

**Interspecific Interactions between Native Brown
Trout and Invasive Brook Trout
Insight into Behaviour and Morphology**

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In memory of J3rgen Johnsson

Abstract

The introduction of non-native species represents a global threat to ecosystems and biodiversity. In Europe, the introduction of the invasive brook trout (*Salvelinus fontinalis*) has led to species displacement and local extinction of native brown trout (*Salmo trutta*) populations. Additionally, several studies have documented a convergence in feeding niche, where brown trout in sympatry with brook trout utilise terrestrial insects to a larger extent. This conflicts with the competitive exclusion principle, as competition should increase divergence between species. In this thesis, I examine behavioural interactions between invasive brook trout and native brown trout at various life stages, and investigate the convergence in feeding niche and its possible effect on morphology and development.

As the juvenile stage constitutes a major bottleneck for salmonid populations, we conducted two experiments assessing the association and territoriality between juvenile brown trout and brook trout, and the influence of inter- and intracohort competition between the species. The results showed that brown trout do not discriminate against either conspecific or heterospecific groups, and that brook trout had a tighter group structure than brown trout groups. Additionally, juvenile brown trout were competitively inferior against brook trout when contesting a territory and took longer to feed and spend more time further away in presence of an adult brook trout. Moreover, as terrestrial insects are more common during the day, we investigated whether the converging feeding niche in sympatry could be explained by differences in diel activity between sympatric and allopatric brown trout. Indeed, sympatric brown trout was more active during the day than allopatric brown trout and showed a stronger association towards other individuals in sympatry. Compared to allopatric brown trout, sympatric brown trout also had a head morphology more typical for drift feeding, suggesting an adaptation to forage on terrestrial insects. Furthermore, terrestrial and aquatic insects differ in relative content of certain omega-3 fatty acids, vital for development of neural tissues. Thus, we examined the relative contribution of aquatic and terrestrial prey in the diet and if this could affect brain volume. Here, we found that brain volume was negatively correlated with higher consumption of omega-3 deprived terrestrial prey.

Collectively, the results show that invasive brook trout have a major impact on native brown trout at an early life-stage and that the change in feeding niche may affect development of neural tissues in brown trout. As most studies have focused on the direct competition between brown trout and brook trout, future studies should focus on direct and indirect effects on other species as well as ecosystem effects. Additionally, a management plan to eradicate or reduce brook trout populations in key ecosystems should be implemented in Sweden.

Keywords: Invasive species, fish, competition, foraging, management

List of papers

- Paper I** Lovén Wallerius, M., Näslund, J., Koeck, B., and Johnsson, J.I. 2017. Interspecific association of brown trout (*Salmo trutta*) with non-native brook trout (*Salvelinus fontinalis*) at the fry stage. *Ethology*, 123: 933-941.
- Paper II** Lovén Wallerius, M., Moran, V., Závorka, L., and Höjesjö, J. Asymmetric competition over space use and territory between native brown trout (*Salmo trutta*) and invasive brook trout (*Salvelinus fontinalis*). *Manuscript*.
- Paper III** Larranaga, N., Lovén Wallerius M., Guo H., Cucherousset J., and Johnsson, J.I. 2018. Invasive brook trout disrupts the diel activity and aggregation patterns of native brown trout. *Canadian Journal of Fisheries and Aquatic Sciences*, 76: 1052–1059.
- Paper IV** Závorka, L., Larranaga, N., Lovén Wallerius M., Näslund, J., Koeck, B., Wengström, N., Cucherousset, J., and Johnsson, J.I. 2020. Within-stream phenotypic divergence in head shape of brown trout associated with invasive brook trout. *Biological Journal of the Linnean Society*, 129: 347-355.
- Paper V** Závorka, L., Lovén Wallerius, M., Kainz, M., Höjesjö, J. Linking brain volume in wild stream-dwelling brown trout with dietary supply of omega-3 fatty acids. *Submitted to OIKOS*, 12-04-2021.

The following papers were published during the course of the doctoral studies but are not included in the dissertation:

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Lovén Wallerius, M., Gräns, A., Koeck, B., Berger, D., Sandblom, E., Ekström, A., Arlinghaus, R., and Johnsson, J. I. 2019. Socially induced stress and behavioural inhibition in response to angling exposure in rainbow trout. *Fisheries Management and Ecology*, 26, 611-620.

Lovén Wallerius, M., Johnsson, J. I., Cooke, S., and Arlinghaus, R. 2020. Hook avoidance induced by private and social learning in common carp. *Transactions of the American Fisheries Society*, 149: 498-511.

Koeck, B., Lovén Wallerius, M., Arlinghaus, R., and Johnsson, J. I. 2020. Behavioural adjustment of fish to temporal variation in fishing pressure affects catchability: an experiment with angled trout. *Canadian Journal of Fisheries and Aquatic Sciences*, 77: 188–193.

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1. Introduction

1.1. Species interactions

During the lifetime of an animal, several opportunities and challenges will arise, from finding food, shelter and mating opportunities, to avoiding predators and hostile environments. These abiotic and biotic factors forces the individual to gradually and constantly assess and adjust its behaviour and physiology in order to survive. The abiotic factors, for instance, may include changes in temperature that forces the individual to find a new environment to avoid costly physiological alterations. The biotic processes include a plethora of interactions between individuals of the same species (intraspecific) or between different species (interspecific) that reside in the environment (Begon, Townsend and Harper, 2006). Hence, the environment offers a dynamic process between abiotic and biotic factors that together forms the ever-changing ecosystem with a range of niches more or less suitable for different organisms. However, increasing anthropogenic environmental change such as habitat loss, climate change and the introduction of non-native species introduces a novel selection pressure that force individuals and species to rapidly adapt or they will risk extinction (Sih, Ferrari, & Harris, 2011). In this thesis, I will present how native brown trout (*Salmo trutta*) at various life-stages respond to the novel competition with the introduced non-native brook trout (*Salvelinus fontinalis*), focusing on behaviour, morphology and foraging.

1.1.1. Inter- and intraspecific interactions

Interspecific interactions refer to the interaction between two or more different species, and can vary in strength and outcome. For instance, the interaction between different species can be harmless for one of them and beneficial for the other (commensalism), while some interactions are beneficial for both species (mutualism). On the other end of the spectrum, interactions may have a negative impact on both individuals (e.g. competition), while some interactions are harmful for one species and beneficial for the other species (e.g. predation). The negative competitive interactions between species may appear as both direct competition, such as displacement of one individual to

obtain resources and habitats, or as indirect competition when two species vary in temporal activity (i.e., day and night active) but feed on the same resource (Begon, Townsend & Harper, 2006). Similarly, intraspecific interactions are the interactions within a species, e.g. competition for mating opportunities, territories and resources, and will mostly have a negative effect on the less competitive individual. Intraspecific interactions are mostly unequal due to size differences between individuals and can occur naturally between individuals as a function of resource acquisition, such that more resources will increase the body size of an individual. The competition between year classes (inter-cohort competition) are most common within a species, as the ecological niche (i.e., habitat use and diet) of an individual will naturally overlap more with other conspecifics (Begon, Townsend & Harper, 2006; Davies, Krebs & West, 2012). Consequently, the competition between juveniles and adult cohorts may lead to habitat displacement and decreased growth of the juveniles (Höjesjö, Kaspersson, & Armstrong, 2016; Kaspersson & Höjesjö, 2009; Kaspersson, Höjesjö, & Bohlin, 2012). The strength of the interactions are generally stronger between cohorts within a species than between species as it can have a major impact in population dynamics (Ward, Webster & Hart, 2003). For instance, the number of surviving juveniles is often negatively related to the density of the adult individuals, creating a density-dependent bottleneck at the juvenile stage (Elliot, 1994).

1.1.2. Phenotypic plasticity and competitive exclusion

As mentioned above, individuals may have to adapt during their lifetime to cope with the abiotic and biotic factors affecting the ever-changing ecosystem. The adjustment within an individual's lifetime is called phenotypic plasticity and can include morphological, physiological and behavioural changes. Specifically, phenotypic plasticity is the ability for one genotype to produce more than one phenotype when interacting with other individuals or exposed to different abiotic condition, and is a well-studied phenomenon in biology (Pigliucci, 2001; Agrawal, 2001). For instance, by accurately responding to biotic variables (e.g. predation), individuals may adapt by changing body morphology in the presence of a predator (Brönmark & Miner, 1992; DeWitt, 1998) or adjust fright behaviour in response to predation pressure (Brown,

Rive, Ferrari, & Chivers, 2006; Giles & Huntingford, 1984). Abiotic conditions may have a similar effect on an individual, such that an increased temperature affects the physiological mechanisms as a response to the temperature changes and help the individual cope with the environment (Egginton & Sidell, 1989; Guderley & Johnston, 1996). An additional phenotypic response that has gained increased attention is animal learning. Animal learning is the process where an individual changes its behaviour with experience (Dill, 1983; Griffin, 2004; Kieffer & Colgan, 1992). By associating and processing stimuli derived from the environment, individuals can acquire experience via private and socially gathered information from other individuals (Heyes, 1994). Overall, these phenotypically plastic responses may indirectly affect all levels of biological organization (Agrawal, 2001) where reduced activity in the presence of a predator (Holopainen, Aho, Vornanen, & Huuskonen, 1997; Van Buskirk & Schmidt, 2000) may cascade through the trophic levels and affect primary consumption and food webs in the ecosystem (Beckerman, Uriarte, & Schmitz, 1997).

