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Within-stream phenotypic divergence in head shape of brown trout associated with invasive brook trout

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Competition with a non-native species can lead to morphological changes in native organisms induced by phenotypic plasticity, and by selection against individuals that do not adjust their morphology to the novel selection pressure. The morphological changes in native organisms are often associated with rapid behavioural responses to competition with the invader. However, knowledge of the interaction between the behaviour and morphology of native organisms competing with a non-native species remains scarce. Here, we investigated the effect of competition with non-native brook trout *Salvelinus fontinalis* on head shape of native brown trout *Salmo trutta* in a stream system where changes in diet and territorial behaviour of sympatric brown trout have previously been demonstrated. We found that sympatric brown trout had smaller eyes, shorter lower jaws and more terminal mouth than allopatric conspecifics. These differences in head shape were highly repeatable over a period of 12 months. Apparent survival indicated that the selection on head shape of brown trout was weaker in the sympatric than in the allopatric stretch of the stream. The results suggest that these changes reinforce divergences of foraging strategies between the allopatric and sympatric brown trout, which can negatively affect their population dynamics and trophic function in the food-web.

ADDITIONAL KEYWORDS: character displacement – morphometric analysis – phenotypic divergence – Salmonidae – species introduction.

INTRODUCTION

Non-native species can induce phenotypic changes in native organisms through predation, parasitism, competition and modification of the recipient ecosystem and are a leading cause of the current biodiversity crisis (Mooney & Cleland, 2001; Strauss *et al.*, 2006; Berthon, 2015). Competitive interactions with non-native species have been demonstrated to affect a broad range of phenotypic traits in native organisms, including circadian activity patterns (Harrington *et al.*, 2009), foraging strategy (Nakano & Furukawa-Tanaka, 1994), diet (McNatty *et al.*, 2009) and morphology (Sharpe & Chapman, 2018). Salmonid fishes express high phenotypic plasticity (Hutchings, 2011; Jacobs *et al.*, 2019) and display particularly large variations in head morphology, which is closely related to their foraging strategies (Adams *et al.*, 2003; Keeley *et al.*, 2005; Parsons *et al.*, 2010). Many stream-dwelling salmonid populations are dimorphic, with a benthic-feeding morph, having shorter jaws and a sub-terminal mouth, and a drift-feeding morph with longer jaws and a terminal mouth (Skúlason & Smith, 1995; Nakano *et al.*, 1999). Furthermore,

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eye size is often related to habitat use and foraging strategy in salmonids, with profundal benthic-foraging individuals having larger eyes than pelagic feeding conspecifics due to differences in light intensity (e.g. in glacial lakes; Piggott *et al.*, 2018). Longer jaws can facilitate social dominance in aggressive territorial interactions, which often includes nipping and mouth fighting in salmonids (Kalleberg, 1958; Abbott & Dill, 1985). Previous studies on salmonids have demonstrated that sympatric, closely related non-native species can induce shifts in foraging strategy and diet (Baxter *et al.*, 2004; Nakano *et al.*, 2019), diel activity patterns (Larranaga *et al.*, 2018) and territorial defence (Blanchet *et al.*, 2007). However, it remains poorly understood how head shape of native salmonids responds to changes in diet and behaviour associated with competition with a non-native species and what roles phenotypic plasticity and selection play in this process.

