N$ in coyotes (Newsome *et al.* 2015) and 60% for $\delta^{13}C$ and 64% for $\delta^{15}N$ 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.

*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, timescales, and sources of plasticity in the different populations. The strength of trophic plasticity of individual marble trout is similar to the

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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 *et al.* 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, Vincenzi et al. 2017, Vincenzi *et al.* 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, i.e. 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.

*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

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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 of 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 changing environmental and ecological features are affecting individual trophic shifts in wild populations.

## Conclusion

Overall, our results show the crucial importance of considering effects of timescales on functional variability at the individual, population, and species level. The present study provides empirical evidence that 1) timescale affects the relative strength of between- and within-individual effects of ontogeny; 2) intra-individual variation on a short-term is higher than medium- and long-term scales; and 3) the trophic trait variability displayed by individuals was similar to the variability measured between populations.

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## Author's contributions

AJC, DJ and CM designed the study, CM, DJ and AJC conducted field work; CM analysed the data and wrote the manuscript and, all authors participated in the improvement of the manuscript and provided editorial advice.

## Data accessibility

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

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## Figure captions

**Figure 1 –** Measurements of the within-individual effect (WIE) of growth on trophic position variation (**A**) and of the between-individual effects (BIE) 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*, $\overline{L_i}$ is the average total length of individual *i* and $\overline{TP_i}$ is the average trophic position of invidual *i*. Different scenarios explaining how within- ($\beta_W$) and between-individual ($\beta_B$) 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 (WIE > 0). (**D**) BIE > $\beta_W$ 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 & Wright, 2000.

**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 and F), medium-term survey for immature (B and G) and mature trout (C and H) and short-term survey for immature (D and I) and mature trout (E and 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 color represents a marble trout population.

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**Figure 3 –** Averaged estimates and corresponding 95% CI of between- ($\beta_B$) and within-individual ($\beta_W$) effects of body size for the three considered timescales (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 $\beta_B$ and $\beta_W$ are displayed by *** and were calculated using Eq. 2, indicated by the sign of $|\beta_B| - |\beta_W|$ (*see Material and Methods*).

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## Tables

**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 | $TP_{ijkm} = \beta_0 + \beta_W (L_{ij} - \bar{L}_i)\, \theta_m + \beta_B\, \bar{L}_i\, \theta_m + v_{0k} + u_{0i(k)} + \varepsilon_{0ijkm}$ |
| Immature | Trophic position | $TP_{ijkm} = \beta_0 + \beta_W L_{ij}\, \theta_m + (\beta_B - \beta_W)\, \bar{L}_i\, \theta_m + v_{0k} + u_{0i(k)} + \varepsilon_{0ijkm}$ |
| Mature | Trophic position | $TP_{ijkm} = \beta_0 + \beta_W (L_{ij} - \bar{L}_i)\, \theta_m + \beta_B\, \bar{L}_i\, \theta_m + v_{0k} + u_{0i(k)} + \varepsilon_{0ijkm}$ |
| Mature | Trophic position | $TP_{ijkm} = \beta_0 + \beta_W L_{ij}\, \theta_m + (\beta_B - \beta_W)\, \bar{L}_i\, \theta_m + v_{0k} + u_{0i(k)} + \varepsilon_{0ijkm}$ |
| Immature | Carbon use | $\delta^{13}C_{corr\ ijkm} = \beta_0 + \beta_W (L_{ij} - \bar{L}_i)\, \theta_m + \beta_B\, \bar{L}_i\, \theta_m + v_{0k} + u_{0i(k)} + \varepsilon_{0ijkm}$ |
| Immature | Carbon use | $\delta^{13}C_{corr\ ijkm} = \beta_0 + \beta_W L_{ij}\, \theta_m + (\beta_B - \beta_W)\, \bar{L}_i\, \theta_m + v_{0k} + u_{0i(k)} + \varepsilon_{0ijkm}$ |
| Mature | Carbon use | $\delta^{13}C_{corr\ ijkm} = \beta_0 + \beta_W (L_{ij} - \bar{L}_i)\, \theta_m + \beta_B\, \bar{L}_i\, \theta_m + v_{0k} + u_{0i(k)} + \varepsilon_{0ijkm}$ |
| Mature | Carbon use | $\delta^{13}C_{corr\ ijkm} = \beta_0 + \beta_W L_{ij}\, \theta_m + (\beta_B - \beta_W)\, \bar{L}_i\, \theta_m + v_{0k} + u_{0i(k)} + \varepsilon_{0ijkm}$ |