As stated in the competitive exclusion principle, two co-existing species that share the same limited ecological niche, whether it being food or space, will eventually lead to one of them becoming extinct or experiencing an evolutionary ecological niche divergence that will reduce competition with the other species (Hardin, 1960). Native community structure consists of species that have co-evolved over several thousands to millions of years, thus, competitive exclusion and coexistence have probably led to niche divergence (Ford, Parkin, & Ewing, 1973; Turcotte & Levine, 2016) or reduced competition over partially overlapping resources, both temporally and spatially. In contrast to these natural predator-prey and competitive interactions between and within species, where defensive tactics (Johnsson 2009) and plastic responses (Agrawal, 2001) have co-evolved, the increasing human-induced environmental change, such as the introduction of non-native species, presents a relatively novel challenge for all organisms and can have far reaching ecological consequences (Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Sih et al., 2011).

A non-native species whose niche overlaps completely or partially with the niche of a native species, could lead to competitive displacement and population decline of the native species (Amarasekare, 2002; Bohn, Asmundsen, & Sparrow, 2008). On the other hand, the increased competition following an introduction of a non-native species may also lead to rapid niche divergence of the native species (Bourke, Magnan, & Rodriguez,

1999; Juncos, Milano, Macchi, & Vigliano, 2015; Rogosch & Olden, 2020). Yet, the main problem with biological invasions is that they constitute a novel interspecific interaction with unknown consequences for the ecosystem or native species (Grether, Peiman, Tobias, & Robinson, 2017). These unknown ecosystem changes may be difficult to predict, but can affect all levels of biological organization; from genetic and behavioural changes on the individual level, to ecosystem changes by altering chemical cycles and energy fluxes (Cucherousset & Olden, 2011). Consequently, the introduction of non-native species may lead to extinction or decimated native populations, and some evidence point out that biological invasions may be one of the main reasons for local animal extinctions and loss of biodiversity today (Bellard, Cassey, & Blackburn, 2016; Clavero & García-Berthou, 2005; Mooney & Cleland, 2001).

1.2. Biological invasions

Biological invasions refer to translocation of species outside of its native range and successful establishment in new regions previously not occupied by the species (Mack et al., 2000). The process of biological invasions can generally be divided into four steps; transport, introduction, establishment and spread (Weis & Sol, 2016). To be classified as a successful species invasion, the species must overcome all steps and barriers to reach the spread stage, where major establishment and environmental dispersal occur. Throughout this process, several barriers with major implications for the species invasion success will occur. One of the first steps in this process is transport, and most notably human mediated transport (Weis & Sol, 2016). For instance, a study from 2017 showed that almost 17,000 species have been introduced worldwide, either passively (e.g. ballast water in shipping) or actively (deliberate transport of organisms into new regions, e.g. as part of game, pet or plant trade) (Seebens et al., 2017). Following a successful transfer, the non-native species must survive in the new environment to be classified as introduced. During this stage in the process, the main concerns (from the introduced individuals' point of view) for a continued journey towards success, are foremost if enough individuals have arrived (i.e., propagule pressure), the phenotype of the individuals arriving, and if the new environment's abiotic conditions are sufficient to sustain reproduction so the

newly introduced species can establish a viable population (Weis & Sol, 2016; Simberloff, 2009). If population growth of the non-native species is rapid and the new environment reaches carrying capacity, the population may disperse and establish populations in new regions. Having reached this stage of the invasion process, the only limiting factors towards further spread will mostly depend on landscape barriers and adequate abiotic conditions for reproduction. If the non-native species impacts its new environment substantially, including native species extinctions, habitat alteration and/or loss of biodiversity, it will be classified as an invasive alien species (IAS) (Russell & Blackburn, 2017a). The definition of an invasive alien species has recently been subjected to some debate since some non-native species may also have a positive effect on species biodiversity (e.g. Briggs, 2017; Tassin *et al.*, 2017). However, in this thesis, I will follow the definitions set up by The Convention on Biological Diversity 2008 and further emphasized in (Russell & Blackburn, 2017b), where they distinguish between *alien species* (AS) and *invasive alien species* (IAS) as the latter having a negative impact on the environment and biological diversity.

Of the 17,000 species that has been introduced worldwide, vascular plants represent almost half (~45%) of the species (Seebens *et al.*, 2017), and 33 of these species has been classified as top 100 of the world's worst IAS. In perspective, 536 species of fish have been introduced outside of their native range, and 8 of these have been classified as top 100 of the world's most IAS (Lowe, Browne, Boudjelas, & Poorter, 2000).

1.3. Brook trout and brown trout introductions

One family of fish that has been introduced world-wide with devastating consequences is the Salmonidae, where numerous species have been deliberately introduced outside of their native range, and two are represented on the top 100 worlds' most invasive species: rainbow trout (*Onchorhynchus mykiss*) and brown trout (Lowe *et al.*, 2000). The main reasons behind the introduction of salmonids can be linked to deliberate stocking to support recreational fisheries (Fausch, 2007; Gozlan, Britton, Cowx, & Copp, 2010) and escapes from aquaculture hatcheries and farms (Stanković, Crivelli, & Snoj, 2015). The deliberate and continuous stocking of large amounts of salmonids have likely facilitated the successful establishment of salmonids due

to increased propagule pressure (Colautti, 2005). Species within the family Salmonidae have now established self-sustaining non-native populations all around the globe (e.g. Klemetsen et al., 2003; Macchio et al., 2008; Lecomte et al., 2013; Hutchings, 2014; Stanković, Crivelli & Snoj, 2015; Hasegawa, 2020). Brown trout is native in northern Eurasia, however, during the late 1800s major introductions of brown trout have led to self-sustaining populations all around the globe (Figure 1) (Freyhof, 2013; Jonsson & Jonsson, 2011; Klemetsen et al., 2003; Muhlfeld et al., 2020).

Brook trout on the other hand is native in north-eastern North America but has been deliberately introduced outside of its native range since the late 1800s (Figure 2) (Aas et al., 2018; Hutchings, 2014; MacCrimmon & Campbell, 1969; MacCrimmon, Gots, & Campbell, 1971; Muhlfeld et al., 2020). The interaction between brown trout and brook trout in sympatry represent a fascinating study system regarding animal invasions in general, and particularly regarding salmonid invasions, due to the reciprocally reversed effect that each species has on the other species outside of their native range (Nyman, 1970; Öhlund, Nordwall, Degerman, & Eriksson, 2008; Spens, Alanärä, & Eriksson, 2007; Waters, 1983, 1999). With the introduction of brown trout and its successful establishment and spread, a significant negative impact on native species has occurred (Korsu, Huusko, & Muotka, 2010), which in some cases has led to local extinctions (e.g. a native galaxiid species in New Zealand) (Townsend, 1996) and ecosystem changes (Simon & Townsend, 2003). For instance, the increased predation on invertebrates by brown trout caused a trophic cascade that increased the biomass of periphyton that changed the nutrient and energy fluxes in the invaded stream (Huryn, 1998). Particularly in North America, the introduction of brown trout has led to population declines of local salmonids in the genera's *Onchorhynchus* and *Salvelinus* (Budy & Gaeta, 2017). In Europe, the introduction of brook trout has led to naturalized populations in most countries across the continent (Hutchings, 2014). Most brook trout (but also brown trout) introductions have been conducted to support local sport fisheries (Welcomme, 1988). In Sweden, the first introduction of brook trout occurred in the region of Jämtland between the years 1891-1892. In the following decades, the species was continuously introduced throughout lakes and rivers in Northern and Middle regions of Sweden (MacCrimmon & Campbell, 1969). As of today, brook trout has established self-sustaining populations in lakes and rivers all over mainland Sweden (HAV, 2016). A recent report published by the Swedish Species Information Centre (ArtDatabanken), covering non-native species and their

impact on biological diversity, classified brook trout at the highest scale on the two categories “ecosystem impact” and “invasion potential”. The combined effects of these two categories classified brook trout on the highest risk category with a potential to affect the ecosystem severely after introduction (Strand, Aronsson, & Svensson, 2018).

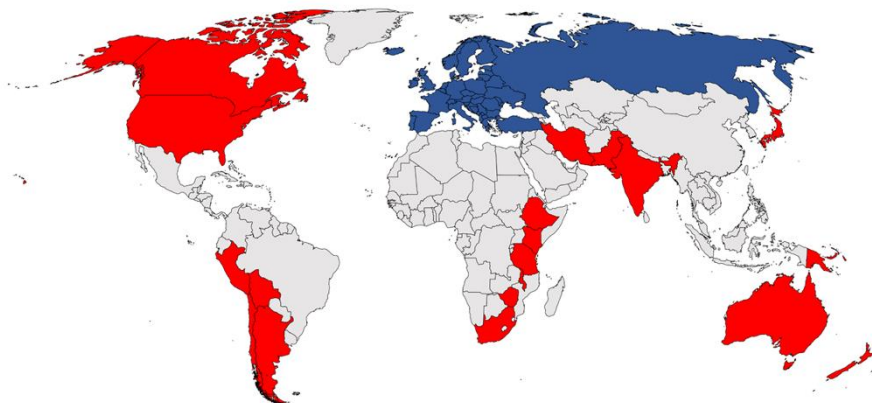


Figure 1. Map over native (blue) and introduced (red) brown trout populations.