Brook trout *Salvelinus fontinalis* is a salmonid native to north-eastern North America, introduced in many parts of Europe since the late 1800s, and now established in numerous streams and lakes, often occurring sympatrically with the European brown trout *Salmo trutta* (MacCrimmon & Campbell, 1969; Hutchings, 2014; Hesthagen *et al.*, 2018). Brook trout generally have a more terminal mouth and in contrast to brown trout feed predominantly on terrestrial drift (Cucherousset *et al.*, 2007; Syrjänen *et al.*, 2011). In European streams, brook trout has been reported to be replacing native salmonids (e.g. Öhlund *et al.*, 2008) and to having negative effects on native biodiversity including rare species, such as the freshwater pearl mussel *Margaritifera margaritifera*, which depends on native salmonids as hosts for its parasitic life-stage (Salonen *et al.*, 2016; Wengström *et al.*, 2016). The coexistence with brook trout can induce a shift in foraging strategy in native brown trout, towards an increased consumption of terrestrial prey, as shown in both Swedish and French streams (Cucherousset *et al.*, 2007; Závorka *et al.*, 2017). Brown trout in sympatry with brook trout have also been found to be more diurnal (Larranaga *et al.*, 2018), have smaller home ranges (Závorka *et al.*, 2017) and a higher tendency to aggregate with other individuals (Larranaga *et al.*, 2018) than their conspecifics in allopatry. These findings indicate changes in ecological niche and territorial behaviour of brown trout when living in sympatry with the non-native brook trout. However, it is not known if such behavioural divergence also leads to differentiation in head shape.

In the present study, using a well-studied model system of native brown trout co-occurring with non-native brook trout in a sub-boreal stream located in southern Sweden, we aimed to quantify: (1) the divergence in head shape of native brown trout in sympatric and allopatric parts of the stream, (2) the repeatability of inter-individual differences in head shape of brown trout, and (3) the effect of inter-individual differences in head shape on summer and winter apparent survival of individuals.

MATERIAL AND METHODS

This study was conducted in the stream Ringsbäcken, situated in southern Sweden (57°40′318″N, 12°59′300″E). Brook trout was probably introduced in this stream in the first half of the 20th century, with the first electrofishing reports indicating a self-reproducing brook trout population dating to 1985 (SERS, 2013). While brook trout has established a population in the upstream section of the stream, brown trout occupy the whole stream, and this separates the stream into two sections with different competition modes: an allopatric (brown trout only) and a sympatric (brown and brook trout co-occurring) section. Sampling was carried out in four 250-m-long sampling sites, three in the sympatric section and one in the allopatric section (see Závorka *et al.*, 2017 for more details on the environmental conditions in the stream). The brown trout population in the study stream is landlocked with no reported lake or seawards migration. Brown trout in similar Scandinavian streams usually reaches maturity between age 3 and age 4 and has an average lifespan of 6 years (Öhlund *et al.*, 2008).

In spring 2015 (7–10 April), all four stretches were sampled by electrofishing (Smith-Root LR-20B, Vancouver, WA, USA) and captured brown trout were anaesthetized (benzocaine; 0.5 mL L^{-1}), measured for fork length and body mass, and tagged with 12-mm PIT-tags (HDX ISO 11784/11785; Oregon RFID, Portland, OR, USA). Each fish was also photographed on its lateral side with a digital camera (Canon PowerShot G16; Canon Inc., Tokyo, Japan), a small pelvic fin clip was collected for stable isotope analysis of their diet, and scale samples were taken from a subsample of individuals for age estimation. All individuals were then released back within their capture section of the stream. In total, 219 brown trout were sampled in this study, 83 from the allopatric and 136 from the sympatric section. Brown trout were significantly larger in sympatry than in allopatry (Welch's *t*-test, $P < 0.001$ for fork length and body mass): mean ± SD fork length and body mass of allopatric trout were 82.73 ± 18.17 mm and 7.15 ± 4.90 g, and of sympatric trout were 102.74 ± 21.01 mm and 13.20 ± 7.11 g, corresponding to subadult brown trout at age 1 and 2 years. A first recapture was performed in summer 2015 (3 and 10 June), during which electrofishing was combined with radio-frequency identification

