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Can personality predict movement patterns and space use in fishes?

A study case on partial-migrating Atlantic cod (*Gadus morhua)* and stream-dwelling Arctic Charr (*Salvelinus alpinus*)

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Dissertation submitted in partial fulfillment of a
Philosophiae Doctor degree in Biology

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Abstract

Individuals within a population often differ predictably in their behaviour compared to other members across time and/or context, often termed personality, which can have major implications for ecology and evolution. Personality includes variation in the levels of risk-taking behaviour (i.e. boldness), exploratory behaviour, activity in a familiar environment, aggressiveness and sociality and often the variables correlate, i.e. they form a behavioural syndrome. The role of consistent differences in movement behaviour within this framework has only been highlighted recently. Additionally, not many studies have examined the influence of seasonal change on behavioural stability or validated laboratory behaviour with natural behaviour. In this thesis, I studied personality, behavioural syndromes and their relation to movement (i.e. local foraging patterns, larger-scale space use and feeding migration) in two fish species, i.e. Atlantic cod (*Gadus morhua*) that exhibit partial migration and a population of stream-dwelling Arctic charr (*Salvelinus alpinus*), which habitat is ideal to study space use. Additionally, I investigated the potential effect of seasonal changes and measurement environment (i.e. laboratory, semi-wild and wild) on personality and movement. The results indicate that personality is present between time intervals, especially for movement-related traits (i.e. activity and exploration, which were identified as two separate traits) and found that this may be related to a feeding migration-linked gene in Atlantic cod. However, no evidence was found for repeatable behaviours across context, i.e. season and environment, in Arctic charr. Additionally, not much evidence for behavioural syndromes was found in these two species. The findings encourage future personality studies to be clear in the definitions used and to take context into account when studying personality. Finally, I examine how personality may have implications for management.

Útdráttur

Einstaklingar af sama stofni sýna oft ákveðið, en ólíkt atferli eftir aðstæðum og tíma, sem getur haft mikla þýðingu fyrir vistfræði og þróun tegunda. Slíkt einstaklingsbundið og endurtekið atferli hefur verið kallað persónuleiki og getur m.a. tengst breytileika í áræðni, könnunaratferli, virkni í kunnuglegu umhverfi, árásargirni og félagsatferli. Þessir eiginleikar geta líka tengst innbyrðis og myndað atferlisheilkenni. Mikilvægi hreyfanleika og fars í þessu samhengi hefur þó aðeins nýlega verið athugað. Einnig hafa fáar rannsóknir verið gerðar á því hvort, og þá hvernig, stöðugleiki atferlis breytist á milli árstíða og hvort þær niðurstöður séu háðar því hvort athuganir fari fram á rannsóknarstofu eða í náttúrulegu umhverfi. Þessi ritgerð fjallar um rannsóknir á persónuleika, atferlisheilkennum og tengslum þeirra við hreyfanleika fiska við fæðunám, nýtingu rýmis og ferða til fæðustöðva. Athugaðar voru tvær fisktegundir, þorskur (Gadus morhua) sem sýnir breytilega farhegðun, og bleikja (Salvelinus alpinus) sem lifir í ám og er því hentug til rannsókna á ferðum einstaklinga í rými. Áhrif árstíðabreytinga og umhverfisaðstæðna á persónuleika og hreyfanleika voru rannsökuð á rannsóknarstofu, við hálfnáttúrulegar og náttúrulegar aðstæður. Í ljós kom að persónuleiki þorsks viðhelst yfir tíma, og þá sérstaklega fyrir hreyfanleika sem tengist virkni og könnunaratferli, og að það mætti hugsanlega rekja til breytileika gens sem tengist fari að fæðustöðvum. Aftur á móti greindist ekki endurtekið atferli á milli ólíks umhverfis og árstíða hjá bleikju. Ekki greindust heldur skýr atferlisheilkenni hjá þessum tveimur tegundum. Fyrir frekari rannsóknir á persónuleika er mikilvægt að nota skýrar skilgreiningar og taka mið af vettvangi rannsóknanna. Að lokum er fjallað um hvernig persónuleiki getur haft þýðingu fyrir nýtingu og stýringu villtra stofna.

Mom, I did it

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List of Papers

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Paper I:

Beukeboom, R. & Benhaïm, D. (manuscript). How to measure exploration? A combined estimation method.

Paper II:

Beukeboom, R., Morel, A., Phillips, J. S., Ólafsdóttir, G. Á., & Benhaïm, D. (2022). Activity vs exploration: Locomotion in a known and unknown environment differs in Atlantic cod juveniles (*Gadus morhua*). Behavioural Processes, 202, 104736. https://doi.org/10.1016/j.beproc.2022.104736

Paper III:

Beukeboom, R., Phillips, J. S., Ólafsdóttir, G. Á., & Benhaïm, D. (2023). Personality in juvenile Atlantic cod ecotypes and implications for fisheries management. Ecology and Evolution, 13(4), e9952. https://doi.org/10.1002/ece3.9952

Paper IV:

Beukeboom, R., Prat, A., Steingrímsson, S.Ó., Benhaïm, D. (manuscript). Consistency and correlation of behavioural traits measured in the laboratory and semiwild conditions: A study case in stream-dwelling Arctic charr (*Salvelinus alpinus*).

Paper V:

Beukeboom, R., Prat, A., Ladurée, G., Steingrímsson, Stefán Ó., Benhaïm, D. (under review at Behavioral Ecology)**.** The influence of seasonality on personality and space use in Arctic charr (*Salvelinus alpinus*).

Author contributions

Table 1. CRediT (Contribution Roles Taxonomy) for the five different papers (I-V).

Author	**Conceptualization**	**Data curation**	**Formal Analysis**	**Funding acquisition**	**Investigation**	**Methodology**	**Project administration**	**Resources**	**Supervision**	**Validation**	**Visualization**	**Writing - Original Draft Preparation**	**Writing - Review and editing**
Rosanne Beukeboom	I-V	I-V	I-V	IV, V	I-V	I-V	I-V			I-V	I-V	I-V	I-V
Antoine Morel					II	II							II
Audrey Prat					IV, V	IV, V							IV, V
Gabrielle Ladurée						V							V
Joseph S. Phillips			II, III										II, III
Guðbjörg Ásta Ólafsdóttir	III			I-III				I-III	II, III				
Stefán Óli Steingrímsson	IV, V			IV, V		IV		IV, V					V
David Benhaïm	IV, V					IV, V		IV, V	I-V				I-V

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1 General introduction

1.1 Consistent behavioural differences

One of the basic tenets observed by Charles Darwin (1809-1882) was that all organisms are unique; i.e. they show a great diversity in traits such as size, colour and gender, but also behaviour, and that this variation was not just noise around an adaptive mean (Dall et al., 2004). These differences have been described between species, between populations of the same species, but also between individuals within the same population (e.g. Aristotle 350 BCE; Darwin, 1859). Although the occurrences of behavioural differences between species and between populations of the same species became generally accepted in the ’60 and ’80 respectively, Wilson (1998) wrote that “now” (1998) was the era to resolve differences within populations. Now, 25 years after Wilson’s “opening of the era”, not only is the existence of behavioural differences within a population widely accepted, the understanding of the complexity of the phenomenon has become visible; researchers in the last decades have not only proven that individuals within a population differ from each other but also that these individual differences are consistent across time and/or context (i.e. individuals show “personality”; Gosling, 2001; Fig. 1a) and thereby is raw material on which natural selection can act.

Based on 30 years of experiments on earthworms, Darwin (1881) noted that some of the individuals seemed to be “timid”, whereas others were more “brave”. More than a century later, Réale and colleagues (2007) proposed five personality axes including the timid-brave axis observed by Darwin: i.e. *shyness-boldness*: “an individual’s reaction to any risky, but not new situation”, *exploration-avoidance:* “an individual’s reaction to a new situation”, *activity*: “the general level of activity […] in a non-risky and non-novel environment”, *aggressiveness*: “the agonistic reaction to the presence or absence of conspecifics” and *sociability*: “an individual’s reaction to the presence or absence of conspecifics, excluding aggressive behaviour” (Réale et al., 2007). However, any repeatable behaviour can potentially be a personality trait, and recently the addition of ‘spatial personality’ as a sixth axis has been discussed (Stuber et al., 2022). These personality traits have often been found to correlate with each other, i.e. they form a behavioural syndrome, for example when bold individuals are also more aggressive (Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, et al., 2004; Fig. 1b). An often described syndrome is the ‘pace-of-life syndrome’, where more active and bold individuals reproduce faster (i.e. they are better in resource acquisition and reproduction), but have a shorter life span (i.e. they experience an increased risk of mortality) (Mittelbach et al., 2014; Réale et al., 2010; Royauté et al., 2018).

Although personality is by definition stable across time and/or context, it can exhibit phenotypic plasticity: “the ability of a single genotype to exhibit a range of different phenotypes in response to variation in the environment” (Forsman, 2015; Fig. 1a). Plasticity can be caused by ecological differences, such as temperature (Biro et al., 2010), photoperiod (Finkemeier et al., 2016), predation pressure (Bell & Sih, 2007; Darby & McGhee, 2019), food predictability (Chapman et al., 2010; Sébastien et al., 2016), presence or absence of conspecifics (Ólafsdóttir & Magellan, 2016) and competition (Wauters et al., 2019). However, as long as rank order remains similar among individuals, personality and behavioural syndromes can still arise, even when average trait values differ between situations and contexts. Interestingly, individuals can also differ consistently in plasticity, i.e. some individuals are more predictable than others (Jolles et al., 2017).

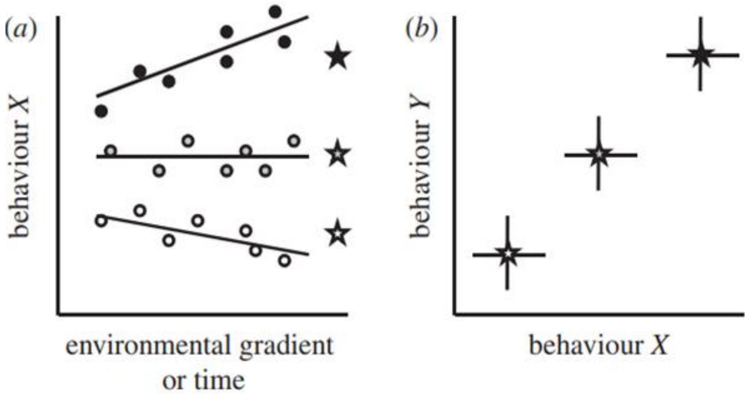


Figure 1. a) Three individuals (black, grey and white dots) show consistent individual variation in response to a changing environmental condition or over time, summarized in a mean personality trait (star). The slopes show that their responsiveness differs (i.e., differences in behavioural plasticity): grey reacts constantly (i.e., no plasticity), while black responds with a stronger increase than white decreases. Regardless of its plasticity, rank order stays the same, i.e. black is always higher, grey is always medium and white is lowest, which indicates personality. b). Two behaviours are correlated, i.e., they form a behavioural syndrome (Figure taken with permission from Dingemanse & Wolf, 2010).

Besides the influence of environmental factors, behavioural differences and syndromes can arise because behaviours may be controlled by underlying factors, such as body size (Darby & McGhee, 2019; Roy & Bhat, 2018), body condition (Morandini & Ferrer, 2019), brain structure (Reddon & Hurd, 2009), age (Holtmann et al., 2017; Stamps & Groothuis, 2010), gender (Ashenden et al., 2017; Krause et al., 2017), parasites (Barber & Dingemanse, 2010), metabolic rate (Careau et al., 2008; Houston, 2010), knowledge, skills and experience (Frost et al., 2006; Mettke-Hofmann, 2014) and hormones (Ruiz-Gomez et al., 2008). Besides extrinsic and intrinsic influences, many behaviours are also linked to genes and are thereby heritable (Dingemanse & Wolf, 2010; Dochtermann & Roff, 2010; Drangsholt et al., 2014; Koolhaas et al., 1999; Lewis & Bates, 2014). Finally, behavioural syndromes can arise because of correlational selection, where the fitness of one trait depends on the fitness of another (Sih & Bell, 2008).

1.2 The role of movement in personality

Movement is an obvious behaviour that occurs from local foraging patterns, and larger-scale home ranges up to even larger-scale migration and dispersal (Abrahms et al., 2017; Shaw, 2020). Movement behaviour has been studied for centuries, for instance, the first report of tagged fish to study movement appeared as early as 1653 (Walton, 1653) and Darwin noted that many animals restrict their movement to specific home ranges (Darwin, 1859). Movement behaviour can be used as a way to maximize growth, reproduction and survival by moving towards favourable conditions (e.g. optimal temperatures, high-quality food patches and mates) and/or away from unfavourable contexts (e.g. high predator pressure, competition) (Bonte & Dahirel, 2017; Parker & Smith, 1990; Van Moorter et al., 2016). Numerous studies show that there are differences in movement behaviour within the population, e.g. sit-and-wait to mobile foraging tactics (Grant and Noakes, 1987; Steingrímsson & Grant, 2011), larger-scale foraging patterns and home ranges (e.g. Börger et al., 2006; Harrison et al., 2015) and partial migration, where only part of the population migrates, while the other part stays resident (Chapman, Brönmark, et al., 2011a).

In the laboratory, movement often finds its way into the personality traits of activity and exploration, which can be repeatable, and even more so than other personality traits (Stuber et al., 2022). However, natural repeatable differences in for example space use during foraging and migration have received less attention (Nilsson et al., 2014; Stuber et al., 2022). Examples can be found in a few studies on the repeatable nature of space use tactics (Harrison et al., 2015; Schirmer et al., 2019; Webber et al., 2020), partial migration (Thorsteinsson et al., 2012) and timing of full migration (Jensen et al., 2020; Tibblin et al., 2016). Natural differences in movement can also correlate with personality axis, for example, bolder fish were more likely to migrate (Chapman, Hulthén, et al., 2011). Another example is that of sociality: as it explains the tolerance of an individual to be in proximity to others, likely, asocial individuals have shown to disperse sooner when population density increases (e.g. Cote et al., 2010).

There is also some evidence for a complete “dispersal syndrome” where bolder, more aggressive and explorative and less social individuals are more likely to disperse (Dingle, 2006; Nilsson et al., 2014; Sih, Bell, Johnson, et al., 2004) and a more general “movement syndrome”, where bold and aggressive individuals have larger home ranges, higher movement rates and little site fidelity compared to shy and less aggressive members of the same population (Michelangeli et al., 2022; Spiegel et al., 2017). The relationship between personality traits and movement is a first (and maybe most visible) example of how personality can influence ecological and evolutionary processes as is described in the next paragraph.

1.3 Why study personality? Consequences for ecology and evolution

It is clear that consistent differences in the life history and fitness (i.e. survival and reproduction) of individuals, can lead to ecological and evolutionary influences on population and ecosystem levels (Dall et al., 2004; Moiron et al., 2020; Fig. 2). Studying personality, including behavioural syndromes and their underlying factors such as genes, has the potential to reveal important relationships between traits and ecological and evolutionary processes, and in some cases, reveal constraints and trade-offs that limit plasticity (Sih et al., 2012; Wolf & Weissing, 2012).

1.3.1 Consequences for individuals

Consistent individual differences can influence life history, including growth, survival and reproductive success, including mate choice (Biro & Stamps, 2008; Mittelbach et al., 2014), and individual movement patterns, including niche specialisation, dispersal and migration (Shaw, 2020; Spiegel et al., 2017; Fig. 2)

Individuals with a certain personality could, for example, increase their fitness by gaining access to the best feeding grounds if they (i) are better at finding these places (i.e. more explorative; e.g. Patrick & Weimerskirch (2014)), (ii) spend more time feeding or mating (i.e. more active; e.g. Montiglio et al. (2016)), (iii) are less afraid of predation or (iv) are better in defending and gaining easier access to mates and food sources (i.e. bolder; e.g. Collins et al. (2019); Krüger et al. (2019); Réale et al. (2000); Ward et al. (2016)), because they can outcompete conspecifics better (i.e. more aggressive, e.g. Coates et al. (2019); Krippel et al. (2017)), or gain more information or protection from their conspecifics (i.e. sociality; e.g. Gartland et al. (2022); Hasenjager et al. (2020)). However, which personality has the better chance of reproduction and/or survival is highly dependent on environmental conditions and a trade-off between costs and benefits (Sih, Bell, Johnson, et al., 2004; Sih et al., 2012). For example, when predator pressure is high, bold individuals have a higher risk of being predated than shy individuals, which may counteract the benefits of more access to food (Balaban-Feld et al., 2019; Dingemanse et al., 2007; Sih et al., 2003).

1.3.2 Consequences for populations

Consistent individual differences can influence population structure, viability and distribution (Bolnick et al., 2011; Forsman, 2015; Fig. 2).

First of all, personality can influence population structure, by influencing its cohesion. For example, bold and more explorative individuals have fewer interactions, but with more different members of the population (Aplin et al., 2013; Croft et al., 2009; Pike et al., 2008). This structure can influence how well information, such as on food location and migration routes can spread (Hoppitt & Laland, 2013). However, the same applies to less favourable conditions, such as the spread of disease (Sih et al., 2018). For example, spider populations that contained 40% bold individuals spread bacteria twice as fast as a population with only 10% bold individuals (Keiser et al., 2016).

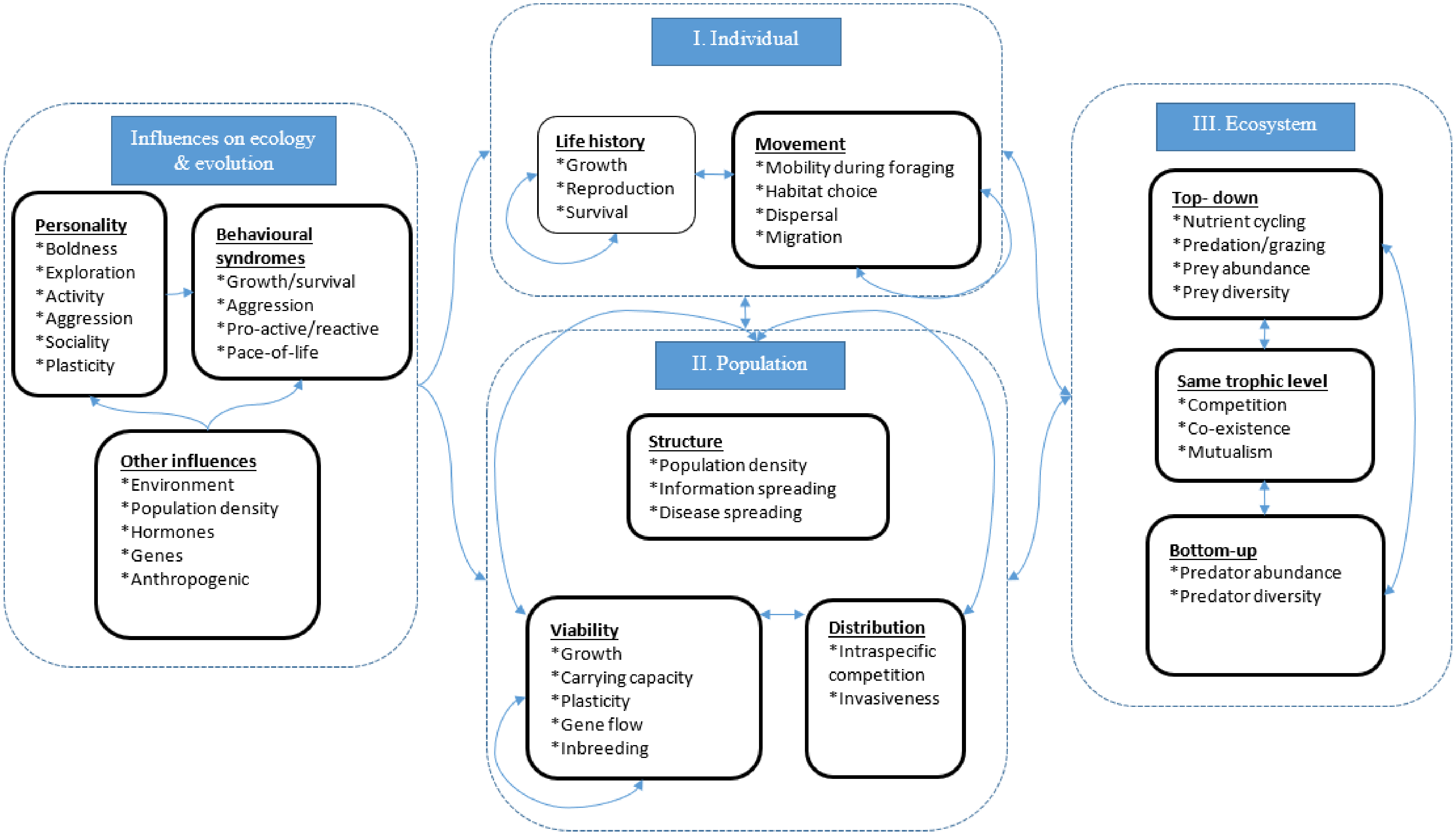


Figure 2. Schematic overview of the consequences of consistent individual differences on the individual level (life history and movement), cascading into population (structure, viability and distribution) and ecosystem effects (top-down, same-level and bottom-up).

Additionally, personality can influence population viability. Populations that contain consistent variation have the ability to be more plastic as a whole and can be thereby more resilient to for example environmental change (Sih et al., 2012). Furthermore, individual food and habitat preferences can expand the available niche of a population and thereby reduce intraspecific competition (Forsman, 2015; Herath et al., 2021). The growth and the total number of individuals that an environment can maintain, i.e. the carrying capacity, is in that case not dependent on the total number of individuals in a population but on the number of individuals with a certain personality type, which can influence population size, growth, productivity and stability (Bolnick et al., 2011). When personality traits specialize, are heritable and consistently differ in their fitness (i.e. not context- or frequency-dependent), this could eventually lead to speciation (Bolnick et al., 2011; Rice, 1987). Speciation may in turn be sped up by (dis)assortative mating based on personality type (Ariyomo & Watt, 2013). The downside is that this also could easily lead to inbreeding and thereby lower a population's viability (Koolhaas et al., 1999).

Finally, personality-dependent distribution cannot only influence intraspecific competition but can also determine how well a population can invade new habitats. Different personality types can facilitate different stages of dispersal and thereby join forces to perform a successful dispersal (Bowler & Benton, 2005; Clobert et al., 2009; Cote et al., 2010; Shaw, 2020). Boldness, for example, may play a role in the decision of departure and lay the way for shy individuals to follow that are more neophobic (Bevan et al., 2018; Chapman, Hulthén, et al., 2011; Found & St. Clair, 2019; Greenberg & Mettke-Hofmann, 2001). After the decision to leave, the physical relocation may be led by individuals who are more active and explorative (Hoset et al., 2011; Reim et al., 2018). Finally, more aggressive individuals may clear the way for arrival at a new patch by competing with other species and the final (temporary) settlement, may be more successful for more sociable individuals (Chapple et al., 2012; Duckworth & Badyaev, 2007). How invasive a population is, is not only determining the success of the population but has also the potential to influence other species and whole ecosystems (Hunter Jr et al., 2021).

1.3.3 Consequences for ecosystems

The studies on the influences of personality on the ecosystem are understudied, but consistent individual differences influencing population dynamics have the potential to cascade and eventually influence biodiversity and ecosystem processes by differences in foraging patterns and transportation of nutrients and other organisms (top-down), by competition, co-existence and mutualism (same trophic level) and by being preyed upon (bottom-up), thereby influencing energy pathways in food webs (Hunter Jr et al., 2021; Fig. 2).

Personality can influence lower trophic levels, for example, repeatable individual differences in litter deposition by crayfish caused primary production to be at similar levels as a double population size would achieve (Raffard et al., 2017). Consistent individual differences in seed dispersal can influence plant fitness, mediated by the individual's differences in habitat choice and dispersal (ingestion and deposition), caching decisions (low vs. high pace-of-life), how well individuals find 'hidden' fruits (boldness/exploration) and the sprouting ability after digestion (metabolic activity) (Zwolak & Sih, 2020). Personality differences in the example of Darwin's earthworms have the potential to influence soil quality (Hunter Jr et al., 2021).

On the same trophic level, personality differences can influence interspecific competition and facilitate co-existence in species with overlapping niches (Milles et al., 2020). For example, two populations of lemmings that overlap in their niches managed to co-exist because of their differences in activity and explorative behaviour (Morris et al., 2019). Shrimp and goby could share the benefits of shared burrows because they had matching activity and vigilance levels (Burns et al., 2019). Shy anemonefish that spend more time in the close vicinity of their host sea anemones, increased their host's growth (Schmiege et al., 2016).

Finally, personality differences can also influence higher tropic levels, i.e. through bottom-up influences as prey, directly (e.g. through more risky behaviour and/or differences in habitat choice) or indirectly (e.g. through differences in body size) (Bolnick et al., 2011). Individual differences in habitat choice in a branch herring stimulated diversification in its predator (Brodersen et al., 2015). Bivalves with different predator escape techniques, i.e. closing or escaping, sustained two otherwise competing snail species (Kent, 1983).

Although the many examples above show that personality can have important consequences on all levels of life for ecology and evolution, some caution needs to be taken to study these topics, which I will describe in the next section.

1.4 How to measure personality (and how not)

1.4.1 Defining personality

The booming, fast-developing field of repeatable behaviour over the last 25 years has led to incongruencies among researchers. To start with, personality is an accepted term to describe these differences, but other terms also have been used; i.e. behavioural individuality, coping style and temperament (Bierbach et al., 2017; Dall et al., 2004; Koolhaas et al., 1999; Réale et al., 2007). Additionally, there are subtle differences in the definition of personality used by different researchers (Sánchez-Tójar et al., 2022). Throughout this thesis, we use "personality" and the most commonly used description: "consistent between-individual differences in behaviour across time and/or context" (Réale et al., 2007; Sánchez-Tójar et al., 2022).

One consensus among researchers in this field has been reached: the same behaviour should be measured more than once to be able to determine repeatability and thereby label a behaviour as personality (Dingemanse & Wright, 2020). Visually, repeatable behaviour can be shown through plotting behavioural reaction norms that show the behaviour per individual for different time periods (see Fig. 1 & II.2). Statistically, personality in the biological literature is usually defined in terms of repeatability ("R", also termed intra-class correlation coefficient (ICC)), i.e. "the proportion of total variance accounted for by differences among groups" (Nakagawa & Schielzeth, 2010). It is based on the "among-individual" variance (σ_{α}^2; also called "between-group", "group-level" or "ID-level") and the "within-individual" variance (σ_{ε}^2; also called "within-group", "residual-level", "data-level" or "observation-level") which can be extracted from the output of generalized linear mixed models that includes the individual as a random effect. Repeatability (R) is then calculated as

$$R = \frac{\sigma_{\alpha}{}^{2}}{\sigma_{\alpha}{}^{2} + \sigma_{\varepsilon}{}^{2}}$$

and thereby ranges from 0 to 1, the latter being perfectly repeatable. Among-individual variation consistency arises when different behaviours occur in the sample, while within-individual consistency occurs when individuals behave similarly between time and/or context (Sih & Bell, 2008). Repeatability can be low either because of high within-individual variation or low between-individual variation. However, it is being debated whether the denominator should include all or any fixed effects and whether all random effects should be included (de Villemereuil et al., 2018; A. J. Wilson, 2018). If for example, we look at the between-individual variation of running time of a marathon for two people. As person A has intensively trained for a year, while person B has not, and we believe this can affect their running time, we include this in the fixed effects of our model. The data show that person A runs the marathon in three hours, while it takes person B six hours. However, if the training time is taken into account, the result will show that there are no between-individual differences. It is therefore important to carefully consider which fixed effects should be included in repeatability estimates and which not (de Villemereuil et al., 2018).

1.4.2 Measuring personality: Test choice

The practical procedure of collecting personality data comes with additional difficulties. First of all, several behaviours may be an indication of the same personality trait. For example, the latency to leave a shelter, the response to a fake predator as well as the inspection of a novel object have all been used as a measure of boldness e.g. (Carter et al., 2012; Réale et al., 2007). On the other hand, one behaviour may be explained as several personality traits. For example, cruising in an open field test may be used as a measure of exploration, boldness or simply a measure of stress tolerance (Carter et al., 2013; Perals et al., 2017). The initial aim of creating personality labels was to provide a working tool, but at the same time, because of the above-named factors, it is very hard to compare personality traits among studies. This is one of the reasons that critics have argued against trait labelling at all (Beekman & Jordan, 2017). However, before-hand verification of which test is eliciting the aimed behaviour and study behavioural entanglement within a test can provide clearance (Carter et al., 2012, 2013; Koski, 2011; Toms et al., 2010). Secondly, behaviours can form complex syndromes and what is adaptive for one personality trait in one situation may show a non-adaptive pattern in another, simply because it is linked to a behaviour that is adaptive (but non-measured). Ideally, several personality traits should therefore be measured (Sih, Bell, Johnson, et al., 2004).

1.4.3 Measuring personality: Short vs. long intervals

As mentioned in 1.4.1, the same behaviour should be measured more than once to be able to determine repeatability (Dingemanse & Wright, 2020). This leads to the next precarious subject of defining the interval between measurements. If the time interval between two measurements is too short, habituation to the test may occur, especially when a test includes a novel feature such as an open field or a novel object (Carter et al., 2013). This may result in lower repeatability if the individual does not experience the second trial similarly to the first trial. On the other hand, not enough time between trials may also cause an unwanted increase in repeatability, because of autocorrelation, where points closer in time are more likely to be the same, due to for example slow changes in hormone levels (Biro & Stamps, 2015; Mitchell et al., 2020; Noonan et al., 2019). On the other hand, a time interval between two trials that is too long can reduce repeatability between measurements, because multiple seasons or developmental stages that induce changes in hierarchies between individuals are included (Cabrera et al., 2021; Stamps & Groothuis, 2010). A meta-analysis showed that long-term repeatability is in general lower than short-term repeatability (Bell et al., 2009). The ideal interval depends unsurprisingly on the life history of the study species (i.e. from minutes in a one-day fly to decades in that of a long-lived species such as a tortoise) and the research questions while finding the balance between the perils above.

1.4.4 Measuring personality: Laboratory vs. field

Personality measurements usually take place in the laboratory, where environmental conditions such as temperature, light and encounter rates with other individuals are under the control of the researcher (Campbell et al., 2009). It provides an environment where controlled experiments can take place, such as the influence of temperature regimes on personality (Biro & Stamps, 2010). However, care should be taken when variables expand out of the limit usually experienced by the study animal. Such a response to extreme conditions usually requires time and natural selection and elicited behaviours by such variables, may be normally out-selected in the wild (Niemelä & Dingemanse, 2014). Additionally, laboratory housing environments are often far from natural and handling stress can easily influence an individual's behaviour which further complicates interpreting behaviour measured in the laboratory, rather than in its natural environment.

On the other hand, while natural measurements are by definition natural, it is often impossible to control for environmental factors, such as temperature and the presence/absence of conspecific or predators. If individuals experience differences in these factors, pseudo-repeatability may arise, where the repeatability of the behaviour is dependent on the (different) environmental conditions experienced (Niemelä & Dingemanse, 2017; Zsebők et al., 2017). It is possible to add such variation to the statistical models used to analyse the data, but whether such an approach is correct is under debate (see 1.4.1 and Wilson (2018)). The minimum to do currently is to be aware of such factors present in the experimental setup and of the influences this may have on the results and conclusions (Biro & Stamps, 2010; Brommer, 2013; Nakayama et al., 2016; Spiegel et al., 2017). Further complications of measuring behaviours directly in the field may arise when individuals disappear (randomly or non-randomly) from the study site which complicates statistical analyses with different sample sizes (Wolak et al., 2012).

Laboratory, as well as field measurements, seem to contribute to crucial aspects of the understanding of personality. It is therefore important to validate that laboratory measurements can explain behaviours in the field before answering ecological and evolutionary questions (Carter et al., 2013; Niemelä & Dingemanse, 2017). Most likely, a validation between laboratory and field studies will result in inconsistencies, (e.g. Mouchet & Dingemanse, 2021), but these irregularities will expand knowledge and lead to further scientific progress.

2 Aims of the thesis

Consistent differences in spatial behaviour, such as space use and movement characteristics have only recently found their way into the personality literature and recent studies acknowledge that this field is highly underrepresented (Nilsson et al., 2014; Spiegel et al., 2017; Stuber et al., 2022). In addition, long-term repeatable behaviour is less studied than short-term behaviour, especially including seasonal differences, and investigating this topic could shed light on how movement remains consistent within a lifespan. Finally, not many studies cross-reference personality traits between laboratory and natural conditions, while these are not necessarily the same (Mouchet & Dingemanse, 2021; Niemelä & Dingemanse, 2014). This thesis collected repeated behavioural data, including acknowledged personality axes and movement data, in the laboratory and field and across different seasons on two fish species (Atlantic cod (*Gadus morhua*) and Arctic charr (*Salvelinus alpinus*); see chapter 1). With this data, this thesis aims to contribute to the above-named gaps by addressing the following topics (Fig. 3):

- Investigate and understand the measurements of the movement-related personality traits exploration and activity (Papers I & II).
- Study among-individual behavioural consistency over time, i.e. short-term intervals (up to a week) for exploration (Papers II-IV), activity (Papers II & IV), boldness (Papers III-V), and sociality (Papers III & IV) and long-term intervals (two months to a year) for exploration, boldness (Papers III & V), and sociality (Paper III).
- Study among-individual behavioural consistent across contexts, i.e. laboratory vs. field (Papers IV&V) and across seasons (Paper V).
- Investigate the link between the measured personality traits and local foraging-related space use (Paper IV), large-scale space use (Paper V) and partial feeding migration (Paper III).
- Investigate behavioural syndromes among the measured traits (Papers II-V).

We expect to find behavioural consistency across time as is found in many species, including fish (Conrad et al., 2011; Gosling, 2008) and across contexts, which is found between laboratory and field (e.g. Závorka et al., 2015) and between seasons (e.g. Harrison et al., 2015; Lukas et al., 2021; Nakayama et al., 2016, 2016; Taylor & Cooke, 2014). Furthermore, we expect to find overall high long-term repeatable movement and space use traits compared to other personality traits as was shown in a meta-analysis of spatial personalities (Stuber et al., 2022). Finally, we expect that all our measured variables are correlated, resembling a pro-active/reactive syndrome (Koolhaas et al., 1999; Sih, Bell, & Johnson, 2004), i.e. where bold, exploration and activity are positively correlated and sociality negatively.