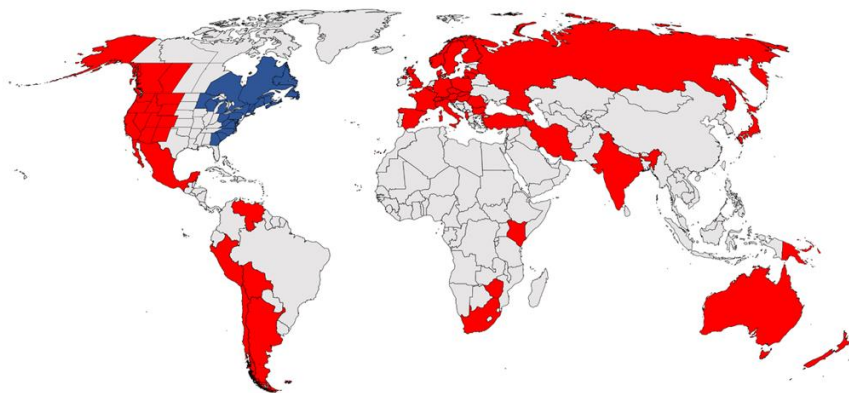


Figure 2. Map over native (blue) and introduced (red) brook trout populations.

1.3.1. Interspecific interactions between brown trout and brook trout

After the introduction of non-native brook trout in Northern Europe, the species has displaced native brown trout from upstream habitats (Korsu, Huusko, & Muotka, 2007). The displacement in some streams has led to a distribution pattern in which allopatric brown trout populations generally inhabit the lower sections of the streams and brook trout inhabit the upstream sections, either as allopatric populations or as sympatric populations consisting of both brown trout and brook trout (Korsu et al., 2007; Závorka et al., 2017). Additionally, brown trout populations were displaced by brook trout in high altitude lake systems across Northern Sweden (Spens et al., 2007). Similarly, the distribution pattern of the two species follow the same pattern in North American stream, where the invasive brown trout displace brook trout from downstream sections in the stream systems and the upstream sections function as refugia for the native brook trout (Fausch & White, 1981; Weigel & Sorensen, 2001). Salmonids in general consists of species that defend territories and resources from exploitation by other individuals. These interactions, which are often aggressive in their nature, fall into the category of interference competition, where chases, nips and other aggressive behaviours are used so displace less competitive individuals (Amarasekare, 2002; Case & Gilpin, 1974). However, after settling the social hierarchies, aggressive interactions tend to decrease as the individuals become more familiar with each other, and less costly displays are used to maintain the rank (Höjesjö, Johnsson, Petersson, & Järvi, 1998; Závorka, Näslund, Aldvén, Höjesjö, & Johnsson, 2015).

It has been suggested that brown trout has a competitive advantage over brook trout in both Sweden and North America (Öhlund et al., 2008; Wagner, Deweber, Detar, & Sweka, 2013). Yet, the direction of the competitive interactions between the species can be affected by laboratory and field experiments (Blanchet, Loot, Grenouillet, & Brosse, 2007; Korsu, Huusko, & Muotka, 2009) and it is likely that several environmental factors can affect the outcome (Spens et al., 2007). In the following paragraphs, I will describe the outcomes of the interactions between brown trout and brook trout regarding growth, long-term displacement and reproduction from studies conducted in both North America and Europe. Additionally, a paragraph will cover the overlap in feeding niche observed in sympatric populations, the link

between diet and fatty acids, and its possible effect on development of neural tissues in salmonids.

1.3.1.1. Growth, feeding and habitat displacement

Studies measuring growth and feeding interactions between brown trout and brook trout have found various effects (Blanchet et al., 2007; Korsu et al., 2009). For instance, in a Finnish study, Korsu, Huusko and Muotka (2009) found that brook trout had a lower growth rate and reduced feeding in presence of brown trout in a laboratory setting. However, this effect was not seen in the field where instead growth of both juvenile and adult brook trout exceeded brown trout growth by the end of the summer. Similar results have been found in studies from Sweden, where Öhlund et al. (2008) found that brown trout were smaller and had a lower growth rate in sympatry with brook trout than in allopatry, and Závorka et al. (2017) found that specific growth rate of brown trout was significantly lower in sympatry than in the allopatric population. Clearly, the effects of laboratory settings can differ from the natural environment and can even show a stronger negative effect (Korsu et al., 2010). In a natural setting the effect of size differences and cohort competition will be more evident, whereas it may be hidden when size matching the two species in the laboratory (Korsu et al., 2009; Taniguchi, Rahel, Novinger, & Gerow, 1998).

The overall results from both lab and field when studying interference competition suggest brown trout is a stronger competitor. For instance, brown trout are more prone to agonistic interactions and feed more than brook trout over a range of temperatures (Taniguchi et al., 1998) and capture more food items than brook trout in a sympatric laboratory setting (Dewald & Wilzbach, 1992). There is also a strong micro-habitat overlap between the species, as indicated by substrate preference (Blanchet et al., 2007) and similar use of riffle and pools in absence of the other species (Dewald & Wilzbach, 1992). In adults, brook trout in sympatry with brown trout spends more time foraging in less preferred habitats (Hitt, Snook, & Massie, 2017) and brown trout displaced brook trout from favorable resting positions and pools (Fausch & White, 1981; Nyman, 1970). Yet, in disagreement with the studies comparing interactions at the adult life stage, Fausch & White (1986) found that brook trout were better at defending

profitable stream positions against equally sized brown trout at the juvenile stage.

1.3.1.2. Long-term replacement and reproduction

Contrary to growth, studies on the survival or reproduction of the two species may capture long-term effects most promisingly, when studying interactions between the two species. For instance, in 12 out of 28 high altitude lakes across northern Sweden, the replacement of brown trout by brook trout took on average 20 years (Spens et al., 2007). Additional studies in stream systems in Finland showed that brook trout increased over a 10 year period and replaced brown trout in small head water streams (Korsu et al., 2007). Similarly, and contrary to predicted patterns in North America, a study by Hoxmeier and Dieterman (2019) found that native brook trout naturally replaced invasive brown trout after more than 20 years of displacement.

There is a clear overlap in reed-site preference and spawning period between the two species (Gunn, 1986; Witzel & MacCrimmon, 1983; Cucherousset et al., 2008). The overlap in spawning period can range from 4 to 6 weeks (Witzel & MacCrimmon, 1983; Cucherousset et al., 2008), with the majority of brook trout spawning earlier during autumn. Brown trout generally starts to spawn 2-3 weeks later. This overlap in spawning period has led to species mismatch and can generate sterile hybrids (tiger trout) (Chevassus, 1979). Such hybridization between the two species can potentially lead to long-term negative effects on their populations as it will impair the reproductive success of individuals in both species (Cucherousset et al., 2008; Grant et al., 2002). Furthermore, Korsu, Huusko & Muotka (2007) found that the density of juvenile brown trout was severely reduced in sympatric populations over a period of 10 years. As the spawning period of brook trout start earlier in the season, there is a possibility for earlier hatching of their offspring in the spring. The number of degree days are rather similar between the two species over a range of temperatures (Crisp, 1981), which would further emphasize the possibility for replacement due to earlier hatching. The long-term trends of reduced brown trout populations in sympatry could also be fuelled by differences in life history between the species, as it has been observed that brook trout mature at a younger age and have a higher proportion of mature females compared with brown trout (Öhlund et al., 2008).

1.3.1.3. Shift in trophic feeding niche, stable isotopes and fatty acids

Stable isotopes in bulk tissue, namely nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$), can be used to quantify food web dynamics and energy transfer in ecological systems (Post, 2002). The use of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) in bulk muscle tissue is especially valuable as it can provide an integrative picture of trophic feeding niche of individuals and species over a period of months. For instance, nitrogen ($\delta^{15}\text{N}$) gets enriched 3-4 ‰ per consumer level (Middelburg, 2014; Post, 2002), whereas carbon ($\delta^{13}\text{C}$) levels can differ in individuals depending on the origin of the carbon (e.g. terrestrial, aquatic or littoral and pelagic) (Peterson & Fry, 1987; Vander Zanden & Rasmussen, 1999). For instance, evidence of trophic niche shift following the introduction of IAS has been shown in lake trout (*Salvelinus namaycush*) by assessing $\delta^{13}\text{C}$ levels. Here, the introduction of smallmouth bass (*Micropterus dolomieu*) and rock bass (*Ambloplites rupestris*) led to a lower trophic position of lake trout, as indicated by higher values of $\delta^{13}\text{C}$ in the muscle tissue due to heavier reliance on a plankton based diet as opposed to the earlier fish diet (Vander Zanden, Casselman, & Rasmussen, 1999). However, contrary to the competitive exclusion principle, several studies have documented a convergence in feeding niche between brook and brown trout by the incidence of stable isotopes. These studies showed that brown trout in sympatry with brook trout change feeding niche towards more terrestrial prey compared to allopatric brown trout populations (Cucherousset, Aymes, Santoul, & Céréghino, 2007; Cucherousset, Závorka, Ponsard, Céréghino, & Santoul, 2020; Závorka et al., 2017). Yet, a study by Horká et al. (2017) evaluated stomach content on a monthly basis in sympatric and allopatric populations of brown and brook trout in northern Czech Republic. Horká et al. (2017) found no convergence in feeding niche for brown trout in sympatry with brook trout, but instead that brook trout change feeding niche towards more terrestrial prey when in sympatry with brown trout. However, the difference between snapshots of stomach content on a monthly basis (Horká et al., 2017) compared to the long-term stability of stable isotopes in muscle bulk tissue (Hesslein, Hallard, & Ramlal, 1993), should favour stable isotopes analyses in providing a more integrative long-term picture of the trophic diet niche of individuals.