(RFID)-scanning using a portable antenna (Oregon RFID) to facilitate detection of tagged fish. In total, 98 individuals were recaptured: 54 in the allopatric section and 44 in the sympatric section. Recaptured fish were transported to the University of Gothenburg, where they were anaesthetized, measured for fork length and body mass, and fin clipped to assess their summer diet by stable isotope analysis. All fish were held for 3 weeks in holding tanks. Fish were subjected to a behavioural trial (open-field test) and respirometry to assess metabolic rates (a subsample of 72 individuals), before being released back to their respective stream sections. No mortality occurred during this period. The results of behavioural and metabolic assessment, and diet analysis have been published in Závorka *et al.* (2017, 2019a). In spring 2016 (18–21 April) all four stretches were sampled for the second recapture using the same sampling method combining electrofishing and portable RFID-scanning. In total, 66 tagged individuals were recaptured, 23 in allopatry and 43 in sympatry. All recaptured brown trout were anaesthetized (benzocaine; $0.5\ \mathrm{mL\ L^{-1}}$), measured for fork length and body mass, and photographed. We used the information from the mark–recapture study as an indicator of apparent survival. Apparent survival for the summer period was measured from the tagging in spring 2015 until the first recapture in summer 2015. Apparent survival for the winter was measured from summer 2015 until the second recapture in spring 2016. Individuals that were not recaptured in summer 2015 but were recaptured in spring 2016 were considered as survivors even in the model for apparent summer survival (i.e. between spring and summer 2015). Apparent survival represents a summary of true survival, site fidelity of individuals and efficiency-driven sampling bias in electrofishing (Bohlin, 1989). Assuming that sampling bias is random, apparent survival provides information about the site-specific selection pressure, as individuals with phenotypes that do not match the local environment are more likely to die or emigrate to a more suitable habitat where they cannot be recaptured (Auer *et al.*, 2018; Näslund *et al.*, 2018).

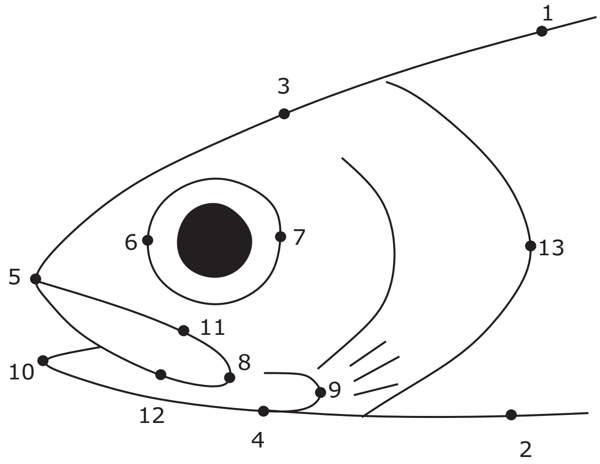

Figure 1. The 13 morphometric landmarks for head morphology of salmonids (adapted from Adams *et al.*, 2003).

MORPHOMETRIC ANALYSES

Thirteen landmarks, representing the main head structures (following Adams *et al.*, 2003; Figure 1), were digitized on individual photographs using tpsDig 2.31 (Rohlf, 2017). Landmarks were then imported into MorphoJ (Klingenberg, 2011) to calculate partial warps, and subsequently examined using principal component analysis (PCA). Inputs to the PCA (i.e. Procrustes-coordinates of individual head shape) were controlled for the allometric effect by using the residuals from allometric regression between the Procrustes-coordinates and the centroid size of the head. The first two partial warps (PC1 and PC2) explained 33.8 and 14.0% of the variance in head morphology, respectively. Hence, 47.8% of the total variance was explained by PC1 and PC2, which were subsequently used in the analysis of individual apparent survival. The first partial warp, PC1, discriminated individuals based on eye size, relative length of the lower jaw and mouth position, with high scores indicating relatively smaller eyes, shorter lower jaws and terminal mouths (Figure 2). The second partial warp, PC2, discriminated individuals based on the length of their upper and lower jaws, with higher scores indicating longer jaws (Figure 2). Overall, morphometric analyses indicated that inter-individual differences were greatest in upper and lower jaws, and in eye size. Therefore, we also measured these three specific morphological traits to evaluate the repeatability of inter-individual differences in these traits during the period of 12 months between tagging and second recapture.