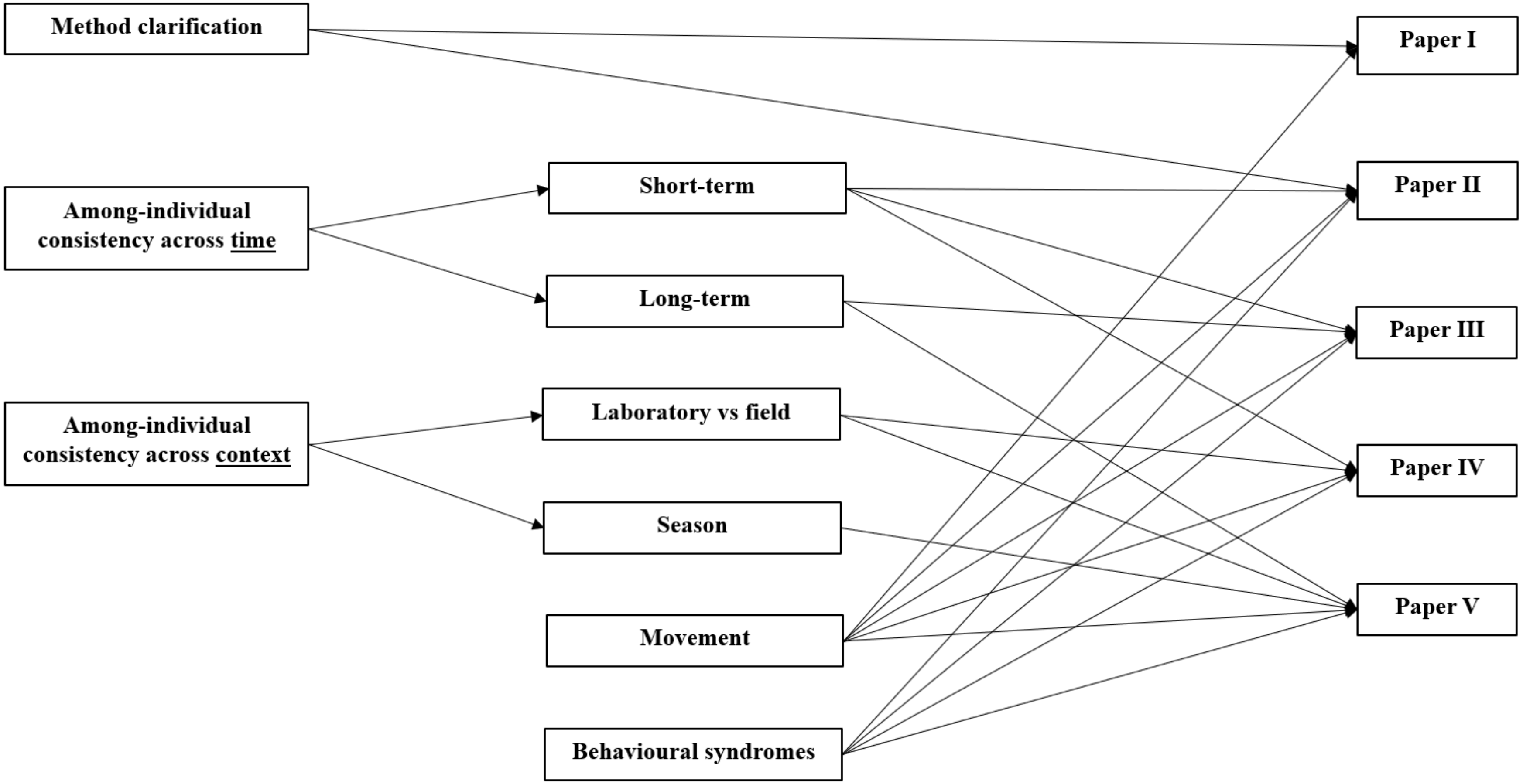


Figure 3. Overview of which aims are addressed in which papers.

3 Study system

The aims were addressed by studying two fish species that were chosen based on their differences in movement patterns. We started with behavioural measurements of marine Atlantic cod juveniles (*Gadus morhua*) as they show partial feeding migration, which has a genetic basis. This data is described in Papers I-III. We then continued studying a stream-dwelling population of Arctic charr (*Salvelinus alpinus)*, as this species shows a broad range of behaviours and its habitat is much more accessible (see 3.1.2). This data is the basis of Papers IV and V.

3.1 Study species and housing

3.1.1 Atlantic cod (*Gadus morhua*; Papers I-III)

Atlantic cod (*Gadus* morhua) is a benthopelagic marine fish of the family Gadidae. The Atlantic cod is widespread throughout the continental shelf on both sides of the North Atlantic Ocean and is an apex predator, which makes it a key species in its ecosystem (Link & Garrison, 2002). However, although the species has few natural predators, it is of high commercial importance and overfishing has reduced the worldwide population size by as much as 99.9% of its historical levels between 1960 and 1990 (Christensen et al., 2003; Hutchings & Reynolds, 2004). Although management measures ranging from a total fishing ban to size-dependent fishing quotas have given the species some space to start a slow recovery, moving away from “critically endangered” to “vulnerable” on the IUCN red list, these measurements are not everywhere as successful, as the recovery has been slow or even non-existent in some populations (Hutchings & Reynolds, 2004). In Iceland, the cod population has been fairly stable since 1983 when quotas were established, but a recent reduction in population size has been detected (*MFRI Assessment Reports*, 2020; G. Pálsson & Helgason, 1990). Interestingly, current measurements are often based on biomass estimates of an assumed homogenous genetic and/or phenotypic group of individuals (Kerr et al., 2017).

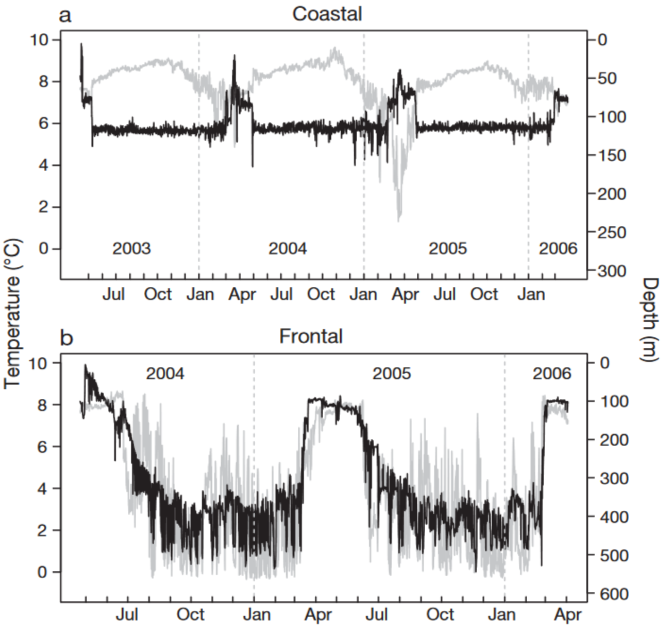


Figure 4. Repeatable depth (black) and temperature (grey) profiles of coastal (resident) and frontal (migratory) Atlantic cod. Reprinted with permission from Thorsteinsson et al. (2012).

However, if individuals differ within a population, personality may play an additional role in management (Olsen et al., 2012; Petitgas et al., 2010).


Figure 5. Individual housing of the cod juveniles in the laboratory in Bolungarvik.

The Atlantic cod is an ideal candidate for studying the theory of personality traits influencing movement, leading to differences in life history and population structure, with potential implications for management. Adults of this species have shown within-population behavioural differences, i.e. non-breeding partial migration (Chapman, Brönmark, et al., 2011b). “Residents” perform feeding migrations close to the shore year-round, while “migrants” take more extensive feeding migrations (100-1000 km) outside the spawning season (June-January; Pálsson & Thorsteinsson, 2003; Fig. 4). Interestingly, both the resident and the migration patterns are consistent over multiple years (Thorsteinsson et al., 2012). In Icelandic cod these movement patterns are genetically linked to the *Pan*I locus; which is located in a large linkage group of numerous genes (Matschiner et al., 2022; Pampoulie et al., 2022). The distribution of individuals carrying the *Pan*I^{AA} genotype is highly skewed towards the migrant behaviour, while individuals carrying Pan *Pan*I^{BB} are skewed towards the frontal behavioural ecotype, although published research during this PhD has shown that *Pan*I^{AA} is a better predictor for residency than *Pan*I^{BB} for migration (Kirubakaran et al., 2016; Pampoulie et al., 2022; Pogson & Mesa, 2004). This genotype provides possibilities for “easy” migration estimates measured in the laboratory to observe movement patterns in the wild.

To address the above-named aims (see Chapter 0), we beach-seined 102 age 0+ cod juveniles in October 2019 in three different fjords around the Westfjords of Iceland to obtain genetic variation (Fig. I.1). They were transported to a laboratory in Bolungarvik, Iceland, and measured for standard length (STL) and weight and housed individually in 9.5-litre tanks (“home tanks”, ~29x21x19cm, water level 16 cm, Aquaneering Inc., Fig. 5). Activity measurements took place in these home tanks, while the other personality traits were collected in an experimental area (see Papers II & III).

3.1.2 Arctic charr (*Salvelinus alpinus*; Paper IV & V)

Arctic charr (*Salvelinus alpinus)* is a member of the Salmonidae family and is the northernmost, circumpolar freshwater species. Charr are mostly found in lakes and the colder, uppermost parts of rivers and streams which are often species-poor and low-productive (Klemetsen et al., 2003). Interestingly, individuals vary majorly in their phenotypic expression (e.g. variation in colour and pigmentation, foraging mobility from sit-and-wait to mobile strategies), ecology (e.g. habitat use; (epi)benthic, pelagic and littoral zone, diet; plankti-, mollusci-, insect- and piscivorous) and life history (e.g. weight at maturity ranging from 0.003 to 12 kg, spawning during different months of the year) and show thereby more variation than most fish (Jonsson & Jonsson, 2001; Klemetsen, 2010; Klemetsen et al., 2003; Sandlund et al., 1992; Tunney & Steingrímsson, 2012).

The population studied in this thesis resides in the upper part of river Grímsá, northern Iceland (N 65.792379, W 19.844413; Fig. 6). This part of the stream is shallow (average 10-50 cm deep) and narrow (1-5 m wide), which makes it an ideal study stream as it limits vertical and horizontal movements respectively (Rasmussen & Belk, 2017). The only natural fish population in this part of the stream is Arctic charr (*Salvelinus alpinus*), but juvenile Atlantic salmon are occasionally released for enhancement purposes of a downstream salmon population. Potential predators include bigger conspecifics, introduced American mink (*Neogale vison*), red-breasted merganser (*Mergus serrator*) and the Arctic tern (*Sterna paradisaea*), although only the latter has been observed around Grímsá and predation pressure is generally low (pers. obs). The stream originates as a run-off stream and a waterfall 4.8 km from the origin blocks upstream fish movement into the study section (Fig. 6; most northern red dot). Three main tributaries flow into this part of the river Grímsá which are all blocked for fish passage upstream, two by a waterfall and one by an artificial road

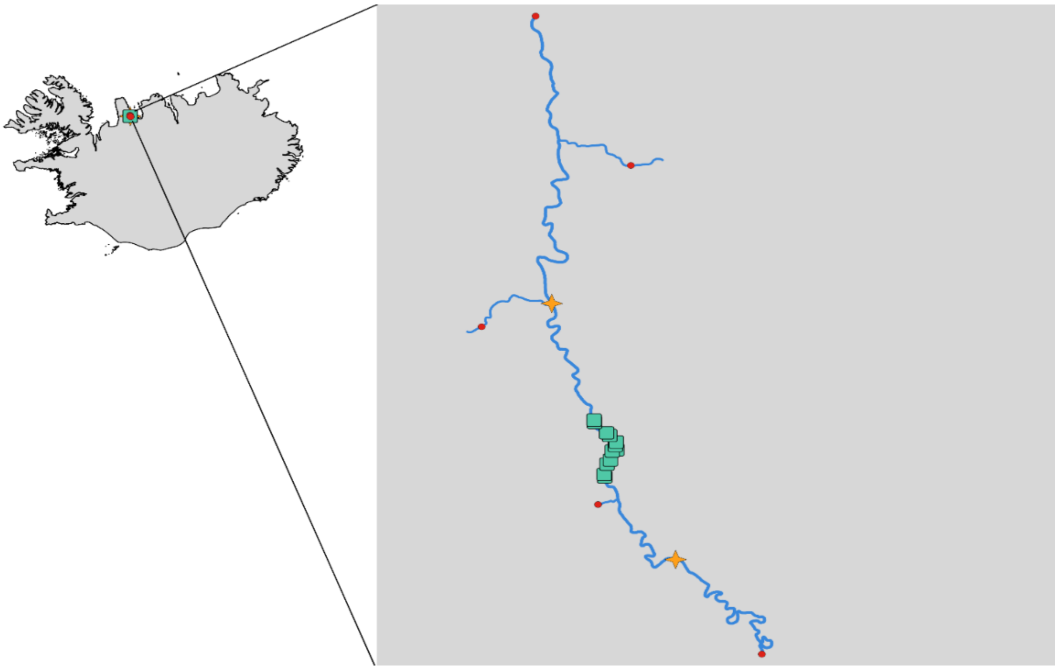


Figure 6. A map of river Grímsá (blue). Stream enclosures from which fish were released are depicted by green squares, the boundaries of the main study stream by the two yellow stars, three waterfalls and one impassable road culvert that confine the distribution of the population by red dots. The arrow indicates north and the flow direction. Map credits: Eric dos Santos & QGIS.

passage (Fig. 6; other red dots). The species is thereby landlocked which may be the reason that individuals stay relatively small (up to 20 cm, pers. obs. SÓS). Charr are opportunistic feeders but feed mainly on drifting invertebrates, which are abundant during summer, but whose numbers reduce with decreasing temperatures with decreasing temperatures (Larranaga, 2016). Higher temperatures have been shown to increase feeding activity in this species in this stream (Larranaga, 2016) and similar streams (Fingerle et al., 2016), but they also stay active during the winter (Klemetsen et al., 2003). The species has been shown to defend territories while feeding, although their home range overlaps more than in other salmonids, and they show different mobility patterns during feeding (Gunnarsson & Steingrímsson, 2011). Specific spawning timing has not been studied in this stream, but sexually mature fish have been observed in October during electrofishing (pers.obs.).

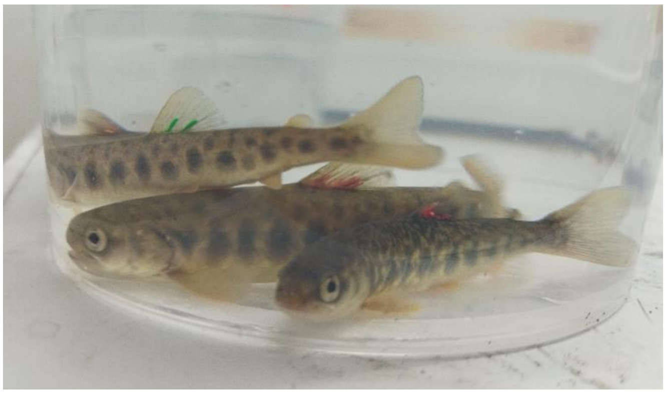


Figure 8. Four Arctic charr recovering from aneasthetics during VIE tagging which allows for individual identification per tank/stream enclosure.

Figure 7. Home tanks of Artic charr in the laboratory

To address the above-named aims, a total of 96 Artic charr of age 1+ were electro-fished (LR-24 electrofisher, Smith-Root, Inc., Vancouver, Wash., USA) on 22 and 23 June 2021 in river Grímsá (Fig. 6). They were transported on a 10-minute drive to the Verið laboratory in Sauðárkrókur (Department of Aquaculture and Fish Biology, Hólar University). Individuals were anaesthetized with 0.3mg/L phenoxyethanol and measured for fork length to the closest 0.1 mm with callipers and body mass to the closest 0.01 g. Then, fish were subcutaneously tagged with visible implant elastomer (VIE; Northwest Marine Technology, Inc., Washington, USA) using different combinations of yellow, green, orange, pink and red in two positions along the dorsal fin (Fig. 7). Subsequently, the fish were randomly assigned to twelve circular grey 120 L tanks (8 fish/tank) with pebbles on the bottom to provide shelter and thereby reduce potential stress, with a constant input of fresh water in the tanks (Fig. 8). Personality traits in the laboratory were measured in an experimental arena (see Papers IV & V). After the laboratory experiments, the fish were transported back to the stream and placed in stream enclosures. Enclosure size was 2.4m (l) x 1.0m (w) x 0.75m (h) which for 8 fish per enclosure is within range of natural densities for stream salmonids (i.e. 3 fish/m^2; Gunnarsson & Steingrímsson, 2011) (Fig. 9; Paper IV). Six metal support posts held the stream enclosures, which were made of a green nylon net (mesh size = 5 mm), allowing for the flow-through of water and drifting prey items (Keeley & Grant, 1997; Klemetsen et al., 2003; Zimmerman

& Vondracek, 2006). The stream enclosures were covered with a sieved local substrate (max ø 2cm). Metal bars with markers were laid out on the bottom to create a 10 cm Cartesian coordinate system which allowed fish position determination (Fig. 9). Three cobbles of similar size were placed in each stream enclosure to provide shelters and crossed strings between the support posts deterred potential avian predation, but presumably without affecting the risk perception of the fish. Water flow was regulated with a wooden sluice gate to be roughly the same in all stream enclosures and water temperatures were measured every hour using HOBO® Pendant® Temperature Data Loggers (UA-002-08) at four stream enclosures. Stream enclosures were at least 10 meters apart and alternated between river bank sides to keep the influence of upstream enclosures on downstream enclosures as low as possible.

Figure 9. Stream enclosures with metal bars on the bottom indicating grids with 10cm markers (grey tape), three cobbles with moss functioning as shelters and white strings to prevent predation. Photograph credit: Kári Heiðar

After the stream enclosure observations, the fish were tagged with passive HDX PIT tags (ICAR-registered, Oregon RFID) by making a small incision in the abdomen. The fish were given three days to recover and after all the fish seemed healthy, the tops of the stream enclosures were lowered, so the fish could leave voluntarily. A day later, all the fish had left the stream enclosures. A week later, data collection started by collecting weekly GPS locations by walking slowly in the river with a mobile reading kit (Oregon RFID) containing a Single Antenna reader (Oregon RFID; range: 30 cm above and below, 15 cm from the side) while moving the scanning device 20-30 cm above the substrate (Fig. 10). When a fish was detected, the date, time, tag number and GPS location were recorded (GPS Logger v. 3.1.7; measurement error max. 2m). The slow walk through the stream only disturbed the fish slightly as fish were returning quickly to its detected location after disturbance (pers. obs) and fish were rarely detected multiple times on the same day, which could have been an indication for a downstream chase.

Figure 10. Weekly river scanning in summer (left) and winter (right) to collect GPS points.

3.2 Data collection

3.2.1 Exploration

In the absence of a predator, juvenile fish have been shown to move freely across an open space (Nordeide & Svåsand, 1990), which most likely serves the function of information gathering (Hughes, 1997). Therefore, an open field test was used as a proxy for exploration, where it is expected that explorative fish swim greater distances and cover a bigger area than non-explorative individuals. For both species, exploration was measured in the laboratory (Paper I-V), and for charr, initial travel distance in the field was used as a more natural measure of exploration (Paper V; Fig. 11).

3.2.2 Activity

Activity in a known environment was measured in the home tank for cod (Papers II & III) and in the stream enclosures for charr (Paper IV; Fig. 11).

3.2.3 Boldness

Boldness was measured in a novel object test for cod, where bold individuals were expected to become more active and approach the novel object, while shy individuals were expected to flee, retreat or become inactive (Toms et al., 2010; Paper III; Fig. 11). For charr, boldness was measured using a shelter test, where several measurements, including the latency to exit and a measure of thigmotaxis, were extracted and then combined in a PCA, where bolder fish were expected to leave the shelter faster and showed less thigmotaxis than shy fish (Toms et al., 2010; Papers IV &V; Fig. 11).

3.2.4 Sociality

Sociality was measured as the interaction with conspecifics, excluding aggressive behaviour, where closer distances to conspecifics indicate more social individuals. In cod, this data was collected using a mirror test (Paper III; Fig. 11). Cod juveniles can show plastic social behaviour, from shoaling to aggression (Meager & Batty, 2007). The mirror test can be used to measure both sociality and aggression, depending on the species and developmental phase. While Villegas-Ríos et al. (2018) used the mirror test as a measure of aggression in adult cod, the life stage where the risk of being predated is minimal, we assume that the mirror test in this study on juveniles elicited social behaviour instead for two reasons. Firstly, the arena was open with no shelter to hide, which has been shown to elicit shoaling behaviour in juvenile cod (Laurel & Brown, 2006). Secondly, aggressive/submissive behaviour often occurs when opponents differ in size (McCormick & Weaver, 2012; Sverdrup et al., 2011) and as the mirror just reflects the fish itself, these size differences are non-existent. In charr, sociality was measured by calculating the mean distance to the closest neighbour during the stream enclosure observations (Paper IV; Fig. 11).

3.2.5 Movement-related behaviour

Local foraging-related movement (small-scale space use) in charr was extracted as the individual home range kernel from the stream enclosure observations (Paper IV&V; Fig. 11). Large-scale movement in charr was extracted from the distances between consecutive GPS points in the stream (Paper V; Fig. 11). Finally, individual partial migration tendency was determined in cod using fin clips to assign the fish to either coastal ($Pan\mathrm{I}^{AA}$), frontal ($Pan\mathrm{I}^{BB}$), or heterozygote ($Pan\mathrm{I}^{AB}$) using PCR analyses as described in Ólafsdóttir et al., (2023); Pampoulie et al. (2006) (Papers II & III; Fig. 11).

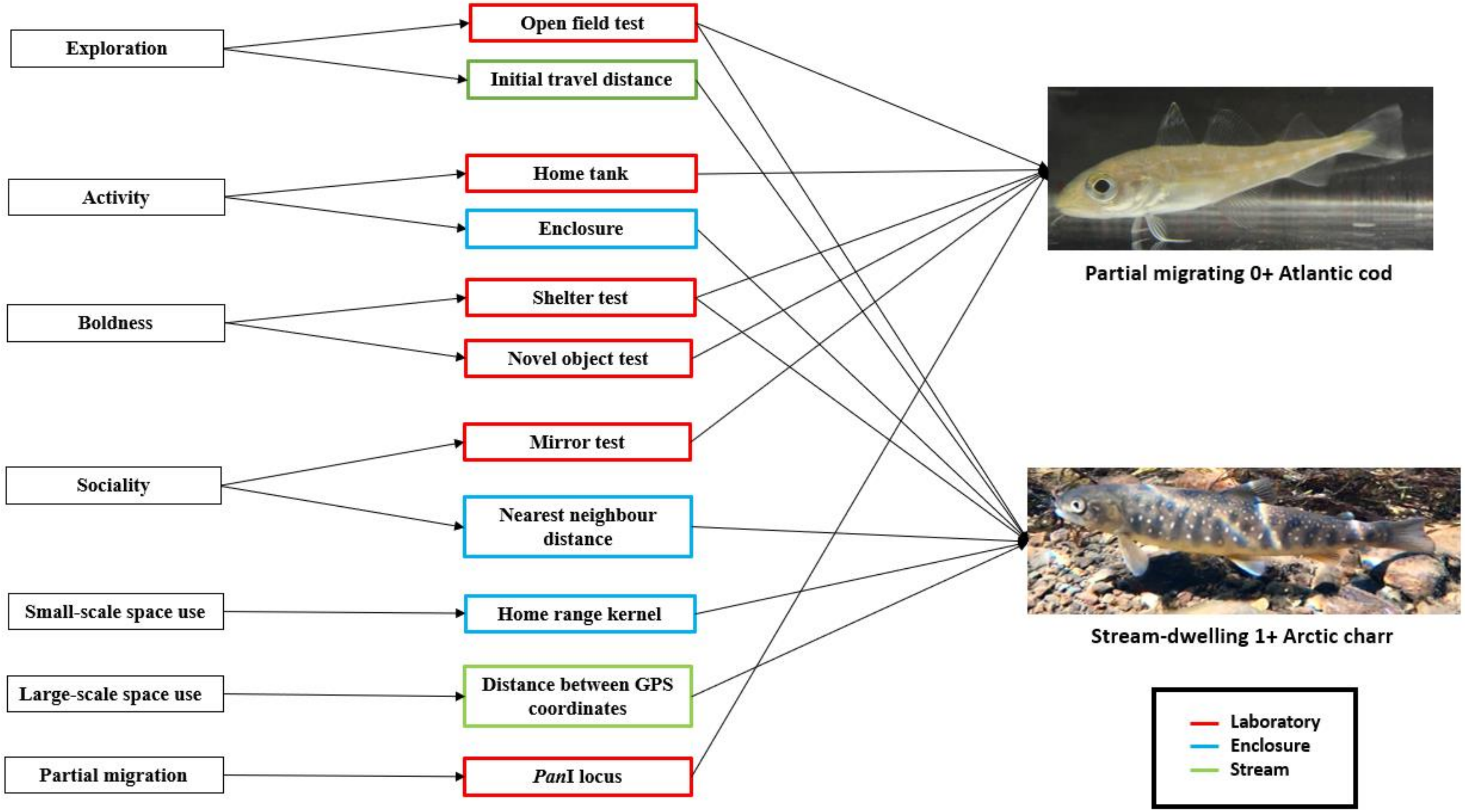
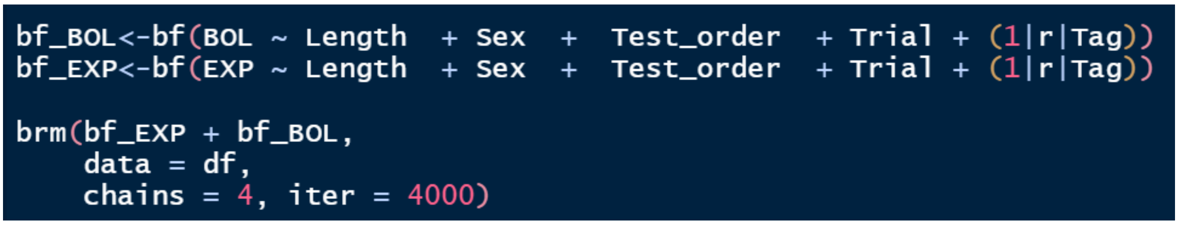


Figure 11. Methods of personality measurements and space use for Atlantic cod and Arctic charr in the laboratory (red), stream enclosures (blue) and stream (green).

3.3 Statistics: Bayesian modelling in R (Paper II-V)

All data were processed and analysed using R v. 4.0.4 (R Core Team, 2022) and all main data analyses are based on Bayesian multivariate modelling using Stan (Carpenter et al., 2017) ran through the “brms” package in R (Bürkner, 2017), thereby avoiding the use of p-value statistics as much as convenient (e.g. Nuzzo, 2014; Rigby, 1999; Wasserstein & Lazar, 2016). The benefit of these models is that multiple models are combined, i.e. the model simultaneously can regress each dependent variable (i.e., the personality traits) against a set of fixed (such as sex and length) and random effects (i.e. Fish ID) while also quantifying the covariance between the dependent variables, i.e. behavioural syndromes (Fig. 12). As the random-effects structure included individual fish identity (ID) as a grouping variable, it was possible to calculate the repeatability of the dependent variables as the ratio of the among-individual variance and the sum of the among-individual and residual-level variances (i.e. personality; see 1.4.1), which were recalculated from the standard deviation (i.e. among-individual variance = sd^2) and sigma (residual-level variance = sigma^2) from the model output. Model convergence was assessed using the standard diagnostics provided by Stan, including the potential scale reduction factor ($\hat{R}$-hat), effective sample size, and visual inspection of trace plots and histograms for each model parameter (Stan Development Team, Version 2.32).



```
bf_BOL<-bf(BOL ~ Length  + Sex  +  Test_order  + Trial + (1|r|Tag))
bf_EXP<-bf(EXP ~ Length  + Sex  +  Test_order  + Trial + (1|r|Tag))

brm(bf_EXP + bf_BOL,
    data = df,
    chains = 4, iter = 4000)
```

Figure 12. Example of R code for running the multivariate model which is able to regress the two models of bf_BOL and bf_EXP simultaneously and estimate their covariance. The addition of the individual fish ID (Tag) as a random effect allows for the calculation of repeatability.

4 General results

First of all, Paper I shows that it is important to take the distance travelled as well as the area covered into account when measuring exploration in an open field test. Furthermore, paper II shows that activity should not be measured in a novel environment, as is regularly found in the literature, despite being clearly defined by Réale et al. (2007), as it thereby intermingles with the definition of exploration (Réale et al., 2007; Fig. 13). Locomotion data of cod in a known and unknown environment showed that locomotion was more consistent and on average higher in the known environment compared to the unknown environment and no relation between both traits was detected. This demonstrates that locomotion in both environments, i.e. the personality axes activity and exploration, most likely have different underlying motivations and should therefore not be confused nor treated as if they reflect the same personality trait.

Secondly, this thesis provides evidence for repeatable behaviours across time, i.e. personality, in cod and charr. Especially movement-related behaviours seemed to be more often repeatable than other personality traits (Fig. 13; green connections). Exploration was repeatable in the short-term (up to one week) in cod (Papers II & III) and in charr (Paper IV), as well as longer-term: across two months in cod (Paper III) and one year in charr (Paper V; Fig. 13. Activity was found to be repeatable across short-term intervals in cod in the laboratory (Paper II) and in charr in stream enclosures (Paper IV), and larger-scale space use based on distances between weekly GPS positions in the stream for charr also turned out to be repeatable, but only in summer (Paper V). On the other hand, local foraging-related space use based on home range kernels in the stream enclosures was not found to be repeatable in charr. Mixed results were found for the less-movement-related traits of sociality, in which repeatability was dependent on species, and boldness which showed short-term repeatability in both species, but not long-term (Fig. 13); red and blue connections). In cod, both traits were only repeatable in the short-term (three days) in one month (March), but not in another (January) and neither was repeatable over a two-month interval (Paper III). In charr, sociality was repeatable over a short-term interval (one week) and not measured long-term, while boldness was repeatable short-term, but not over long-term intervals (Papers IV & V).

Thirdly, this thesis found no strong evidence for repeatable behaviour across contexts as no correlations were found between the laboratory and the field (Papers IV & V), nor between seasons (Paper V; Fig. 13). A trend was visible for a correlation between exploration measured in the laboratory and the field (Paper V).

Finally, no evidence was found for behavioural syndromes for any of the measured traits in both species (Papers II-V), except for one behavioural syndrome between sociality and activity, where less social charr were less active (Paper IV; Fig. 13). However, a trend was visible for a possible relation between exploration and a feeding migration-linked allele (*Pan*I) in cod, where residents were more explorative than heterozygotes, but no data on migratory cod was available (Papers II & III; Fig. 13).

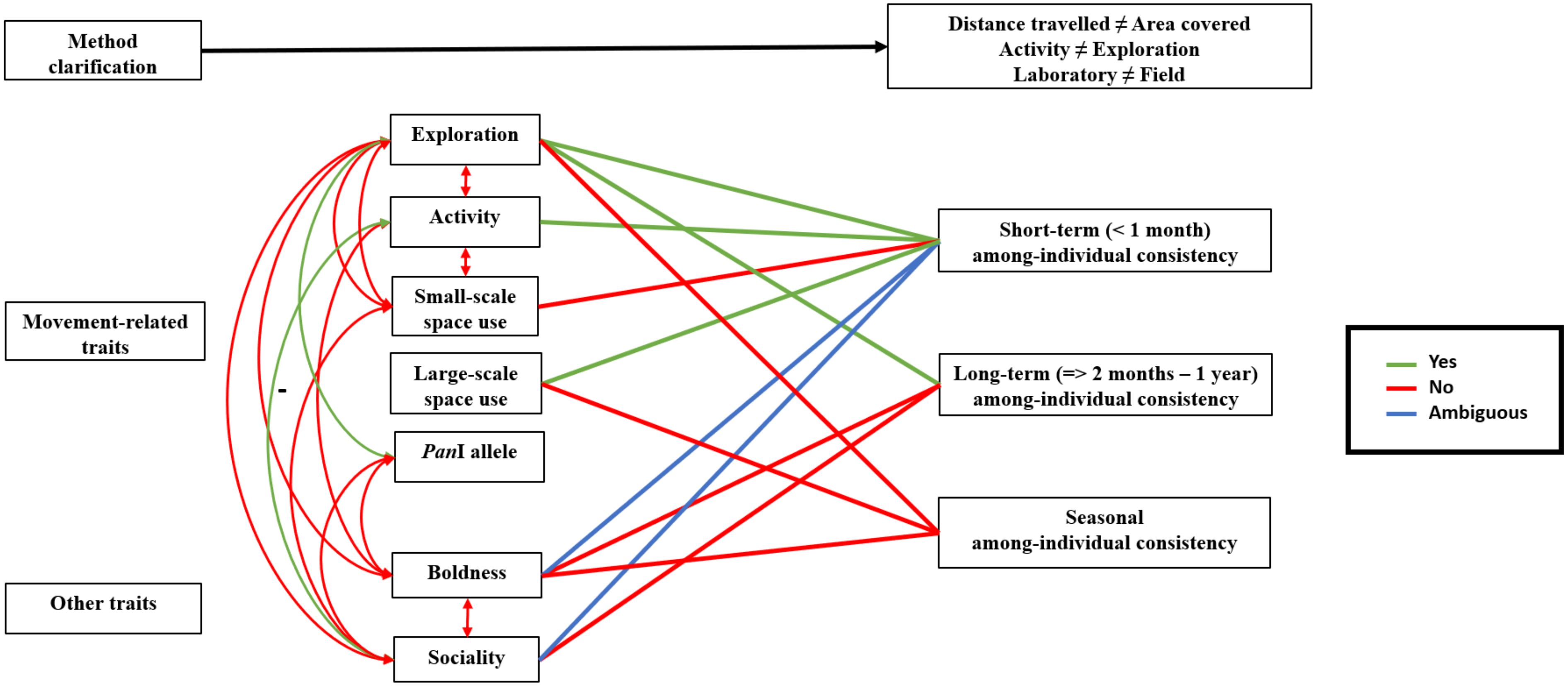


Figure 13. Overview of the main results of the thesis, including results indicating methods clarification, short-, long- and seasonal behavioural consistency of movement-related and other traits and behavioural syndromes. Green connections confirm the existence, while red rejects this connection and blue indicates ambiguous results.

5 General conclusion and further directions

This thesis aimed to investigate the role of personality on movement-related behaviour. All papers presented in this thesis together show clearly that fish display behavioural among-individual consistency across time, especially for the behaviours underlying movement, such as activity, exploration and large-scale space use. The results from all papers indicate that these measurements are more repeatable, more often repeatable and across longer time intervals than other personality traits (such as boldness and sociality) which supports similar findings recently summarized (Stuber et al., 2022). The reasons for these findings may lay in the fact that individuals are similarly bound by external constraints, which are often the same across situations and are thereby more susceptible to pseudoreplication (Spiegel & Pinter-Wollman, 2022; Vander Wal et al., 2022). However, the finding suggests a possible genetic basis of exploration in Atlantic cod, which may be another explanation for highly repeatability personality traits. Regardless of the cause, consistent individual differences in movement may have implications for ecology and evolution on the individual level and can cascade into population and ecosystem consequences (see 1.3). Personality may therefore play an important role in management strategies as we describe in Paper IV. Additionally, except for temperature, no other environmental conditions were measured in this thesis and future research should include the effect of for example substrate size and stream flow and aim for experimental manipulations of such external factors to study their influence on repeatable movement behaviour.

On the other hand, the papers on Arctic charr within this thesis linking laboratory measurements with measurements in the field and linking behaviours across different seasons, show that there is not much evidence for consistency across contexts. This implies that care should be taken while using laboratory measurements to explain natural behaviours and that researchers should be aware that seasonal differences may influence the repeatability of behaviour. Future studies should therefore ideally test predictions in multiple contexts.

The results of this thesis also show not much evidence that the behavioural traits are related to each other, i.e. that they are forming behavioural syndromes. Most likely these behavioural estimates are based on separate underlying mechanisms and have thereby the ability to develop or, if heritable, to evolve independently from each other.

Furthermore, as some results are consistent between Atlantic cod and Arctic charr, such as short-term repeatable exploration, activity and boldness, these results may apply to other fish species and even other taxa. In other cases, such as in the case of sociality, results have shown to be more species-specific. Further research is needed to establish whether these differences are indeed species-, environmental- or method-specific.

Finally, there seems to be no perfect way (yet) to define and study personality. Studies seem to be accepted as long as definitions, measurements and experiments are clearly explained and substantiated. In this thesis, I aimed to approach the inconsistencies in the field by

- defining personality and the used traits clearly in every paper
- aiming for substantiated hypotheses and methods
- combining several personality traits and other possible influences
- recognizing potential caveats in the methods
- being cautious while interpreting results
- discussing potential caveats

However, the field is still majorly evolving as even the big names in the field are acknowledging: “We ourselves have made many, if not all, of the aforementioned “mistakes” in our past publications, but we have always tried not to repeat them once a superior approach has been recommended.” (Dingemanse & Wright, 2020). Getting around in the field is being aware of its weaknesses and difficulties which I have tried to lay out along the way. Nonetheless, besides the difficulties, this journey has let me through very interesting concepts of animal behaviour along the way and I hope I managed to bring you along with me.

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Paper I

Brief communication: How to measure exploration? A combined estimation method.
Authors: Rosanne Beukeboom, David Benhaïm

Summary

In this short communication, we demonstrate that achieving a good measurement of exploration often does not only include the total distance travelled but also a measure of space use. As none of the available behaviour-tracking software provides a measure of space use in their output summary, we provide an easy way to calculate such a measure from the available position data provided by the software and a method to determine the best proxy for exploration.