The observed prey shift from aquatic towards more terrestrial prey in sympatric brown trout populations may also have far-reaching consequences for the development of individuals. For instance, long-chain

polyunsaturated fatty acids (PUFA), such as eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) are vital subsidies for cell membrane and neural tissue development (Farkas et al., 2000; Twining et al., 2016). However, aquatic and terrestrial prey differ in their content of these fatty acids. While terrestrial prey contain less of these vital nutrients, aquatic prey contain more (Twining et al., 2019). The reason behind the difference in composition originate from the primary producers in the terrestrial and aquatic ecosystems. In aquatic ecosystems, primary producers such as algae contain both EPA and DHA (Twining et al., 2016) which are readily available for benthic invertebrates and the subsequent predation by fish. In terrestrial ecosystems, primary producers are rich in the short-chain PUFA alpha-linolenic acid (ALA), which is not readily available for usage in vital tissues. While ALA can be converted into the long chain PUFAs EPA and DHA by some animals, the conversion rate is low in aquatic animals (Koussoroplis, Nussbaumer, Arts, Guschina, & Kainz, 2014). Thus, it is likely that the observed prey shift in brown trout may lead to higher intake of terrestrial preys rich in short-chain ALA, over aquatic prey rich in vital long-chained EPA and DHA (Brett et al., 2017). The possible deficiency may affect storage of EPA and DHA in muscle and fat tissue (Ebm, Guo, Brett, Bunn, & Kainz, 2021), which could negatively affect brain development (Lund, Skov, & Hansen, 2012). DHA deficiency, has also been linked to decreased responsiveness against a simulated predator (Lund, Höglund, Ebbesson, & Skov, 2014), as well as decreased visual responsiveness and activity (Benítez-Santana et al., 2007; Oberg & Fuiman, 2015).

2. Research aims

The overall aim of this thesis was to increase the knowledge about interspecific interactions between native brown trout and non-native brook trout at various life stages. More specifically, I wanted to highlight the neglected interactions at the juvenile stage, which constitute a major bottleneck for salmonids (Elliott, 1989). Additionally, the thesis aims to describe the patterns behind the observed niche shift from aquatic to terrestrial prey in sympatry and its possible links to morphological plastic changes and brain development. Specifically, I wanted to study:

The association and territoriality between the species at the fry stage, which constitute a major bottleneck for salmonids, and the influence of inter- and intracohort competition over territory and space use between the species (**Paper I** and **Paper II**).

Whether diel activity patterns can explain the shift in feeding niche previously reported in sympatric brown trout populations (**Paper III**).

How brown trout in allopatry and sympatry with brook trout differ in morphological attributes related to the niche shift in prey (**Paper IV**).

How an increased predation on polyunsaturated fatty acids (PUFA) deficient terrestrial prey in sympatry, compared to PUFA rich aquatic diet in allopatry, could affect development of vital organs such as the brain (**Paper V**).

3. Methods

3.1. Experimental overview

Here, I will give a brief overview of the experimental setup for the papers included in the thesis. Most of the fish used in the experiments originated from an area South East of Borås (WGS84 decimal [lat, long]: 57.670827°N, 12.988458°E), Sweden. The population of brown trout and brook trout in three streams (Ringsbäcken, Lindåsabäcken and Kovraån) covered in the thesis are all divided into a downstream allopatric brown trout section and an upstream sympatric section with both brown trout and brook trout. Collection of fish, either to bring to the lab for behavioural studies (**Paper I** and **Paper II**), for field experiments and tissue sampling (**Paper III** and **Paper V**) or morphometric analysis (**Paper IV**), were conducted using electro-fishing (LUGAB L- 600; Lug AB, Luleå, Sweden; DC, 200–300 V; or Smith-Root LR-20B, Vancouver, Washington, USA). For more detailed explanation of experimental setup, procedure and statistical analysis, see the method section in the papers described.

3.1.1. Behavioural studies in the lab

In **Paper I** and **Paper II**, brown trout and brook trout of different age classes (young of the year (0+) and yearling (1+)) were mainly collected (but see **Paper I**) from the sympatric and allopatric sections of Ringsbäcken (Figure 3) and brought back to the animal facility at University of Gothenburg. Together with my co-authors of **Paper I**, I conducted two consecutive experiments that assessed the behaviour of 0+ brown trout; in the first experiment, we examined whether single focal brown trout fry choose to associate with a group of seven conspecific brown trout or a group of seven heterospecific brook trout in a binomial choice test (Figure 4). For the second experiment (**Paper I**), we tested a similar association but this time the fish could swim around freely in a larger arena (65 × 45 cm). The focal 0+ brown trout was initially separated with a cylinder (10.5 cm diameter) from the stimuli group consisting of either five brown trout or five brook trout. After releasing the focal brown trout, it could swim around freely in the arena and distance from the nearest neighbor and area of the stimuli group was measured.



Figure 3. Picture of Ringsbäcken showing a sympatric section with both brown trout and brook trout (top), and an allopatric section with only brown trout (bottom).

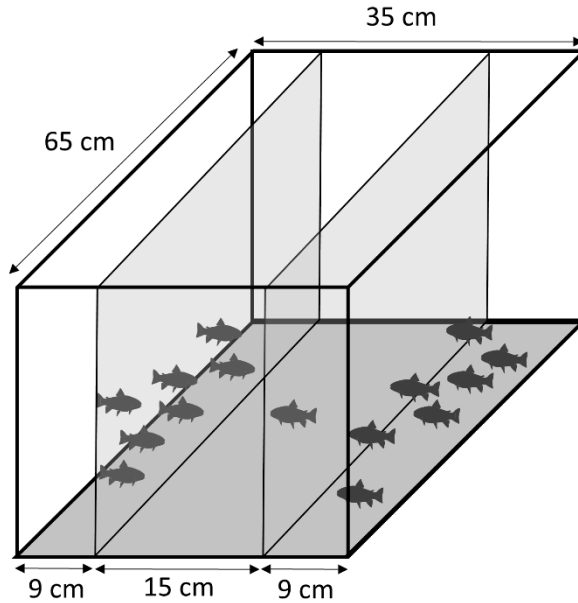


Figure 4. Schematic figure of the setup in **paper I** showing the first experiment where both side compartments had groups that the focal brown trout could associate with. In the other treatments, one of the compartments was left empty to test whether the 0+ brown trout prefer to associate with a group of fish or an empty side. Association was measured as brown trout being within 5 cm of one of the two compartments.

In **Paper II**, we also did two consecutive experiments. First, we assessed the space use and time to feed by a 0+ brown trout or brook trout in the presence of a 1+ hetero- or conspecific individuals, placed in a separate compartment (Figure 5). Here, we measured the proportion of time spent close to the other compartment and how long time it took for the 0+ individual to start feeding over two consecutive days. During day 1, no 1+ individual was present in the other compartment, whereas day 2 had a 1+ individual in the other compartment. For each day, the transparent wall in the middle was first covered with an opaque divider, and later uncovered, rendering two measurements of time spent close to the other compartment each day. Two during the first day without a large 1+ individual and two during the second day when a large 1+ individual was present.

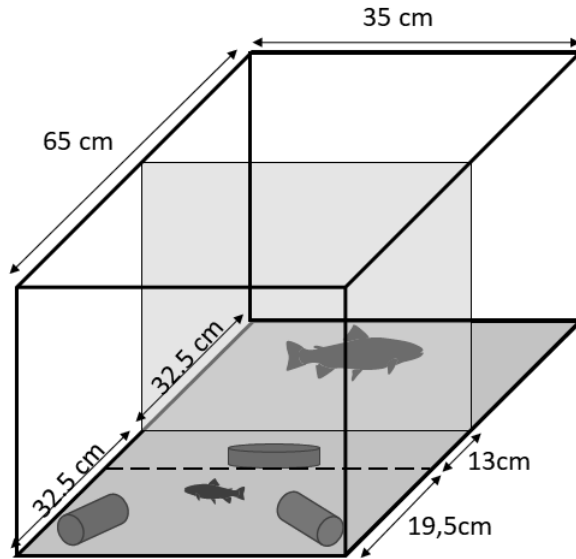


Figure 5. Setup of experiment I in **paper II**. The dashed line represent the zone used to measure space use close to the larger I+ individual. Within this zone, we introduced food (chironomidae) over the petri dish. The setup shown here represent the scenario when the opaque divider had been removed.