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**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 & 2.

| Parameter | Statistical description | Biological description | References |
|---|---|---|---|
| $\beta_0$ | Model intercept | | van de Pol and Wright 2009 |
| $\beta_W$ | 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 |
| $\beta_B$ | 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 |
| $\beta_W - \beta_B$ | Difference between within- and between-individual effects, statistical method to assess the statistical differences between intra-specific variation components | If $\beta_w - \beta_b = 0$, strength of trophic shifts is similar both within-individuals during ontogeny and between-individuals;<br>If $\beta_w - \beta_b > 0$, trophic shifts in TP or $\delta^{13}C_{corr}$ is driven by ontogenetic changes within | van de Pol and Wright 2009 |

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| | | | |
|---|---|---|---|
| | | individuals<br>If $\beta_w - \beta_b < 0$, trophic shifts in TP or $\delta^{13}C_{corr}$ is driven by the differences among individuals | |
| $V_{pop}$ | 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) | Dingemanse and Dochtermann 2013 |
| $V_{ind}$ | Within-individual (residual) variance for phenotype for *y* | Average within-individual plasticity in response variable towards stimulus that are statistically unaccounted in the model (e.g. morphology, behavior, personality, sex, etc.) | Dingemanse and Dochtermann 2013 |

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**Table 3** – Variance decomposition of best linear mixed models fixed effects for immature and mature trout and trophic traits. 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.

| **Size** | **Predictor** | **Trophic Position** | | | | | | **$\delta^{13}C_{corr}$** | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | ***Df*** | **S.Sq** | **Var. Exp. (%)** | **F-value** | **$R^2M - R^2C$** | **AICw** | ***df*** | **S.Sq** | **Var. Exp. (%)** | **F-value** | **$R^2M - R^2C$** | **AICw** |
| **Immature** | | | | | | 0.15 – 0.44 | *0.712* | | | | | 0.39 – 0.51 | *0.659* |
| | $\beta_w$ | 1,138 | 0.096 | 2.56 | 1.74 | | | 1,138 | 0.428 | 9.29 | 17.19 | | |
| | $\beta_B$ | 1,138 | 0.592 | 15.69 | 10.69 | | | 1,138 | 0.210 | 4.57 | 8.45 | | |
| | $\theta_m$ | 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** | | | | | | 0.56 – 0.65 | *0.622* | | | | | 0.34 – 0.49 | *0.885* |
| | $\beta_w$ | 1,325 | 3.450 | 5.14 | 38.52 | | | 1,325 | 1.097 | 11.79 | 30.27 | | |
| | $\beta_B$ | 1,325 | 1.725 | 2.57 | 19.26 | | | 1,325 | 1.297 | 13.89 | 35.66 | | |
| | $\theta_m$ | 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 | | |

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**Table 4 –** Estimation of variance components (mean [95% CI]) of the random effects in *Eq. 1* for both trophic traits (TP, trophic position and $\delta^{13}C_{corr}$) and trout maturity classes. $V_{pop}$ is the variance of *population* random effect and $V_{ind}$ is the residual variance, i.e. the within-individual variance.

| **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] |

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## Supporting Information

$\delta^{15}N$ and $\delta^{13}C$ biplots can be found in the online additional supporting information.

**Appendix S1 –** Graphical representation of raw data of trout, benthic macroinvertebrates and terrestrial arthropods from the six studied streams for the different sampling campaigns.