Introduction

Studies aiming at unravelling consistent individual differences (i.e. personality) within populations are numerous. Verification of the methods used to collect personality data is therefore important (Carter et al., 2013). The personality trait "exploration", which is defined as "an individual's reaction to a new situation" (Réale et al., 2007) is often measured in an open field test (Perals et al., 2017). There are two common ways to extract a measure of exploration from this open field test, either manually, or by using software.

Studies that collect data on exploration manually often include measurements of mobility level, e.g. the total number of line crossings (Bajer et al., 2015; Favati et al., 2016) and space use, e.g. the number of unique areas visited (Bell & Stamps, 2004; Galib et al., 2022; Kaiser et al., 2018; Schürch & Heg, 2010), or a combination of those, e.g. the time to reach a specific area (Kaiser et al., 2018; Rödel & Meyer, 2011).

Commercially available video tracking software, such as Ethovision XT (Noldus et al., 2001) and LoliTrack (Loligo® Systems, Viborg, Denmark) and freeware, such as ToxTrac (Rodriguez et al., 2018) have been developed to increase speed, improve accuracy and make the standardization of the analysis of behavioural data in general easier. Besides providing the raw x/y position of one or multiple individuals, it also provides 'summary statistics', which includes variables that could be an indication of exploration, such as the total distance travelled and mobility rate. However, an output summary of the total area covered is not provided.

Some researchers have continued in the same line with the manual methods by extracting the same variables with the help of the software, for example by dividing the arena virtually into multiple zones. However, as the output does not provide summary statistics of space use, these measurements are still as 'rough' as the manual methods, e.g. time spent in the border/center (Eilam, 2003; Tran et al., 2021), the total number of areas visited (Lamb, 2018) or a combination of these (Alstott & Timberlake, 2009; Michelangeli et al., 2020), sometimes combined into a PCA (Edenbrow & Croft, 2011; Horback & Parsons, 2018).

In addition, the absence of summary statistics for space use might unintentionally encourage studies to investigate and report only measurements that are included in the summary, i.e. the total distance travelled while ignoring space use, (e.g. Bierbach et al., 2017; Guenther et al., 2014; Niemelä et al., 2019; Polverino et al., 2016; Santostefano et al., 2017; Scherer et al., 2017; Stewart et al., 2012), but see Beukeboom et al. (2022); Boulton et al. (2014); Cote et al. (2010); and Ramesh et al. (2022).

This brief communication aims to show the importance of including or at least verifying the correlation between distance travelled and area covered as a measurement of exploration and provides an easy method to calculate a measurement of the total area covered with adjustable resolution from raw x/y coordinates that can be extracted from the automated tracking software.

Methods

In 2019, 96 Atlantic cod juveniles (*Gadus morhua*) were subjected to an open field test (40x80 cm) for five minutes to study individual differences in exploration within the population (see for details Beukeboom et al., 2022, 2023). Their tracks were analysed with Ethovision (v. 15, Noldus, The Netherlands). For the purpose of this brief communication, all movement tracks were examined and three different types of movement patterns were discovered, e.g. stress behaviour (Fig. 1A), thigmotaxis (Fig. 1B) and regular swimming behaviour (Fig. 1C).

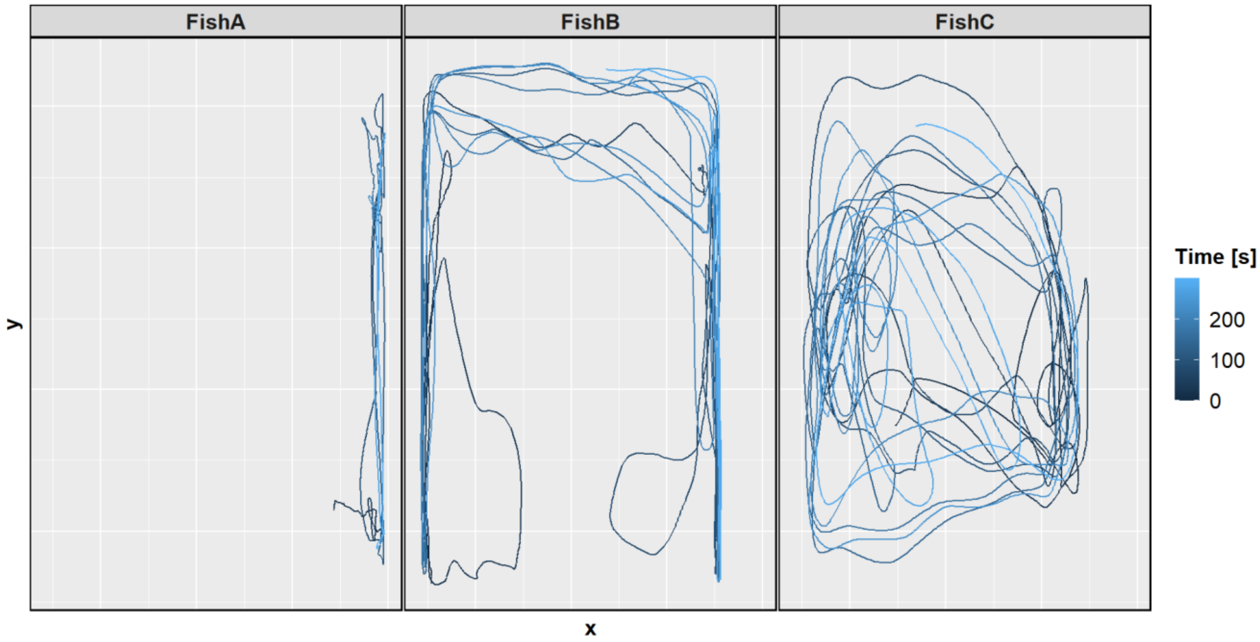

Figure 1. Movement tracks of three different Atlantic cod juveniles during 5 minutes (300 seconds) of an open field test.

The total distance travelled (DT) can be extracted from the summary of Ethovision. Alternatively, DT can be calculated by retrieving the raw x/y coordinates from the software and applying the Pythagorean theorem, which is not being discussed here. The total area covered (AC) can be calculated using the same raw x/y coordinates in the following way:

1. *Determination of resolution*
   The resolution of how much surface an individual is covering is dependent on the number of decimals of the x/y coordinates. The more decimals, the higher the number of unique x/y pairs and a higher correlation with the DT. The coordinates provided by the software are dependent on the input of the calibration settings but are usually too detailed (up to four decimals) to provide a biological meaning. Researchers should decide for their own studies how detailed the resolution should be and thereby how many digits they should use while applying rounding (Table 1, columns 4&5). This is for example dependent on the size and speed of movement of the study species: it might be useful to determine the space use of a beetle in millimetres (e.g. Schuett et al., 2018), while meters might be more useful in that of a shark (e.g. Finger et al., 2016).
2. *Pair the x/y coordinates to create positions (Table 1, column 6).*
3. *Find the total number of unique pairs (Table 1, column 7)*

Table 1. The first seven seconds of a track show the process from raw x/y coordinates to a total area covered (AC).

Time (s)	**X**	**Y**	**X (round to 0 digits)**	**Y (round to 0 digits)**	**XY (paste)**	**Unique XY (cumulative)**
0	1.27333	1.79976	1	2	1-2	1
1	1.45398	2.01877	1	2	1-2	1
2	1.56523	2.26223	2	2	2-2	2
3	1.88390	2.92539	2	3	2-3	3
4	1.88337	2.98183	2	3	2-3	3
5	2.00762	3.87827	2	4	2-4	4
6	2.66012	3.85639	3	4	3-4	5
7	3.00123	3.88109	3	4	3-4	5
					Total AC	**5**

In this example, the x/y coordinates were rounded to the nearest integer, which created a 1 cm resolution. As the open field test took place in an arena with 40*80 cm dimensions, total AC is limited to a maximum of 3200 unique data points. As we show real data, we interpolated the distance travelled for Fish A and B based on their previous behaviour to match the distance travelled with fish A to support the goal of this article.

Results and discussion

If we would base our exploration score solely on the distance travelled, we would conclude that there were no differences in exploration rate (i.e. 2400 cm including interpolation for all fish; Fig. 2). However, when taking the total area covered into account, we would conclude that fish A is the least explorative (AC=200), followed by fish B (AC = 800) and finally fish C (AC = 1350; Fig. 2). Consequently, the correlation between DT and AC for Fish A is non-existent, for fish B around 0.5 and close to 1 for fish C. Only in the last case, a single measurement would represent exploration as well as the use of both. In this case, it is probably best to continue with only a measurement of distance travelled, as this measurement is not statistically ceiled (i.e. there is a maximum number of unique x/y coordinates available) and can thereby capture the most variation between individuals.

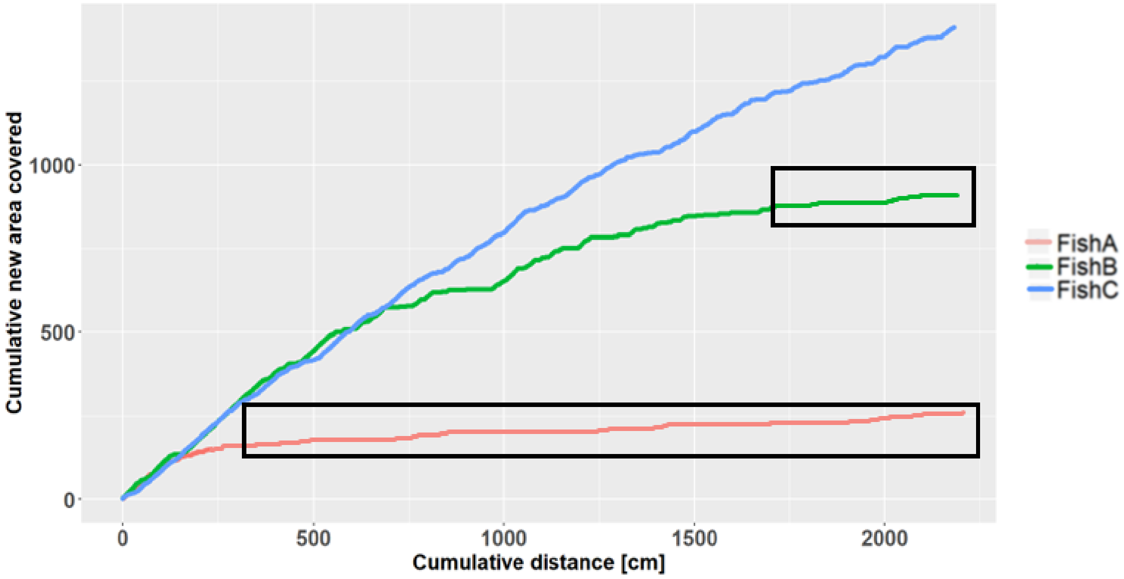

Figure 2. Correlation between distance travelled and new area covered for three different fish. The data within the black squares is interpolated, predicted on the fish's previous behaviour.

Conclusion

This short communication aimed to show that using only the distance travelled might not be enough to capture an individual's exploration tendency and that a measure of space use should ideally be included to provide a full understanding of this personality trait. Additionally, this short communication provides an easy way to extract such measurement of space use (i.e. total area covered) from behavioural-tracking software, even though it is not automatically provided in the summary statistics.

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Paper II

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Activity vs exploration: Locomotion in a known and unknown environment differs in Atlantic cod juveniles (*Gadus morhua*)

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ABSTRACT

Individuals within a population often behave differently and these differences can be consistent over time and/or context, also termed "animal personality". Animal personality has been commonly classified into five axes with studies aiming to validate these axes. One subject that has surprisingly not received full attention yet is the difference between the two personality axes "activity" and "exploration-avoidance", i.e. behaviour in a known vs an unknown environment. Despite this clear difference in definition, many studies measure activity in an unknown environment and term it activity, while underlying motivations between the two environments are different.

This study aimed to detect the two personality traits "activity" and "exploration" in Atlantic cod juveniles, and to investigate whether they support the distinctive definitions proposed by previous authors. This study showed significant consistency in locomotion variation in both environments, i.e. personality. In addition, the two environments clearly elicited different behaviours; Atlantic cod juvenile behaviour was more repeatable and they moved more in the known vs the unknown environment, and no correlation of the proportional locomotion between the two was found. This demonstrates that locomotion in both environments, i.e. the personality axes "activity" and "exploration", should not be confused nor treated as if they reflect the same personality trait.

1. Introduction

Individuals within a population often behave differently, and these differences can be consistent over time and/or context, also termed "animal personality" (Gosling, 2001). The persistence of these differences in almost every population/species examined suggests that natural selection is maintaining multiple personality types/continuums, rather than just being "noise around [one] adaptive mean" (Dall et al., 2004). Personality can affect fitness directly i.e., by substantially influencing growth (Adriaenssens and Johnsson, 2011), reproductive success (Ariyomo and Watt, 2013; Monceau et al., 2017) and dispersal/migration (Chapman et al., 2011; Cooper et al., 2017). These direct fitness effects can subsequently influence population dynamics (Arlinghaus et al., 2017; Cote et al., 2010), eventually cascading into effects on communities and ecosystems (Bolnick et al., 2011).

Animal personality has been commonly classified into five axes (shyness-boldness, exploration-avoidance, activity, sociality, and aggressiveness; Réale et al., 2007). Although many studies have measured proxies of these personality traits, fewer studies have raised questions about whether those truly characterize the underlying trait of interest. Guidelines have been laid out to validate different interpretations of certain personality traits (Carter et al., 2013); such as the "novel object test" vs "antipredator response" (Carter et al., 2012), the use of the "open field test" for both a measure of exploration and boldness (Finger et al., 2016; Perals et al., 2017; Toms et al., 2010) and the influence of different starting boxes for the "emergence test" (Näslund et al., 2015). However, one subject that has surprisingly not received full attention yet is the difference between the two personality axes "activity" and "exploration-avoidance"; defined respectively as "the general level of activity of an individual […] in a non-risky, non-novel environment" and "an individual's reaction to a new situation", including new habitats, new food and novel objects (Réale et al., 2007).

The term "activity" has a very broad meaning, and the definition of

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"general level of activity" by Réale et al. (2007) is open to many interpretations; including "locomotion activity" (the actual movement from one place to another), "movement" (which may or may not include stationary activity), "baseline activity", "open-field activity", "motor activity", "foraging activity", "mating activity" and "metabolic rate" (see Table S1 for an overview). Analyzing these definitions is beyond the scope of this article, but it seems crucial to define the type of activity that is being measured in a given context because of the differences in underlying behavioural motivations (Hughes, 1997).

What is less open to interpretation according to Réale et al. (2007) is that activity is thought to reveal itself in a known (and un-risky) environment, while exploration is believed to expose itself in an unknown (novel) environment, which is not a new insight (Bindra, 1968; Kelley, 1993). A Google Scholar search for the terms "animal personality" AND "activity" AND "exploration" AND "Réale" from 2008 onwards (a year after the publication of the definitions proposed by Réale et al.) resulted in 2130 matches. Two of these matches were reviews showing that the study of activity as a personality trait is generally underrepresented. For example, Moiron et al. (2020) collected 28 articles for a meta-analysis on the influence of behavioural differences on survival, comprising mammals, fish, insects, molluscs, reptiles and birds, and only reported one article that measured activity in a known environment. Even more striking are the 27 articles that Cabrera et al. (2021) collected for a review of the development of personality across ontogeny comprising mammals, birds, reptiles, cephalopods, arachnids, amphibians, insects and fish. Fourteen articles of the 26 mentioned activity as a personality trait, but only two of those 14 measured activity in a known environment (Table S1). Another three articles defined a known environment after habituation for only 2–24 h, without providing a rationale for such a time (Table S1). To determine whether behaviour in a known and unknown environment is interchangeable, these traits would ideally be tested on the same individuals within the same time period. However, only four of the articles that measured activity in a well-defined known environment also measured exploration (i.e. behaviour in an unknown environment), but only one compared actual locomotion behaviour in both environments. In the first study on larvae and juvenile lake frogs (*Rana ridibunda),* general activity was measured as the time spent active and time spent in the open in their holding tanks, while exploration was measured as the latency to move into an open arena (Wilson and Krause, 2012). In the second study on zebra finches (*Taeniopygia guttata*), activity was measured as the number of flights in their home cage, while exploration was measured as the number of perches visited and latency to visit all perches in an open field test (Wuerz and Krüger, 2015). In the third study on Eastern chipmunks (*Tamias striatus),* activity was measured as locomotion acceleration in their natural environment, while exploration was measured as the number of lines crossed in an open field test (Gharnit et al., 2020). In the fourth (and oldest) study on Wister lab rats, locomotion was measured in both their home tank and the experimental setup (Vezina and Stewart, 1984). Additional scanning through the search results besides these two reviews did not reveal much extra information, except that activity was still recently studied in an unknown environment (e.g. Galib et al., 2022, Lundgren et al., 2021; Santicchia et al., 2021; Table S1). To our knowledge, there are no recent studies assessing both activity and exploration using the same measurements in both a known and unknown environment, which makes it difficult to determine possible behavioural differences between the two environments.

Treating locomotion in a novel environment as a proxy of activity could lead to "[…] misinterpreting results, putting the development of animal personality theory at risk" (Carter et al., 2013). For example, Herde and Eccard (2013) reported a behavioural syndrome between activity and exploration in common voles, but as percentage moving (used as a proxy for activity) and frequency of head-through-hole (used as a proxy for exploration) were both measured in an unknown environment, it might just indicate that both experiments measured exploration, rather than forming an actual behavioural syndrome. It is therefore important to further explore locomotion in a known and unknown environment, to get a better understanding of what is actually being measured and whether the division between the two environments made by Réale et al. (2007) holds.

In this study, both locomotion (the movement from one location to another) in a known (home tank; HT) and unknown (open field test; OFT) environment were investigated in Atlantic cod juveniles (*Gadus morhua*). The data were collected as part of a larger project studying the influence of personality on movement, specifically "partial migration", where one part of the population consistently migrates, while the other part stays always resident. Personality has been shown to be present in adult Atlantic cod (Villegas-Ríos et al., 2018) and adult cod partial migration has been shown to be consistent on the individual level over multiple years (Thorsteinsson et al., 2012). Insight into the link between personality and partial migration could be used to better predict and sustain population dynamics; for example, the migratory and non-migratory subpopulations might differ in their susceptibility to (over)fishing (Mittelbach et al., 2014). To draw conclusions about how personality can influence population dynamics, it is necessary to study personality at multiple life stages, including juveniles, account for among-population variation and subsequently establish a consistent terminology around movement proxies. We aim to answer the following questions: (1) Do Atlantic cod juveniles show consistent among-individual variation in locomotion (i.e. personality) in a known (activity) and unknown (exploration) environment? and (2) Is individual locomotion correlated between known and unknown environments? We hypothesize that juveniles show behavioural consistency at an early age as is the case in other fish species (Biro et al., 2010; Polverino et al., 2016). Secondly, if locomotion in the two environments belongs to different functional categories (Budaev and Brown, 2011; Kelley, 1993), we expect no correlation of this behaviour between the two environments, i.e., discriminant validity. However, a correlation might be found if the two environments elicit similar behaviours, i.e., convergent validity, or if the behaviours are part of a behavioural syndrome (Sih et al., 2004).

2. Methods

One hundred two age 0 + cod juveniles (weight range = 0.75–4.39 g and mean = 1.87 g; standard length range = 3.83–7.55 cm and mean = 5.72 cm) were beach seined from the 3rd to the 12th of October 2019 in three different fjords around the Westfjords of Iceland (Fig. 1) to obtain maximal genetical behavioural variation. They were transported to a laboratory in Bolungarvik, Iceland and housed individually in 9.5-litre tanks (~29×21×19cm, water level 16 cm, Aquaneering Inc.). The recirculating system contained freshwater mixed with marine salt to achieve a natural salinity of 30 ± 2‰, a temperature of 11 ± 1 °C, ammonia levels of < 0.5 ppm, oxygen levels of 10.4 ± 0.1 mg/L and a constant photoperiod of 12:12 (7 AM-7 PM GMT). The water circulated through the Aquaneering system, passing through all the tanks, a biofilter, sieves (mesh size 25 μm), and a UV light for sterilization. Every tank had a grey PVC pipe to provide shelter to the fish. Fish were fed twice a day alternating fresh shrimp and defrosted bloodworms daily ad libitum. On the experimental days, feeding took place after the experiment to avoid any differences in feeding motivation. The water temperature of the experimental tank for the OFT (10.3–12.2 °C) was manually controlled to match the temperature of the home tank. After the first trial of the OFT experiments, the fish were measured for weight and standard length.

2.1. Behavioural experiments

2.1.1. Home tank measurements (known environment)

Between October 28 and November 4, 2019, HT experiments were run first to keep the level of disturbance as low as possible. Locomotion in the home tank was video recorded for seven minutes during three

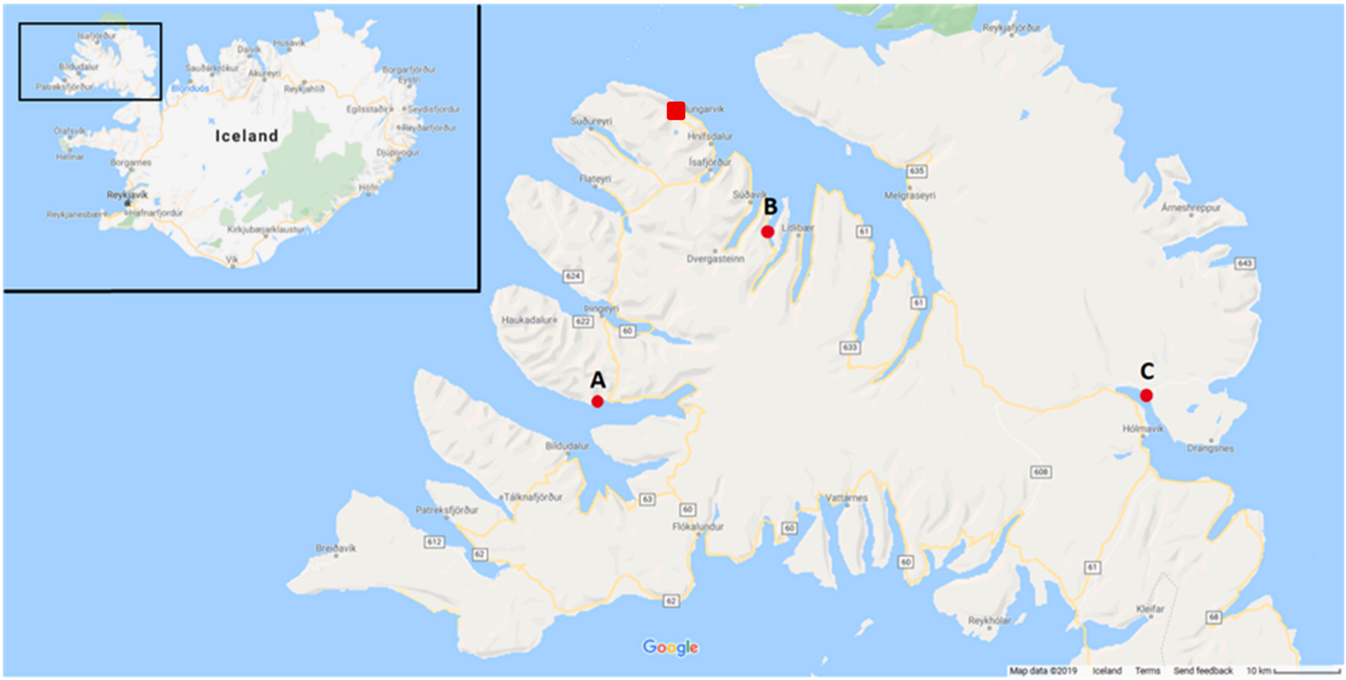

Fig. 1. Sample sites in the Westfjords of Iceland. (A) Arnarfjörður (65°46′′01.6"N 21°42′′03.6"W), (B) Seyðisfjörður (65°57′′22.7"N, 22°49′′30.3"W) and (C) Steingrimsfjörður (65°45′′45.1"N, 23°17′′55.9"W). Red square: laboratory in Bolungarvik.

trials (day 1, 2, and 5) by a camera that was placed in front of the home tank. During the analysis, the first two minutes of each video were discarded to account for the minimal disturbance of the camera placement. The remaining five minutes were analyzed using Solomon coder (V. beta 19.08.02) and scored for time performing “locomotion” (the actual displacement of the body), “stationariness” (moving, but without displacing), and hiding “in shelter”. Subsequently, the proportion of time that the fish was performing locomotion within the experimental five minutes was calculated.

2.2. *Open field test (unknown environment)*

Between November 5 and 28, 2019, locomotion in an OFT was video recorded during three trials (day 1, 7 and 20). The fish was gently captured with a dipnet out of its home tank and placed in a shelter (26 L; 40×40×40 cm, water level 16 cm) and after five minutes of acclimation, the door was lifted. The fish was given five minutes to leave the shelter. If it did not leave voluntarily, it was gently forced out using a dip net into the arena (51 L; 80 × 40 × 40cm, water level 16 cm). The arena was substantially larger than the home tank and had blue walls contributing to its novelty relative to the home tank. As soon as the fish entered the arena, the shelter was closed and the fish was recorded from above for five minutes. Those video recordings were analyzed with a video-tracking software (Ethovision, Noldus, v. 15.0) and the total distance travelled, the total area covered (total unique x/y coordinates rounded to the nearest integer) and moving/non-moving were extracted, which are all measurements commonly used as proxies of exploration. The threshold for moving was set to start when the centre point of the fish moved 1.5 cm/s and stopped at 1.25 cm/s and a smoothing parameter of 0.1 was set, which set the sample points to the previous location until the distance moved was more than 0.1 cm. The moving measurement was transformed into proportional locomotion. Total area covered and total distance travelled were both highly correlated with proportional locomotion (PEARSON: $r = 0.98$; CI 95 % [0.97–0.99]; $P = <0.001$; $r = 1.00$; CI 95 % [0.99–1.00]; $P = <0.001$ respectively) and therefore only proportional locomotion was used in further analysis to match the HT analysis.

All the experiments in the larger study, including the OFT used in our study, were designed to be analyzed with Ethovision. However, in the home tank more importance was given to the welfare of the fish i.e., the Aquaneering system, which consequently did not meet the requirements for using the tracking software to analyse the data. To assure that any differences found between the two environments were not explained by the different methods used, 16 randomly selected OFT videos across trials (10 %), but from 16 different fish, were analyzed using the manual home tank method and compared to the Ethovision output of the same videos. There was a strong correlation between the two methods (PEARSON: $r = 0.97$; CI 95 % [0.93–0.99]; $P = <0.001$), and the two methods resulted in similar locomotion values ($\bar{x}_{HT} = 0.31$, $\bar{x}_{OFT} = 0.32$, Paired t-test; $t = -0.77$, $P = 0.455$). We thereby ruled out any significant influence of the measuring method on the results.

2.3. *Genotyping*

In June 2020, at the end of the overall project, the fish were euthanized with phenoxyethanol (1.6 mg/L) and fin clips were taken to assign the fish to either coastal (*Pan*I^{AA}), frontal (*Pan*I^{BB}), or heterozygote (*Pan*I^{AB}) using PCR analyses as described in Pampoulie et al. (2006). Allelic type was included in this study because it might influence movement as coastal cod behave mainly as residents, frontal as migratory (Thorsteinsson et al., 2012) and heterozygotes are thought to behave like any of the homozygotes (Pampoulie et al., 2008) or show intermediate behaviour, but are more likely to show resident behaviour (Árnason et al., 2009).

2.4. *Statistics*

All data were analyzed using R v. 4.0.4 (R Core Team, 2021). The proportional locomotion measurements were arcsine squared-root transformed (expressing variation on an un-constrained scale) and then scaled per environment using z-scoring (subtracted the mean and divided by the standard deviation). To investigate the differences between locomotion in the two environments, a Bayesian multivariate linear model using Stan (Carpenter et al., 2017) was run using the ‘brms’ package (Bürkner, 2017). The model simultaneously regressed each dependent variable (i.e., HT and OFT locomotion) against a set of fixed and random effects while also quantifying the covariance between the dependent variables. Several fixed effects that could influence locomotion were evaluated for collinearity: weight (g), standard length (cm), Fulton's condition factor ($K = Weight / Length^3 \times 100$), and specific growth rate ($SGR = \Delta$ ln(weight) * 100 / Δ day). Pearson correlations revealed that K was not correlated with any of the others, while the other three were correlated to each other (Table S2). Therefore, scaled measurements of K and SGR were included as fixed effects. The full model was fitted with the environment as the independent variable (HT vs. OFT), transformed proportional locomotion as the dependent variable, the four fixed effects of SGR, K *Pan*I allele and trial with individual fish identity added as a random factor. To determine whether the fish handling in the OFT (gently pushing the fish out of the shelter (N = 65) vs leaving the shelter voluntarily (N = 97)) influenced their locomotion behaviour, it was added as a binary covariate for the OFT.

The random-effects structure included individual fish identity (ID) as a grouping variable, allowing us to calculate the repeatability of HT and OFT locomotion as the ratio of the among individual variance and the sum of the among individual and residual-level variances (i.e. personality) (Johnson and Koch, 2011). Moreover, the model estimated covariances between HT and OFT at both the ID and residual levels. The among individual covariance quantified the degree to which locomotion in the two environments was correlated among individuals across multiple trials (i.e. behavioural syndrome), while the residual level covariance quantified the degree to which locomotion was correlated among observations independently of the identity of individuals.

The model was run for 4000 iterations (2000 for warmup and 2000 for sampling), four chains, and all other parameters set to their defaults. Convergence was assessed using the standard diagnostics provided by Stan, including the potential scale reduction factor ($\widehat{R}$), effective sample size, and visual inspection of trace plots and histograms for each model parameter. Unless otherwise noted, we used posterior modes for point estimates and higher posterior density with 95 % coverage for uncertainty intervals ($UI_{95\ \%}$), respectively calculated using the map_estimate and hdi functions from the "coda" package (Plummer et al., 2006).

2.5. *Ethical note*

The number of fish and the procedures (fishing, handling, fin-clipping and the behavioural tests) were chosen to adhere to strict ethical guidelines, but an ethics committee approval for the research project was not required by Icelandic regulation (Act No. 55/2013 on Animal Welfare).

3. Results

The initial set-up should have led to 306 trials (102 individuals x 3 repetitions) per experiment (HT and OFT). However, some fish experienced weight loss and mortality, because of the incapability of adjusting to the laboratory food, which is not uncommon for the transfer from the wild to the lab. To get a more reliable dataset with fish that successfully adjusted to the laboratory conditions and therefore were expected to show more "natural" behaviour, the fish that lost weight in the month preceding the experiments and those that died in the week after the experiments were excluded. Of the 102 0 + juvenile cod caught in October 75 were residents (*Pan*I^{AA}); 17 heterozygotes (*Pan*I^{AB}) and largely underrepresented was the migratory allele with four individuals (*Pan*I^{BB}). After excluding fish that lost weight, there was only one fish with the *Pan*I^{BB} allele, which was excluded from further analysis. Two other fish missing all of the OFT experiments were also excluded. The final data set used for analysis consisted of 56 fish, which included 51 fish with a complete data set, four fish missing one OFT trial and one fish missing a HT trial, leading to 162 observations. The missing trials were all caused by video failure; the fish underwent the experiment, but the analysis was lost.

These 56 cod juveniles increased in weight from the start to the end of the experiments (one month) from $\bar{x} = 1.98 \pm$ SD 0.71 (start) to $\bar{x} = 3.10 \pm 1.24$ gr (end), had a mean Fulton's condition factor of 0.98 ± 0.09 (start) and 0.98 ± 0.07 (end) and a specific growth rate of 1.51 ± 0.76 % body weight/day (start-end). Forty-five fish (80 %) were assigned to the *Pan*I^{AA} allele and 11 (20 %) were heterozygotes (*Pan*I^{AB}). The proportional locomotion ranged from 0.00 to 1.00 (median = 0.84) in the HT and from 0.02 to 0.95 (median = 0.26) in the OFT (Fig. 2). The model converged, with $\widehat{R} = 1$, well-mixed chains, and no extreme trails visible in the trace plots (Figs. S3).

3.1. *Repeatability*

Among individual variances of both proportional locomotions in the HT and OFT were unambiguously different from zero, indicating individual repeatability in these behaviours. In the HT, among individual variance exceeded the residual variance such that the behaviour was highly repeatable (R=0.64; $UI_{95\ \%}$=[0.49, 0.76]; Fig. 3). In contrast, in the OFT the residual variance exceeded the among individual variance, resulting in lower repeatability (R=0.34; $UI_{95\ \%}$=[0.14, 0.52]; Fig. 3).

3.2. *Fixed effects*

In the OFT, fish tended to move less with lower condition factors (K), although $UI_{95\%}$ overlapped zero (Fig. 4, Table S4). In contrast, K did not appear to affect HT locomotion, and SGR did not influence movement in either of the environments. In both environments, resident cod (*Pan*I^{AA}) moved more, as did cod that left the shelter voluntarily before the OFT (Fig. 4; Table S4). Cod in the HT moved similarly during the first two trials (Δ 1 day), but decreased movement in the third trial (Δ 5 days), while cod in the OFT moved less in the second trial compared to the first (Δ 7 days), but went back to similar levels in the third trial (Δ 21 days; Table S4).

3.3. *Differences between locomotion in the HT and OFT*

The covariance of locomotion in the two environments was close to zero with $UI_{95\%}$ strongly overlapping zero (Fig. 3, Table S4). Additionally, the proportional locomotion in the HT was higher than locomotion in the OFT (Fig. 4, Table S4). Finally, no visual association was apparent when plotting the locomotion values in both environments with their corresponding regression lines based on among individual and residual-level covariances (Fig. 5; See S5 for details on the calculation of the regression line from the multivariate linear model).

4. Discussion

This study evaluated whether locomotion measurements in known and unknown environments are repeatable in Atlantic cod juveniles and to what extent these behaviours vary independently as distinctive personality traits as defined by Réale et al. (2007). To do so, we measured locomotion in a known (home tank) and unknown (open field test) environment repeatedly for individual fish. Using these data, we aimed to answer the following research questions: (1) Do Atlantic cod juveniles show consistent among-individual variation in locomotion (i.e. personality) in a known (activity) and unknown (exploration) environment?, and (2) Is individual locomotion correlated between known and unknown environments? We found that activity and exploration behaviour were repeatable and different from each other amongst the 56 Atlantic cod juveniles measured. Specifically, the fish were more active in the known environment and there was no covariance between locomotion in the two environments, supporting the hypothesis that activity and

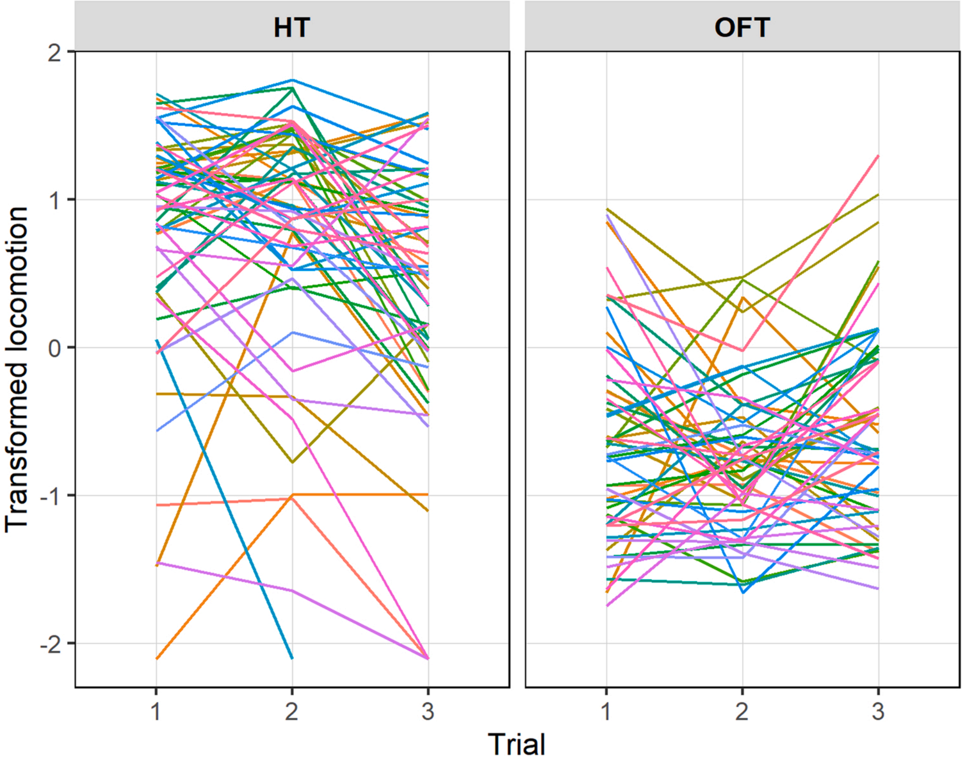

Fig. 2. Z-scored arcsine squared-root transformation of the proportion of locomotion in a known (HT) and unknown (OFT) environment for three different trials (HT; Oct28-Nov4, Day 1, 2 and 5) and (OFT; Nov5–27; day 1, 7 and 20). Lines/colours represent the 56 individual fish.