In the second experiment (**Paper II**), we assessed agonistic interactions between 0+ brown trout and 0+ brook trout. Specifically, we investigated if a size disadvantage of 0+ brown trout could be compensated by manipulating its prior residence duration in a territory (Johnsson & Forser, 2002). In this experiment, we used smaller tanks ($24 \times 18 \times 13$ cm) divided into two equally sized compartments to separate the two heterospecific individuals before they could contest the territory. First, agonistic interactions and contest duration were measured when the two species had similar residence duration in the territory, and secondly we manipulated residence duration for the brown trout, giving them either 2 days or 4 days in the territory as opposed to 3 days for the brook trout.

3.1.2. Field studies

In **Paper III**, we built and set up enclosures in Ringsbäcken to assess if brown trout originating from either allopatry or sympatry differed in diel activity and aggregation pattern. The enclosures were manipulated to mimic sympatric and allopatric conditions by stocking some with both species and some with only brown trout. All fish were tagged with visible implant elastomer to facilitate observations of diel activity and aggregation patterns. During the length of the experiment, fish were observed on average every third day. In **Paper IV**, we wanted to measure if the previously observed diet changes in sympatric brown trout also would affect plastic traits such as head shape, and if head morphology was related to survival of the individuals. In a mark-recapture study conducted over a year in Ringsbäcken, brown trout from sympatry and allopatry were tagged, photographed and released back into the stream. Survival was estimated using apparent survival, which combine true survival, site-fidelity and sampling bias during electrofishing. To assess head morphology, all individuals were photographed. The photographs were digitized in TpsDig 2.31 (Rohlf, 2017) by using 13 different landmarks (following Adams, Woltering and Alexander, 2003) measuring e.g. length of the upper and lower jaw, eye size and overall size of the head. In **Paper V**, we investigated the effects of increased consumption of terrestrial prey in sympatric brown trout (Cucherousset et al., 2020; Závorka et al., 2017), and its possible influence on brain development. Brown trout were sampled in both allopatric and sympatric sections of Ringsbäcken (Figure 3), Lindåsabäcken and Kovraån, all within the same catchment area. Two small clips of the pelvic fin were taken from all collected brown trout, one for stable isotope analysis and one for genetic analysis. Additionally, a subsample of individuals at each study section were dissected for tissue analysis of lipids and brain measurements. Terrestrial and aquatic insects were sampled at each site to estimate abundance of insects and facilitate analysis of stable isotopes and lipid content of the fish. Lipid analysis and stable isotopes were analysed at WasserCluster Lunz, Austria.

4. Results and discussion

4.1. Summary of results

Paper I – Association during the fry stage

In **Paper I**, the focal brown trout showed no discrimination against conspecific or heterospecific groups when presented at the same time (Figure 6). Additionally, the lack of species-specific preference was further confirmed when one side was left empty, as the focal brown trout showed a strong association response towards both heterospecifics and conspecifics in preference to the empty side (Figure 6).

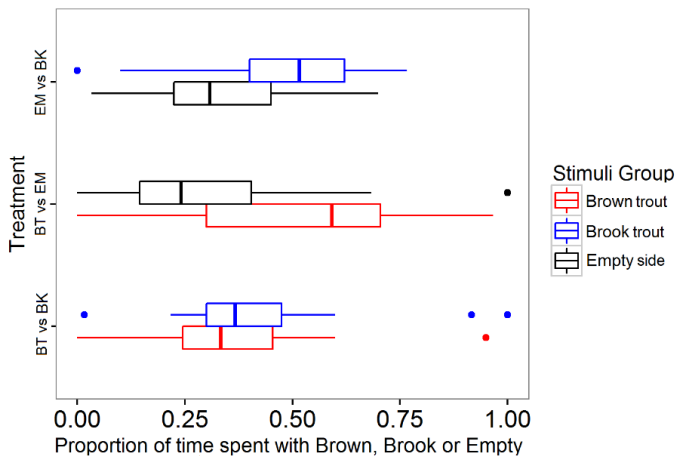


Figure 6. Association patterns of 0+ brown trout in **Paper I**, shown as the proportion of time spent close towards the compartments having a group of brown trout (BT), brook trout (BK) or when one of the compartments were empty (EM).

Paper I also demonstrated that the focal brown trout showed a stronger association towards the group of brook trout than towards the group of brown trout when it could move around freely. Additionally, larger 0+ brown trout showed a stronger association towards the group of brook trout than smaller brown trout did, and groups of brown trout were more dispersed than groups of brook trout. Collectively, the results from **Paper I** showed that brown trout do not discriminate against juvenile brook trout when having the choice between conspecifics and heterospecifics. Additionally, the two species show distinct responses in group structure that may facilitate stronger association towards heterospecific brook trout than conspecific brown trout.

Paper II – Antagonistic interactions and inter-cohort association

In **Paper II**, brown trout and brook trout did not differ in proportion time spent close to the middle of the tank during the first day. However, during the second day, after removing the opaque divider, 0+ brook trout spent significantly more time close to the larger 1+ brown trout than 0+ brown trout in presence of a larger 1+ brook trout (Figure 7). Likewise, brook trout in presence of a larger 1+ brown trout were faster to consume the offered food than were brown trout in presence of a larger 1+ brook trout. Brook trout won 13 and brown trout 7 territorial contest in the equal residence experiment. When manipulating residence duration of brown trout into two or four days and increasing size difference such that all brook trout were larger, brook trout won most of the territorial contest. Additionally, the 4-day residence advantage increased both contest duration and number of agonistic interactions between the species, compared to the 2-day residence (Figure 8). Taken together, the results from **Paper II** show that 0+ brown trout and brook trout respond differently towards larger heterospecifics, and that brook trout may have a competitive advantage over brown trout at the juvenile stage.

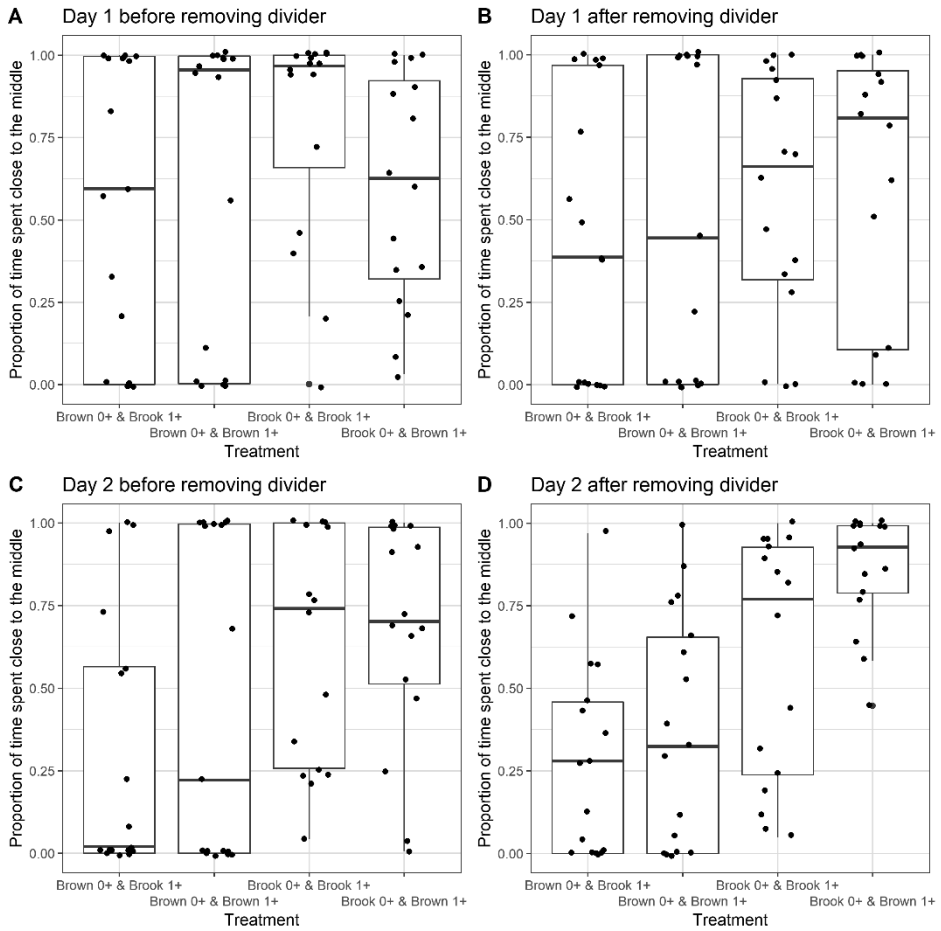


Figure 7. Experiment in Paper II showing the proportion of time 0+ brown trout and 0+ brook trout spent close to the compartment housing the larger 1+ individual. A and B show day 1 when no 1+ individual was present in the other compartment, (A) before and (B) after removing an opaque divider. C and D show day 2 when a 1+ individual was present on the other side (C) before and (D) after removing the opaque divider.