STATISTICAL ANALYSES

Discriminant function analysis was used to assess the effect of competition mode (allopatry vs. sympatry with brook trout) on head shape of brown trout adjusted for centroid size of the head. The significance of the difference between competition mode was tested by a permutation test with 1000 iterations. We quantified the adjusted repeatability of three morphological traits closely linked to the morphological variation described by PC1 and PC2 (i.e. length of the lower and upper jaws, and eye size). Adjusted repeatability was calculated using the intra-class correlation coefficient given by linear mixed models (LMMs), including

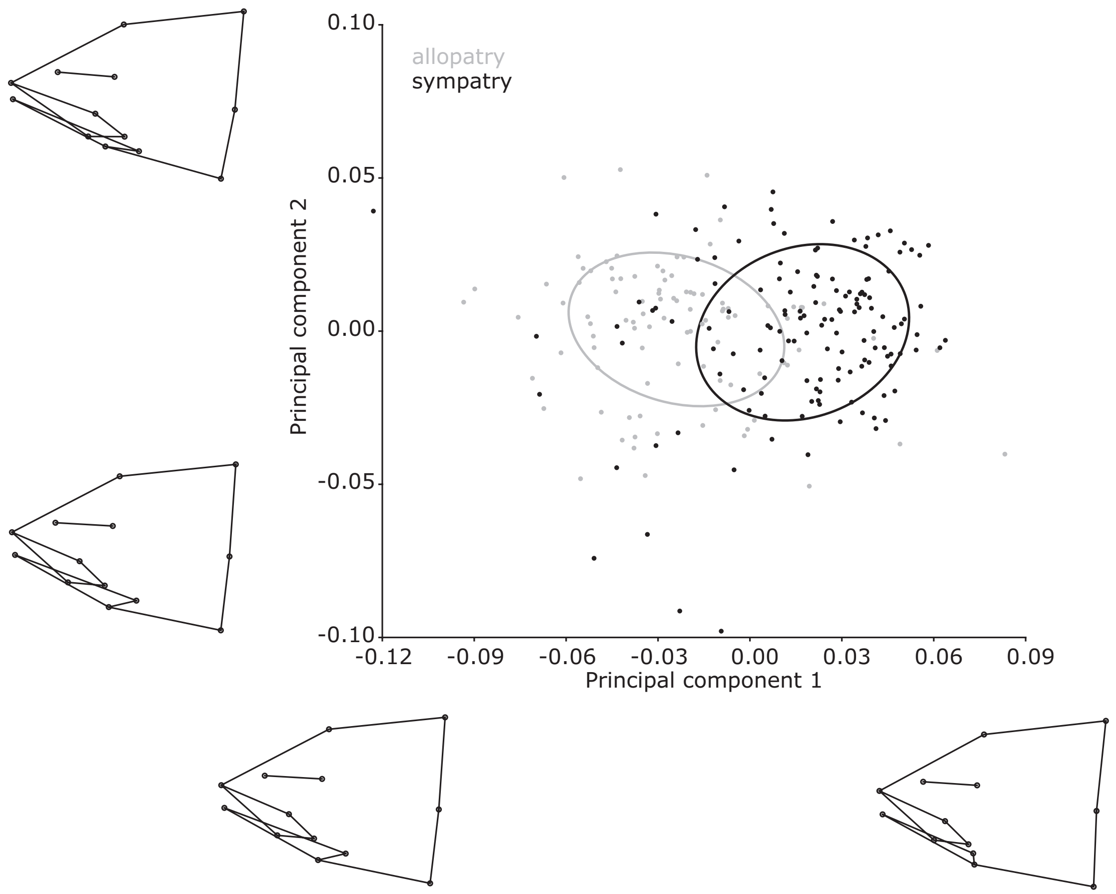

Figure 2. The two main partial warps (PC1 and PC2) of overall head shape variation controlled for centroid size. Head shapes corresponding to the minimum and maximum values of each PC are depicted along the axes. Grey and black full circles and ellipses covering 50% of the datapoints in each group correspond to allopatric and sympatric brown trout, respectively.