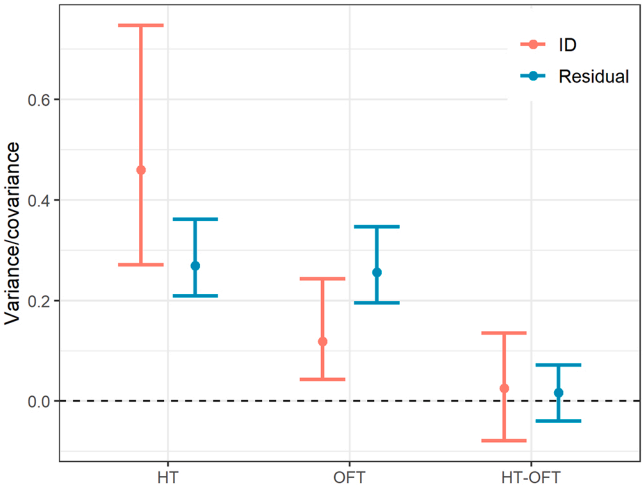

Fig. 3. Posterior modes and their corresponding uncertainty intervals for the variances and pairwise covariance of HT and OFT, on both the ID level (red) and residual level (blue). The black dashed line indicates zero.

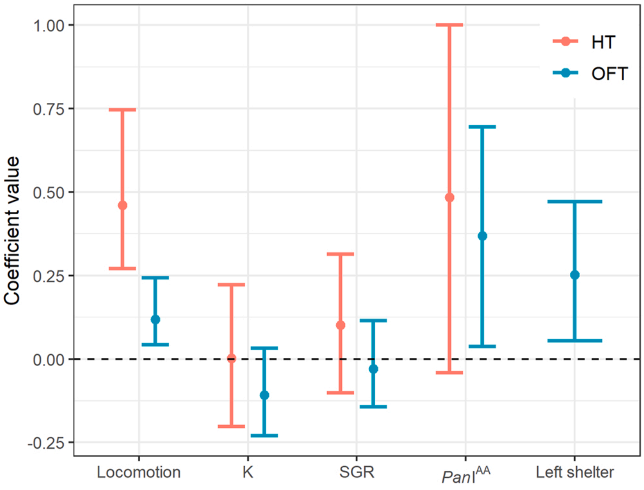

Fig. 4. Posterior modes and their corresponding 95 % uncertainty intervals for the fixed effects *K*, *SGR* and *Pan*I allele for the HT (red) and OFT (blue) and fish that left the shelter voluntarily (only OFT). The black dashed line indicates zero. Because the non-categorial fixed effects were z-scored, the co-efficient values are presented in units of standard deviation.

exploration should be treated as two distinct personality traits.

Hypothesis 1. Personality in Atlantic cod juveniles.

Locomotion in both environments showed significant consistency in behavioural variation, i.e. personality. To the best of our knowledge, this is the first evidence that Atlantic cod juveniles show personality in early life, in addition to what is shown in adults (Villegas-Ríos et al., 2018). The repeatability found in this study for activity (0.64 over three repetitions within 5 days) is difficult to compare to other studies of fish because time intervals between trials are rarely the same, which could influence the results (Biro and Stamps, 2015). Additionally, not many studies have measured activity in a known environment (Table S1). Examples in the literature show ranges from 0.25 to 0.35 in Ward's damselfish fish over 11 repetitions within two weeks (Biro, 2012) to 0.72 in mosquitofish measured 12 times within six days (Biro et al., 2020). The repeatability found in this study for exploration (0.34) is lower than the 0.5 found in adult Atlantic cod (Villegas-Ríos et al., 2018), although they used a different measurement for exploration (i.e., latency to exit a shelter). Polverino et al. (2016) showed that repeatability of exploration in mosquitofish increased during development (juveniles; 0.06, subadults; 0.21, adults; 0.48), which also could explain the lower repeatability found in this study on juveniles compared to

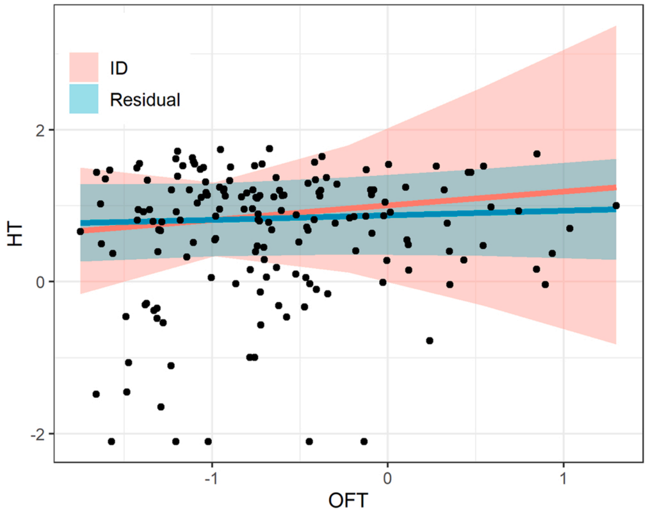

Fig. 5. Association of proportion of locomotion between home tank (HT) and open field test (OFT), with regression lines based on among individual (ID, red) and residual-level (blue) covariances. Posterior medians and 95% quantiles were used for point estimates and uncertainty intervals to preserve the linearity of the regression line (whereas posterior modes and highest density intervals would not). See S5 for details on the calculation of the regression line from the multivariate linear model.

adults. This topic should be studied in more detail, over a longer time period, to get more insight into the development of personality in Atlantic cod.

Hypothesis 2. Locomotion in a known vs an unknown environment does not correlate.

Our study showed that the HT and OFT elicited different behaviours; locomotion was more repeatable in the HT (0.64) than in the OFT (0.34), fish moved more in the HT compared to the OFT and no covariance in locomotion between the two was found. The higher repeatability for locomotion in a known environment suggests that physiological processes, such as metabolic rates and daily routine, are more consistent than the motives behind exploration, such as fear or curiosity (Biro et al., 2018; Careau et al., 2008; Hughes, 1997; Nilsson et al., 2014). However, metabolic rate was not measured in the current study, nor have other motivations been studied, so further research is needed.

The literature review (Table S1) revealed that only four studies measured activity as a personality trait in a known environment and exploration in an unknown environment on the same individuals: zebra finches (Wuerz and Krüger, 2015), frogs (Wilson and Krause, 2012) and rats (Vezina and Stewart, 1984), although only Vezina and Stewart (1984) used locomotion as a measurement in both environments. Only Vezina and Stewart (1984) and Wuerz & Krüger (pers. comm.) reported the direction of those differences and found that both rats and zebra finches respectively, were more active in an unknown environment compared to their home environment, the opposite of what is found in the current study. Prior experiences with predators vs naivety could influence a first reaction to an unknown environment, e.g. curiosity vs cautiousness (Kelley, 1993). These different reactions to an unknown environment, related to wild vs captivity is demonstrated in rats (Mitchell, 1976), rainbow trout (Biro et al., 2007), but also in adult resident Atlantic cod itself (Meager et al., 2011). This most likely explains why the wild-caught cod in the current study are showing less locomotion activity in an unknown vs a known environment. Interestingly, even though the choice of a bigger tank size for the OFT compared to the HT could have directly contributed to greater movement simply due to the larger available area, our results show the opposite, which suggests that the two environments truly elicited different locomotion behaviour. Three studies found no correlation between their activity and exploration measurements which supports the results found in our study (see introduction; Vezina and Stewart, 1984; Wilson and Krause, 2012; Wuerz & Krüger, pers. comm.). One study found that activity patterns were correlated with exploration measurements, although activity was not repeatable (Gharnit et al., 2020). This is not necessarily in conflict with our study, as a correlation between activity and exploration, when measured correctly, could indicate the existence of a behavioural syndrome (Sih et al., 2004). Other correlations between traits can be found such as the proportional locomotion in an OFT used as a measurement of exploration in this study to boldness, especially in the first minute after start of test (i.e. time until first movement) (Burns, 2008; Toms et al., 2010).

Interestingly, cod carrying the *PanI*^{AA} allele moved more in both environments than the heterozygotes, despite its uneven distribution (*PanI*^{AA}, 80 %, *PanI*^{AB}, 20 %). These behavioural differences between the alleles are contradictory to the result from a study that found that heterozygotes were mainly behaving as residents (Árnason et al., 2009). Whether heterozygotes behave more like migrants, are showing intermediate behaviour (Pampoulie et al., 2008) or show behaviour that is unrelated to the other alleles remains to be investigated.

5. Conclusion

This study shows evidence for the hypothesis that locomotion in a known vs an unknown environment is not the same, at least in Atlantic cod juveniles. This result is consistent with what was implicitly found in the four previous studies that measured both traits on the same set of individuals (Gharnit et al., 2020; Vezina and Stewart, 1984; Wilson and Krause, 2012; Wuerz and Krüger, 2015). Together, these results provide support for the two distinctive personality traits “activity” and “exploration”, as defined by Réale et al. (2007). The difference between activity and exploration is most likely explained by different motivations in the different contexts (Budaev and Brown, 2011; Kelley, 1993), but further research is needed to collect data on other species and the nature of these differences to strengthen those findings. We therefore call out to the research community to be more careful and definite when defining these personality traits to avoid mislabeling and work together towards a clearer development of the personality theory.

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Declarations of interest

none.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.beproc.2022.104736.

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Paper II - Supplementary materials

*Table S1**:** An overview of articles that are mentioning activity as a personality trait.*
OFT= Open field test, NM= Not measured

				Activity				**Exploration**	
Authors	**Year**	**Species**	**Referenced in**	**Definition**	**Test environment**	**Known environment?**	**Measurement**	**Test environment**	**Measurement**
Bell & Stamps	2004	Three-spined stickleback (*Gasterosteus aculeatus*)	Cabrera et al. (2021)	Activity in a known environment	New tank (12 hours habituation)	Maybe	Total number of arenas visited, number of movements	NM	NM
Biro	2012	Ward's damselfish (*Pomacentrus wardi)*	NA	Activity	Home tank	Yes	Midpoint crossed and time active (movement of 0.5 time body length)	NM	NM
Biro et al.	2010	Lemon damselfish (*Pomacentrus moluccensis)*	NA	Activity	Home tank	Yes	Total distance in three minutes	NM	NM
Biro et al.	2010	Coral reef fish (*Pomacentrus moluccensis*)	NA	Activity	Home tank	Yes	Total distance in three minutes	NM	NM
Biro et al.	2020	Mostquitofish (*Gambusia holbrooki*)	NA	Spontaneous activity	Home tank	Yes	Scan samples active/inactive. Proportion of time spent moving	NM	NM
Bosco et al.	2017	Desert funnel-web spider (*Agelenopsis lisa*)	Cabrera et al. (2021)	Foraging and exploration activity	OFT	No	Time active	OFT	Distance traveled
Boulton et al.	2018	Sheepshead swordtail (*Xiphophorus birchmanni*)	Cabrera et al. (2021)	Activity	OFT	No	Time in trial spent moving at >1.5 cm.s−1 [%]	NM	NM
Brodin	2009	Damselfly (*Lestes congener)*	Cabrera et al. (2021),	Activity	Home cage	Maybe	Head over gridline, 1 observation per 10	NM	NM

			Kelley et al. 2015				minutes, for 140 minutes		
Burns	2008	Trinidadian guppy (*Poecilia reticulata*)	NA	Activity	Isolation tank (2-4 days)	Maybe	Number of areas per second	OFT, novel object test	Swimming rate. Latency to emerge
Colléter & Brown	2011	Rainbowfish (*Melanotaenia duboulayi*)	NA	Activity	Home tank	Yes	Number of transects crossed	NM	NM
Dingemanse et al.	2009	Three-spined stickleback *(Gasterosteus aculeatus*)	NA	Activity in a non-novel environment	New tank (2/4 hours habituation)	Maybe	Number of boundary crossings	New tank	Square change
Dosmann et al.	2015	Belding's ground squirrels (Urocitellus beldingi)	NA	Activity	Hole board apparatus	No	Number of lines crossed	Hole board test	Number of head dips
Galib et al.	2022	Signal crayfish (*Pacifastacus leniusculus*)	NA	Activity	OFT	No	Total time moving	OFT	Unique grid squares
Gharnit et al.	2020	Eastern chipmunk (*Tamias striatus*)	NA	Activity	Own habitat	Yes	Accelerations	OFT	Number of lines crossed
Gyuris et al.	2012	Fire bugs (*Pyrrhocoris apterus)*	Cabrera et al. (2021)	General activity	OFT	No	Mean and variance of step size, mean and variance of turning angles	OFT	Number of objects visited, time to reach the wall
Herde & Eccard	2013	Common voles (*Microtus arvalis*)	NA	Activity	Barrier test & OFT	No	1-0 sampling every 10 seconds	Hole-test: cage with four holes (similar to housing cage?)	Head through hole

Horback & Parsons	2018	Pig (*Sus scrofa*)	Cabrera et al. (2021)	Activity	OFT	No	Duration of standing, lying down and walking (among others)	Human approach test and OFT	Many measurements leading to a PCA score
Horváth et al.	2016; 2019	Carpetan Rock Lizards (*Iberolacerta cyreni*)	NA	Activity	Home box	Yes	Total distance moved	NM	NM
Hoset et al.	2021	Root voles (*Microtus oeconomus*)	NA	Locomotor activity	OFT	No	Time spent walking	OFT	Number of compartments visited within unit of time
Kaiser et al	2018	Speckled wood butterfly (*Pararge aegeria)*	Cabrera et al. (2021)	Activity	OFT	No	Number of transitions between squares	OFT	Number of squares visited at least ones
Kanda et al.	2012	Siberian dwarf hamster (*Phodopus sungorus*)	Kelley et al. (2015)	Activity	Tunnel maze	No	Many measurements	NM	NM
Kelley et al.	2015	Squirrel (*Tamiasciurus hudsonicus*)	Cabrera et al. (2021)	Activity (in response to a novel object)	OFT	No	Walk. Moving in the arena. May be walking or running. (and many others)	NM	NM
Kobler et al.	2011	Bullhead (*Cottus perifretum*)	Mittelbach et al. (2014)	Activity vs novel environment activity (exporation)	New tank (12 hours habituation)	Maybe	Distance moved	Tank with new food item, OFT	Number of squares crossed in OFT, interest in maggot as novel object
Lartigue et al.	2020	Parasitoid wasp (*Trichogramma evanescens*)	NA	Activity	OFT	No	Time active, mean active time	OFT (different area)	he total area explored per unit time and (2) the mean sinuosity of the pathway
Lundgren et al.	2021	Jungle fowl (*Gallus gallus*)	NA	Activity	OFT	No	Number of boundary crossings	OFT	Latency to visit all arenas

McGhee & Travis	2010	Bluefin killifish (*Lucania goodei*)	Mittelbach et al. (2014)	Mating behaviour activity	OFT	No	Number of aggressive behaviours and courtship	NM	NM
Minassian et al.	2016	Mice (*Mus* musculus*)*	NA	Activity	Hole-test	No	Locomotion	Hole-test	Head through hole
Monceau et al.	2017	Mealworm beetle (*Tenebrio molitor)*	Cabrera et al. (2021)	Activity	OFT	No	Number of transitions between sections	OFT	Number of transitions between sections
Müller & Müller	2015	Mustard leaf beetle (*Phaedon cochleariae)*	Cabrera et al. (2021)	Activity	OFT	No	Covered distance, amount of movements, turning angles < 90° and variance of turning angles	NM	NM
Niemelä et al.	2015	Cricket (*Gryllus campestris*)	Moiron et al. (2020)	Baseline activity	In front of burrow	Yes	Total time spent moving with 5 minutes	NM	NM
Pasquet et al	2015	Northern pike (*Esox lucius*)	NA	Activity	Maze/novel object	No	Time spent swimming	Maze/novel object	Latency to leave start box, number of arms/zones visited
Polverino et al.	2016	Eastern mosquitofish (*Gambusia holbrooki*)	Cabrera et al. (2021)	(Swimming) activity	OFT	No	Distance moved, not actively swimming, and time spent in shelter	NM	NM
Santicchia et al.	2021	Eurasian red squirrels (Sciurus vulgaris)	NA	Activity	OFT	No	Mobility	OFT	Hole board test
Schuster et al.	2017	Eurasian harvest mouse (*Micromys minutus*)	NA	Activity	OFT/Y maze	No	Total distance moved	Novel object test/Y maze	Time exploring, time spent in unknown arm of Y maze

Smith & Blumstein	2010	Trinidadian guppy (*Poecilia reticulata*)	Mittelbach et al. (2014)	General activity	OFT	No	Number of different areas, total time spent moving	Novel object	Latency, number and distance of appraoch
Taylor et al.	2012	North American red squirrels (*Tamiasciurus hudsonicus*)	NA	Activity	OFT	No	Many variables in PCA	OFT	Many variables in PCA
Vezina & Stewart	1984	Wistar lab rats	NA	Activity	Home cage	Yes	Locomotion	Activity cage (OFT)	Locomotion
von Merten et al.	2017	Shrew (*Neomys fodiens, Sorex araneus, Sorex minutus, Neomys anomalus*)	NA	Activity	OFT	No	Total count of lines crossed	NM	NM
White & Wilson	2019	Trinidadian guppy (*Poecilia reticulata*)	Cabrera et al. (2021)	Activity	OFT	No	Moving at >4 cm s−1	NM	NM
Wilson & Godin	2010	Bluegill sunfish (*Lepomis macrochirus*)	NA	General activity in open arena	OFT	No	Distance traveled	NM	NM
Wilson & Krause	2012	Lake frog (*Rana ridibunda*)	Cabrera et al. (2021), Kelley et al. 2015	Activity	Home tank	Yes	Proportion active/in open	OFT	Latency to first activity, total activity
Wuerz & Krüger	2015	Zebra finch (*Taeniopygia guttata*)	Cabrera et al. (2021)	General activity	Home cage	Yes	Number of flight, number of perches visited, position diversity index	Novel environ ment	Number and latency of seven possible positions and latency to enter the novel environment
Závorka et al.	2015	Brown trout (*Salmo trutta*)	NA	Activity	OFT	No	Number of crossing between squares	NM	NM

Zhao et al.	2016	Chestnut thrush (*Turdus rubrocanus*)	NA	Activity	OFT	No	Counts of walking, hopping and flying	NM	NM
Zidar et al.	2017	Red junglefowl (*Gallus gallus*)	NA	Activity	OFT/Novel object test	No	Activity	OFT/Novel object test	Latency to explore

Table S2. Correlation matrix of possible effects on locomotion.

	STL	W	SGR
W	0.981		
SGR	0.496	0.461	
K	0.124	0.280	-0.103

Table S4. Posterior modes and uncertainty intervals of the model output in variances/ covariance of the two environments (HT and OFT). Bold values showing parameters that influenced locomotion.

	HT		*OFT*	
Predictor	*Posterior mode*	*UI 95%*	*Posterior mode*	*UI 95%*
ID-level				
Locomotion	0.46	0.27 – 0.75	0.12	0.04 – 0.24
K	0.00	-0.20 – 0.22	-0.11	-0.23 – 0.03
SGR	0.10	-0.10 – 0.31	-0.03	-0.14 – 0.11
Allele (PanI^{AA})	0.48	-0.04 – 1.00	0.37	0.04 – 0.69
Trial 2	0.00	-0.21 – 0.20	-0.24	-0.48 – 0.04
Trial 3	-0.43	-0.63 – -0.24	0.02	-0.18 – 0.21
Shelter	0.25	0.05 – 0.47		
Residual-level				
Locomotion	0.27	0.21 – 0.36	0.26	0.20 – 0.35
HT-OFT		*Posterior mode*	*UI 95%*	
ID-level		0.03	-0.08 – 0.14	
Residual-level		0.02	-0.04 – 0.07	

S5. Calculation of the regression lines in the figure 5.

To visualize the association between HT and OFT locomotion, we calculated regression lines from the multivariate model based on either the ID- or residual-level correlations and standard deviations (related to the covariances and variances). Specifically, we calculated the slope of the relationship between HT and OFT as

$$m = \rho_{HT,OFT}\ (\sigma_{HT} / \sigma_{HT,OFT})$$

using correlation coefficient (ρ) and standard deviations (σ) estimated from the model at either the ID- or residual level. We calculated the y-intercept by relating the predicted mean value of HT ($\bar{y}$) to the predicted mean value of OFT ($\bar{x}$):

$$\bar{y} = m\bar{x} + b,$$

which yields

$$b = \bar{y} - m\bar{x}\,.$$

We calculated $\bar{y}$ and $\bar{x}$ using the fixed effects from the model, averaged over different levels of the categorical predictors. Using the slope (m) and intercept (b) calculated we were able to generate a best-fit regression line based on the estimates from the multivariate linear model for both the ID- or residual-levels.

Paper III

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RESEARCH ARTICLE

Personality in juvenile Atlantic cod ecotypes and implications for fisheries management

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Abstract

Animals show among-individual variation in behaviors, including migration behaviors, which are often repeatable across time periods and contexts, commonly termed "personality." These behaviors can be correlated, forming a behavioral syndrome. In this study, we assessed the repeatability and correlation of different behavioral traits, i.e., boldness, exploration, and sociality, and the link to feeding migration patterns in Atlantic cod juveniles. To do so, we collected repeated measurements within two short-term (3 days) and two long-term (2 months) intervals of these personality traits and genotypes of the *Pan* I locus, which is correlated with feeding migration patterns in this species. We found high repeatabilities for exploration behavior in the short- and long-term intervals, and a trend for the relationship between exploration and the *Pan* I locus. Boldness and sociality were only repeatable in the second short-term interval indicating a possible development of stability over time and did not show a relation with the *Pan* I locus. We found no indication of behavioral syndromes among the studied traits. We were unable to identify the existence of a migration syndrome for the frontal genotype, which is the reason that the link between personality and migration remains inconclusive, but we demonstrated a possible link between exploration and the *Pan* I genotype. This supports the need for further research that should focus on the effect of exploration tendency and other personality traits on cod movement, including the migratory (frontal) ecotype to develop management strategies based on behavioral units, rather than treating the population as a single homogeneous stock.

KEYWORDS
Atlantic cod, behavioral syndrome, management, migration, *Pan* I, personality

TAXONOMY CLASSIFICATION
Applied ecology, Behavioural ecology, Environmental sustainability, Movement ecology

1 | INTRODUCTION

Animals show among-individual variation in behaviors, which when repeatable across time periods and contexts are commonly termed "personality" (Dingemanse & Wright, 2020). Personality can significantly influence life history, ecology, and evolution (Biro & Stamps, 2008; Wolf & Weissing, 2012), thereby acting on individual, population, and ecosystem levels (Bolnick et al., 2011; Cote et al., 2017; Hunter Jr et al., 2021; Mittelbach et al., 2014; Réale et al., 2010). One such example is personality in migration behavior (Bowler & Benton, 2005), where migration is defined as a (usually seasonal) round-trip (Stenseth & Lidicker, 1992).

Personality-based migration patterns can lead to personality-related differences in individual life history, such as growth rate and survival (Clobert et al., 2009) because time and energy are spent on dispersion, rather than on foraging or immunity but with the benefit of the possible discovery of better feeding grounds (Raffard et al., 2022). Furthermore, an optimal mix of personalities in a population can influence its survival by supporting the different stages (departure, translocation, and settlement) differently (Bowler & Benton, 2005; Cote, Clobert, et al., 2010). For example, bolder individuals might be more successful in the decision to depart (Bevan et al., 2018), more explorative individuals might be better in the translocation, and less aggressive individuals might thrive better in settlement (Duckworth & Badyaev, 2007). Finally, behavioral differences in migration can influence ecosystems in a variety of ways, such as personality-related prey abundance reduction (Cote et al., 2017; Raffard et al., 2022) and seed migration abilities (Snell et al., 2019; Zwolak & Sih, 2020).

Réale et al. (2007) provided a terminology for studying personality by defining five broad categories (i.e., shyness-boldness, exploration-avoidance, activity, sociability, and aggressiveness). Out of these five categories, three are often found to be correlated to migration (Coates et al., 2019; Cote et al., 2017; Cote, Fogarty, et al., 2010), i.e., *shyness-boldness*: "an individual's reaction to any risky, but not new situation," *exploration-avoidance*: "an individual's reaction to a new situation" and *sociability*: "an individual's reaction to the presence or absence of conspecifics, excluding aggressive behavior" (Réale et al., 2007). These traits all act on the decisions of whether, when, and where an individual should migrate (Shaw, 2020). For example, bolder great tits (Dingemanse et al., 2003) and killifish (Fraser et al., 2001) dispersed over greater distances than shyer individuals. Bolder wild elk (Found & St. Clair, 2019), lizards (Damas-Moreira et al., 2019), and common roach (Chapman, Hulthén, et al., 2011) were more likely to disperse than their shyer counterparts. More explorative lizards (Damas-Moreira et al., 2019; Michelangeli et al., 2017), voles (Hoset et al., 2011), and butterflies (Reim et al., 2018) dispersed further than less explorative individuals. Finally, asocial mosquitofish (Cote et al., 2017) and yellow-bellied marmots (Blumstein et al., 2009) dispersed further than social individuals and asocial lizards dispersed earlier with higher population densities (Cote & Clobert, 2007).

Boldness, exploration, and sociality are often correlated, where higher levels of boldness and exploration and lower levels of sociality are positively related to migration occurrence and distance, forming a migration syndrome (Bevan et al., 2018; Clobert et al., 2009; Coates et al., 2019; Comte & Olden, 2018; Nilsson et al., 2014). These syndromes can be underpinned by physiological traits, e.g., hormone levels and corresponding genes (Réale et al., 2007), life history, and morphological traits, but the latter two have shown to be of less importance (Dingle, 2006). Correlated behaviors limit plasticity and might constrain animals in their ability to behave optimally in every situation (Conrad et al., 2011). This means that personality traits ideally should not be studied without consideration of other traits, because it could only reveal the cost or benefit of the behavior in a particular context while ignoring the possible influence of other traits of equal importance, which carry their own costs and benefits (Sih, Bell, & Johnson, 2004).

The Atlantic cod (*Gadus morhua*) is an ideal candidate for studying the theory of personality traits influencing migration, leading to differences in life history and population structure, with potential implications for management. This species is widespread throughout the continental shelf on both sides of the North Atlantic Ocean and is an apex predator, which makes it a key species in its ecosystem (Link & Garrison, 2002). Although the Atlantic cod has few natural predators, it is of high commercial importance and overfishing has reduced the worldwide population size by as much as 99.9% of its historical levels between 1960 and 1990 (Christensen et al., 2003; Hutchings & Reynolds, 2004). Management measures ranging from a total fishing ban to size-dependent fishing quotas have given the species some space to start a slow recovery, moving away from "critically endangered" to "vulnerable" on the IUCN red list (Sobel, 1996). However, current measurements that are often based on biomass estimates of an assumed homogenous genetic and/or phenotypic group of individuals (Kerr et al., 2017), are not everywhere as successful, as the recovery has been slow or even nonexistent in some populations (Hutchings & Reynolds, 2004). This leads to the search for other factors than biomass as facilitators of recovery, such as behavioral mechanisms, i.e., the transfer from quantitative to qualitative quota (Olsen et al., 2012; Petitgas et al., 2010).

In Iceland, the cod population has been fairly stable since 2002 when quotas were established, but a recent reduction in population size has been observed (MFRI Assessment Reports, 2020). The life cycle of the Icelandic cod starts as larvae on a multitude of spawning grounds spread around the country (Marteinsdottir et al., 2000; Sólmundsson et al., 2015). Part of the larvae drift off to deeper waters, but most of them drift to shore where they settle for the first four years of life. After four years, the individuals begin to show nonbreeding partial migration (Chapman, Brönmark, et al., 2011). "Residents" or "coastal cod" perform feeding migrations close to the shore year-round, while "migrants" or "frontal cod" make more extensive feeding migrations (100–1000 km) outside the spawning season (June–January) (Pálsson & Thorsteinsson, 2003). These migration differences result in differences in habitat use by the two ecotypes during the feeding season; coastal are mainly found in water that is shallower (<200 m) and warmer (x̄ 7.3°C) water than where frontal reside (200–600 m; x̄ 4.6°C) (Pálsson & Thorsteinsson, 2003; Robichaud & Rose, 2004; Thorsteinsson et al., 2012). Consequently, these differences in habitat use during the feeding season by the two ecotypes have led to differences in life history traits (Jónsdóttir et al., 2008; McAdam et al., 2012). Interestingly, both the coastal and the frontal migration patterns are consistent over multiple years, i.e., coastal fish remain close to shore, while the frontal always performs its long-distance feeding migration (Thorsteinsson et al., 2012).

The two ecotypes do not only differ in behavior but also possess different morphological (McAdam et al., 2012) and genetic characteristics, such as the ancient evolutionary stable pantophysin locus (*Pan* I; Kirubakaran et al., 2016; Pampoulie et al., 2008; Pogson & Mesa, 2004). The *Pan* I locus codes for an integral membrane protein, which is expressed in cytoplasmic transport vehicles (Windoffer et al., 1999). The function related to the behavioral ecotypes remains unclear, but the gene resides in a supergene (Linkage group 1, LG1; Matschiner et al., 2022; Pampoulie et al., 2022), comprising the rhodopsin gene related to dim light perception (Andersen et al., 2015; Berg et al., 2016; Pampoulie et al., 2015), and genes encoding for hemoglobin-induced temperature preference (Petersen & Steffensen, 2003), brain function and potentially swim bladder function (Kirubakaran et al., 2016). In the Icelandic cod population, the distribution of individuals carrying the *Pan* I^{AA} genotype is highly skewed towards the coastal behavioral ecotype, while individuals carrying *Pan* I^{BB} are skewed towards the frontal behavioral ecotype (Pampoulie et al., 2008), although a recent study showed that the *Pan* I^{AA} is a better indicator for residency than *Pan* I^{BB} is for migratory behavior (Pampoulie et al., 2022). The behavior of heterozygotes (*Pan* I^{AB}) is ambiguous: they have been shown to behave like either of the homozygotes (Pampoulie et al., 2008), show coastal behavior (Árnason et al., 2009), or differ from coastal behavior (Beukeboom et al., 2022).

Given the evidence that personality can be linked to migration, that Atlantic cod show different migration patterns and the existence of unanswered questions regarding population management, this study focuses on unraveling the link between personality and migration in Atlantic cod juveniles. Studying juveniles specifically allows for investigating the initiation and development during the early life stages (Petitgas et al., 2010; Polverino et al., 2016). As juveniles might face different challenges than adults, personality change can be expected during ontogeny, i.e., developmental plasticity, which can influence behaviors expressed later in life (Bowler & Benton, 2005; Polverino et al., 2016; Schuster et al., 2017; Stamps & Groothuis, 2010). So far, most studies including *Pan* I have focused on adults (Fevolden et al., 2012), while juveniles are important for the recruitment of the Icelandic stock (Jonasson et al., 2009).

To get insight into the link between personality and migration, we measured personality over short- (3 days) and long-term (2 months) intervals, aiming to answer the following specific research questions: (1) Do Atlantic cod juveniles show consistent behavioral individual differences for exploration, boldness, and sociality, i.e., personality, in the short-term (3 days) and long-term (2 months)?; (2) Do these behavioral differences correlate, forming a behavioral syndrome? (3) Can *Pan* I be integrated forming a migration syndrome together with these personality traits, i.e., are cod carrying the *Pan* I^{BB} more explorative, bolder, and more (a)social than cod carrying the *Pan* I^{AA}?

We predicted that Atlantic cod juveniles show consistent individual differences in bold, explorative, and sociality behavior within short- (3 days) and long-term (2 months) intervals, as juvenile Atlantic cod have shown differences in other behaviors, that these behaviors are repeatable and that this continues into adulthood (Beukeboom et al., 2022; Hansen et al., 2008; Hart & Salvanes, 2000; Villegas-Ríos et al., 2018; Zimmermann et al., 2012). We predicted that juvenile cod show a behavioral syndrome, where a higher boldness and exploration and lower sociality are correlated as already shown in adult cod and other fish species (Coates et al., 2019; Cote, Fogarty, et al., 2010). Finally, we predicted that the migration type, identified by *Pan* I genotypes, can be integrated forming a migration syndrome, where cod carrying the *Pan* I^{BB} are bolder, more explorative, and less social, while cod with the *Pan* I^{AA} are shyer, less explorative and more social. This assumption is based on the link between *Pan* I and migration behavior (Pampoulie et al., 2008, 2022; Thorsteinsson et al., 2012) and that exploratory behavior has a genetic basis in adult cod (Drangsholt et al., 2014). Getting insight into these questions will increase our knowledge about how personality could be linked to susceptibility to the harvesting of Atlantic cod and thereby provides input for population management tools.

2 | METHODS

The methods followed the same protocol as described in Beukeboom et al., 2022; 102 age 0+ cod juveniles (weight range = 0.75–4.39 g and mean = 1.87 g; standard length range = 3.83–7.55 cm and mean = 5.72 cm) were beach seined from the 3rd to 12th of October 2019 in three different fjords around the Westfjords of Iceland to obtain genetical variation. They were transported to a laboratory in Bolungarvik, Iceland, and housed individually in 9.5-L tanks (~29 × 21 × 19 cm, water level 16 cm, Aquaneering Inc.). The recirculating system contained freshwater mixed with marine salt to achieve a natural salinity of 30 ± 2‰, a temperature of 11 ± 1°C (November) and 10 ± 1°C (December–June), ammonia levels of <0.5 ppm, oxygen levels of 10.4 ± 0.1 mg/L and a constant photoperiod of 12 h:12 h (7 AM–7 PM GMT). The water circulated through the Aquaneering system, passing through all the tanks, a biofilter, sieves (mesh size 25 μm), and a UV light for sterilization. Every tank had a gray PVC pipe to provide shelter to the fish. Fish were fed twice a day alternating defrosted shrimp and bloodworms daily ad libitum. On the experimental days, feeding took place after the experiment to avoid any differences in feeding motivation. Every month, after the first trial of the open field experiments (see below), the fish were measured for weight and standard length. In November, a set of trial experiments was performed, which are presented in Beukeboom et al., 2022.

2.1 | Behavioral tests

Of the initial 102 caught individuals, 43 were included in the analysis (see Results). Each individual underwent a cycle of a shelter test (ST, boldness), open field test (OFT, exploration), novel object test (NOT, boldness), and mirror test (MT, sociality) during four trials: January 19–21 (Trial A), January 22–24 (Trial B), March 15–17 (Trial C), and March 18–20 (Trial D) (Figure 1). All fish started with the ST, followed by the OFT. Consecutively, 20 fish were subjected to first the NOT and then the MT, while the rest ($N=23$) received the MT first and then the NOT to take any influence of the NOT or MT test order into account (Figure 1). In addition, all fish were tested in the same overall order to standardize the intervals between the tests for each fish. Data in the ST was collected manually, while OFT, NOT, and MT videos were analyzed with video-tracking software (Ethovision, Noldus, v. 15.0). A smoothing parameter of 0.1 was set in the video-tracking software, which set the sample points to the previous location until the distance moved was more than 0.1 cm, which removed any noise of moving pixels due to imperfect light conditions, as this was found to be appropriate for the setup we used (Beukeboom et al., 2022). The water temperature of the experimental tank ranged from 9.2 to 11.5°C.