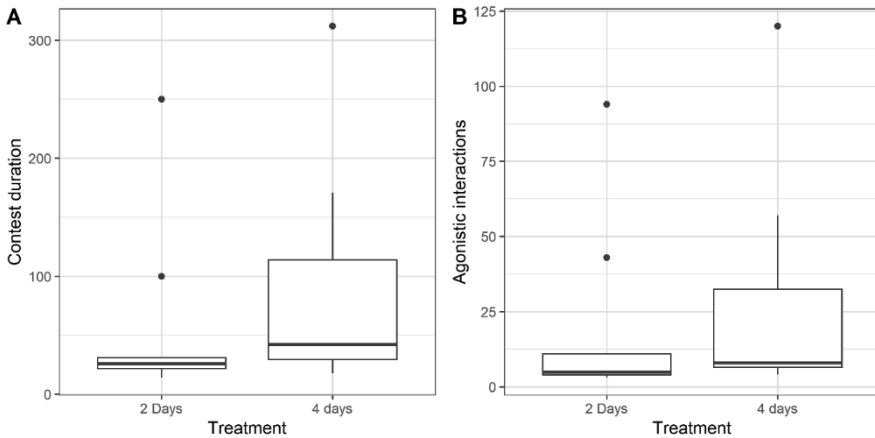


Figure 8. Experiment in **Paper II** showing the difference in A) contest duration and B) number of agonistic interactions between 0+ brown trout and 0+ brook trout when brown trout (the weaker competitor) had a prior territorial residence duration of either 2 days or 4 days.

Paper III – Diel activity and association of yearlings

In **Paper III**, we found that brown trout of allopatric origin were more active during the night than during the day compared to brown trout originating from sympatry, which were more active during the day. Additionally, brown trout of allopatric origin were less active during the night when placed in a sympatric setup (Figure 9). The change in diel activity was most evident when comparing diel activity between two periods (i.e., the first seven days against the last 21 days of the experiment). Here, allopatric brown trout became more day active when placed in sympatry with brook trout, whereas sympatric brown trout became more night active when placed in allopatry during the second period as opposed to the first period (Figure 10). A similar association pattern as in **Paper I** was also seen in **Paper III**, where individuals in a sympatric setup were both more aggregated than individuals in the allopatric setup, and brown trout of sympatric origin were more aggregated than brown trout of allopatric origin. Overall, **Paper III** showed distinct differences in diel activities in brown trout from allopatric and sympatric populations, and that released competition with brook trout can reverse the diel activity of brown trout to become more night active.

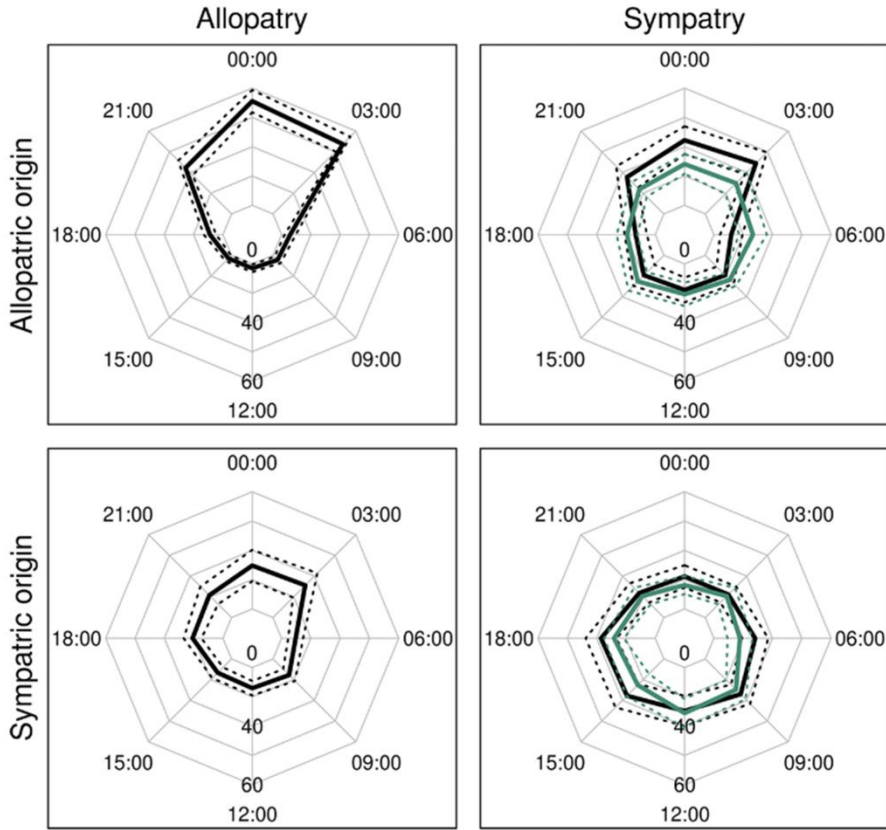


Figure 9. The diel activity of brown trout (black) and brook trout (green). Origin (left) indicate where the fish was originally caught in the river, whereas Allopatry and Sympatry (top) represent how the enclosures were manipulated. For example, the top row refers to brown trout caught in allopatry (allopatric origin) and placed in either allopatric condition (left panel) or novel sympatric condition (right panel) with brook trout.

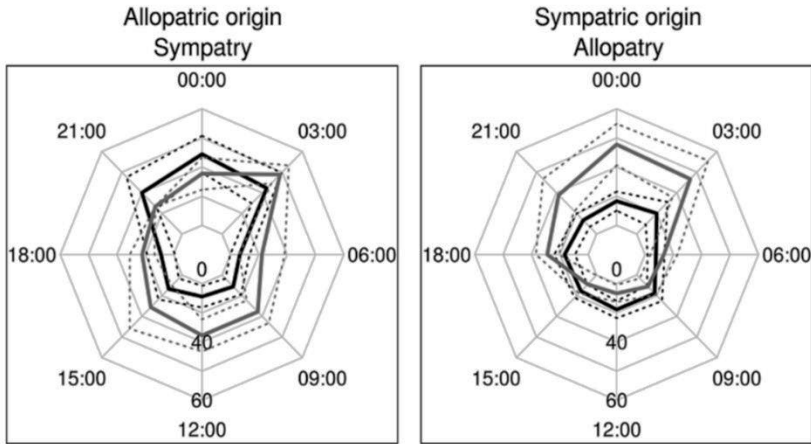


Figure 10. Change in diel activity between brown trout originating from allopatry and sympatry placed in sympatry or allopatry, respectively. The black line represent period 1 and the grey line represent period 2 of the study. Period 1 accounts for the first seven days, while period 2 accounts for the final 21 days of the experiments.

Paper IV – Morphological differences

In **Paper IV**, we found strong evidence of morphological differences in head-shape between allopatric and sympatric brown trout. Brown trout living in sympatry with brook trout had a terminal mouth, smaller eyes, and lower jaw compared to allopatric brown trout (Figure 11). Additionally, apparent survival after 12 months showed that individuals with a longer jaw had lower survival in the allopatric population compared to the sympatric population. Collectively, **Paper IV** showed that allopatric and sympatric brown trout from the same river show differences in head morphology and that there is a strong selection against certain morphologies in the allopatric population.

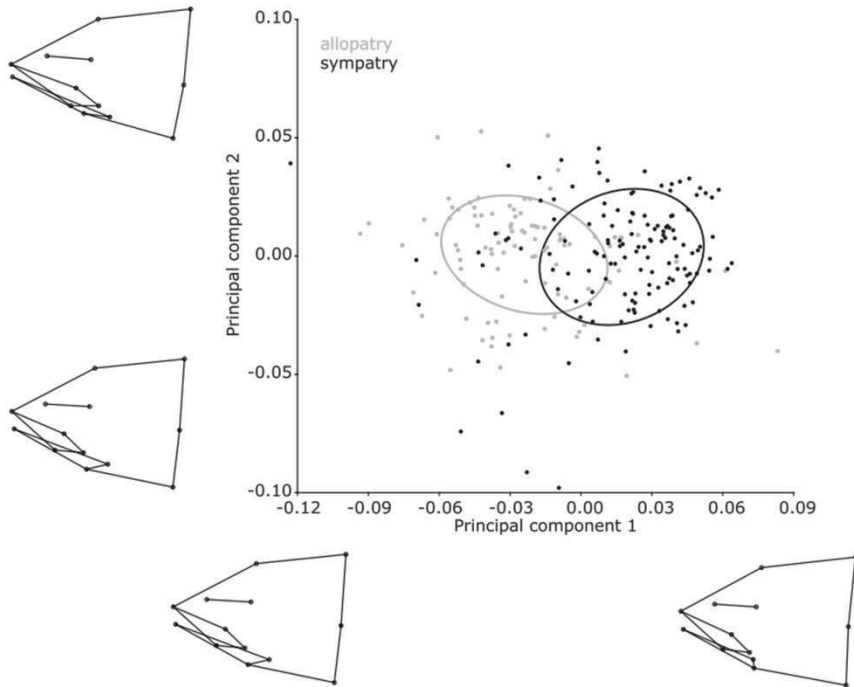


Figure 11. The two main partial warps of overall head shape variation between allopatric (grey) and sympatric (black) brown trout. Principal component 1 discriminate individuals based on eye size, length of lower jaw and mouth position, with high scores indicating smaller eyes, short lower jaw and terminal mouth. Principal component 2 discriminate individuals based on length of upper and lower jaws, with high scores indicating longer jaws.