fork length and competition mode as independent factors and individual identity as a random intercept (Nakagawa & Schielzeth, 2010). The effects of fork length, and PC1 and PC2 in interaction with the competition mode (i.e. allopatry or sympatry) on summer and winter apparent survival rate were tested by a generalized linear model (GLM) using a binomial distribution (logit link-function). All statistical analyses were performed using R 3.4.3 (R Development Core Team, 2015).

RESULTS

Head shape was significantly affected by centroid size ($P < 0.001$); this allometric effect explained 12.1% of the variation and indicated that individuals with a larger head had relatively smaller eyes, stouter head and more terminal mouth. We found that after accounting for this allometry, head shape of allopatric and sympatric brown trout was significantly different (Procrustes distance = 0.042; $P < 0.001$; Figure 3). Cross-validated discriminant function analysis based on head shape indicated that individuals could be assigned to the allopatric and sympatric groups with a probability of 81 and 82%, respectively (Figure 3). Sympatric brown trout had smaller eyes, shorter lower jaw and more terminal mouth than allopatric brown trout (Figure 3).

Relative lengths of the upper jaw [$R_{adj} = 0.756$ (95% CI: 0.647, 0.845)] and lower jaw [$R_{adj} = 0.776$ (95% CI: 0.665, 0.861)] were highly repeatable. Relative eye size was also highly repeatable, albeit less so than jaw length [$R_{adj} = 0.613$ (95% CI: 0.441, 0.748)]. Repeatability of these morphological traits was similar between allopatric and sympatric brown trout (Figure 4).

Apparent summer survival did not differ significantly between the allopatric and sympatric section ($\chi^2 = 1.072$, $P = 0.300$) and was not related to head shape of individuals (PC1: $\chi^2 = 1.523$, $P = 0.217$; PC2: $\chi^2 = 1.656$, $P = 0.198$). However,