2.2 | Shelter test (ST)

The shelter test is commonly used as a measure of boldness (see for an overview Toms et al. (2010)), where bolder fish have a shorter exit time. The fish was gently captured with a dipnet out of its home tank and placed in a shelter (26 L; 40×40×40 cm, water level 16 cm) and after five minutes of acclimation, the door was lifted. The fish was given 5 min to leave the shelter, and the latency to exit was recorded. If it did not leave voluntarily, it was gently forced out using a dip net into the arena (51 L; 80×40×40 cm, water level 16 cm) and given a maximum score of 300 s. Unfortunately, in 95 out of 158 ST trials (60.1%), fish did not leave the shelter voluntarily. This was most likely due to the test duration being too short, which resulted in insufficient variation in this behavior. This original boldness measurement was therefore excluded from further analysis, but a binary factor (left shelter y/n) was included in our models to account for any influence of the fish being pushed out of the shelter rather than leaving voluntarily.

2.3 | Open field test (OFT)

In absence of a predator, juvenile cod have been shown to move freely across an open space (Nordeide & Svåsand, 1990), which most likely serves the function of information gathering (Hughes, 1997). Therefore, the OFT was used as a proxy for exploration, where it is expected that explorative fish swim greater distances and cover bigger areas than nonexplorative individuals. The test was carried out as follows: as soon as the fish entered the arena during the ST (51 L; 80×40×40 cm, water level 16 cm, Figure 1), the shelter was closed and the fish was video recorded for five minutes. The total distance traveled and the total area covered (i.e., traversed, calculated by using the total unique x/y coordinates rounded to the nearest integer) were extracted. Area covered and distance traveled (both log-transformed) were highly correlated (PEARSON: $r=0.97$; CI 95% [0.96–0.98]; $p<0.001$). Because the area covered is statistically ceiled (i.e., there is a maximum number of unique X/Y coordinates available), the total distance traveled was used in further analysis, to catch the maximum variation possible.

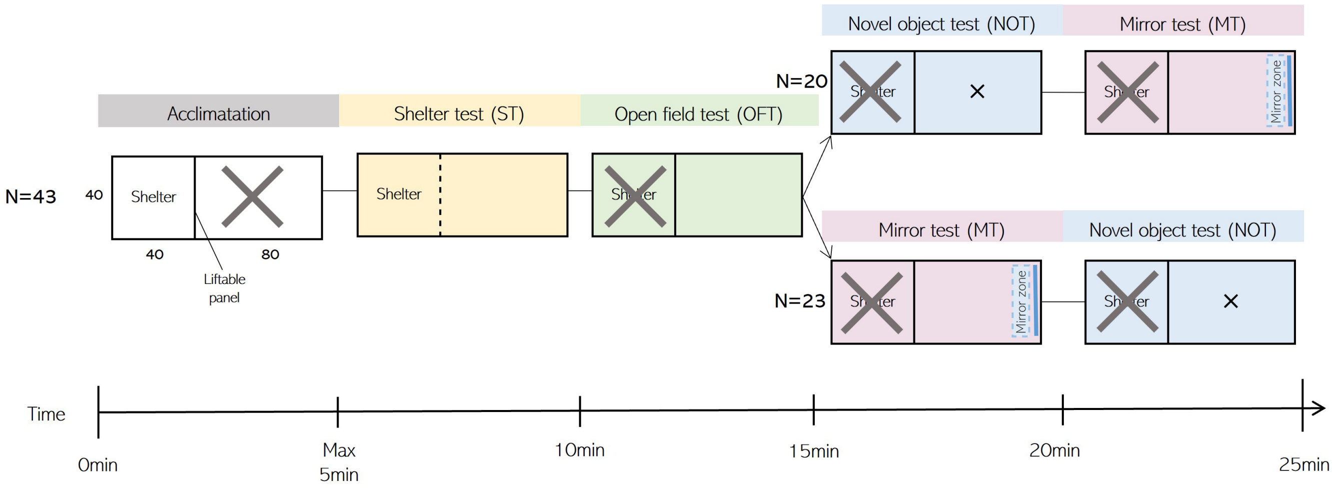

FIGURE 1 Experimental setup of the four different tests. Dimensions are in centimeters, crossed areas are inaccessible during the experiment.

2.4 | Novel object test (NOT)

The novel object test was used as a measure of boldness, where shy individuals are expected to flee, retreat, or freeze, while bold individuals are expected to become more active and approach the novel object (Toms et al., 2010). The NOT was carried out after the OFT ($N=20$) or after the MT ($N=23$). When present, the mirror was removed, and a novel object was dropped in the middle of the arena (Figure 1). In January, this was a red, tin can (ø 6 cm, 113 cm^2) and in March this was a blue plastic pipette tip rack (13 × 10 cm; 117 cm^2) to reduce habituation to the object. Five minutes were video recorded and the mean distance to the object was extracted as a proxy for boldness.

2.5 | Mirror test (MT)

Cod juveniles can show plastic social behavior, from shoaling to aggression (Meager et al., 2018). The mirror test can be used to measure both sociality and aggression, depending on the species and developmental phase. While Villegas-Ríos et al. (2018) used the mirror test as a measure of aggression in adult cod, the life stage where the risk of being predated is minimal, we assume that the mirror test in this study on juveniles elicited social behavior instead for two reasons. Firstly, the arena was open with no shelter to hide, which has been shown to elicit shoaling behavior in juvenile cod (Laurel et al., 2004). Secondly, aggressive/submissive behavior often occurs when opponents differ in size (McCormick & Weaver, 2012; Sverdrup et al., 2011), and as the mirror just reflects the fish itself, these size differences are nonexistent. The MT was carried out after the OFT ($N=20$) or after the NOT ($N=23$). When present, the object was removed, and a mirror was placed opposite the shelter door (Figure 1). Five minutes were video recorded, and the total time spent in a 10 cm zone in front of the mirror was extracted as a proxy of sociality. After the experiment, visual inspection of the videos for aggressive and/or social behaviors confirmed our decision; social behaviors, such as repeated approaches to the mirror at cruising speed and "hanging around" the mirror were highly represented, and aggressive behaviors such as accelerations towards the mirror, biting or c-shaping were absent (Sverdrup et al., 2011).

2.6 | Genotyping

In June 2020, at the end of the overall project, the fish were euthanized with phenoxyethanol (1.6 mg/L) and fin clips were taken to assign the fish to either coastal (*Pan* I^{AA}), frontal (*Pan* I^{BB}), or heterozygote (*Pan* I^{AB}) using PCR analyses as described in Pampoulie et al. (2006).

2.7 | Statistics

All data were analyzed using the same method as in Beukeboom et al. (2022) using R (v. 4.1.2; R Core Team, 2021). We fit multivariate linear mixed models to estimate the repeatabilities of and the correlations between the total distance traveled (OFT), mean distance to object (NOT), and time spent in the mirror zone (MT). The models were fit using the Bayesian software Stan (Carpenter et al., 2017) run via the "brms" package (Bürkner, 2017). We ran four separate models containing four different subsets of the data: short-term (Δ 3 days) for January (trials 1 and 2; SJ) and March (trials 3 and 4; SM) and long-term (Δ 2 months) for the first trials (trial 1 and 3; LA) and the second trials (trial 2 and 4; LB) of each month. The models simultaneously regressed each dependent variable (i.e., OFT, NOT, and MT estimates) against a set of fixed and random effects while also quantifying the covariance between the dependent variables. The fixed effects of weight (g), standard length (cm), Fulton's condition factor ($K = Weight/Length^3 \times 100$), and specific growth rate ($SGR = \Delta$ ln(weight) *100/Δ day) that could influence the personality estimates were evaluated for collinearity. Pearson correlations revealed that all measurements were substantially correlated (Figure A1) and therefore only SGR was included in the analysis. The three personality estimates and SGR were scaled using z-scoring (subtracted the mean and divided by the standard deviation) separately for the subset of data used in each model. The full version of each model was fit with the scaled personality measurement as response variables (i.e., total distance traveled, mean distance to object, and total time in the mirror zone), the four fixed effects of genotype, SGR (since the previous month for short-term, January–March for long-term), trial and shelter leave (y/n). We include a binary covariate to indicate the order in which fish were tested for the NOT and MT. The random-effects structure included individual fish identity (ID) as a grouping variable, allowing us to calculate the repeatability of the personality estimates as the ratio of the among-individual variance and the sum of the among-individual and residual-level variances (Johnson & Koch, 2011). Moreover, the model estimated covariances between the personality estimates at both the ID and residual levels. The among-individual covariance quantified the degree to which the personality estimates were correlated among individuals across multiple trials (i.e., behavioral syndrome), while the residual level covariance quantified the degree to which the personality estimates were correlated among observations independently of the identity of individuals. The model was run for 4000 iterations (2000 for warmup and 2000 for sampling), four chains, an adapted delta of 0.9, and all other parameters set to their defaults. Convergence was assessed using the standard diagnostics provided by Stan (Bürkner, 2017; Carpenter et al., 2017), including the potential scale reduction factor ($\hat{R}$), effective sample size, and visual inspection of trace plots and histograms for each model parameter. We used medians for point estimates and quantiles with 95% coverage for uncertainty intervals ($\text{UI}_{95\%}$).

2.8 | Ethical note

The number of fish and the procedures (fishing, handling, finclipping, and behavioral tests) were chosen to adhere to strict ethical guidelines, but an ethics committee approval for the research project was not required by Icelandic regulation (Act No. 55/2013 on Animal Welfare).

3 | RESULTS

The 102 0+ juvenile cod caught in October 2019 consisted mainly of coastal cod (*Pan* I^{AA}; $N=75$), with substantially fewer heterozygotes (*Pan* I^{AB}; $N=17$) and very few migratory individuals (*Pan* I^{BB}; $N=4$). The *Pan* I locus of six fish could not be determined due to failing analysis. A high mortality rate ($N=56$) caused by the incapability of adjusting to the laboratory food, which is not uncommon for the transfer from the wild to the lab, caused a major reduction in the sample size. Additionally, the individuals with unknown genotypes, fish that lost weight between January and March, and fish that had a condition factor below the mortality threshold of 0.8 (Marteinsdottir & Begg, 2002), were removed. This left only one individual with the migratory genotype. Therefore, we only analyzed data from the coastal and heterozygotes, comprising a final dataset of 43 fish. Although all fish performed the experiments, which should have led to 540 observations (43 fish * 3 tests * 4 trials; 90 per subset), video failures reduced the number to 328 trials (83 observations in the models SJ, SM, and LA; 79 in LB). The 43 individuals gained weight from the start to the end of the experiments (January–March) from $\bar{x}$ 6.48 ± SD 3.07 (start) to 10.05 ± 6.18 gr (end), had a mean Fulton's condition factor of 1.08 ± 0.10 (start) and 1.09 ± 0.12 (end) and a specific growth rate of 0.78 ± 0.30% body weight/day (start-end). Thirty-five were assigned as coastal (*Pan* I^{AA}) and eight were heterozygotes (*Pan* I^{AB}). All models converged with $\hat{R}=1$, had well-mixed chains, and no extreme trails were visible in the trace plots. The total distance traveled ranged from 49.2 to 4147.7 cm ($\bar{x}=1318.2$ cm), the mean distance to the object ranged from 14.2 to 36.6 cm ($\bar{x}=25.7$ cm) and the total time in the mirror zone from 0.0 to 282.1 s ($\bar{x}=82.8$ s).

3.1 | Repeatabilities

Among-individual variance (ID) of total distance traveled in the OFT (i.e., exploration) was unambiguously different from zero both in the short-term and long-term models, indicating individual repeatability for this trait. Among-individual variance exceeded the within-individual (residual) variance in the short-term intervals, such that the behavior was highly repeatable (January: $R=0.80$; $UI_{95\%}=[0.62, 0.89]$; March: $R=0.56$; $UI_{95\%}=[0.27, 0.75]$, Figures 2–4, Table A1). By contrast, the residual variance exceeded the among-individual variance in the long-term intervals, resulting in lower repeatability (Trial A: $R=0.48$; $UI_{95\%}=[0.16, 0.70]$;

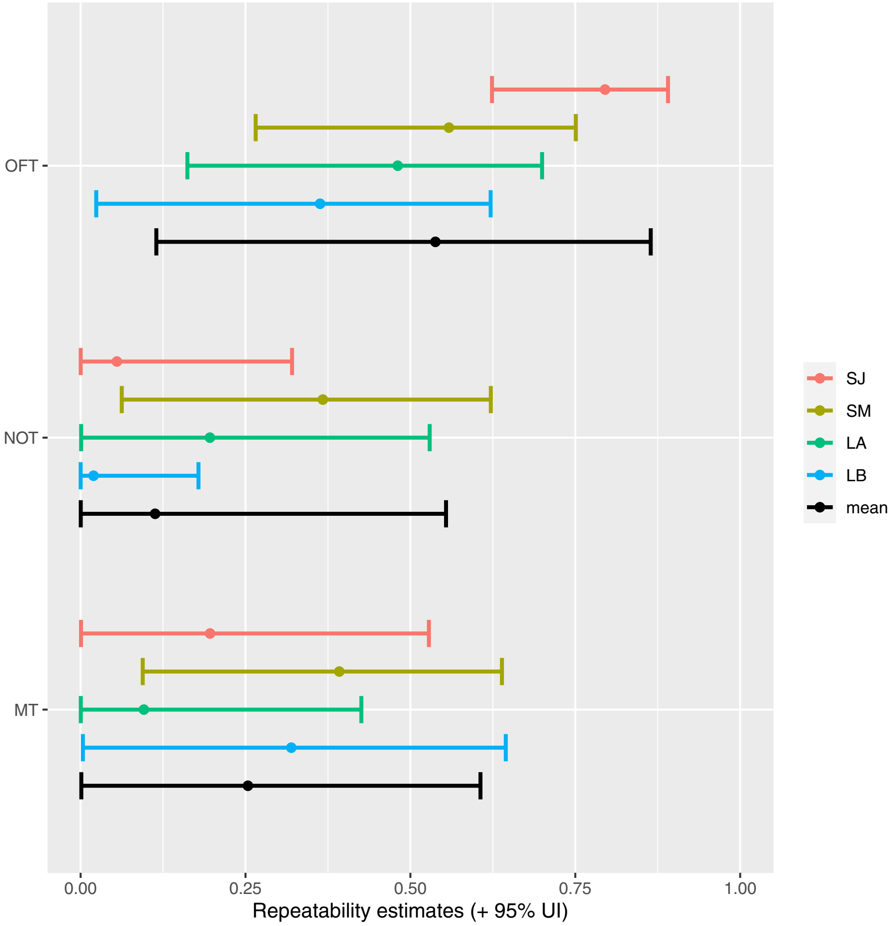

FIGURE 2 Repeatabilities and their 95% UI short-term (three days) intervals within January (SJ) and March (SM) and between two months (long-term) intervals for the first and second trials (LA; LB) and their combined mean (black) for exploration (OFT), boldness (NOT) and sociality (MT). Estimates with a median away from zero and error bars non-bordering 0 are considered repeatable.

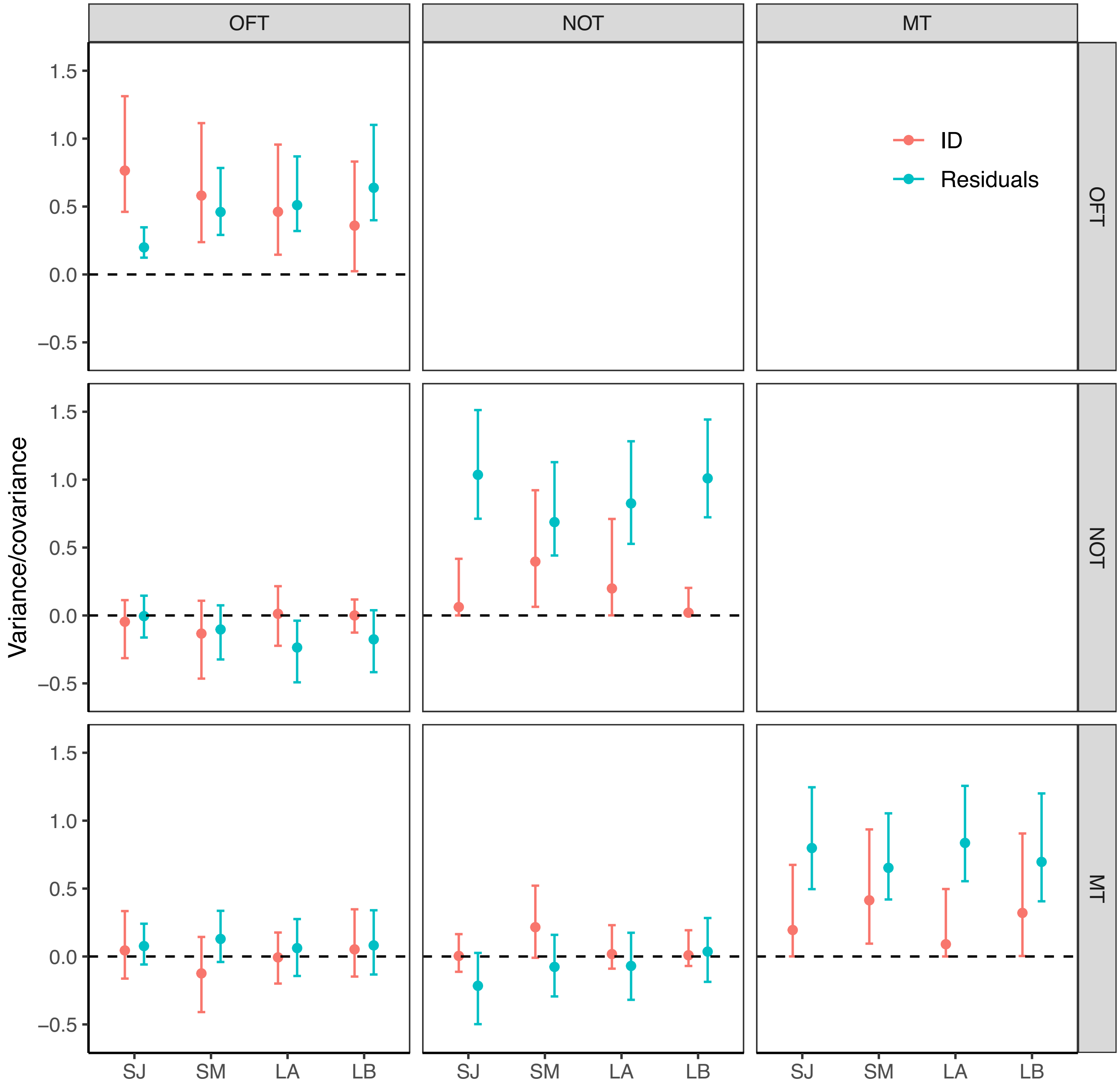

FIGURE 3 Medians and their corresponding 95% uncertainty intervals for the variances and pairwise covariances of exploration (OFT), boldness (NOT), and sociality (MT) for the two short-term (3 days; SJ and SM) and long-term (2 months; LA and LB) models on both the ID (red) and residual level (blue). The dashed line indicates zero.

Trial B: $R = 0.36$; $UI_{95\%} = [0.02, 0.62]$, Figures 2 and 3, Table A1). Repeatabilities for mean distance to object in the NOT (i.e., boldness) and time spent in front of the mirror in the MT (i.e., sociality) was overall low, although in both cases, the short-term interval in March was repeatable (Table A1). This increase in repeatability between the short-term models of January and March was mainly caused by an increase in the among-individual variance and to a lesser extent a decrease in the residual variance (Figures 2 and 3, Table A1). These patterns are also visible in the raw data, where OFT has short lines on its axis and NOT and MT long lines (Figure 4).

3.2 | Behavioral syndromes

Covariances of the pairwise combination of the three estimates (OFT-NOT, NOT-MT, and OFT-MT) for all four models (SJ, SM, LA, and LB) were all close to zero with $UI_{95\%}$ strongly overlapping zero (Figure 3, Table A2). Additionally, no visible association was apparent on the ID level (no apparent increasing or decreasing dot patterns), nor on the residual level (lines not pointing in the same direction) when plotting all combinations of the personality traits pairwise (Figure 4). These results show no evidence of a behavioural syndrome between any of those traits.

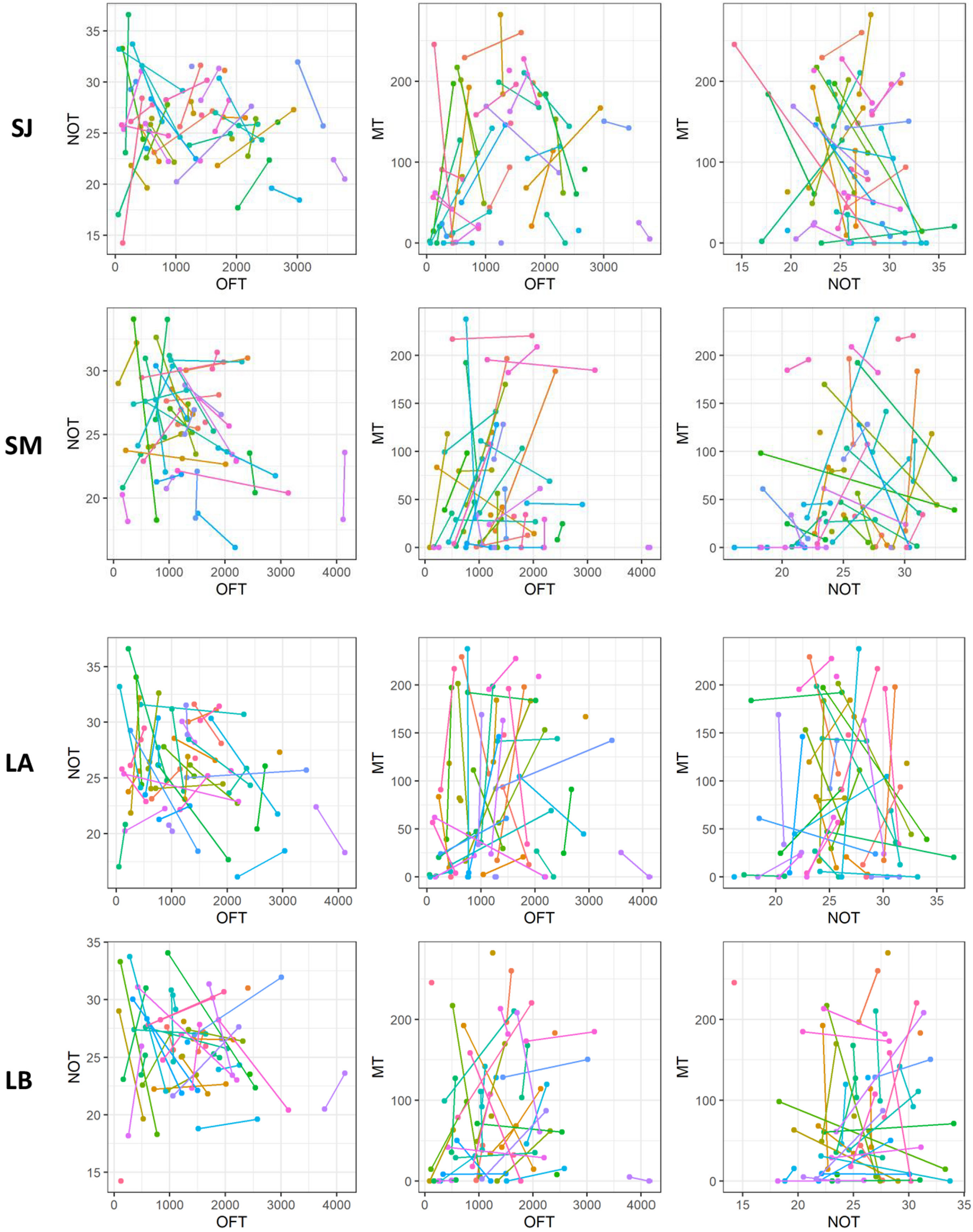

FIGURE 4 Pairwise combinations of exploration (OFT), boldness (NOT), and sociality (MT) on the short-term for January (SJ) and March (SM) and long-term correlation for trials A (LA) and B (LB) of January and March. Connected/colored dots are estimates for the same individual. Within axis distance (i.e., short or long) indicates repeatability, overall dot pattern (i.e., decreasing/increasing or no pattern) indicates a behavioral syndrome and the direction of the lines (i.e., similar or different) indicates a correlation on the residual level.

3.3 | Fixed effects

The *Pan* I genotype shows a trend to influence the total distance traveled during the OFT, with the most uncertainty in the short-term January and the least in the long-term first trial: coastal individuals tended to move more than heterozygotes. The *Pan* I genotype did not show to influence the mean distance to object, nor the total time spent in the mirror zone (Figure 5, Table A2). A trend was also visible for specific growth rates in the OFT as all estimates are away from zero but with slightly overlapping $UI_{95\%}$. Fish with a higher SGR might travel longer distances during the OFT. A similar trend was visible for the NOT; faster-growing fish were on average closer to the object, with the strongest evidence for this in the long-term models where point estimates and uncertainty intervals were farther from zero. A final trend was visible for the MT; fish with a higher SGR spent less time in the mirror zone in the short-term interval in January, but no influence was visible in the other models, where point estimates were close to zero with strongly zero-overlapping uncertainty intervals (Figure 5, Table A2). The order of the experiments, shelter leave, and trial number had no clear effects on the personality traits (Table A2, Figure A2).

4 | DISCUSSION

In this study, we aimed to examine the link between personality and migration tendencies, using the migration-linked *Pan* I locus in Atlantic cod juveniles. To do so, we collected repeated measurements within short- (3 days) and long-term intervals (2 months) of exploration, boldness, and sociality and genotypes for the *Pan* I locus. Using this data, we aimed to answer the following research questions: (1) Do Atlantic cod juveniles show personality over short- (3 days) and long-term (2 months) intervals for boldness, exploration, and sociality?; (2) Do these behavioral differences correlate into behavioral syndromes? (3) Can *Pan* I be integrated to form a migration syndrome with these personality traits? We found that exploration behavior was repeatable in the short- and long-term intervals, with a possible link with the *Pan* I locus, where coastal fish might be more explorative than heterozygotes. By contrast, boldness and sociality were only repeatable in the second short-term interval. Moreover, the personality estimates were not correlated to each other at the individual level, indicating the lack of any behavioral syndrome. We were unable to identify the existence of a migration syndrome for the frontal genotype, which is the reason that the link between personality and migration remains inconclusive, but we demonstrated a possible link between exploration and the *Pan* I genotype, which supports the need for further research on this topic.

4.1 | Personality in Atlantic cod juveniles

Exploration was found to be repeatable between three-day intervals but also between two months. Although it is difficult to compare repeatabilities across studies with different time intervals

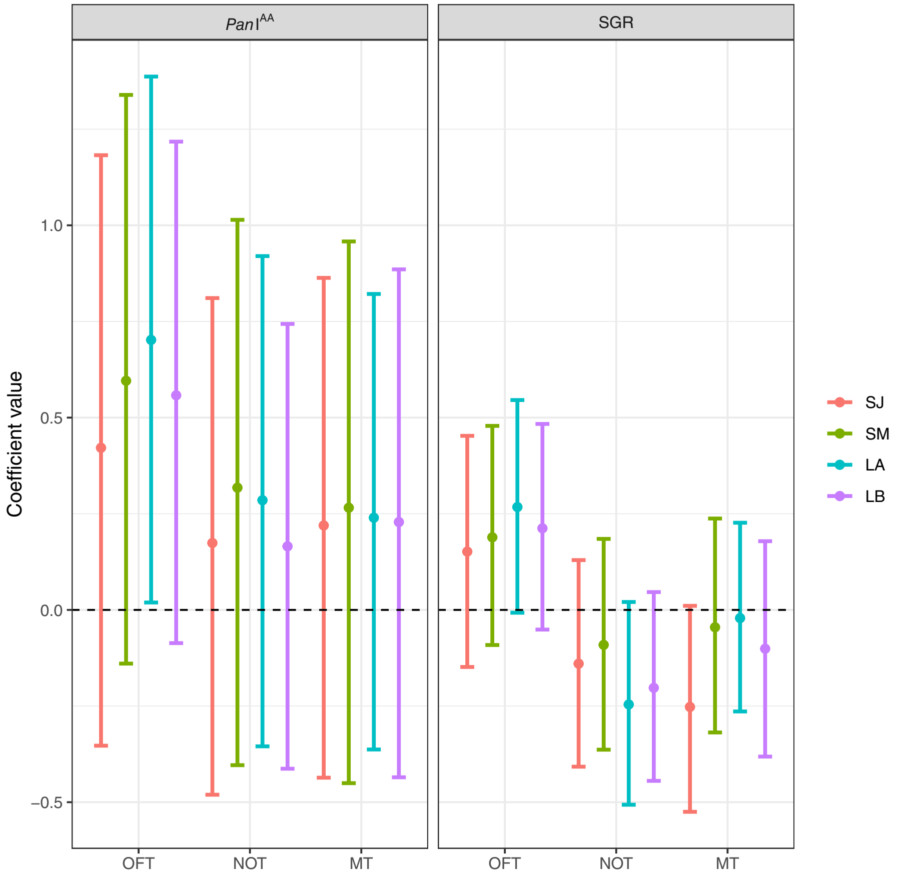

FIGURE 5 Medians and their corresponding 95% uncertainty intervals for the fixed effect of Pan I genotype and specific growth rate (SGR) for exploration (OFT), boldness (NOT), and sociality (MT) for the two short-term (SJ and SM) and long-term (LA and LB) models. The dashed line indicates zero. Because SGR was z-scored, the co-efficient values are presented in units of standard deviation.

between trials(Biro & Stamps, 2008), the short-term repeatability found in this study is higher than that was found in a study on adult Atlantic cod (Villegas-Ríos et al., 2018) and the long-term repeatability is similar to a previous study on cod juveniles at an earlier age (Beukeboom et al., 2022). The higher repeatabilities found for the short-term compared with the long-term intervals in this study for exploration were also found in a meta-analysis (Bell et al., 2009). This supports the finding that cod show consistent individual differences in exploration behavior, i.e., personality both at juvenile and adult stages whereas boldness and sociality seem to be more plastic at this developmental stage. Both were only repeatable in the short-term interval in March, mainly caused by an increase in the among-individual variance and to a lesser extent to a decrease in the within-individual variance compared with January. This indicates that boldness and sociality strengthen with fish age as was found in cichlids (Budaev et al., 1999) and mosquitofish (Polverino et al., 2016), but further research over a longer time period is needed.

4.2 | Behavioral/migration syndrome

This study found no evidence that exploration, boldness, and sociality were correlated in Atlantic cod juveniles and thereby not indicating a full-suit behavioral syndrome for migration, as was found in Nilsson et al. (2014). The lack of a behavioral syndrome could be explained by environmental changes in cod natural habitat that might favor the plasticity of these traits (Sih, Bell, Johnson, & Ziemba, 2004). Further research with a larger sample of individuals, including frontal individuals, is needed to confirm this result (Garamszegi et al., 2012).

Of the three personality traits measured, only exploration showed a tendency of being influenced by the *Pan* I locus in both the short- and long-term intervals, where coastal individuals traveled greater distances than heterozygotes and therefore are believed to be more explorative. Interestingly, in a previous study, the same pattern was found at an earlier stage of development i.e., up to five months earlier (Beukeboom et al., 2022). This strengthens the support for a stable link between personality, development, and the migration-linked *Pan* I locus in Atlantic cod. Moreover, this correlation in combination with the high repeatability of exploration gives support to the idea that exploration has a heritable basis as was found in adult cod (Drangsholt et al., 2014) and thereby has the potential to form a basis of personality-based evolution (Bell, 2008; Dochtermann et al., 2015). There is no current evidence for a relationship between exploratory behavior and heritability in other fishes (e.g., brown trout: Kortet et al. (2014); zebrafish: Lamb (2018)), but a genetic basis was found in great tits (Drent et al., 2003; Mouchet et al., 2021).

Due to a lack of the migratory genotype in our study, we could not link personality to the *Pan* I locus for this ecotype as intended and are therefore unable to draw any conclusions about the link between personality and migration. We also could not study how coastal and heterozygotes behave compared with the frontal ecotype. It is possible that a behavioral syndrome is only detectable when correlating coastal with frontal cod, which remains to be investigated. Interestingly, the fact that we failed to catch migratory individuals using the beach seining method (i.e., fishing in shallow water of <1.5 m), suggests that cod of the frontal ecotype migrate soon after developing past the larval stage. This is supported by data on Atlantic cod juveniles in Sweden where coastal cod juveniles were also more likely to be found in shallower water, with a decrease in abundance with increasing depth (Henriksson et al., 2022).

4.3 | Implications for fisheries management

Although there is an increasing recognition that personality plays an important role in ecology and population dynamics, it has not much been applied in fisheries management yet (Berger-Tal et al., 2016; Diaz Pauli & Sih, 2017; Merrick & Koprowski, 2017; Shumway, 1999; Watters et al., 2003). The management of the Icelandic cod stock is currently based on quota, gear selectivity, and temporary fisheries closures (i.e., protected areas), but these management measures/tools are focused on fish size, productivity, and environmental improvement but do not consider fish behavior (Fisheries Management, 2022; Jaworski et al., 2010; Ólafsdóttir & Jakobsdóttir, 2021; Pampoulie et al., 2022).

An often-suggested method to include behavioral variation into population management is the intended use of mixed-gear fishing methods that together are unselective for personality type. For example, angling and longlining select for boldness and activity (Härkönen et al., 2014), pots and traps select for boldness and exploration, gill nets select for bold and active individuals, trawlers select for shyness, activity, sociality (MFRI Assessment Reports, 2020), and seining on shyness (Diaz Pauli and Sih (2017) and reference therein). As the *Pan* I locus is part of a supergene located in the LG1 (Berg et al., 2016; Matschiner et al., 2022) containing hundreds of genes maintained by selection processes and strongly discriminating the coastal and frontal behavioral ecotypes, the trend of a correlation of the exploration to the *Pan* I genotype could be representative of the difference in the exploration capacity of the coastal and frontal behavioral ecotypes. If this is the case, then unmanaged use of fishing gear that is unintentionally selected for personality, might deplete one of the behavioral ecotypes and thereby lose migration-related features, genomic structural variants (Matschiner et al., 2022; Pampoulie et al., 2022), and other variation in the population that could affect population growth and recovery and eventually cause unwanted fisheries-induced evolution (Árnason et al., 2009; Hutchings et al., 2007; Nusslé et al., 2011; Smith & Blumstein, 2013; Walsh et al., 2006; Ward et al., 2016). It might for example partly explain the *Pan* I genotype fluctuations observed in Icelandic waters (Árnason et al., 2009; Jakobsdóttir et al., 2011). Evidence that size-selective harvesting can cause a change in available personality types has already been shown in zebrafish (Sbragaglia et al., 2019) and in rainbow trout, where bold and fast-growing fish were more vulnerable to fisheries (Biro & Post, 2008). Although no direct studies have focused on the relationship between catching method and personality in Atlantic cod, some studies have made efforts to examine how personality influences space use of cod (Villegas-Ríos et al., 2018), how harvesting targets deep vs shallow water cod (Olsen et al., 2012), how specific gear unintentionally targets cod that behave differently (Bøe, 2014) or are in poor condition (Ovegård et al., 2012), and how cod react to trawling in and in front of the net (Handegard & Tjøstheim, 2005; Rosen et al., 2012). Implementing mixed-gear methods might also increase the accuracy of estimating the stock biomass, which is commonly underlying quota determination (Morgan, 1997). For example, when fishing methods specifically select bold individuals, it can increase average timidity in the population, and the remaining individuals are therefore harder to catch. This could lead to an underestimation of the total population size (Andersen et al., 2018; Arlinghaus et al., 2017). It is therefore important to include personality in fisheries management. Which specific fishing methods are selecting for the different behavioral ecotypes in Icelandic cod and how these methods need to be arranged remains to be investigated.