Paper V – Fatty acids and development

In **Paper V**, reliance on terrestrial carbon was higher in sympatric than allopatric brown trout populations, indicating higher consumption of terrestrial prey in sympatry. While there was no difference in brain volume between allopatric and sympatric brown trout populations across the three streams (Figure 12b), there was an overall effect of smaller brain volume with increasing reliance of terrestrial carbon (Figure 12c). Terrestrial and aquatic prey contained similar amount of the omega-3 short-chained polyunsaturated

fatty acid ALA, but aquatic prey contained more of the omega-3 long-chained polyunsaturated fatty acid EPA. A path model indicated that an increased reliance of terrestrial carbon would increase the content of ALA and decrease the content of DHA in the tissues. The increased relative content of ALA and decreased relative content of DHA was also associated with smaller brain volume in brown trout. In summary, **Paper V** showed that brown trout living in sympatry with brook trout have a higher content of terrestrial carbon in their diet that negatively correlated with brain volume. Additionally, the increased consumption of terrestrial invertebrates in sympatry negatively affected the fatty acid composition in the tissues, which might affect brain volume.

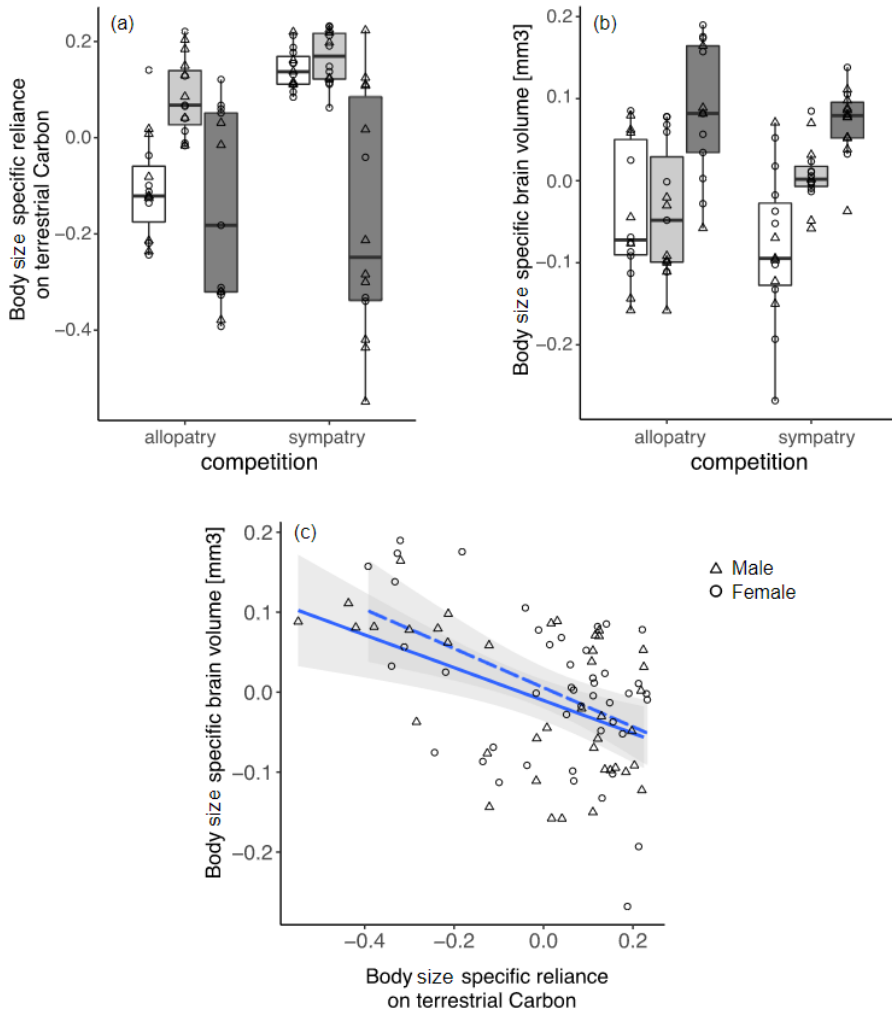


Figure 12. The reliance of carbon from terrestrial prey between A) allopatric and sympatric brown trout and B) difference in brain volume between allopatric and sympatric brown trout, and C) linear regression over reliance of terrestrial carbon and brain volume. The greyscale represents the different streams, white = Kovraån, light grey = Lindåsabäcken and dark grey = Ringsbäcken.

4.2. Discussion and management

In summary, the results show that juvenile brown trout and brook trout behave differently regarding group composition, association and territorial interactions (**Paper I** and **II**). For instance, juvenile brook trout had a tighter group structure than brown trout (**Paper I**) and brown trout showed strong avoidance behaviour against larger heterospecific brook trout compared to juvenile brook trout in presence of a large heterospecific brown trout (**Paper II**). Territorial interactions at the juvenile stage showed that brook trout was a stronger competitor by displacing brown trout from a territory (**Paper II**). We also found that brown trout became more day active when living in sympatry with brook trout, compared to night active allopatric brown trout (**Paper III**). Additionally, sympatric brown trout showed plastic changes in head morphology that may be linked with a change in feeding niche towards more terrestrial prey (**Paper IV**). Furthermore, brown trout living in sympatry with brook trout consume more terrestrial prey than allopatric brown trout. The higher predation on long-chained PUFA deprived terrestrial prey, as opposed to long-chained PUFA rich aquatic prey, may have negatively affected brain volume of brown trout (**Paper V**).

Overall, the displacement of brown trout is not solely dictated by brook trout being stronger competitor compared to brown trout. Rather it is likely a combined effect of habitat preferences (Korsu, Heino, Huusko, & Muotka, 2012), competition between the species (Fausch & White, 1981) and life-history differences, such as earlier maturity (Öhlund et al., 2008) and earlier spawning in brook trout (Cucherousset et al., 2008). In general, such combined effects make it difficult to predict the outcome following an introduction of non-native species. Only focusing on one factor could lead to misinterpretations and wrongly classifying an invasive alien species (IAS) as merely an alien species (AS). Most previous studies have focused on the interactions between brown and brook trout during the adult stage (but see Fausch and White, 1986). Thus, brown trout may be competitively superior against brook trout as adult, but inferior at the juvenile stage. Inferior competitive ability at the juvenile stage, in combination with suitable and available habitats for the brook trout could explain some of the conundrums regarding the displacement of brown trout by brook trout in Europe.

So far, no studies have focused on behavioural differences (i.e. “personalities”: Réale et al., 2010; Sih et al., 2012) and whether some brown

trout phenotypes are more likely to be displaced by brook trout. For instance, some phenotypes may benefit more from the social interactions with brook trout (**Paper I** and **Paper III**), be more prone to social learning (Kurvers et al., 2010; Trompf & Brown, 2014) and adopt the terrestrial feeding strategy of brook trout. This hypothesis could explain the results in **Paper IV** and **Paper V**, where phenotypically plastic changes in head-shape and higher reliance of terrestrial prey differed between allopatric and sympatric populations. Yet, as smaller brain size has been linked to DHA deficiency (Lund et al., 2012), our findings about increased reliance on terrestrial prey and smaller brain volume (**Paper V**) could have major fitness implications for brown trout. For instance, small brain volume may negatively affect learning performance (Kotrschal et al., 2013), foraging behaviour (Wilson & McLaughlin, 2010) and behavioural plasticity (Herczeg et al., 2019), which could reduce their flexibility to switch between terrestrial and aquatic prey. Additionally, as DHA may also be important for somatic growth (Brett et al., 2017), the reduced predation of DHA rich aquatic prey could also explain the reduced growth previously observed in brown trout living in sympatry with brook trout (Závorka et al., 2017). Collectively this could lead to a downward spiral, where sympatric brown trout rely on low quality terrestrial prey that affects behaviour, cognitive abilities and growth, ultimately decreasing their competitive ability against the invasive brook trout.

4.2.1. Foraging and prey choice

The mechanisms behind the niche shift in prey consumption between allopatric and sympatric brown trout is not fully understood (Cucherousset et al., 2007, 2020; Závorka et al., 2017), but possible explanations could include learning and morphological trait changes in presence of the brook trout (**Paper IV**). The above mentioned earlier spawning period of brook trout (Cucherousset et al., 2008) in combination with similar incubation period across a range of temperature (Crisp, 1981; Grant et al., 2002) could result in earlier hatching of brook trout eggs compared to brown trout. This could affect the information transfer in streams where the two species co-exist and the social environment for juvenile brown trout when starting exogenous feeding. Thus, brown trout that are associating and observing brook trout feeding on mainly terrestrial prey falling in the stream could facilitate social learning (Brown & Laland,

2011; Magnhagen & Staffan 2003; Laland, 2004; White & Gowan, 2014) about feeding niche that might affect morphological traits such as head shape (**Paper IV**) and the development of neurological tissues such as eyes and brain (**Paper V**). The results presented in **paper I**, where brown trout did not discriminate against a group of heterospecifics further emphasize this possible explanation. Yet, these results are in conflict with **paper II**, where strong territorial interactions between the species occurred. However, the effect of group size and laboratory environment may influence this behaviour. In a different scenario, the association with a group of brook trout at the juvenile stage may function as a dilution effect to avoid predators (Delm, 1990; Foster & Treherne, 1981; Magnhagen, Braithwaite, Forsgren & Kapoor, 2008). Thus, by showing stronger association with a group of brook trout could further facilitate the social information even under short periods. Additionally, the association with brook trout at the juvenile stage could explain the patterns of changed diel activity presented in **paper III**. As terrestrial prey is more common in the drift during the day, the changed diel activity from nocturnal to diurnal could also explain the prey choice and niche shift in brown trout. The increased predation on terrestrial prey falling in the stream might relax the predation pressure on benthic invertebrates. This in turn, could increase the activity and density of benthic invertebrates, such as grazers and shredders, and affect the fluxes of nutrients in the ecosystem. Yet, the large-scale ecosystem effects following an introduction of invasive brook trout remains to be studied.