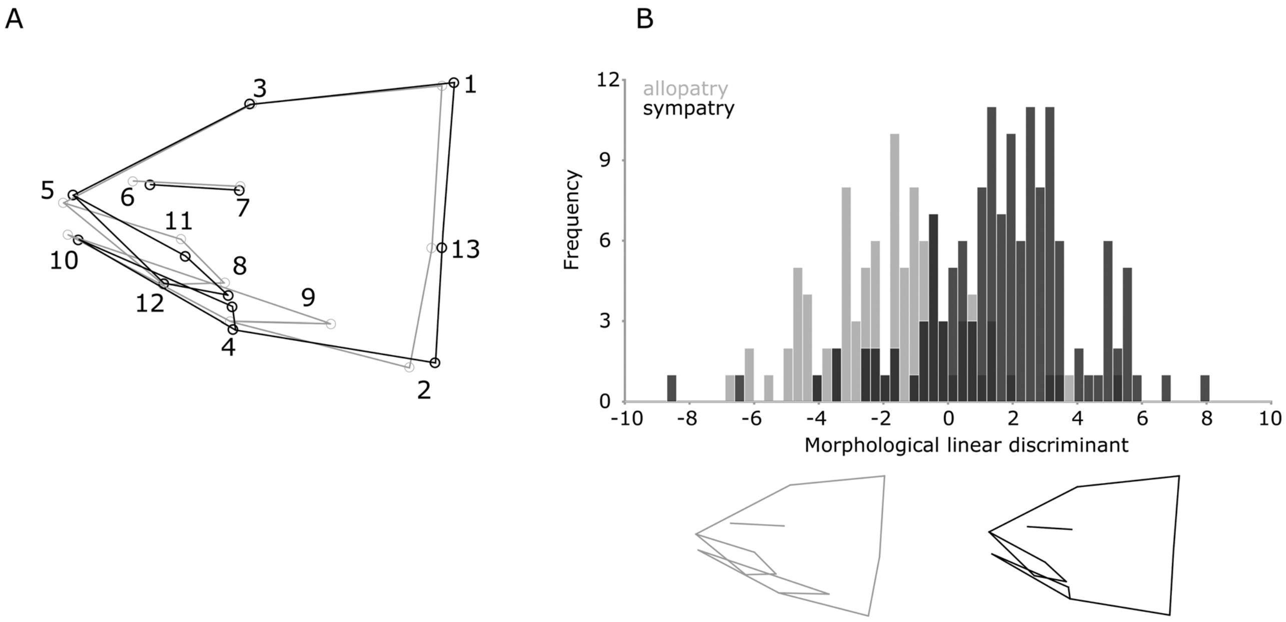

Figure 3. Mean head shapes (A) and distribution of the morphological linear discriminant value (B) of allopatric (grey) and sympatric (black) brown trout.

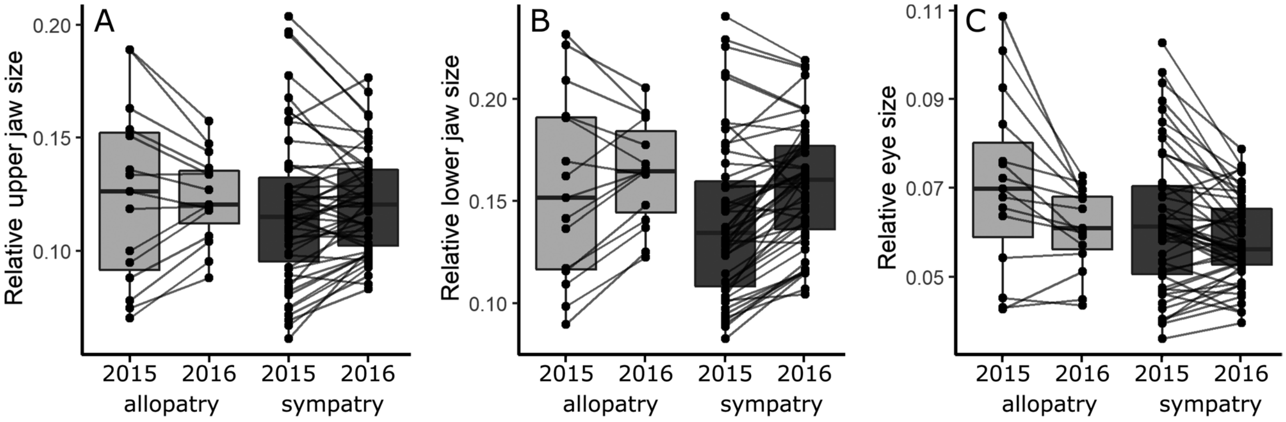

Figure 4. Inter-individual differences in upper and lower jaw, and eye size in allopatric (light grey) and sympatric (dark grey) brown trout in spring 2015 and spring 2016. Values corresponding to the same individual across the two samplings are connected with a line across boxplots. Jaw and eye sizes are displayed relative to individual fork length, following recapture at the end of the study.

apparent summer survival was negatively associated with the fork length of individuals ($\chi^2 = 19.758$, $P < 0.001$; Figure 5A). Apparent winter survival was affected by the interaction between head shape (i.e. PC2) and competition mode, indicating that individuals with longer jaws had lower survival, but that this relationship was weaker in sympatry than in allopatry ($\chi^2 = 4.880$, $P = 0.027$; Figure 5B). There were no significant effects of PC1 ($\chi^2 = 0.739$, $P = 0.390$) and fork length ($\chi^2 = 0.447$, $P = 0.504$) on apparent winter survival.