Another method used to manage fish populations is the use of MPAs, which aim to protect fish populations against overharvesting and can benefit the fish industry by a spillover of adults, eggs, and larvae beyond the boundaries of the MPAs and into the fished areas. Recent studies suggest that protection by MPAs can affect the behavior of individuals living inside it. For instance, individuals of protected populations typically have a decreased wariness and flight initiation distance compared with fish outside these areas (Bergseth et al., 2016; Januchowski-Hartley et al., 2015), which might increase the chance of being caught when leaving the protected area (Alós et al., 2015; Diaz Pauli & Sih, 2017). In turn, individual behavior can affect the effectiveness of MPAs. Fish that are more mobile have a higher chance of moving outside the MPA, where their risk of being harvested is higher (de Benito-Abelló et al., 2022; Dwyer et al., 2020; Mee et al., 2017; Parsons et al., 2010; Pilyugin et al., 2016; Thorbjørnsen et al., 2021; Villegas-Ríos et al., 2021), especially when fishing pressure on the edges of the reserves is high (Kellner et al., 2007). In this case, if movement behavior has a heritable component, MPAs might cause evolutionary changes within the populations, by favoring resident rather than migratory behavior. This in turn might influence the yield and eventually change the available gene pool in the species (Villegas-Ríos et al., 2017, 2021). It is therefore important to integrate individual variation in spatial behavior into MPA design and implementation (Claudet et al., 2006; McDermott et al., 2017).

5 | CONCLUSION

This study shows the first evidence of repeatable exploration behavior and a possible link between this behavior and the migration-linked *Pan* I locus in the Icelandic cod population, which could have implications for stock management. In a recent study, it was shown that the attribution of *Pan* I to determining migration tendency is more complex than previously assumed. The coastal cod (*Pan* I^{AA}) is staying close to the coast as previously thought, but the correlations between the frontal cod genotype (*Pan* I^{BB}) and long-distance migrations are more ambiguous around Iceland (Pampoulie et al., 2022). Further research should therefore move away from solely using the *Pan* I as a determination of migration type when continuing research on personality-linked stock management.

AUTHOR CONTRIBUTIONS

Rosanne Beukeboom: Conceptualization (equal); data curation (lead); formal analysis (equal); investigation (lead); methodology (lead); software (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Joseph S. Phillips:** Formal analysis (equal); writing – review and editing (equal). **Guðbjörg Ásta Ólafsdóttir:** Conceptualization (equal); funding acquisition (lead); resources (lead); writing – review and editing (supporting). **David Benhaïm:** Supervision (lead); validation (equal); writing – original draft (supporting); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

All data underlying the results in this articles are available at Dryad doi: 10.5061/dryad.79cnp5j07.

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APPENDIX A

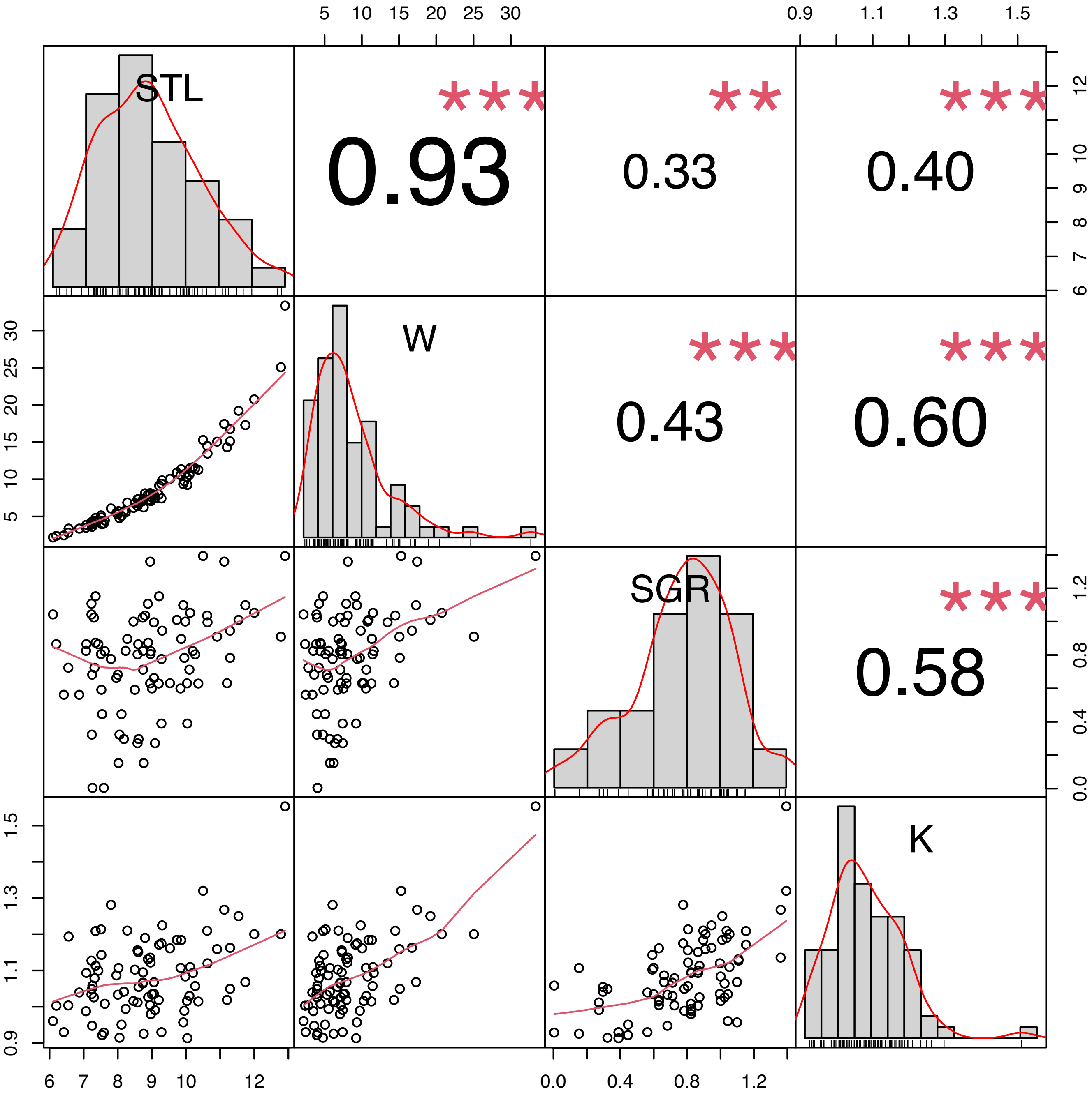

FIGURE A1 Pearson correlation matrix of possible effects on the personality estimates.

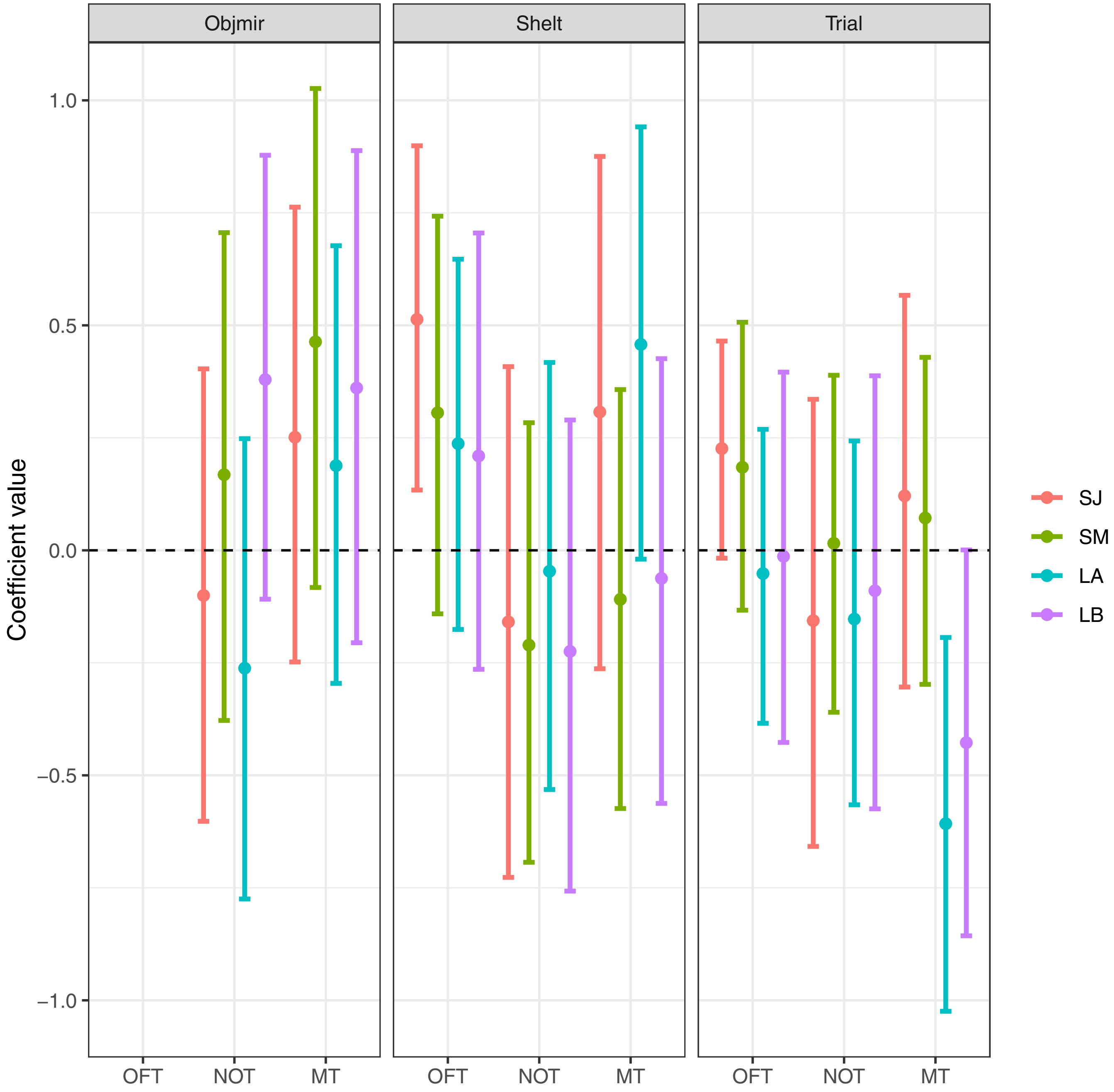

FIGURE A2 Median and 95% uncertainty intervals of the covariances of the four models (SJ, SM, LA and LB) between the pairwise personality measurements (OFT, NOT and MT).

TABLE A1 Median and 95%uncertainty intervals of the four models (SJ, SM, LA, and LB) invariances of the three personality measurements (OFT, NOT, and MT) and the fixed effects (Allele, SGR, Trial, Test order, and Shelter leave).

SJ	**OFT**		**NOT**		**MT**	
Predictor	**Median**	**UI 95%**	**Median**	**UI 95%**	**Median**	**UI 95%**
ID level						
Measurement	0.76	0.46 to 1.31	0.06	0.00 to 0.42	0.19	0.00 to 0.67
Allele (*Pan* I^{AA})	0.42	−0.35 to 1.18	−0.17	−0.48 to 0.81	0.22	−0.44 to 0.86
SGR	0.15	−0.15 to 0.45	−0.14	−0.41 to 0.13	−0.25	−0.52 to 0.01
Trial	0.23	−0.02 to 0.47	−0.16	−0.66 to 0.34	0.12	−0.30 to 0.57
Shelter leave	0.51	0.13 to 0.90	−0.16	−0.73 to 0.41	0.31	−0.26 to 0.88
Object/Mirror order			−0.10	−0.60 to 0.40	0.25	−0.25 to 0.76
Residual level						
Measurement	0.2	0.12 to 0.35	1.04	0.71 to 1.51	0.8	0.50 to 1.25
SM	**OFT**		**NOT**		**MT**	
Predictor	**Median**	**UI 95%**	**Median**	**UI 95%**	**Median**	**UI 95%**
ID level						
Measurement	0.58	0.24 to 1.11	0.4	0.06 to 0.92	0.41	0.09 to 0.67
Allele (*Pan* I^{AA})	0.60	−0.14 to 1.34	−0.32	−0.40 to 1.01	0.27	−0.45 to 0.96
SGR	0.19	−0.09 to 0.48	−0.09	−0.36 to 0.18	−0.05	−0.32 to 0.24
Trial	0.18	−0.13 to 0.51	0.02	−0.36 to 0.39	0.07	−0.30 to 0.43
Object/Mirror order	0.31	−0.14 to 0.74	−0.21	−0.69 to 0.28	−0.11	−0.57 to 0.36
Shelter leave			0.17	−0.38 to 0.71	0.46	−0.08 to 1.03
Residual level						
Measurement	0.46	0.29 to 0.78	0.69	0.44 to 1.13	0.65	0.42 to 1.05
LA	**OFT**		**NOT**		**MT**	
Predictor	**Median**	**UI 95%**	**Median**	**UI 95%**	**Median**	**UI 95%**
ID level						
Measurement	0.46	0.15 to 0.96	0.20	0.00 to 0.71	0.09	0.00 to 0.50
Allele (*Pan* I^{AA})	0.70	0.02 to 1.39	0.29	−0.35 to 0.92	0.24	−0.36 to 0.82
SGR	0.27	−0.01 to 0.55	−0.25	−0.51 to 0.02	−0.02	−0.26 to 0.23
Trial	−0.05	−0.38 to 0.27	−0.15	−0.57 to 0.24	−0.61	−1.02 to −0.19
Object/Mirror order	0.24	−0.18 to 0.65	−0.05	−0.53 to 0.42	0.46	−0.02 to 0.94
Shelter leave			−0.26	−0.77 to 0.25	0.19	−0.30 to 0.68
Residual level						
Measurement	0.51	0.32 to 0.87	0.83	0.53 to 1.28	0.84	0.55 to 1.26
LB	**OFT**		**NOT**		**MT**	
Predictor	**Median**	**UI 95%**	**Median**	**UI 95%**	**Median**	**UI 95%**
ID level						
Measurement	0.36	0.02 to 0.83	0.02	0.00 to 0.20	0.32	0.00 to 0.91
Allele (*Pan* I^{AA})	0.56	−0.09 to 1.22	0.17	−0.41 to 0.74	0.23	−0.44 to 0.89
SGR	0.21	−0.05 to 0.48	−0.20	−0.44 to 0.05	−0.10	−0.38 to 0.18
Trial	−0.01	−0.43 to 0.40	−0.09	−0.57 to 0.39	−0.43	−0.86 to 0.00
Object/Mirror order	0.21	−0.26 to 0.71	−0.22	−0.76 to 0.29	−0.06	−0.56 to 0.43
Shelter leave			0.38	−0.11 to 0.88	0.36	−0.21 to 0.89
Residual level						
Measurement	0.64	0.40 to 1.10	1.01	0.72 to 1.44	0.7	0.41 to 1.20

TABLE A2 Median and 95% uncertainty intervals of the covariances of the four models (SJ, SM, LA, and LB) between the pairwise three personality measurements (OFT, NOT, and MT).

SJ		OFT		NOT		MT	
	Predictor	**Median**	**UI 95%**	**Median**	**UI 95%**	**Median**	**UI 95%**
NOT	ID	−0.05	−0.31 to 0.11				
	Residual	0.00	−0.16 to 0.15				
MT	ID	0.04	−0.16 to 0.33	0.00	−0.11 to 0.16		
	Residual	0.08	−0.06 to 0.24	−0.22	−0.50 to 0.03		
SM		**OFT**		**NOT**		**MT**	
	Predictor	**Median**	**UI 95%**	**Median**	**UI 95%**	**Median**	**UI 95%**
NOT	ID	−0.13	−0.46 to 0.11				
	Residual	−0.10	−0.32 to 0.07				
MT	ID	−0.12	−0.41 to 0.14	0.22	−0.01 to 0.52		
	Residual	0.13	−0.04 to 0.34	−0.08	−0.29 to 0.16		
LA		**OFT**		**NOT**		**MT**	
	Predictor	**Median**	**UI 95%**	**Median**	**UI 95%**	**Median**	**UI 95%**
NOT	ID	0.01	−0.22 to 0.22				
	Residual	−0.24	−0.49 to −0.04				
MT	ID	−0.01	−0.20 to 0.18	0.02	−0.09 to 0.23		
	Residual	0.06	−0.14 to 0.28	−0.07	−0.32 to 0.17		
LB		**OFT**		**NOT**		**MT**	
	Predictor	**Median**	**UI 95%**	**Median**	**UI 95%**	**Median**	**UI 95%**
NOT	ID	0.00	−0.13 to 0.12				
	Residual	−0.18	−0.42 to 0.04				
MT	ID	0.05	−0.15 to 0.35	0.01	−0.07 to 0.19		
	Residual	0.08	−0.13 to 0.34	0.04	−0.19 to 0.28		

Paper IV

Title: Consistency and correlation of behavioural traits measured in the laboratory and semi-wild conditions: A study case in stream-dwelling Arctic charr (*Salvelinus alpinus*)

Authors: Rosanne Beukeboom, Audrey Prat, Stefán Óli Steingrímsson, David Benhaïm

Summary

Individuals within a population often differ predictably in their behaviour compared to other members even when average population behaviour may vary due to for example exposure to different environmental or behavioural stimuli, often termed ‘personality’. Personality is usually measured in the laboratory to have maximal experimental control, but which is often very different from the species' natural environment. Semi-natural stream enclosures have been used to study more natural salmonid behaviour, but have barely been used to study personality. Here, we study exploration and boldness in the laboratory and foraging-related activity, sociality and space use (95% home range kernel) in semi-natural stream enclosures in Arctic charr, to determine whether stream enclosures are suitable to measure personality and whether laboratory measurements can explain more natural behavioural measurements. All defined personality traits were found repeatable, except for space use, where movement-related traits (i.e. exploration and activity, except space use), were more repeatable than boldness and sociality within context. Furthermore, one behavioural syndrome was detected within the stream enclosures, i.e. more active fish were less social. We conclude that stream enclosures are suitable for measuring personality traits, but that the traits measured in this study either differ in underlying motivations or field observations cannot represent laboratory measurements. To disentangle these two explanations, future studies should aim to measure the same personality traits within both environments.

Keywords: personality, boldness, exploration, activity, sociality, space use, laboratory, stream enclosures, behavioural syndrome, validation

Introduction

Individuals within a population often differ predictably in their behaviour compared to other members even after accounting for environmental stimuli (Gosling, 2001). These consistently different behaviours over time and across context, often termed ‘personality’, include variation in the levels of risk-taking behaviour (i.e. boldness), exploratory behaviour, activity in a familiar environment, aggressiveness and sociality and often have been found to correlate, i.e. they form a behavioural syndrome (Conrad et al., 2011; Sih, Bell, Johnson, et al., 2004; Sih & Bell, 2008). These behaviours are involved in all aspects of daily life, such as foraging, habitat use and antipredator behaviour (Dall et al., 2004; Réale et al., 2007) and as such, personality and behavioural syndromes, have been shown to impact life history, ecology and evolution (e.g. Biro & Stamps, 2008; Cabrera et al., 2021; Dingemanse & Wolf, 2010; Réale et al., 2007; Sih, Bell, & Johnson, 2004; Sih & Del Giudice, 2012; Smith & Blumstein, 2008; Wolf & Weissing, 2012; Zwolak & Sih, 2020). Understanding why these differences exist and why evolution is not leading to one optimal behaviour as has been assumed in the past (Dall et al., 2004), has become one of the major challenges in evolutionary and behavioural ecology (Dall et al., 2012; Wolf et al., 2007). In addition to being of fundamental importance, insight into repeatable and correlated behaviours can help understand population structure and can thereby influence the decision-making process regarding sustainable management and conservation (MacKinlay & Shaw, 2023). Although the study of consistent among-individual behavioural differences has received plenty of attention in the last decades, it is still considered a relatively new field with many knowledge gaps.

The opening up of this relatively new field results in a lack of consensus regarding the terminology to describe these behaviours to get insights into what we are actually observing (e.g. personality, coping style, temperament, individuality; Bierbach et al., 2017; Dall et al., 2004; Koolhaas et al., 1999; Réale et al., 2007) and the methods to measure these individual differences (Carter et al., 2012, 2013; Dingemanse & Wright, 2020; Perals et al., 2017; Toms et al., 2010). Additionally, personality studies often take place in the laboratory (e.g. by using different types of apparatus such as open field, novel object or mirror test), where environmental conditions such as temperature and light are under the control of the researcher, and are usually performed without the interference of other individuals (Campbell et al., 2009). However, these conditions are often far from natural, and while researchers aim to answer ecological questions, the assurance that laboratory measurements are within the natural range experienced by the population and/or are explaining what is happening in the field is often neglected (Carter et al., 2013; Niemelä & Dingemanse, 2014) or proven otherwise (e.g. Mouchet & Dingemanse, 2021). On the other hand, while measurements in the field are by definition natural, it is often impossible to control such above-named variables which themselves create variation in behaviour, although they can in some cases be statistically accounted for during the analysis of the data (Borenstein et al., 2009; Hertel et al., 2020). Failing to account for these differences may confound behavioural with environmental differences and thereby cloud conclusions (Biro & Stamps, 2010; Brommer, 2013; Nakayama et al., 2016; Spiegel et al., 2017). Several studies have started to investigate whether behaviours studied in the laboratory can explain ecological processes and their impact on fitness in the wild (Adriaenssens & Johnsson, 2011; Dingemanse et al., 2004; Höjesjö et al., 2002; Závorka et al., 2015). However, these studies are often based on tagged animal tracking, rather than direct behavioural observations (but see Herborn et al., 2010), as finding animals back after release for observation can be a time-consuming, if not an impossible, task.

In salmonid behavioural research, an often used tool to observe natural behaviour, such as foraging and territoriality, is a stream enclosure positioned in the river of the fish’s origin, which provides an intermediate solution for the difficulty of combining laboratory with observational field data (Blanchet et al., 2008; Church & Grant, 2018; Larranaga & Steingrímsson, 2015; Lindeman et al., 2015). These stream enclosures promote all aspects of the natural environment, including the presence of other individuals and the flow-through of river water and prey items (Zimmerman & Vondracek, 2006), while the fish of interest stay within vision. The only obvious difference between the fish in the stream enclosure with its free-living counterpart is that it is limited in its large-scale space use, but the size of the stream enclosure and the species can be chosen accordingly to reduce such fencing effects (Johnsson & Näslund, 2018). The opportunity to study repeatable behaviour such as the established personality traits activity, aggressiveness and sociality, but also the repeatable nature of possible personality-related behaviours such as foraging mode and territoriality (Larranaga, 2016; Lindeman et al., 2015) in a near-natural environment has not been exploited yet (but see Church & Grant, 2018).

One of the salmonid species ideal to study personality and behavioural syndromes is the Arctic charr (*Salvelinus alpinus*), because of its high behavioural diversity. This species is the northernmost, circumpolar freshwater species and is mostly found in lakes and the colder, uppermost parts of rivers and streams which are often species-poor and low-productive (Klemetsen et al., 2003). Interestingly, individuals of this species vary majorly in their phenotypic expression (e.g. variation in colour and pigmentation, foraging mobility from sit-and-wait to mobile strategies), ecology (e.g. habitat use; (epi)benthic, pelagic and littoral zone, diet; plankti-, mollusci-, insect- and piscivorous and mobility; movers vs stayers) and life history (e.g. weight at maturity ranging from 0.003 to 12 kg, spawning during different months of the year) and show thereby more variation than most fish (Grant & Noakes, 1987; Klemetsen, 2010; Klemetsen et al., 2003; Sandlund et al., 1992; Tunney & Steingrímsson, 2012).

Personality, i.e. among-individual behavioural consistency in boldness (reaction to a risky, but not new situation), exploration (reaction to a new situation) and social behaviour (reaction to the presence/absence of conspecifics, excluding aggressive behaviour) (Réale et al., 2007) have already been demonstrated in Arctic charr in the laboratory (Benhaïm et al., 2023; Horta-Lacueva et al., 2021; Philip et al., 2022). Although no direct data seems to be available on repeatable activity in a familiar environment in this species, it has been shown that standard metabolic rate often underlying activity, is repeatable in Arctic charr (Cutts et al., 2001). Direct measurements of activity as a personality trait have been demonstrated in other fish species (Beukeboom et al., 2022; Biro, 2012; Biro et al., 2020; Cote et al., 2010; Pike et al., 2008; Wilson & Godin, 2009). Correlations between these traits often follow a pro-active/reactive syndrome, where bold, exploration and activity are positively correlated and sociality negatively (Conrad et al., 2011; Koolhaas et al., 1999; Sih, Bell, & Johnson, 2004).

The relationship between these personality traits and foraging-related behaviour, such as foraging-related space use (here: the size of the 95% home range kernel where the individual often travels in search for food; Burt, 1943, p. 351) in fish as well as the repeatability of space use has received less attention (but see Stuber et al., 2022; Wilson & McLaughlin, 2007). Some relationships can be hypothesized by combining other studied behaviours. For example, if we assume that fish can acquire more food with increasing home range size (Tunney & Steingrímsson, 2012) and that bolder fish are also more dominant (Sundström et al., 2004), and combine this with the knowledge that charr mainly reside in low-productive waters (Klemetsen et al., 2003), it is expected that bolder fish will use a larger space for foraging (Nakano, 1995; Pike et al., 2008). Consequently, as bolder fish are expected to defend this territory, this will likely result in lower levels of sociality for bolder fish (Croft et al., 2009; Pike et al., 2008). Bold fish may also be more active during the day than shy fish, as the latter may reduce their daytime activity to avoid competition with bolder fish (Larranaga, 2016; Stamps, 2007). Alternatively, if smaller fish have a smaller home range, they may increase their activity to compensate for this smaller home range (Blanchet et al., 2008; Borkowski, 2000). Studies have shown that more explorative fish have a higher chance of encountering others and are therefore more social, although this may be sex-dependent (Cote et al., 2010; Gartland et al., 2022; Michelangeli et al., 2020). As more social fish are closer to others they are expected to have to compete more for food and will therefore need a larger home range to fulfil their foraging demands (Lindeman et al., 2015; Wilson & McLaughlin, 2007). Additionally, social individuals may be more active as they benefit from the protection of shoaling (Hamilton, 1971). Finally, body length increased activity and territory size in charr (Benhaïm et al., 2003; Gunnarsson & Steingrímsson, 2011), but did not affect boldness (Benhaïm et al., 2023).

Although several studies have observed the behaviour of this species in the laboratory e.g. (Benhaïm et al., 2003, 2020; Cutts et al., 2001; Leblanc et al., 2011; Philip et al., 2022), in stream enclosures (Fingerle et al., 2016; Larranaga, 2016) and in the field (Gunnarsson & Steingrímsson, 2011; Heggenes & Saltveit, 2007), there is to the best of our knowledge only one study on a closely related species that linked personality behaviours in the laboratory with personality-related behaviours in (semi)-natural conditions (Wilson & McLaughlin, 2007). In this study, we investigate the existence of personality and repeatable space use during foraging of stream-dwelling Arctic charr measured in a laboratory and semi-natural stream enclosures and investigate whether they are correlated. Specifically, we are aiming to answer the following questions:

1. Do stream-dwelling Arctic charr show among-individual consistency in exploration and boldness traits (i.e. personality) over short-term (one week) time intervals in the laboratory and do these behaviours correlate, i.e. do they form a behavioural syndrome?

2. Do stream-dwelling Arctic charr show short-term (one week) among-individual consistency in foraging activity and sociality in the field and do they form a behavioural syndrome?
3. Is space use during foraging repeatable across time in stream-dwelling Arctic charr?
4. Are there correlations (i.e. behavioural syndromes) between the measured behavioural traits in the laboratory and the stream enclosures, i.e. can behaviours measured in the lab explain behaviours in the wild?

We expect that all our measured variables are correlated, resembling a pro-active/reactive syndrome (Koolhaas et al., 1999; Sih, Bell, & Johnson, 2004), i.e. where bolder charr are more explorative and more active, but less social. Additionally, we predict that more proactive Artic charr use more space during forging. However, correlations between behaviours measured in the laboratory (boldness and exploration) and behaviours in a more natural environment (activity, sociality and foraging-related space use) also depend on whether laboratory experiments are suitable to explain natural behaviour.

Methods

A total of 96 Artic charr (*Salvelinus alpinus*) of age 1+ (mean (range): weight: 6.7 (2.5-17g); fork length: 8.8 (6.6-11.8) cm) were electro-fished (LR-24 electrofisher, Smith-Root, Inc., Vancouver, Wash., USA), which is considered low-harm (Arnekleiv et al., 2004), on 22 and 23 June 2021 in river Grímsá, northern Iceland (N 65.792379, W 19.844413; Fig. 1). This population of Arctic charr is landlocked between the origin of this run-off stream and a big waterfall, 4.8 km downstream and the only natural population in this part of the stream (except juvenile salmon sporadically being released for fishing purposes downstream, pers. obs.). After capture, the fish were transported on a 10-minute drive to the Verið laboratory in Sauðárkrókur (Department of Aquaculture and Fish Biology, Hólar University College). Individuals were anaesthetized with 0.3mg/L phenoxyethanol and measured for fork length to the closest 0.1 mm with callipers and body mass to the closest 0.01 g. Then, fish were tagged with visible implant elastomer (VIE; Northwest Marine Technology, Inc., Washington, USA), which has no impact on growth or survival in other freshwater species (Goldsmith et al., 2003) using different combinations of five colours (yellow, green, orange, purple and red) in two positions along the dorsal fin. Subsequently, the fish were randomly assigned to twelve circular grey 120 L tanks (8 fish/tank) with pebbles on the bottom to provide shelters and thereby reduce potential stress. There was a constant input of fresh water in the tanks and the water temperature ranged from 4.1-6.4°C (mean 5.25 °C), which is within the natural range.

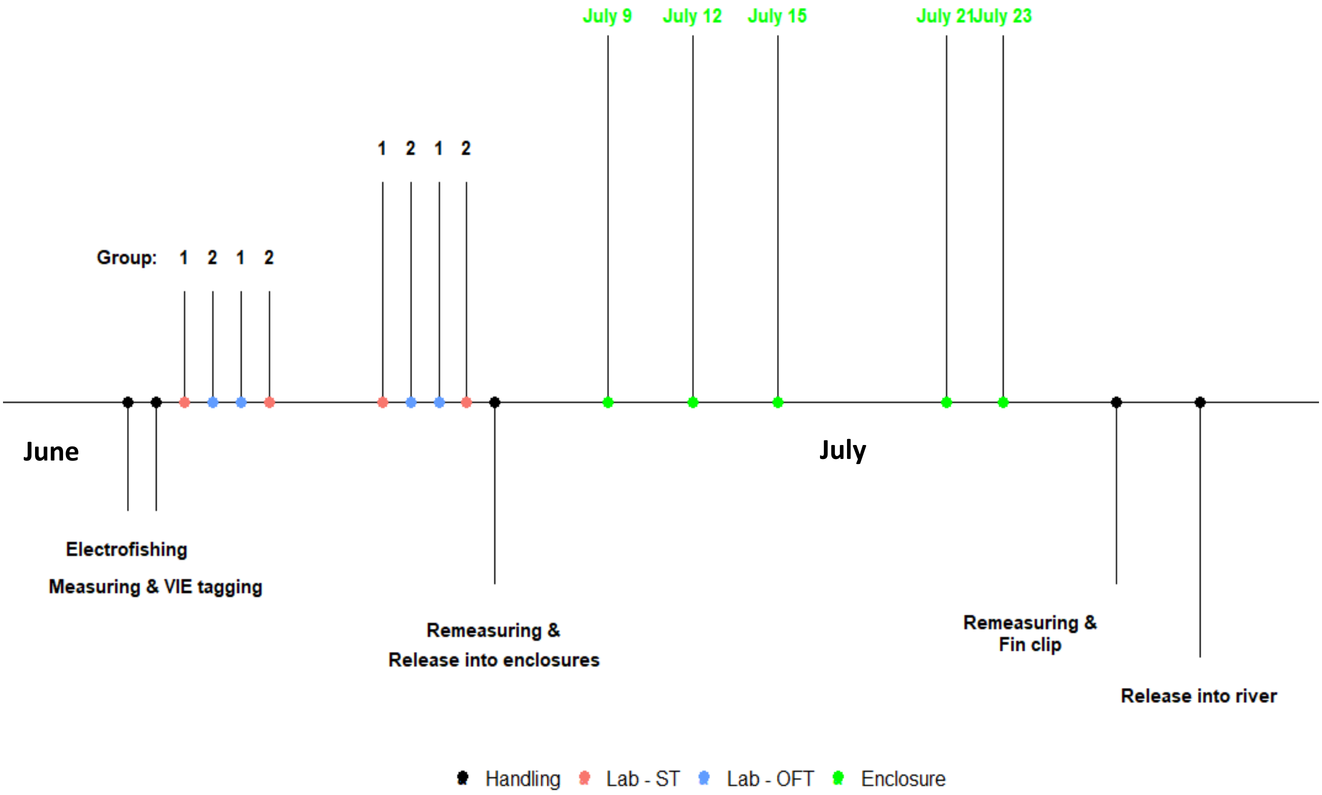

Figure 1. Time line from the moment of electrofishing (June 22, 2021) until release back into the river (July 30, 2021), including the shelter test (blue) and open field test (blue) in the laboratory for group 1 that received the shelter test first and group 2 that received the open field test first and the enclosure observations (green).

Laboratory trials

Not all fish could be tested on the same day. The first trial took place on June 24 and 25; after a minimum of 24 hours of habituation in the lab, the first group (56 fish) were subjected to a Shelter Test (ST) and on the next day, the other 40 fish (Group 2) were subjected to an Open Field Test (OFT) (Fig. 1; red and blue respectively). On June 26, Group 1 received the OFT and on June 27 Group 2 received the ST. This pattern was repeated one week later (July 1-4; Trial 2; Fig. 1). The alternation of the test order allowed taking any test order effect into account in the statistical model. To increase the capacity of the behavioural observations, four tests were performed in parallel in different arenas (Fig. 2). Water in the trial tanks was changed in between trials to remove any cues from previous fish.

Shelter Test (boldness)

In the ST, the focal fish was placed in an arena (39.7 cm x 29.5 cm x 6 cm) with shelter (6 cm x 14 cm; Fig. 2) and after five minutes of habituation, the door was lifted and the arena was filmed for 20 minutes using a camera (Basler Ace acA 1920-150µm, Germany) at 30 frames per second placed 110 cm above the arena. Video tracking software (Ethovision 15.0, Noldus, The Netherlands) was used to divide the arena into entry (2.5 x 6 cm), border (5 cm from the arena edge; as a measure of thigmotaxis; Sneddon, 2003) and centre (the arena minus shelter, border and centre) zones (Fig. 2). Subsequently, the software was used to extract the latency to exit the shelter with full body (s), total time spent in shelter, entry, centre, and border zone (s), frequency to enter shelter, entry, centre and border zones, total distance traversed (cm), absolute angular velocity (degrees/s) and mean velocity (body lengths/s) as in (Benhaïm et al., 2020). Fish that did not leave the shelter, were assigned the maximum score of 1200 seconds for time in the shelter and latency to exit and zero for the other variables. A Kaiser-Meyer-Olkin criterion performed with the EFAtools package in R (Steiner et al., 2023) performed on the 12 measurements of the ST indicated that our data was suitable for Principal Component Analysis (PCA; all variables > 0.704, overall value = 0.879; Budaev, 2010). The PCA was run on the first trial using the “prcomp” function in R. As the first axis explained 70.16% of the variation in the data and showed a gradient from fish spending the most time in the shelter to spending all their time in several areas of the arena, this axis was used as the boldness score (BOL). Individual repeated measurements (i.e. trial 2) were predicted from these scores using the “predict” function to take repeated measurements into account (R Core Team, 2022; Toms et al., 2010). All boldness scores were multiplied by -1 so lower scores would represent shyer individuals.