4.2.2. Indirect effects on a red listed bivalve

Bivalves constitutes a vital part of the ecosystem in limnic and fluvial environments as they are filter feeders and increase retention of nutrients (Hoellein, Zarnoch, Bruesewitz, & DeMartini, 2017). The mussel excretion increase the flux of nutrients in the ecosystem as it is readily available as food for other benthic organisms and may increase overall productivity of the ecosystem and density of benthic organisms (Howard & Cuffey, 2006). Of the eleven species of great mussels in Sweden, the freshwater pearl mussel is the only one that is restricted to stream environments. Although the freshwater pearl mussel has viable populations all over Sweden, habitat alteration, acidification and pearl fishing have decimated the populations

(Naturvårdsverket, 2005). It has been classified as endangered by the IUCN red list (Moorkens, Cordeiro, Seddon, von Proschwitz, & Woolnough, 2018) and is nationally protected in Sweden (Artdatabanken, 2020). An unforeseen and indirect threat to freshwater pearl mussel populations involves the interaction between brown and brook trout. The complex life cycle of the freshwater pearl mussel begins with the release of parasitic glochidia larvae. The larvae are highly host specific and attach to the gills of native salmonids, specifically brown trout and Atlantic salmon (*Salmo salar*) (Hastie & Young, 2001). After 8-10 months, the larvae release from the host and dig down in the sediment until they are large enough to start filtering at the sediment surface, which can take 5-10 years. After an additional 10-15 years, the mussels become sexually mature and can reproduce (Moorkens et al., 2018; Naturvårdsverket, 2005). Given the host-specificity of freshwater pearl mussel in Europe, the habitat exclusion and reduction of brown trout populations by brook trout can potentially have far-reaching negative effects on freshwater pearl mussel populations. If the freshwater pearl mussel cannot find a suitable host for its larvae, the population will slowly die off. Only a few studies have investigated the host suitability of brook trout for glochidia larvae in Europe, with overall negative result regarding infestation rate (Jung et al., 2013; Salonen, Marjomäki & Taskinen, 2016; Lovén Wallerius et al., In prep). As brook trout is a host for freshwater pearl mussel in North America (Smith, 1976), the low host suitability in Europe is concerning. Additional concerns are the physiological and behavioural impairments for the host following infestation of glochida. For instance, increased metabolic rate (Filipsson et al., 2017) and reduced feeding (Filipsson et al., 2018; Österling, Ferm, & Piccolo, 2014) after glochidia infestation may increase the competitive advantage of brook trout over brown trout in sympatric populations (Salonen et al., 2016). Consequently, the displacement of brown trout by brook trout may increase in streams with freshwater pearl mussel. However, given that the turnover rate of freshwater pearl mussels spans over decades, the monitoring and decline of the populations may be unnoticed. As the freshwater pearl mussels can live over a 100 years (Naturvårdsverket, 2005), the plausible event of a non-reproducing mussel population due to a lack of hosts could probably be reversed by targeted management actions to reduce brook trout populations and increase brown trout populations via stocking.

4.2.3. Management of Invasive Alien Species

A successful establishment and spread of an invasive species is often followed by management actions to prevent further spread of the species, or management programs that aim to eradicate the invasive species completely (Britton, Gozlan, & Copp, 2011; Keller, Geist, Jeschke, & Kühn, 2011; Robertson et al., 2020). While the management of invasive species is associated with high costs (Diagne et al., 2021), few targeted actions have completely eradicated the invasive species after successful establishment (Genovesi, 2005). In addition, eradication programs are often time-consuming (Bogich, Liebhold, & Shea, 2008), and uncertainties of complete eradication of the invasive species remain (Myers, Simberloff, Kuris, & Carey, 2000; Rout, Thompson, & McCarthy, 2009). This constitutes a further problem as a given management technique could target a non-random sample of the populations, and the individuals that remain could consist of individuals with a different genotype that may have a different impact on the ecosystem (Závorka et al., 2018). Consequently, management programs should apply non-selective techniques, while aiming to reduce further spread of the IAS (Britton, Gozlan & Copp, 2011). Thus, single targeted actions in specific areas may provide feasible management actions to eradicate local populations of the invasive species, rather than aiming at complete nationwide eradication.

Various methods can be used to control or eradicate invasive fish in general and salmonids in particular. While the use of the chemical rotenone would be a highly cost and time-efficient measure in aquatic environments aiming at eradicating IAS, the compound is highly toxic and targets all organisms in the water body (Ling, 2002). The use of rotenone would have devastating consequences for the ecosystem and the harm of the chemical would most likely outweigh the harm from the IAS. However, thorough risk and benefit assessments of large-scale invasive management efforts must be considered, and if necessary, some aggressive methods could be justified (Kopf et al., 2017). In North America, successful methods using gill netting eradicated brook trout and rainbow trout from a lake over the course of 2 years (Knapp & Matthews, 1998). Although, gill netting could be a successful management tool applicable to lakes, the passive by-catch of other fish species constitutes a major problem. The use of electrofishing to remove invasive brown trout in Minnesota did not completely eradicate the brown trout population over a 6-year period, but the resident brook trout population grew larger and increased in abundance (Hoxmeier & Dieterman, 2016). While gill netting and electrofishing show promising effects, both have pros and cons regarding specificity of targeted species, efficiency and time. As some streams

are connected to lakes, the combination of targeted electrofishing in the stream, while using gill netting in the lake could be a promising measure to reduce the possibility of invasion from the lake after successful removal via electrofishing. In that case, the brown trout population would be protected in the stream and could colonize the lake after successful removal of brook trout. Another fascinating management method involves the use of genetically modified brook trout males into YY-males, rather than the normal XY-males. When the YY-males reproduced, all offspring would be males, and over time the population will consist of males only (Schill, Heindel, Campbell, Meyer, & Mamer, 2016). Although not tested in wild, simulation models combining electrofishing/gill netting and recurrent release of the YY broodstock show that this method could potentially eradicate brook trout in some instances (Day et al., 2021; Schill, Meyer, & Hansen, 2017).

It is evident that no management method to control IAS in the aquatic environment is better than the other. Rather, the choice of method to eradicate or reduce brook trout populations would depend on the targeted environment (i.e. stream, river or lake) and the amount of collateral damage that could be acceptable (i.e. the risk of reducing other species and damaging the ecosystem) (Kopf et al., 2017). Likewise, many management programs targeting invasive fish are often focused around a relatively short period of time, which could influence the method used and potential management success (Britton, Gozlan and Copp, 2011). For instance, highly specific but time-consuming methods such as electrofishing should be conducted over several years to assure that all brook trout individuals are caught. As of today, the use of electrofishing to remove brook trout from streams could be the most promising measure as it reduces damage on native fish species. However, as it requires active capturing, combining active electrofishing with other passive capturing methods could increase the overall efficiency of the management effort. Additionally, the time-consuming efforts using electrofishing could benefit by focusing the measure on specific periods during the year. If brook trout hatch earlier and have a competitive advantage over brown trout at an early stage (**Paper II**), focusing the electrofishing effort in early spring or in autumn during spawning could be a time-efficient management effort to reduce brook trout offspring that would increase the likelihood of brown trout survival during hatching.

In Sweden, two recently funded projects are working to evaluate different methods to reduce and remove brook trout populations. One is focusing on removing brook trout populations by combining electrofishing and stocking of large amounts of brown trout in two streams in the county of Jämtland (Personal communication, Gunnar Öhlund). The other project will evaluate various removal methods and monitor possible ecosystem effects

following the removal of brook trout (Naturvårdsverket, grant number: 2020-00048).

4.2.4. Conclusion and future perspective

It is clear that brook trout should be considered an IAS given the evidence of competitive displacement and negative effects on development and feeding niche of native brown trout. Future studies should focus on carefully designed removal experiments and study the long-term effects on the ecosystem but also the behavioural and phenotypic response of brown trout after brook trout removal. Yet, complete removal of brook trout from Sweden will most likely never occur due to its widespread distribution across Sweden. Future management and removal efforts should target stream systems and lakes with high ecological values. However, before such attempts, studies that evaluate certain methods considering both efficiency and time should be conducted and a nation-wide management plan on how to deal with brook trout should be considered.

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