DISCUSSION

Salmonids display large intraspecific morphological variation and evidence suggests that this variation of shapes is underpinned by genetic divergence (Stelkens *et al.*, 2012), by expression of regulatory genes (Jacobs *et al.*, 2019) and by phenotypic plasticity (Adams *et al.*, 2003). Morphological changes in salmonids can be rapid and previous studies have demonstrated that distinct morphs can develop in several weeks in response to changes in diet quality (Adams *et al.*,

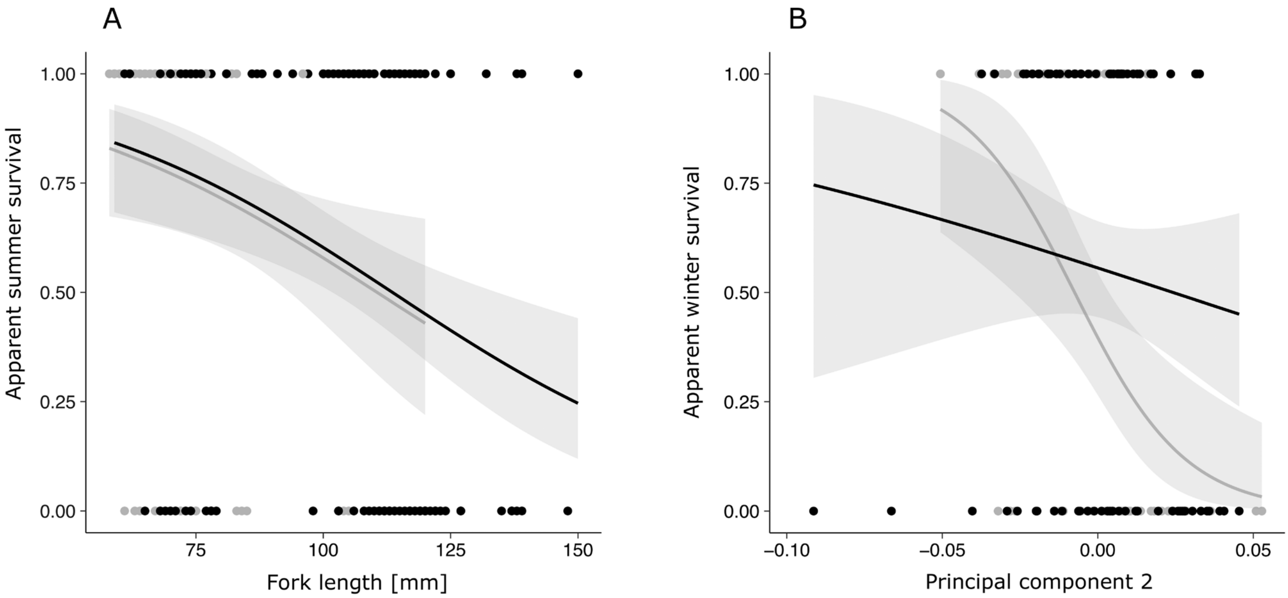

Figure 5. Relationship between (A) apparent summer survival (i.e. the proportion of recaptured individuals) and fork length, and between (B) apparent winter survival and head shape (i.e. PC2) of individuals in allopatry (grey) and sympatry (black). Shaded areas indicate 95% confidence intervals.

2003) or water flow rate (Pakkasmaa & Piironen, 2000). Here, native brown trout that coexist with non-native brook trout displayed a different head shape (i.e. smaller eyes, shorter lower jaw and more terminal mouth) than allopatric conspecifics within a single stream. Moreover, we found that this morphological divergence among individuals was highly repeatable over a period of 12 months and that selection pressure on head shape was stronger in the allopatric than in the sympatric population.