Fig. S1 – Huda Grapa

Fig. S2 – Upper Idrijca

Fig. S3 – Studenc

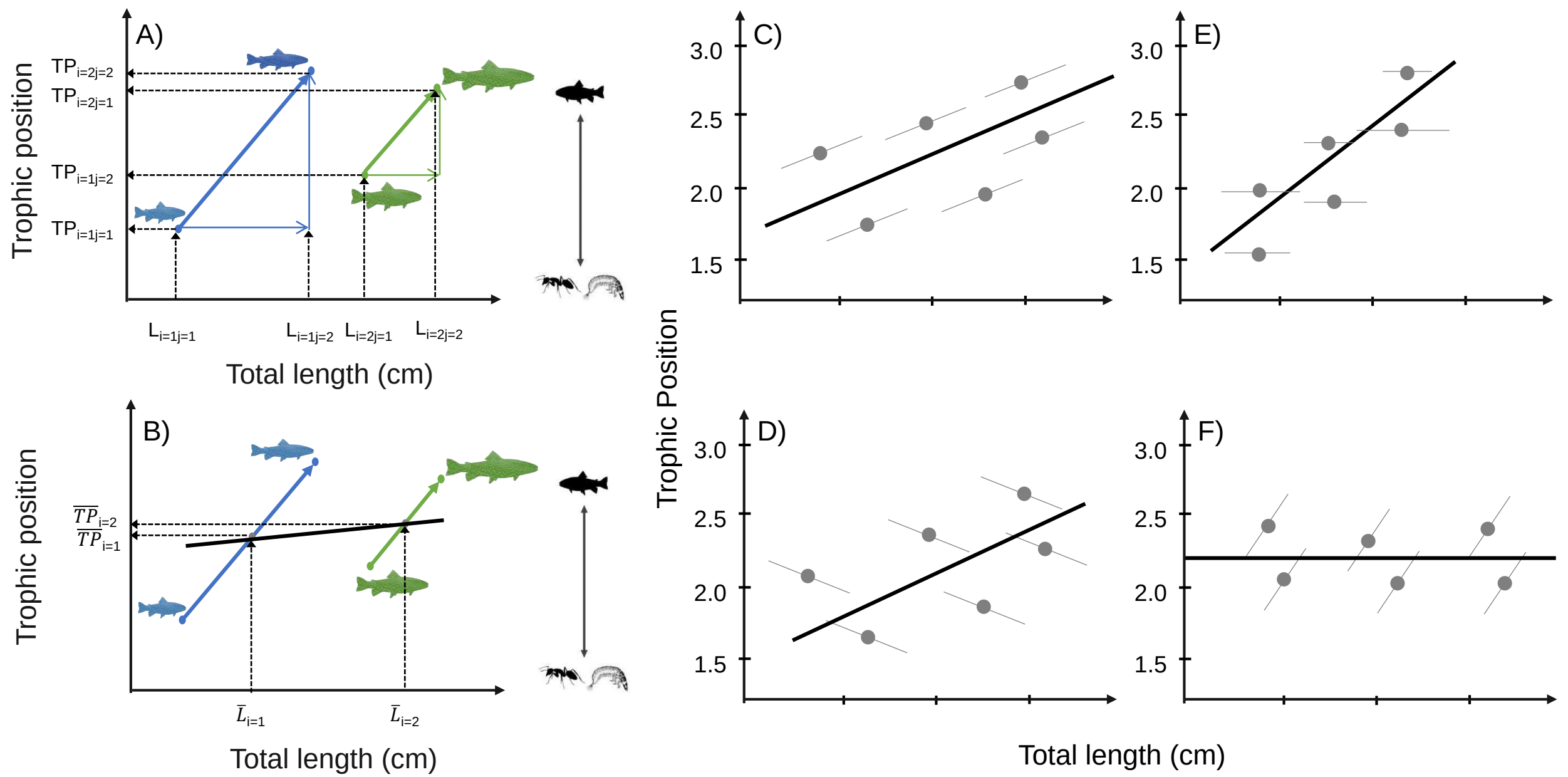
Fig. S4 – Lipovscek

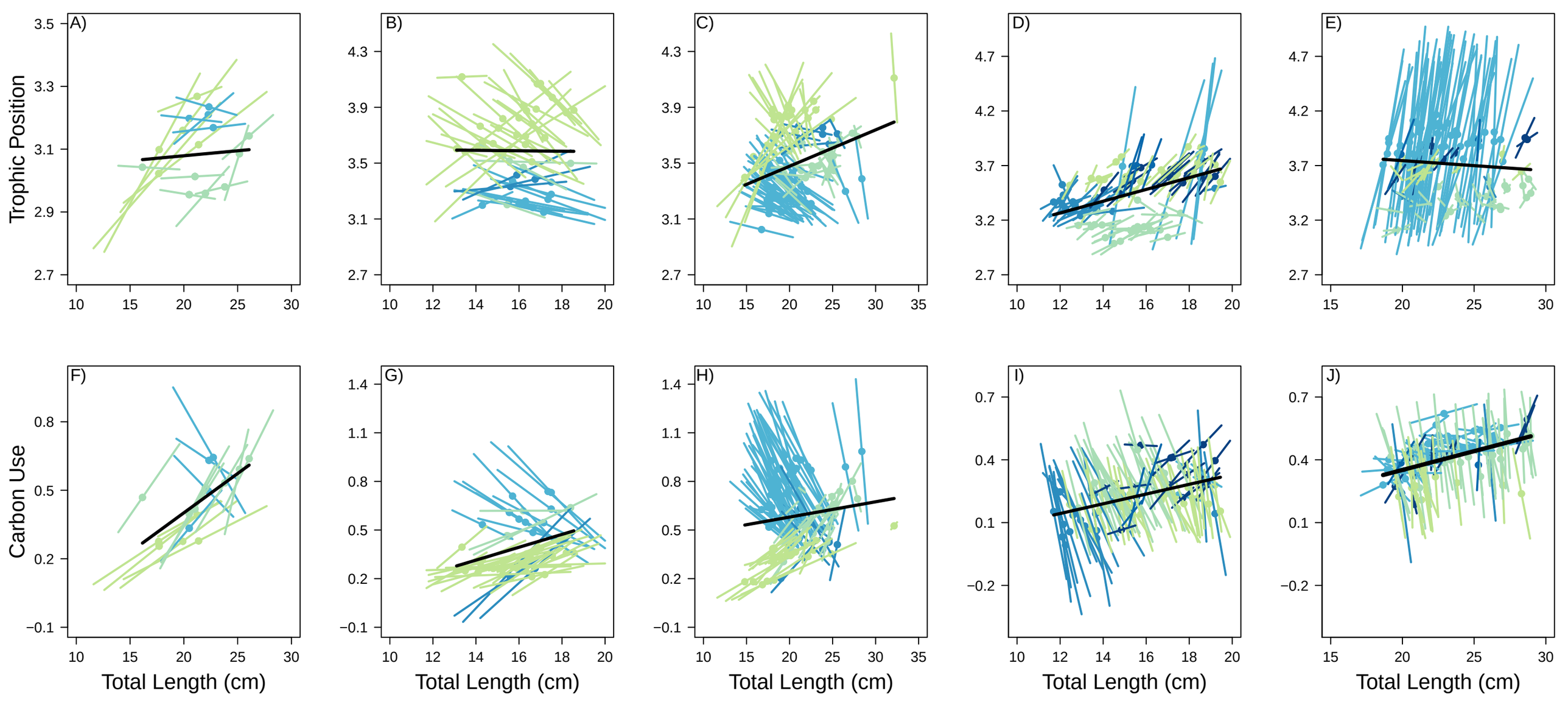
Fig. S5 – Svenica

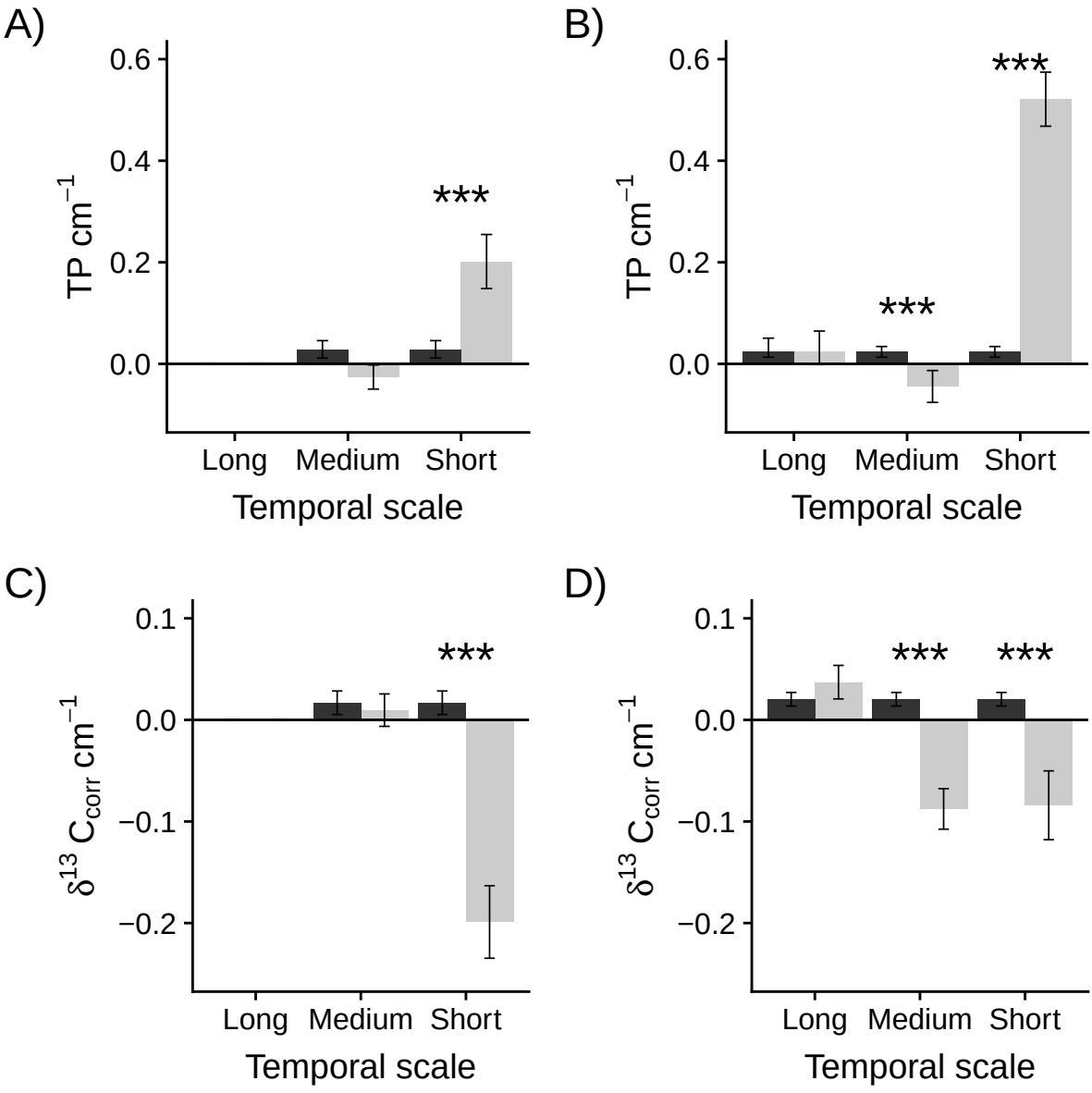
Fig. S6 - Trebuscica

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A)
Trophic position
$TP_{i=2j=2}$
$TP_{i=2j=1}$
$TP_{i=1j=2}$
$TP_{i=1j=1}$
$L_{i=1j=1}$
$L_{i=1j=2}$
$L_{i=2j=1}$
$L_{i=2j=2}$
Total length (cm)
B)
Trophic position
$\overline{TP}_{i=2}$
$\overline{TP}_{i=1}$
$\bar{L}_{i=1}$
$\bar{L}_{i=2}$
Total length (cm)
C)
E)
D)
F)
Trophic Position
3.0
2.5
2.0
1.5
Total length (cm)


A)
B)
C)
D)
E)
F)
G)
H)
I)
J)
Trophic Position
Carbon Use
Total Length (cm)
Total Length (cm)
Total Length (cm)
Total Length (cm)
Total Length (cm)


A)
B)
C)
D)
TP cm$^{-1}$
$\delta^{13}$ C$_{corr}$ cm$^{-1}$
0.6
0.4
0.2
0.0
0.1
−0.1
−0.2
***
Long
Medium
Short
Temporal scale