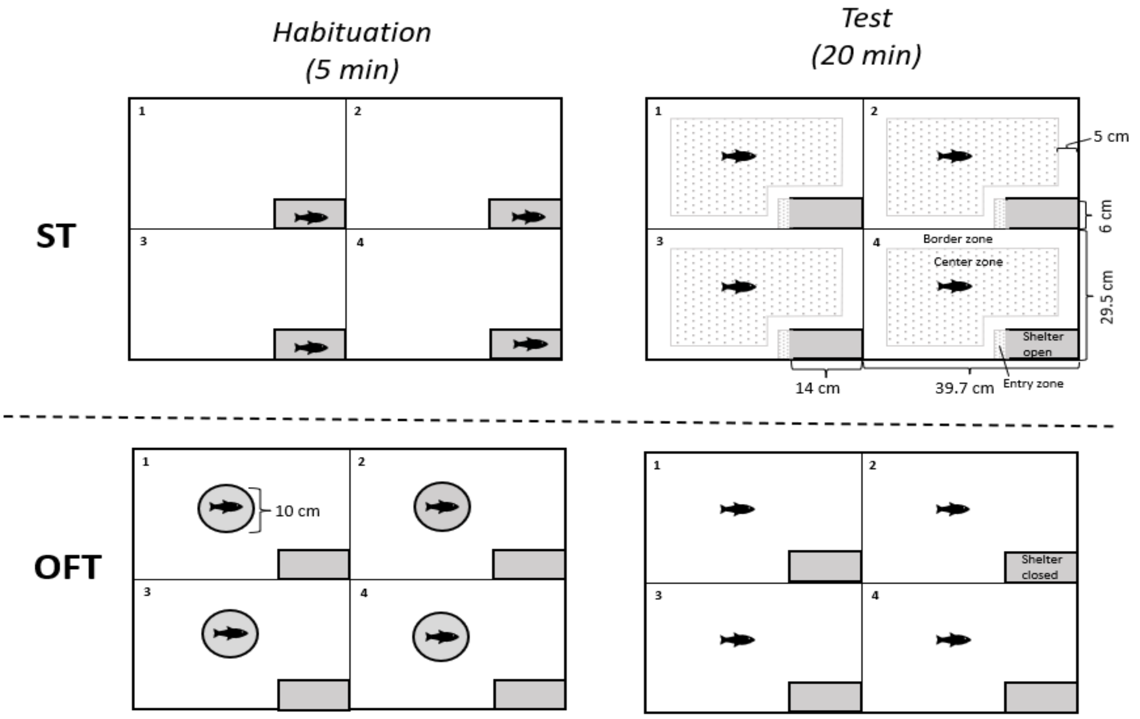

Figure 2. Setup of the trial tanks for the shelter test (ST) and the open field test (OFT). Both tests start with a habituation period of five minutes (ST in shelter, OFT in container) and the test of 20 minutes. In the ST, the arena is divided into shelter (14 (l) x 6.5 (w) x 6.5 (h), water level 6cm), entry (2.5cm), border (5cm) and centre zone. During the OFT, the shelter is closed.

Open Field Test (exploration)

The OFT followed the same protocol as the ST, except that habituation took place in an upside-down plastic white container (Ø10 cm) placed in the middle of the arena (Fig. 2). Additionally, the shelter was permanently closed so that the individual was always visible. These videos were likewise analysed with Ethovision and the total distance travelled and the total area covered (total unique x/y coordinates rounded to the nearest integer) were extracted, which are both measurements commonly used as proxies of exploration. The total distance travelled and the total area covered extracted from the OFT were highly and significantly correlated (PEARSON: r = 0.82; CI 95 % [0.78 –0.86]; P = <0.001) and therefore only the total distance travelled was used in further analysis as this measurement is not statistically ceiled and therefore has the potential to capture the most variation between individuals.

Scan observations in stream enclosures (activity, sociality and space use)

Directly after the laboratory trials (July 5th, Fig. 1), all fish were anaesthetized, remeasured and retagged where necessary. The fish were then transported back to their native stream where they were released into 12 stream enclosures in the same groups as established in the laboratory to keep established social interactions (Magnhagen & Staffan, 2005). Stream enclosure size was 2.4m (l) x 1.0m (w) x 0.75m (h) which for 8 fish per stream enclosure are within-range of natural densities for stream salmonids (i.e. 3 fish/m^2; Gunnarsson & Steingrímsson, 2011) (Fig. 3). Six metal support posts held the stream enclosures, which were made of a green nylon net (mesh size = 5 mm), allowing for the flow-through of water and drifting prey items (Keeley & Grant, 1997; Klemetsen et al., 2003; Zimmerman & Vondracek, 2006). The stream enclosures were covered with sieved local substrate (max ø 2cm). Metal bars with markers were laid out on the bottom to create a 10 cm Cartesian coordinate system which allowed fish position determination (Fig. 3). Three cobbles of similar size were placed in each stream enclosure to provide shelters and crossed strings between the support posts deterred potential avian predation, but presumably without affecting the risk perception of the fish. Water flow was regulated with a wooden sluice gate to be roughly the same in all stream enclosures and water temperatures were measured every hour using HOBO® Pendant® Temperature Data Loggers (UA-002-08) at four stream enclosures. Temperatures during observations ranged from 8.6 to 16.0°C (mean: 11.5 °C). Stream enclosures were at least 10 meters apart and alternated between river bank sides to keep the influence of upstream enclosures on downstream enclosures as low as possible. The up-down temperature gradient during the observations between the first and last stream enclosure ranged from 2.2-2.7°C (mean 2.6°C). This difference was an interplay of the time of day of the observation (i.e. stream enclosures 1 to 4 were always observed earlier in the day than 5:12) and a natural downstream increase of temperature from stream enclosures 1 to 12.

Scan observations started after three days of habituation to the stream enclosures and were performed on July 9, 12, 15, 21 and 23 between 9.30 and 17.00 by four different observers so that all fish could be observed once on the same day (Fig. 1; green). The observers always observed the same three stream enclosures to enhance fish identification. The observer walked quietly to a stream enclosure and stood motionless beside it for five minutes. Juvenile Arctic charr responded only weakly to overhead stimuli and always resumed their natural behaviour after a maximum of two minutes (pers. obs.). The observation took place from above and started after five minutes of habitation to the observers' presence. A stream enclosure was observed for 60 minutes per day, and every two minutes for every fish, the nose position (x/y coordinate to the nearest 10 cm using the metal bar grid) and behaviour were recorded, i.e. searching for food (S; swimming in the water column), resting (R; resting motionless on the bottom), or hiding (H; not visible) (Larranaga & Steingrímsson, 2015).

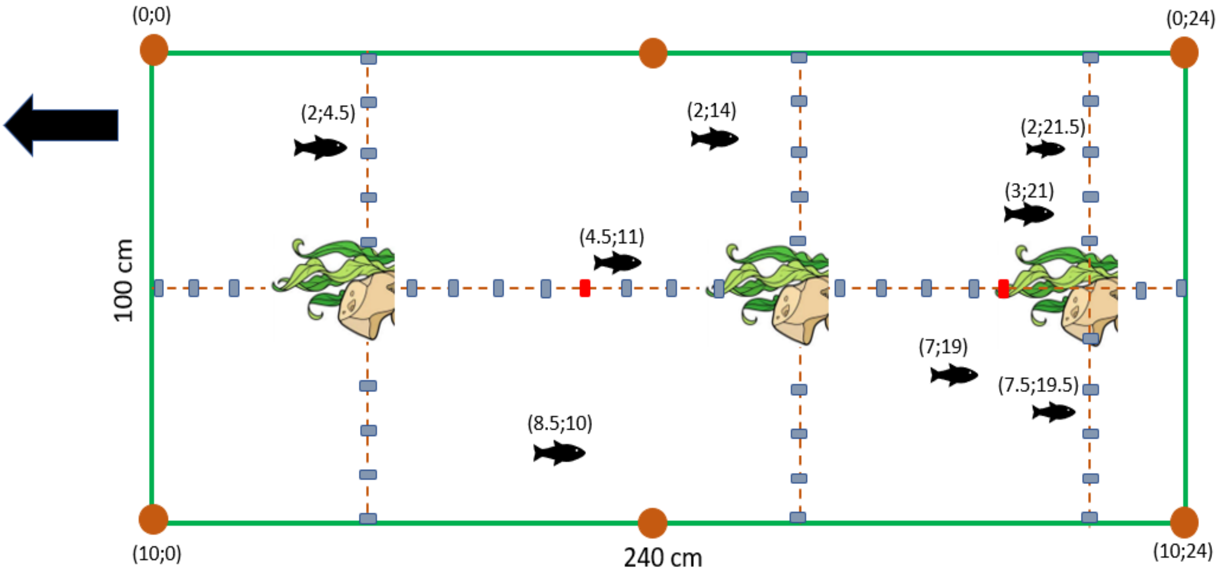

Figure 3. Stream enclosures with metal bars on the bottom indicating grids (dotted line) with 10cm markers (grey squares) and three cobbles with moss functioning as shelters containing eight fish with their Cartesian coordinates as an example. Arrow indicates

A measure of activity (ACT) was calculated as the number of actively swimming observations (S) against the number of total observations (Swimming + Resting + Hiding). Arctic charr have been shown to perform schooling behaviour on multiple occasions (Breau et al., 2007; Cunjak & Power, 1986; Larranaga, 2016). A measure of sociality (SOC) was therefore determined by calculating the minimum distance to any other fish in any 2-minute period. Averaged within each day, including swimming and resting behaviour (i.e. a measure of nearest neighbour distance; Gartland et al., 2022; McBride, 1971). Only fish with more than 15 or more known X/Y coordinates (i.e. those that were hiding less than 50% of the time) were included as previous studies have shown that charr in this stream show stable behaviour, i.e. at least for 15 minutes (Larranaga, 2016). This measurement was multiplied by -1 so that more social individuals had a higher score. A measure of space use during foraging (SPU) was determined for the same subset of fish used for the sociality measurements by calculating a 2-dimensional 50% and 95% home range kernel (White & Garrott, 2012) with the kernelUD function from the adehabitatHR package (Calenge 2006). After inspection of graphs with different smoothing parameters (h), h was set to 0.1 and boundaries were set as the actual boundaries of the stream enclosures. The mean number of visible fish (i.e. S or R) per stream enclosure per day was calculated separately as this can influence the calculations of SOC and SPU. A week after the last observations (July 29, Fig. 1), the top of the stream enclosures was lowered and the fish could leave the stream enclosures when they were ready, which they all had done the next day.

Sexing

Sex was determined by taking a fin clip of each study fish when they were PIT-tagged and DNA was extracted using the instructions and materials from a NucleoMag Tissue kit for DNA purification from cells and tissue (Macherey-Nagel GmbH Co. KG). An 18s control marker was used for species identification and an SDY marker was used to identify the males (Yano et al., 2013).

Statistics

All data were analysed using R v. 4.1.3 (R Core Team, 2022) and ran using multivariate linear mixed models using the Bayesian software Stan (Carpenter et al., 2017) run via the ‘brms’ package (Bürkner, 2017). All numeric variables were scaled using the ‘scale’ function in R (i.e. z-scoring; subtracted the mean and divided by the standard deviation), except for ACT, which was treated as a binomial variable.

To determine whether laboratory estimates of exploration and boldness were repeatable and correlated, we ran one model that included exploration (EXP) and boldness (BOL) scores as dependent variables, length, sex, mean temperature of the experimental tank (end-start/2), test order and trial as fixed effects and fish ID as a random effect (Table 1). Because only exploration was found to be repeatable, we omitted boldness from further analysis. The repeatability of exploratory behaviour allowed us to calculate a single ‘stable’ exploration score for every individual (EXPi) by extracting the random effects estimates from the model output using the ‘ranef function’ based on medians from brms. As sex was a stable fixed effect between the two trials, it was included in this ‘stable’ score by adding the median of the slope of sex to the random effect intercept of exploration for the males as female was the reference level. This value was consecutively used in Model 2 (see below).

To determine whether field observations of activity, sociality and foraging-related space use were repeatable and correlated, we ran a second model that included ACT, SOC and SPU as dependent variables, the possible influence of length, the temperature at the start of the observations, and sex as a fixed effect and fish identity nested in stream enclosure as random effects (Table 1). As ACT had a binomial distribution, an observational sequence as a dummy random effect (i.e. 1|dummy) was added to create an observational residual that allowed for calculating the repeatability of this trait. Observer identity was included as a fixed effect for the field models to facilitate the calculation of the covariances. Running the models with the observer in the fixed, nested random effect and without, did not influence the overall model output. For SOC and SPU, the additional fixed effect of the mean number of active fish was included (mean number of active fish per stream enclosure and date) as this may influence these measurements. Finally, to test whether laboratory estimates could explain field estimates, we added EXPi as a fixed effect for ACT, SOC and SPU.

Table 1. Overview of the variables included in the two Bayesian models

Model 1	BOL ~ Length + Sex + Temp + Test order + Trial + (1|ID) EXP ~ Length + Sex + Temp + Test order + Trial + (1|ID)
Model 2	ACT ~ EXPi + length + sex + temp + Observer + date + (1 | Enclosure/ID) + (1|Dummy) SOC ~ EXPi + length + sex + temp + # active fish + Observer + date + (1| Enclosure/ ID) SPU ~ EXPi + length + sex + temp + # active fish + Observer + date + (1| Enclosure/ ID)

Both models were run with 4 chains and 4000 iterations (2000 warm-up and 2000 for sampling) and Model 2 with an additional adapt delta of 0.99 to obtain full convergence, while all other settings were set to their default. As the random-effects structure of both models with EXP, BOL, ACT, SOC and SPU as dependent variables included individual fish identity (ID) as a grouping variable, it was possible to calculate the repeatability of these variables as the ratio of the among-individual variance and the sum of the among-individual and residual-level variances (i.e. personality) (Johnson & Koch, 2011; Nakagawa & Schielzeth, 2010), which were recalculated from the standard deviation (i.e. among-individual variance = sd^2) and sigma (residual-level variance = $sigma^2$) from the model output. For the binomial ACT, the residual variance was calculated as the observational variance + pi^2/3 (Nakagawa & Schielzeth, 2010). Furthermore, the models estimated covariances between all dependent variables within the models (i.e. BOL-EXP, ACT-SOC, ACT-SPU and SOC-SPU). Convergence was assessed using the standard diagnostics provided by Stan including the potential scale reduction factor R-hat, effective sample size, and visual inspection of trace plots and histograms for each model parameter (Bürkner, 2017; Carpenter et al., 2017). We report medians and 95% quantiles of the variances and covariances.

Ethical note

The number of fish and the procedures (electrofishing, handling, fin clipping, behavioural tests and stream enclosure use) were chosen to adhere to strict ethical guidelines and approved by the Icelandic Food and Veterinary Authority (MAST; 2021-09-05). Permission to return the fish from the lab to their natal stream was approved separately at the date of release (ÍSLGJ13321).

Results

Both models converged with R-hat = 1, had well-mixed chains, and no extreme trails visible in the trace plots.

Laboratory data

Ninety-six fish received the ST and OFT twice (Trial 1 and 2), but five observations were excluded because of one fish for which the length was measured wrongly and for two fish the sex could not be determined because of failing analysis, which resulted in 187 observations. Fifty-one of these fish (27%) did not leave the shelter during the shelter test. BOL ranged from -2.73 to 9.53 (median = -0.86) and EXP from 459 to 7521 cm (median = 2347 cm). Of the 96 individuals in the laboratory, 57 were female, 37 were male and the gender of two fish could not be established. The mean water temperature in the laboratory trial tanks ranged from 5.1 to 8.25 °C (mean 5.88 °C).

EXP and BOL were both repeatable, with between- and within-individual variances different from zero, where EXP was more repeatable than BOL (Fig 4, 5, Table S1). The covariance of BOL and EXP was close to zero with UI95% strongly overlapping zero (Table S2; Fig. 6). There was a trend visible that fish were overall more explorative in the second trial, while they did not vary in boldness. Finally, longer fish were bolder and marginally more explorative, while no influence of temperature or sex was observed (Figure 7, Table S1).

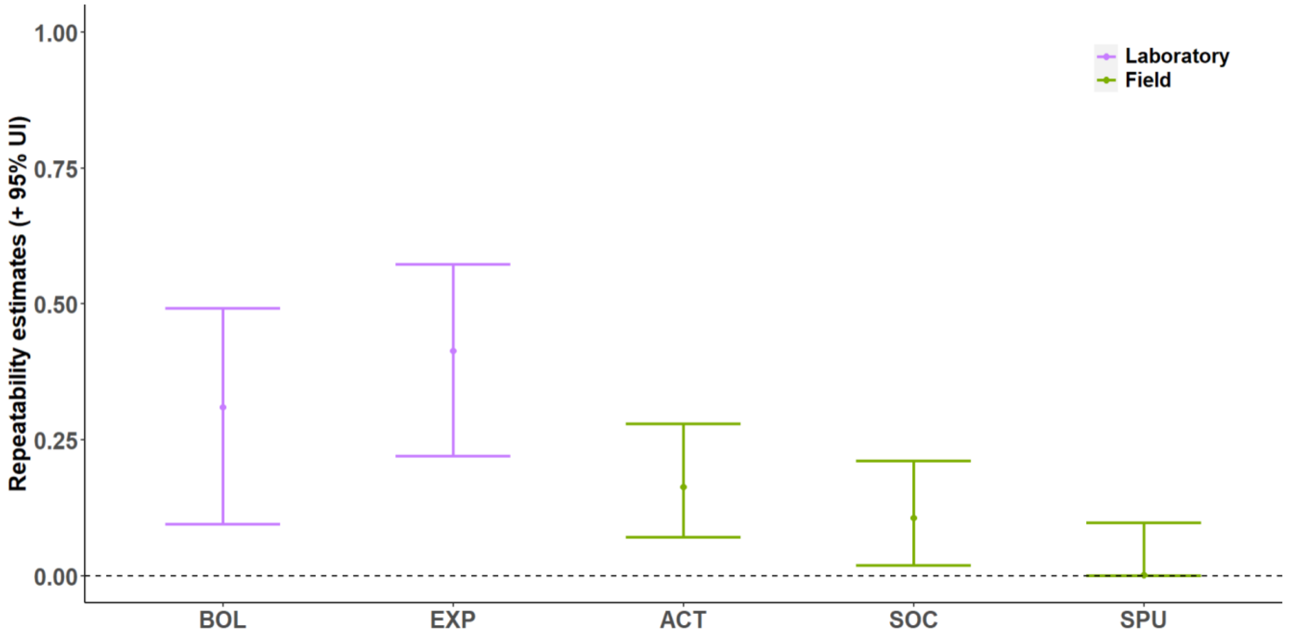

Figure 4. Repeatability of variable in the laboratory (purple), i.e. boldness (BOL) and exploration (EXP), and in the enclosures (green), i.e. activity (ACT), sociality (SOC) and local foraging space use (SPU).

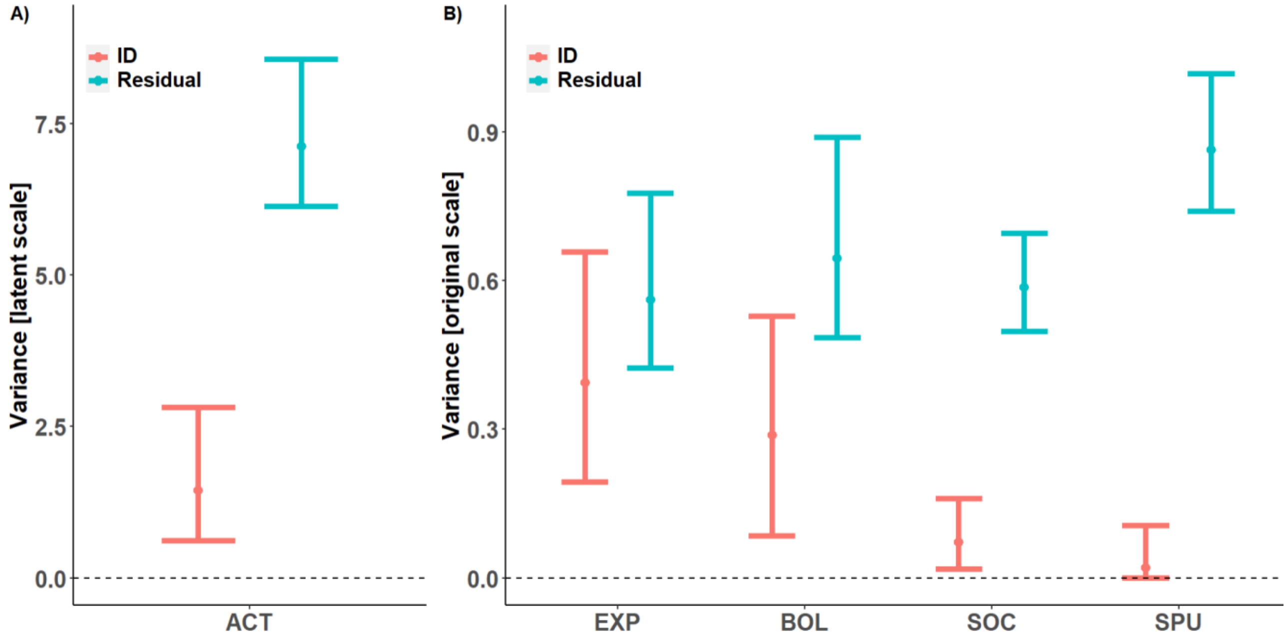

Figure 5. Between- (ID, red) and within-individual (Residual) variances of (A) activity (ACT) on the latent scale and (B) exploration (EXP), boldness (BOL), nearest neighbour distance (SOC) and 95% home range kernel (SPU) on the original scale with medians and 95%UI. Dashed line indicates zero.

Stream enclosures

ACT scores could be calculated for all fish, while fish had on average four repetitions (range 1-5) for SOC and SPU. Three fish had only one repetition for these variables, which consequently were not included in the calculation of within-individual variance, but were included to contribute to the between-individual variance. This resulted in a total of 340 observations of 91 individuals. Stream enclosure temperatures at the start of the observations ranged from 10.2-16.0°C (mean 11.5°C). Because the 50% and 95% home range kernel estimates were highly correlated (linear regression: $r2 = 0.787$, $P < 0.001$), only 95% kernel UD's are reported (as in Steingrímsson & Grant, 2011). Activity ranged from 0 to 1 (median 0.97), sociality from 0.05-1.35 m (median = 0.44 m) and 95% home range kernel from 0.14 – 1.76 m^2 (median = 0.57 m^2).

ACT and SOC were both marginally repeatable, with between- and within-individual variance away from, where ACT was slightly more repeatable than SOC (Fig. 4, 5; Table S1). ACT and SOC were also correlated, where less social individuals were more active (Fig. 6; Table S2). SPU was not repeatable, with between-individual variance close to zero, while residual variance was different from zero with non-zero overlapping 95% confidence intervals (Fig 4, 5; Table S1). SPU was not found to be correlated to ACT or SOC (Fig. 6, 7, Table S2). Higher temperatures increased activity and sociality marginally and longer fish were marginally more active and more social. None of the fixed effects influenced SPU and sex did not influence any of the measured traits (Fig 6, 7, Table S1).

Figure 6. Pairwise covariances of exploration (EXP), boldness (BOL), activity (ACT), sociality (SOC) and space use (SPU) with posterior medians and 95%UI. Dashed line indicates zero.

Correlation between the laboratory and field

No evidence was found that EXP and BOL measured in the laboratory influenced ACT, SOC, or SPU measured in the stream enclosures (Fig. 6).

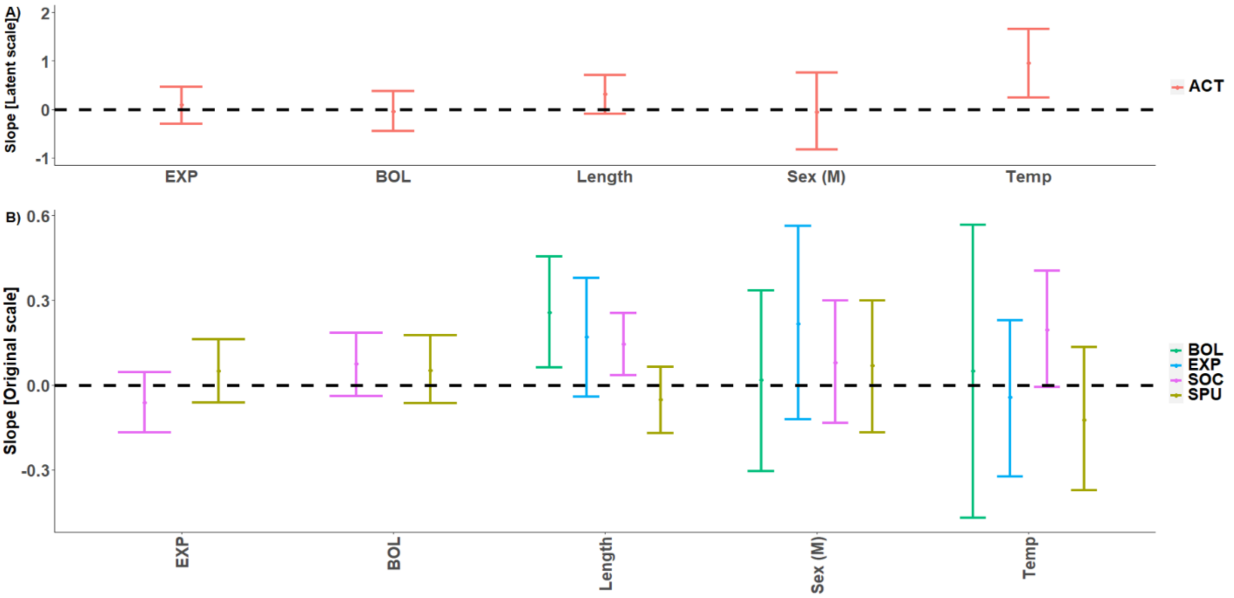

Figure 7. Median slopes and 95%UI of the fixed effects of individual exploration, boldness, fish length, sex and temperature for A) activity (ACT; red) on the latent scale and B) boldness (BOL; green), exploration (EXP; blue), sociality (SOC; purple) and 95% home range kernel (SPU; brown) on the original scale. Dashed line indicates zero.

Discussion

In this study, we aimed to explore personality and behavioural syndromes within and between laboratory and field observations in a natural land-locked population of Arctic charr. We did this by extracting two personality traits from laboratory trials (boldness and exploration) and combining these with two personality traits (activity and sociality) and one measure of foraging-related space use extracted from observations in semi-natural stream enclosures in the river of origin. We found short-term (i.e. one week) repeatable exploration in the laboratory, repeatable activity and sociality behaviour and a correlation between these in the stream enclosures, but no indication that lab exploratory behaviour measured in the laboratory could explain behaviour in the stream enclosures.

Laboratory

We found that exploration and boldness were repeatable at the individual level, while no difference for boldness was found. Exploration has been found to be repeatable in many other fish species (e.g. Beukeboom et al., 2022, 2023; Bierbach et al., 2017; Cote et al., 2010; Kobler et al., 2009; Wilson & Godin, 2009), summarized in Conrad et al. (2011), but is also widespread throughout the animal kingdom (Bell et al., 2009; Gharnit et al., 2020; Herde & Eccard, 2013; Stuber et al., 2022; Wuerz & Krüger, 2015; Zidar et al., 2017). Repeatable boldness was also found in other Arctic charr populations in Iceland (Benhaïm et al., 2023; Horta-Lacueva et al., 2021; Philip et al., 2022).

We did not find evidence for a behavioural syndrome between exploration and boldness. Although to the best of our knowledge, this correlation has not been studied in Arctic charr before, data on other fish species is incongruent (summarized in Conrad et al. (2011)). The absence of correlation is most likely because the traits evolved separately which is due to independent functional roles (Sih, Bell, Johnson, et al., 2004).

Stream enclosures

While foraging activity and sociality have been studied before in this species in different conditions (e.g. Larranaga, 2016), the current study shows that these behaviours are also consistent over time. We found that the amount of active foraging and sociality (i.e. based on the mean nearest neighbour distance) were marginally repeatable and that fish were more active and less social at higher temperatures, but that sex did not influence these behaviours. A similar study in stream enclosures on Atlantic salmon (Church & Grant, 2018) found no repeatable activity, which may be an additional difference between salmonid species (Gunnarsson & Steingrímsson, 2011; Klemetsen et al., 2003). However, repeatable activity and sociality exist in many other species across the animal kingdom, (e.g. Hanson et al., 2007; Krause et al., 2017); summarized in Gartland et al. (2022) and Stuber et al. (2022)). The increase of activity with increasing temperature has been observed in this species in a similar river (Fingerle et al., 2016; Larranaga, 2016), but is also commonly observed in other salmonids (e.g., Bartolini et al., 2015; Blanchet et al., 2008; Breau et al., 2007; Jonsson & Jonsson, 2009), probably because of a link with metabolic rate (Biro & Stamps, 2010; Careau et al., 2008; Cutts et al., 2001). The relationship between temperature and sociality is more ambiguous, as, interestingly, both mean population activity and sociality increased with temperature, but were negatively correlated at the individual level. Fish studies on temperature on sociality and activity are scarce and measure activity as tail-beat frequency, rather than the amount of time active as in the current study (e.g. Bartolini et al., 2015; Pritchard et al., 2001). Studies including wider temperature regimes can achieve more insight into the link between sociality, activity and temperature, for example by comparing these traits in different rivers with different temperature ranges (Larranaga, 2016). One explanation of why asocial fish are more active in the current study may be that they have better-established territories than fish that were showing themselves less.

Space use (i.e. the 95% home range kernel) during foraging was not repeatable, did not correlate with foraging-related activity or sociality and was not influenced by temperature, length or sex. Space use was only found marginally repeatable and also did not correlate with other personality traits in the common bully (Kerr & Ingram, 2021). Space use may be therefore determined by unmeasured environmental variables, rather than underlying personality traits, such as food availability as this has been shown to influence territory size (Gunnarsson & Steingrímsson, 2011; Keeley & Grant, 1995). Additionally, fish may have been restricted in their space use, which reduced between-individual variation (Johnsson & Näslund, 2018; Lindeman et al., 2015).

Laboratory vs field

We found that the laboratory measurements of exploration and boldness were more repeatable than the field observations of activity, sociality and space use. This is in contrast to what was found in a meta-analysis, which found that measurements in the field were more repeatable (Bell et al., 2009). However, lower repeatability in the field measurements can be explained by unmeasured and thereby uncontrolled influences, such as food availability, compared to the more controlled environment in the laboratory (Mouchet & Dingemanse, 2021). The observed difference in repeatability in this study was mainly caused by a higher between-individual variation in the laboratory, as within-individual variation was similar between the laboratory and the field, which may be another indication that environmental factors may have played a role. Interestingly, within environments, the traits underlying moving, i.e. exploration and activity are both more repeatable than other personality traits within the same context which was also found in a meta-analysis (Stuber et al., 2022). However, the unrepeatable space use measurement does not correspond with this.

Our results partially provide evidence for the pro/reactive axis as more active fish were less social, but no evidence was found that this also included exploration or boldness (Koolhaas et al., 1999). This is in contrast with for example Farwell & McLaughlin (2009) who show that bolder salmonids measured in the laboratory were moving more during foraging in the field. The choice of observing rather than experimenting in the natural environment, to keep the conditions as natural as possible, causes the possible reasons for the absence of a correlation between the laboratory and field measurements to be four-fold. First of all, the laboratory observations were carried out in isolation, while the fish were observed in a group in the stream enclosures. A recent study showed that solitary boldness behaviour was not correlated with boldness behaviour when in a group (Philip et al., 2022) and although this behaviour was not measured in both contexts in the current study, the presence of other individuals may have also influenced the other behaviours. Secondly, the lack of correlation between laboratory and stream enclosure observations may indicate that the different personality traits and the measurement of space use are expressions of different underlying characters (Mouchet & Dingemanse, 2021). For example, the sociality of a fish may have nothing to do with how explorative an individual is and may therefore be triggered by different ecological and evolutionary mechanisms (Sih, Bell, & Johnson, 2004). Thirdly, the laboratory and field observations differed in their number of observations which may have influenced the results. The choice of the number of repetitions in the laboratory is a result of a trade-off between the number of repetitions and the need to reduce the time in the laboratory and minimize habitation to the tests, which may influence behaviour itself. The fourth and final explanation may be that the laboratory environment has been too artificial and was therefore not able to measure natural behaviour or even elicit new behaviours (Carter et al., 2013; Niemelä & Dingemanse, 2014). In that case, caution needs to be taken when explaining natural processes using laboratory measurements. However, Farwell & McLaughlin (2009) found several correlations between laboratory and field measurements, so only further experiments including measuring the same behaviour in both the laboratory and the field can disentangle these hypotheses. Ideally, we would have measured the same behaviours in the laboratory and stream enclosures. However, we wanted to focus on natural and well-described behaviours in salmonids. For example, exploration is supposed to be measured in a novel environment, which is hard to create in stream enclosures without losing its natural aspect.

Conclusion

The findings in this study contribute to the knowledge about consistent individual differences in stream-dwelling fish and provide an example of how to measure personality traits in more natural conditions compared to the often used laboratory studies. Although non-natural, laboratory studies provide more controlled environments, it is essential to compare these studies with natural behaviour before drawing any conclusions, ideally studying the same behaviour in both environments. Although inconsistencies may arise and increase as this study has shown, it induces further scientific progress on how nature works. Future studies should focus on measuring the same personality traits in the laboratory and field.

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Paper IV - Supplementary materials

Table S1. Medians and 95% uncertainty intervals of the variances of exploration (EXP) and boldness (BOL) in the laboratory and activity (ACT), sociality (SOC) and the 95% home range kernel (SPU) and fixed effects of length, sex, temperature, trial and test order. Covariances away from zero with non-zero overlapping UI95% appear in bold and trends (median away from 0 and UI95% <.0.10 overlapping 0) in italics.

	BOL ***Original scale***		***EXP*** ***Original scale***		***ACT*** ***Latent scale***		***SOC*** ***Original scale***		***SPU*** ***Original scale***	
Predictor	*Median*	*UI 95%*	*Median*	*UI 95%*	*Median*	*UI 95%*	*Median*	*UI 95%*	*Median*	*UI 95%*
Repeatability	**0.31**	**0.09 – 0.49**	**0.41**	**0.22 – 0.57**	**0.16**	**0.07 – 0.28**	**0.10**	**0.02 – 0.21**	0.00	0-0.10
Between-individual	**0.29**	**0.09 – 0.53**	**0.39**	**0.19 – 0.66**	**1.44**	**0.61 – 2.81**	**0.07**	**0.02 – 0.16**	0.02	0 – 0.11
Within-individual	**0.64**	**0.48 – 0.89**	**0.56**	**0.42 – 0.78**	**7.12**	**6.13 – 8.55**	**0.59**	**0.5 – 0.69**	**0.86**	**0.74 – 1.02**
Length	**0.26**	**0.06 – 0.46**	*0.17*	*-0.04 – 0.38*	*0.32*	*-0.09 – 0.71*	**0.14**	**0.04 – 0.25**	-0.05	-0.17 – 0.06
Sex (male)	0.02	-0.31 – 0.33	0.22	-0.12 – 0.56	-0.05	-0.83 – 0.75	0.08	-0.13 – 0.30	0.07	-0.17 – 0.30
Temperature	0.05	-0.47 – 0.57	-0.04	-0.32 – 0.23	**0.95**	**0.24 – 1.65**	*0.20*	*-0.01 – 0.40*	-0.12	-0.37 – 0.13
Trial (2)	*-0.06*	*-0.29 – 0.17*	*0.24*	*0.03 – 0.47*						
Test order (OFT first)	*-0.42*	*-0.79 – -0.05*	*-0.41*	*0.75– -0.07*						

Table S2. Medians and 95% uncertainty intervals of the covariances of the pairwise measurements of exploration (EXP) and boldness(BOL) in the laboratory, and in activity (ACT), sociality (SOC) and 95% home range kernel (SPU) and the effect of EXP on ACT, SOC and SPU. Covariances and slopes away from zero with non-zero overlapping UI95% appear in bold and trends in italics.