The smaller eyes, shorter lower jaw and more terminal mouth of sympatric brown trout are characteristic of drift-feeding morphs of salmonids that specialize on terrestrial prey (Piggott *et al.*, 2018; Nakano *et al.*, 2019). This corresponds to previous findings that brown trout in sympatry with brook trout have higher proportions of terrestrial prey in their diet (Cucherousset *et al.*, 2007; Závorka *et al.*, 2017), because terrestrial prey are more common in the drift than on the stream bottom (Nakano & Furukawa-Tanaka, 1994). Terrestrial resources, in contrast to aquatic resources, contain limited amounts of unsaturated omega-3 fatty acids (Závorka *et al.*, 2019b), which are essential dietary micro-nutrients necessary for the development of neural tissues such as brain and eyes (Sargent *et al.*, 1999). The lower nutrition of the terrestrial diet of sympatric brown trout could be a reason for the development of smaller eyes (Iglesias *et al.*, 2018; Piggott *et al.*, 2018), although this remains to be tested. Reduced eye size of sympatric brown trout may also be related to the increase of daytime activity of sympatric brown trout, as compared to allopatric conspecifics (Larranaga *et al.*, 2018). Divergence of head shape seen between sections within a single stream could also be related to sexual segregation of individuals, such as due to different habitat preferences of males and females (Stelkens *et al.*, 2012; Nitychoruk *et al.*, 2013). However, a recent screening of individuals in our experimental stream indicated that there was no difference in sex-ratio between allopatric and sympatric sections (L. Závorka *et al.*, unpublished data). The head shape of sympatric brown trout indicates a convergence in foraging strategy of the native species to non-native drift-feeding brook trout (Syrjänen *et al.*, 2011). This result is in contrast to a previous study demonstrating divergence of head shape in sympatric salmonids competing for similar resources (Nakano *et al.*, 2019). This discrepancy could be explained by the short evolutionary history of the competitive interaction between brook and brown trout in our study stream.

Inter-individual differences in ecologically important morphological traits (i.e. length of upper and lower jaws and eye size) were highly repeatable in age 1+ and 2+ subadults over a period of 12 months. The apparently limited head shape plasticity of subadult brown trout in this study probably makes individuals sensitive to imposed selection pressures, as they apparently cannot adjust their head shape to new environmental cues during this life stage. Hence, selection could result in increased mortality or emigration of individuals with a head shape mismatching the environmental pressure and result in changes to the genetic structure of the population (Auer *et al.*, 2018). Indeed, we observed a significant selection on head shape at this ontogenetic stage as individuals with long jaws (i.e. high scores in PC2) had overall a lower apparent winter survival (i.e. they displayed greater probability of mortality or emigration from the sampling sites). Importantly, we also found that this mode of selection pressure tended to be weaker in sympatry than in allopatry. Furthermore, the negative correlation between apparent summer survival in the whole stream and fork length of brown trout may also be a consequence of seasonal downstream migration of larger individuals, particularly those with an active behavioural type (Näslund *et al.*, 2018). The reduction in selection pressure on head shape of sympatric subadult brown trout can potentially have negative effects on individual fitness later in their life (e.g. during reproduction; Järvi, 1990). A possible negative effect on reproduction of brown trout is corroborated by previous findings that brown trout have higher maturation age and lower fecundity in sympatry with non-native brook trout than in allopatry (Öhlund *et al.*, 2008).

Previous studies in the same system have indicated that the divergence in head shape was associated with changes in diet and territorial behaviour of sympatric brown trout (Závorka *et al.*, 2017; Larranaga *et al.*, 2018). However, this complex phenotypic response to competition with non-native brook trout apparently leads to niche convergence with the invader and does not prevent a reduction in fitness and population growth of sympatric brown trout (Öhlund *et al.*, 2008; Závorka *et al.*, 2017). These findings indicate that native fish species often fail to sufficiently adapt their behaviour (Blanchet *et al.*, 2007) and morphology (Geladi *et al.*, 2019) to biological invasion, which can cause long-term decreases in their population size (Öhlund *et al.*, 2008; Geladi *et al.*, 2019).

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