	EXP		***ACT***		***SOC***		***SPU***	
	Median	*UI 95%*	*Median*	*UI 95%*	*Median*	*UI 95%*	*Median*	*UI 95%*
BOL	0.06	-0.09 – 0.22	-0.04	-0.44 – 0.37	0.07	-0.04 – 0.19	0.05	-0.07 – 0.18
EXP			0.09	-0.19 – 0.47	-0.06	-0.17 – 0.05	0.05	-0.06 – 0.16
ACT					**-0.22**	**-0.45 – -0.06**	0.07	-0.05 – 0.02
SOC							-0.01	-0.05 – 0.02

Paper V

Title: The influence of seasonality on personality and space use in Arctic charr (*Salvelinus alpinus*)

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Summary

Animals often differ consistently in behaviour within populations, i.e. personality, which may be a result of responding differently to changes within their environment, for example by moving towards favourable and/or avoiding unfavourable conditions. Seasonality can act directly on movement behaviour, but the influence of personality is less clear. Here, we investigated the consistency of seasonal, long-term (one year) exploration and boldness estimates in the laboratory, initial dispersal from release (a natural measure of exploration), seasonal large-scale space use in the field, and the correlation between these variables. Stream-dwelling Arctic charr were assessed for boldness and exploration in the laboratory in two summers and intervening winter. In between these measurements, the fish roamed freely in their stream of origin, where weekly GPS positions were collected in summer and early winter as an indication of natural space use. Laboratory exploration was found to be repeatable within and between summers, but not between summer and winter whereas boldness was repeatable within summer, but only marginally repeatable from summer to winter and not between consecutive summers. Furthermore, distances between consecutive GPS positions in the field were repeatable within summer, but not within winter, nor between seasons. Finally, small-scale laboratory exploration did explain natural larger-scale exploration of Arctic charr marginally, but not space use in the field. This study contributes to the knowledge of the influence of seasonal change on behavioural consistency and repeatable space use in the field and shows that the link between the laboratory and natural behaviour is not straightforward.

Keywords: field, laboratory, long-term repeatability, personality, seasonality, space use

Introduction

Animals can respond behaviourally to changes within their environment, for example by moving towards favourable (e.g. optimal temperatures, high-quality food patches) and away from unfavourable conditions (e.g. high predator pressure, competition) thereby presumably maximizing their growth, reproduction, and survival (Bonte & Dahirel, 2017; Parker & Smith, 1990; Van Moorter et al., 2016). Interestingly, individuals within populations differ in their spatial behaviour (including movement characteristics and space use) on small scales, such as differences in feeding patterns, medium-scale territory size and home range (Amy et al., 2010; Gunnarsson & Steingrímsson, 2011), as well as on larger scales, such as dispersal and partial migration (Bowler & Benton, 2005; Chapman, Brönmark, et al., 2011; Cote et al., 2010). Consequently, getting an insight into how animals are distributed in both space and time, i.e. where they are found, how much space they use, when they use certain spaces, and if this behaviour is stable across time and context, provides information on how an individual perceives and reacts to the environment, thereby reflecting its states and needs. This information can in turn guide population management and conservation decisions (Allen & Singh, 2016; Ronce, 2007). Individual territories, for example, have been shown to influence the carrying capacity of a population (Grant & Kramer, 1990; López-Sepulcre & Kokko, 2005).

The observed movement and space use differences within a population are often repeatable within individuals, i.e. some individuals move more or occupy consistently more space compared to other members of the population on multiple occasions under different circumstances (Nakagawa & Schielzeth, 2010; Nilsson et al., 2014; Stuber et al., 2022). Behaviours that show low within- and high between-individual variation (i.e. that are repeatable) across time and/or contexts, are often termed ‘personality’ or ‘temperament’ (Dall et al., 2004; Sih, Bell, & Johnson, 2004). These behaviours are commonly divided into five axes: i.e. boldness, exploration, activity, sociality, and aggression (Réale et al., 2007). Spatial behaviour has not been fully integrated into the personality literature, but it has been referred to as ‘spatial personality’ (Stuber et al., 2022). Spatial behaviour underpins the recognized movement-related axis ‘exploration-avoidance’ (i.e. response to a novel environment, often measured as distance travelled or area covered in an open field test) and ‘activity’ (general activity in a known environment; Réale et al., 2007; Stuber et al., 2022). Interestingly, spatial behaviour is more repeatable than any of the other axes, even after taking habitat availability into account (Stuber et al., 2022).

Exploration and activity, as well as spatial behaviour, may be correlated to other personality traits, such as boldness and aggression (Chapman, Hulthén, et al., 2011; Höjesjö et al., 2007; Michelangeli et al., 2022) forming a behavioural syndrome (Sih, Bell, Johnson, et al., 2004). Furthermore, spatial behaviour can be sex-dependent (e.g. Bowler & Benton, 2005; Croft et al., 2003; Michelangeli et al., 2022) and underpinned by physiological (e.g. metabolic rate), neuroendocrine, or genetic variation (Careau et al., 2008; Doligez et al., 2009; Gervais et al., 2020; Koolhaas et al., 2007; Pampoulie et al., 2022; van Oers & Mueller, 2010). In fact, personality traits may influence the distribution of individuals across their environment more than habitat characteristics (Spiegel et al., 2017). Consistent individual differences within spatial behaviour may lead to consistent individual differences in feeding opportunities and predation encounters, and thus affect growth rate and survival (Biro & Stamps, 2008; Moiron et al., 2020). This can influence population dynamics and success (Bastille-Rousseau & Wittemyer, 2019; Bowler & Benton, 2005; Hoch et al., 2019; Milles et al., 2020; Spiegel et al., 2017) and in turn have evolutionary consequences (Sih et al., 2012; Smith & Blumstein, 2008; Webber et al., 2020; Wolf & Weissing, 2012).

Environmental changes, often induced by changes between seasons, frequently affect spatial behaviour per se (e.g. Bremset, 2000; Turbek et al., 2018; Turrisi et al., 2021). Seasonal differences at higher latitudes are especially influential, as abiotic factors, such as temperature and light conditions show remarkable differences between seasons, causing significant fluctuations in food availability and predator presence. Ectotherms especially depend directly on environmental temperatures for their metabolism (Biro et al., 2010; Cutts et al., 2001; Michelangeli et al., 2022). Although the average movement or space use of a population might vary between seasons, personality can still be present if enough variation persists, and the hierarchy among members of the population holds. Several studies on fish show that this can indeed occur (Cutts et al., 2001; Harrison et al., 2015; Nakayama et al., 2016; Taylor & Cooke, 2014), but see Hanson et al. (2010) and Hoch et al. (2019).

Consistent differences in spatial behaviour have only recently found their way into the personality literature and recent studies acknowledge that this field is highly underrepresented (Nilsson et al., 2014; Spiegel et al., 2017; Stuber et al., 2022), but see Kobler et al., 2011, for an example. In addition, long-term behaviour is less studied than short-term behaviour, especially across seasons, and studying this can shed light on how movement remains consistent within a lifespan. Finally, not many studies confirm correlations between measurements in laboratory and natural conditions, while these are not necessarily the same (Mouchet & Dingemanse, 2021; Niemelä & Dingemanse, 2014).

In this study, we focus on the medium-scale individual movement behaviour of a land-locked stream fish (Arctic charr; *Salvelinus alpinus*) in the river Grímsá in northern Iceland, which experiences a strong seasonal change in terms of water *temperatures* (from near freezing up to 17°C in water temperature), daylight (3 hours of daylight in winter to no sunset in summer) and ice cover. Charr in this stream stay relatively small (up to 15-20 cm, Steingrímsson pers. comm.) and are opportunistic feeders but feed mainly on drifting invertebrates, which are abundant during summer, but whose numbers reduce with decreasing temperatures (Larranaga, 2016). Higher temperatures have been shown to increase feeding activity in this species in this stream (Larranaga, 2016) and similar streams (Fingerle et al., 2016), but Arctic charr also stay active during the winter (Klemetsen et al., 2003). Arctic charr defend territories while feeding, although these overlap more than in other salmonids; they also are more mobile during prey search (i.e. foraging mode) than related species (Gunnarsson & Steingrímsson, 2011; Tunney & Steingrímsson, 2012). Specific spawning timing has not been studied in this stream, but sexually mature fish have been observed in October during electrofishing (pers.obs.).

We collected short- and long-term repeated measurements of exploration and boldness in the laboratory in two consecutive summers and intervening winter and combined this with initial dispersal from release as a measure of natural exploration and distances between consecutive weekly GPS locations in summer and winter as a measure of space use. We thereby extend the study on short-term repeatability between laboratory and field on the same Arctic charr individuals (Paper IV) to season-dependent long-term repeatability specifically by asking the following research questions:

1. Are laboratory estimates of boldness (shelter test) and exploration (open field test) of Artic charr repeatable and correlated between seasons?
2. Can laboratory estimates of boldness and exploration explain initial travel distance from release (i.e. a natural measure of exploration) in their natal stream in Arctic charr?
3. Are weekly consecutive GPS locations in the field (i.e. space use) of stream-dwelling Arctic charr repeatable within and between seasons?
4. Can laboratory estimates and/or initial travel distance explain space use in the field?

We found short-term repeatable exploration and boldness behaviour in this subset of fish in the laboratory, (described in Paper IV), so we only focus on seasonality and long-term behaviour in our hypotheses. First, we expect to find overall high long-term repeatable exploration and space use (Stuber et al., 2022), while boldness has the potential to be repeatable long-term, but is understudied. Secondly, we predict that exploration measured in the laboratory correlates with exploration measured in the field (Harrison et al., 2015; Závorka et al., 2015) and while this has not been correlated to boldness before, bolder fish may outcompete shyer individuals and are therefore more likely to find a suitable habitat first, which may result in a lower initial travel distance. Thirdly, we predict that during summer, fish are more explorative and use more space compared to the early winter as low feeding activity as an energy-saving strategy is expected, but we expect no difference in boldness behaviour (Bremset, 2000; Cunjak & Power, 1987; Mulder et al., 2018). Fourthly, regardless of these average trait values, we expect to find repeatable exploration, boldness, and space use and a consistent movement syndrome between seasons (Harrison et al., 2015; Lukas et al., 2021; Nakayama et al., 2016; Taylor & Cooke, 2014). Finally, we expect that regardless of season, this behavioural syndrome manifests along a gradient of ‘stayers’ that are less explorative, bolder, have a smaller initial dispersal distance, and use less space to ‘movers’ that are more explorative, have a higher initial dispersal distance and use more space as found among other freshwater fish species (Chapman, Hulthén, et al., 2011; Conrad et al., 2011; Fraser et al., 2001; Grant & Noakes, 1987; Gunnarsson & Steingrímsson, 2011; Harrison et al., 2015; Knaepkens et al., 2004; Nilsson et al., 2014; Radinger & Wolter, 2014; Rodríguez, 2002; Závorka et al., 2015).

Methods

The study took place in a landlocked part of the river Grímsá, northern Iceland (N 65.792379, W 19.844413; Fig. 1; Larranaga, 2016). The stream section used for this study is shallow (typically < 50 cm deep) and narrow (1-5 m wide), which makes it an ideal study stream study space use as it limits vertical and horizontal movements respectively (Rasmussen & Belk, 2017). The stream originates as a run-off stream and a waterfall 4.8 km from the origin blocks upstream fish movement into the study section (Fig. 1). Three main tributaries flow into this part of the river Grímsá which are all blocked for fish passage upstream, two by a waterfall and one by an artificial road passage (Fig. 1; red dots). The only natural fish population in this part of the stream is Arctic charr (*Salvelinus alpinus*), but juvenile Atlantic salmon are occasionally released for enhancement purposes of a downstream salmon population and predator pressure is low (pers. obs.).

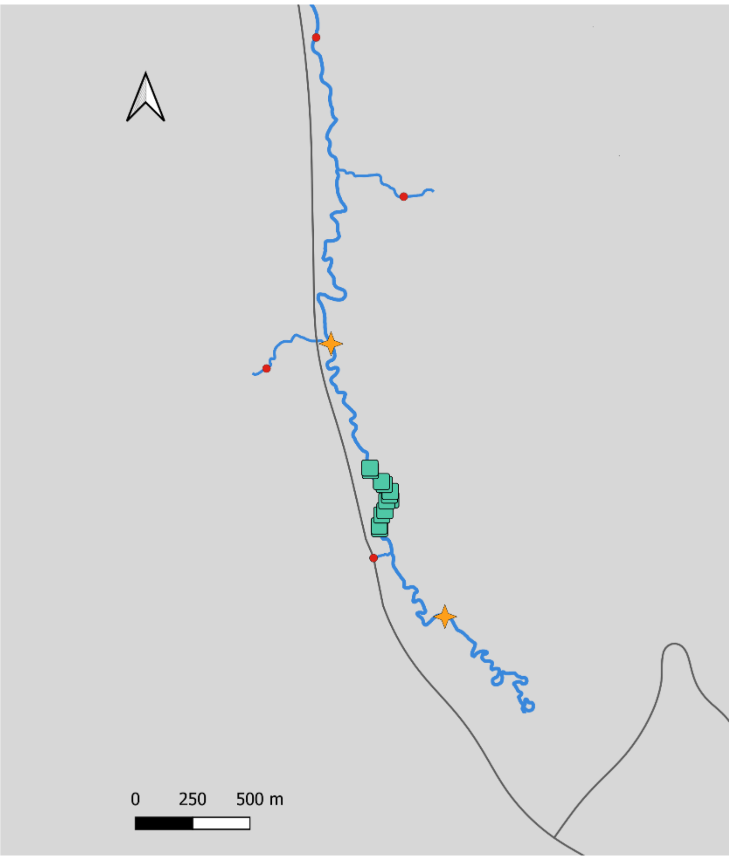

Figure 1. A map of river Grímsá (blue). Stream enclosures from which fish were released are depicted by green squares, the boundaries of the main study stream by the two yellow stars, three waterfalls, and one impassable road culvert that confine the distribution of the population by red dots. The arrow indicates north and the flow direction. Map credits: Eric dos Santos & QGIS

A total of 96 Arctic charr of age 1+ were electrofished on June 22-23, 2021 (LR-24 electrofisher, Smith-Root, Inc., Vancouver, Wash., USA) (Fig. 2). They were transported on a 10-minute drive to the Verið laboratory in Sauðárkrókur (Department of Aquaculture and Fish Biology, Hólar University). Individuals were anaesthetized with 0.3mg/L phenoxyethanol and measured for fork length to the closest 0.1 mm with callipers and body mass to the closest 0.01

g (PESOLA® PPS200, CH-6340 Baar, Switzerland). Then, fish were subcutaneously tagged with visible implant elastomer (VIE; Northwest Marine Technology, Inc., Washington, USA) using different combinations of yellow, green, orange, pink, and red in two positions along the dorsal fin. Subsequently, the fish were randomly assigned to twelve circular grey 120 L tanks (8 fish/tank) with continuous water flow and cobbles on the bottom to provide shelters and potential stress.

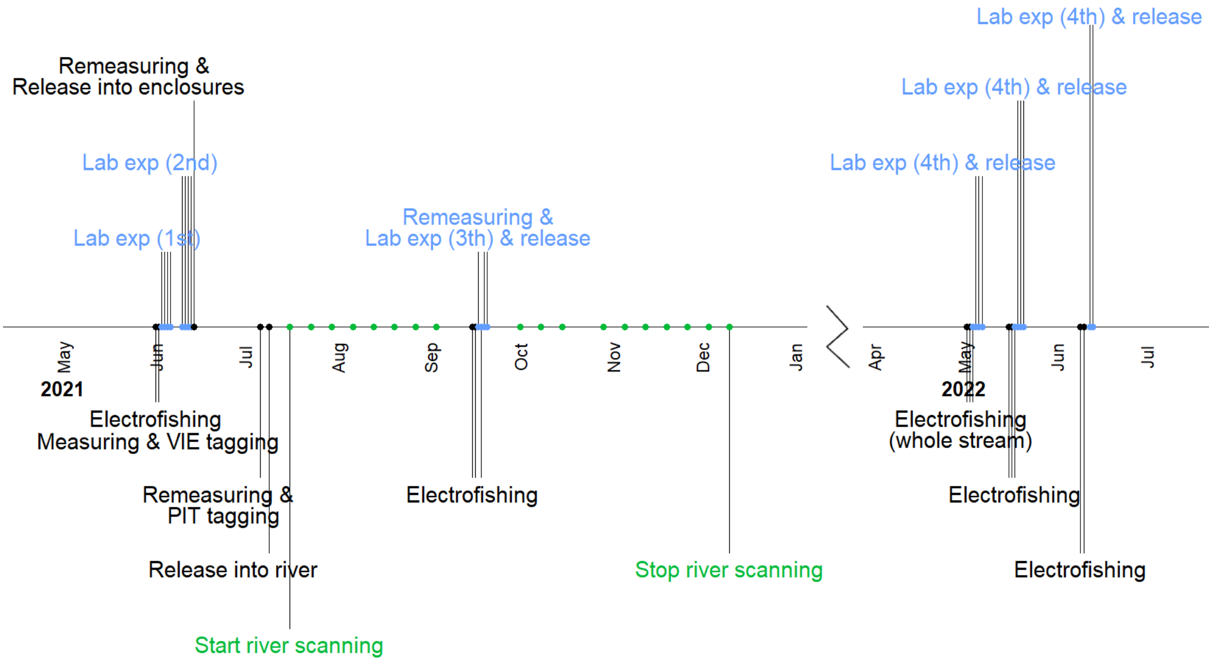

Figure 2. Timeline of transport from and to the river, measuring and tagging (black), laboratory experiments (blue) and river scans (green).

Laboratory trials

These trials were the same as described in Beukeboom (2023) and Philip et al. (2022). Not all fish could be tested in one day (Fig 2; blue). After 24 hours of habituation in the lab, on June 24, the first group (56 fish) was subjected to a Shelter Test (ST) for boldness assessment, and on the next day (June 25), the other 40 fish (Group 2) were subjected to an Open Field Test (OFT) for exploration assessment. On June 26, Group 1 received the OFT and on June 27 Group 2 received the ST. This pattern was repeated one week later (July 1-4; Trial 2), after three months (October; Trial 3), and one year (June 2022, Trial 4; Fig. 2). The alternation of the test order allowed for taking any test order effect into account during the analysis. To increase the capacity of the laboratory tests, four tests were performed in parallel in separate arenas. Water in the trial arenas was changed between trials to remove any cues from previous fish. The mean water temperature in the trial arenas ranged from 4.5 to 8.7 °C (mean 5.8 °C).

Shelter Test

In the ST, the focal fish was placed in an arena (39.7 cm x 29.5 cm x 6 cm) with a shelter (6 cm x 14 cm) and after five minutes of habituation, the shelter door was lifted and the arena filmed for 20 minutes using a camera (Basler Ace acA 1920-150µm, Germany) at 30 frames per second placed 110 cm above the arena (Paper IV; Philip et al., 2022). Video tracking software (Ethovision 15.0, Noldus, The Netherlands) was used to divide the arena virtually into an entry (2.5 x 6 cm), border (5 cm from the edge), and centre (the centre arena minus shelter, border, and entry) zones. Subsequently, the software was used to extract the latency to exit the shelter with full body (s), total time spent in shelter, entry, centre, and border zone (s), frequency to enter these zones, total distance moved (cm), absolute angular velocity (degrees/s) and mean velocity (body lengths/s) (Benhaïm et al., 2020). Fish that did not leave the shelter were assigned the maximum score of 1200 seconds for the total time in the shelter and the latency to leave the shelter and zero for the other variables. A Kaiser-Meyer-Olkin criterion performed with the EFAtools package in R (Steiner et al., 2023) performed on the 12 measurements of the ST indicated that our data was suitable for Principal Component Analysis (PCA; all variables > 0.704, overall value = 0.879) (Budaev, 2010). The PCA was run on the first trial using the "prcomp" function in R. As the first axis explained 70.16% of the variation in the data and showed a gradient from fish spending the most time in the shelter to spending all their time in several areas of the arena, this axis was used as the boldness score (BOL). Individual repeated measurements (i.e. trials 2, 3, and 4) were predicted from these scores using the "predict" function to take the repeated nature measurements into account (R Core Team, 2022; Toms et al., 2010). All boldness scores were multiplied by -1 so lower scores would represent shyer individuals.

Open Field Test

The OFT followed the same protocol as the ST, except that habituation took place in an upside-down plastic white container (Ø 10 cm) which was placed in the middle of the arena (Paper IV). Additionally, the shelter was permanently closed so that the individual was always visible. These videos were also analyzed with Ethovision and the total distance travelled and the total area covered (total unique x/y coordinates rounded to the nearest integer) were extracted, which are both measurements commonly used as proxies of exploration. The total distance travelled and the total area covered extracted from the OFT were intended to be used as measurements of exploration. Both measurements were highly and significantly correlated in Trial 1 and 2 (Paper IV) and this pattern was even stronger in Trial 3 and 4 (PEARSON: $r = 0.87$; CI 95 % [0.79 –0.93]; $P < 0.001$). Therefore, only the total distance traveled was used in further analysis as this measurement is not statistically ceiled (i.e.not bounded by the maximum size of the arena as is the case with the area covered) and therefore can capture the most variation between individuals.

Field: Tagging and tracking

Directly after the laboratory trials (July 5th; Fig. 2), all fish were anaesthetized and remeasured. The fish were then transported back to their native stream where they were released into 12 stream enclosures in the same groups as established in the laboratory for enclosure observations (Fig. 1). The results of these observations can be found in Beukeboom (2023) and will not be further discussed here. The enclosure observations ended on July 27 and 41 fish were tagged with passive 12 mm (0.1 g, >6.9 cm fork length) and 55 fish with 14 mm (0.25 g, >8.7 cm) HDX PIT tags (ICAR-registered, Oregon RFID) by making a small incision in the abdomen (Fig. 2). The tag sizes were chosen to limit the influence on growth and mortality conform a study on the influence of the tags on salmonids (Vollset et al., 2020). However, the 14 mm was a newly released tag and therefore linearly interpolated from the available data taking weight and length into account. After tagging, the fish were given three days to recover in the enclosures and observed for deviant behaviour. All fish seemed healthy and on July 30, the top size of each enclosure was lowered, so the fish could leave whenever they felt ready. A day later, all the fish had left the enclosures (Fig. 1, 2).

Tracking

Solar-panelled Multiple Antenna Readers (Oregon RFID) were stationed at the up- and downstream ends of the study section (total length 1.8 km; Fig 1), combined with a tuner (Oregon RFID) and American Wire Gauge that functioned as an antenna to detect fish that left the study section. Antenna functioning was monitored with a Marker Tag (Oregon RFID). The manual scanning took place between these two stationary antennas and started on August 6, 2021, a week after the release of the fish, and was performed weekly after that (Fig. 2, green dots). This weekly time interval allowed enough time for individuals to sample and experience heterogeneous environments and thereby reduce autocorrelation (Hodder et al., 2007; Noonan et al., 2019; Postlethwaite & Dennis, 2013). The scanning took place between 9.00-17.00 and took around 5,5 hours per day. It was done by walking slowly downstream in the river with a mobile reading kit (Oregon RFID) containing a Single Antenna reader (Oregon RFID; range: 30 cm above and below, 15 cm from the side) while moving the scanning device 20-30 cm above the substrate. When a tagged fish was detected, the date, time, tag number, and GPS location were recorded (GPS Logger v. 3.1.7). Measurement error was obtained from the snap distance between the river vertex and the actual GPS point using the “riverdist” package and was on average 4.7m (range 0.13 – 24.0) (Tyers, 2017). The slow walk through the stream did not appear to disturb the fish as they (i) returned quickly to their detected location after disturbance (pers. obs) and (ii) were rarely detected multiple times (48 out of 1161 cases, 4% and never more than once) on the same day, which would have indicated a downstream chase. On 6, 7, and 9 October 2021, tagged fish were recaptured via electrofishing the study section twice, their location recorded and then brought to the laboratory to repeat one cycle of the ST and OFT. After this, each fish was remeasured and weighed, and released at its respective capture location (Fig. 2). Weekly scanning was resumed two weeks after the release (October 22) and conducted until the river became inaccessible on December 30 because of snow cover. Between May 23 and June 2022, the whole stream (4.8 km) above the downstream waterfall, including the side streams, (Fig. 1) was electrofished three times to recapture as many tagged fish as possible and to reduce any potential bias from fish that had moved out of the study section. Once recaptured, the study fish received a final round of laboratory tests and body measurements (Fig. 2). After the tests, the fish were released at their place of capture. All longitudinal distances between consecutive weekly GPS positions were calculated using the package ‘riverdist’ (Tyers, 2017) based on a manually drawn path with Google Earth Pro with added vertices every 5 meters. The distance between the point of release and the GPS location collected in the first week after the first release, i.e. initial distance travelled, was interpreted as a natural measure of exploration. Following consecutive weekly GPS positions, divided between summer and winter, were interpreted as a measure of space use.

Sexing

Sex was determined by taking a fin clip of each study fish when they were PIT-tagged and DNA was extracted using the instructions and materials from a NucleoMag Tissue kit for DNA purification from cells and tissue (Macherey-Nagel GmbH Co. KG). An 18s control marker was used for species identification and an SDY marker was used to identify the males (Yano et al., 2013).

Statistics

All data were analyzed using multivariate linear mixed models with the Bayesian software Stan (Carpenter et al., 2017) via the ‘brms’ package (Bürkner, 2017) in R v. 4.1.3 (R Core Team, 2022). All numeric variables were scaled using the ‘scale’ function in R (i.e. z-scoring; subtracted the mean and divided by the standard deviation).

To determine whether laboratory estimates of exploration and boldness were repeatable and correlated between seasons, we ran three models with the same model specifications which included EXP and BOL as dependent variables, length, sex, test order, and trial as fixed effects, and fish ID as a random effect (Table 1), but on three different subsets i.e. within the 1st summer (Trials 1&2), summer and winter (Trials 1&3) and between the 1st and 2nd summer (Trials 1&4; Table 1). The temperature in the test arenas did not influence measurements and was therefore not included in the model (Paper IV). The first model containing trials 1 and 2 was slightly different from the one run in (Paper IV), and therefore also included here.

To calculate a single 'stable' exploration and boldness score for every individual (EXPi and BOLi) the random effects estimates were extracted from the model output using the 'ranef function' based on medians from brms. As sex was a stable fixed effect between the two trials, it was included in this 'stable' score by adding the median of the slope of sex to the random effect intercept for the males as female was the reference level. This value was consecutively used as a predictor variable for initial travel distance (i.e. the distance between the enclosure of release and the first scan GPS point; INI). This model also included length and sex as fixed effects (Table 1).

Because laboratory exploration was not repeatable between summer and winter and boldness only marginally with big confidence intervals, and only one laboratory measurement in the winter prevented the calculation of short-term repeatability in that season, 'stable' exploration and boldness were only analyzed in combination with space use in the summer. We ran two separate models. The first model (ModA) contained a subset of the summer distances, excluding initial travel distance, with the distance between consecutive GPS points in the field (DIS) as a dependent variable, EXPi, BOLi, INI, length, sex, and the number of field data points (n_dist) as fixed effects (Table 1). The second model (ModB) contained the winter subset for DIS as the dependent variable and only included length, sex, and n_dist as fixed effects. Both models included fish ID as a random effect (Table 1). Finally, to determine the repeatability of space use and the difference in average space use between summer and winter, we calculated DISi separately for summer and winter in the same way as we calculated EXPi and BOLi. We then ran a model with DISi as a dependent variable, season, sex, and length as fixed effects, and fish ID as a random effect (Mod C).

Table 1. Overview of the data and models used to answer the four research questions.

Research question	**Laboratory data**	**Field data**	**Model**
RQ1	Trial 1&2 Trial 1&3 Trial 1&4		BOL ~ Length + Sex + Test_order + Trial + (1|ID) EXP ~ Length + Sex + Test_order + Trial + (1|ID)
RQ2	'Stable' EXP (EXPi) & BOL (BOLi)	Initial travel distance (INI)	INI ~ EXPi + BOLi + Length + Sex
RQ3&4 (ModA)	'Stable' EXP (EXPi) & BOL (BOLi)	Initial travel distance (INI) All consecutive distances between GPS points (DIS) for the summer	DIS ~ EXPi + BOLi + INI + Length + Sex+ n_dist
RQ3 (ModB)		All consecutive distances between GPS points (DIS) for winter only	DIS ~ Length + Sex + n_dist + (1|ID)
RQ3 (ModC)	'Stable' DIS (DISi)	DISi for summer and winter separately	DISi ~ Season + Length + Sex + (1|ID)

All models were run with 4 chains and 4000 iterations (2000 warm-up and 2000 for sampling) and all other settings were set to their default with two exceptions: the model used for RQ1, trials 1&2 which was run for 8000 iterations (4000 warmups, and 4000 for sampling), with an adapt delta of 0.9 and the model for RQ1, trials 1&4 which was run with an adapt delta of 0.9 to acquire full convergence and high bulk effective sample size. As the random-effects structure of the models with EXP, BOL, and DIS as dependent variables, included individual fish identity (ID) as a grouping variable, it was possible to calculate the repeatability of these variables as the ratio of the among-individual variance and the sum of the among-individual and residual-level variances (i.e. personality) (Johnson & Koch, 2011; Nakagawa & Schielzeth, 2010). The models to answer RQ1 also estimated covariances between BOL and EXP at both the ID and residual levels. The among-individual covariance quantified the degree to which the two variables were correlated among individuals across multiple trials (i.e. behavioural syndrome), whereas the residual level covariance quantified the degree to which they were correlated among observations independently of the identity of individuals. Convergence was assessed using the standard diagnostics provided by Stan, including the potential scale reduction factor R-hat, effective sample size, and visual inspection of trace plots and histograms for each model parameter (Carpenter et al., 2017). We report medians and 95% quantiles of the variances and covariances.

Ethical note

The number of fish and the procedures (electrofishing, handling, fin clipping, behavioural tests, PIT tagging, and tracking) were chosen to adhere to strict ethical guidelines and approved by the Icelandic Food and Veterinary Authority (MAST; 2021-09-05). Permission to transport the study fish from the laboratory to their natal stream was approved by MAST at the date of their release (ÍSLGJ13321 and ÍSLGJ24221).

Results

Laboratory data

All 96 individuals were subjected to trials 1 and 2 of the ST and OFT in June 2021 (see also Paper IV). Of these, 38 fish were recaptured and remeasured in October 2021, and 18 in June and July 2022 of which 10 were also recaptured in October. During VIE-tagging, 4 fish died because of human error and were replaced by spare fish. These spare fish did not perform laboratory trials but were included in the scanning data for the stream. Fork length ranged from 6.6-11.8 cm at first catch (mean 8.8 cm) to 9.0-14.2 cm (mean 11.2cm) in the summer of 2022 and was accidentally not measured for one fish. Of the 96 fish, 57 were male, 37 were female and 2 remained unknown, because of failed genetic analysis. These three fish with missing data were excluded from further analysis.

Field data

A sharp natural drop in temperatures occurred on September 26, 2021, and temperatures after that did not reach the same levels as before. This provided a natural split between ‘summer’ ranging from the time of release (July 30) to September 26 and ‘winter’ from September 26 to December 30 when the river was covered in snow and became inaccessible. Summer water temperatures (mean 8.29°C; range = [2.73 - 16.9°C]) were significantly higher than the water temperatures in the early winter (mean = 1.85°C, range = [0.12- 4.73°C]; t= 84.06, df=1442, p< 0.001).

Ninety-six individuals were released in the river, but three fish were accidentally tagged with an FDX tag which could not be detected by the HDX scanner, although one fish was retrieved during electrofishing in October based on its VIE tag. Both solar-panelled stationary antennas were working irregularly due to day length shortening and weather conditions but still detected 23 individuals on 102 unique days. Eight stationary antenna detections of six individuals could be matched with the scanning dates (+/- 1 day) and were added to the manual scanning data. This resulted in a total of 942 fish detections up to December 30; 493 detections on eight scanning days in summer (mean = 62 fish/day, range = 50-71), 449 detections on nine scanning days in winter (mean = 50 fish/day, range = 35-58) (Fig. 2). Ninety-one out of 93 detectable fish (98%) were detected at least once after release. Individuals were detected on average 5.6 times (range = 1-8) in summer and 4.6 times (range = 1-9) in winter. Individuals with only one sampling point (summer: N = 3; winter N = 17) were not removed from the data set as suggested by Dingemanse & Dochtermann (2013) and Nakagawa & Schielzeth (2010).

All fish that were detected during the first week of scanning were detected upstream of their respective enclosure of release. The distance between the points of release and the first scan (N= 64) was much higher (median= 370 m, range = 46 to 1071 m) than the distance between consecutive points in the summer (median = 13 m, range = 0 – 602m) and winter (median = 12 m, range = 0 – 290 m) and could therefore be used as initial dispersal distance as planned (Fig. 3; *sensu* Harrison et al., 2015; Závorka et al., 2015). In summer as well as in winter, ~30% of the distances between consecutive GPS points were less than 5m, partly due to a group of fish repeatedly found at one location where a side stream entered the study stream (Fig. 1).

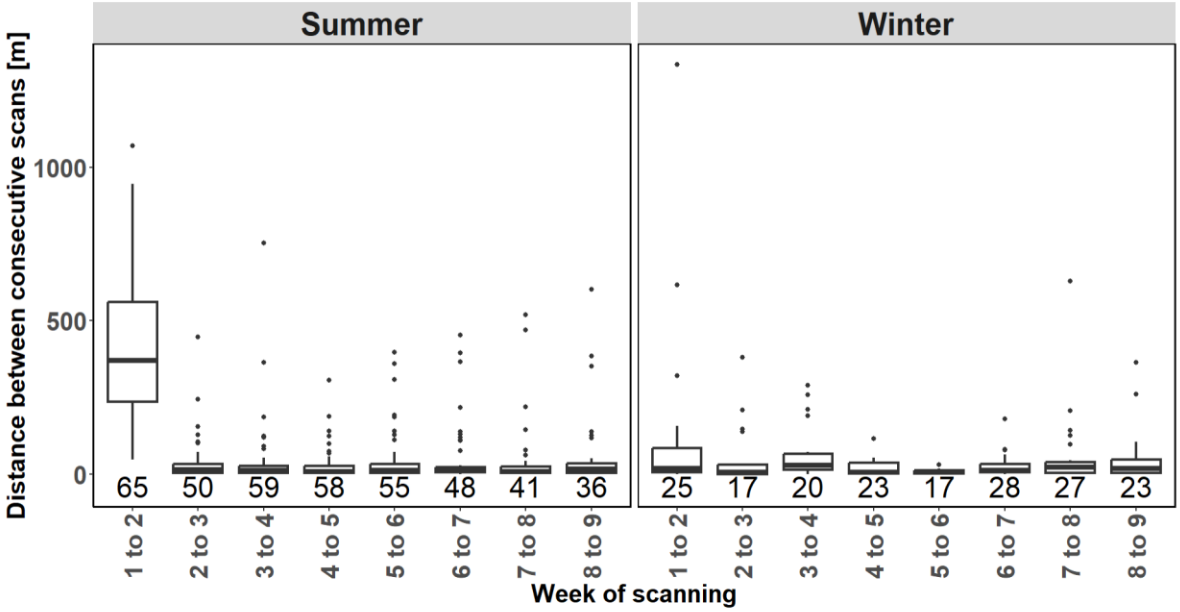

Figure 3. Distances between weekly scanning points of Arctic charr in the river Grímsá. Numbers below the boxplots indicate the sample size.

RQ1: Repeatability and correlation of exploration and boldness in the laboratory between seasons.

Exploration was repeatable within summer (one week: R=0.42; UI95 %=[0.22, 0.58]; Paper IV), between summers (one year: R=0.72; UI95 %=[0.30, 0.90]), but not between summer and winter (four months: R=0.21; UI95 %=[0.00, 0.53]; Fig 4). Boldness was repeatable within summer (R=0.31; UI95 %=[0.07, 0.50]; Paper IV) and marginally between summer and winter (R=0.34; UI95 %=[0.04, 0.61], but not between summers (R=0.26; UI95%=[0.00, 0.64]). Average boldness and exploration behaviour between trials only differed short-term within summer, but not long-term between summer and winter, nor between summers. The marginal and non-repeatable estimates all exhibited low between- and high within-individual variances

(Table S1). The covariances between exploration and boldness within the 1st summer and between summer and winter were close to zero with zero overlapping 95%UI intervals, whereas between summers a trend was visible where bolder individuals were more explorative (Table S1). Covariances on the residual level were present between summer and winter and trends for within and between summer. A trend was present that larger fish were bolder and more explorative within summer and bolder between summer and winter, but not between summers (Table S1). Sex did not influence boldness or exploration in any of the models (Table S1).

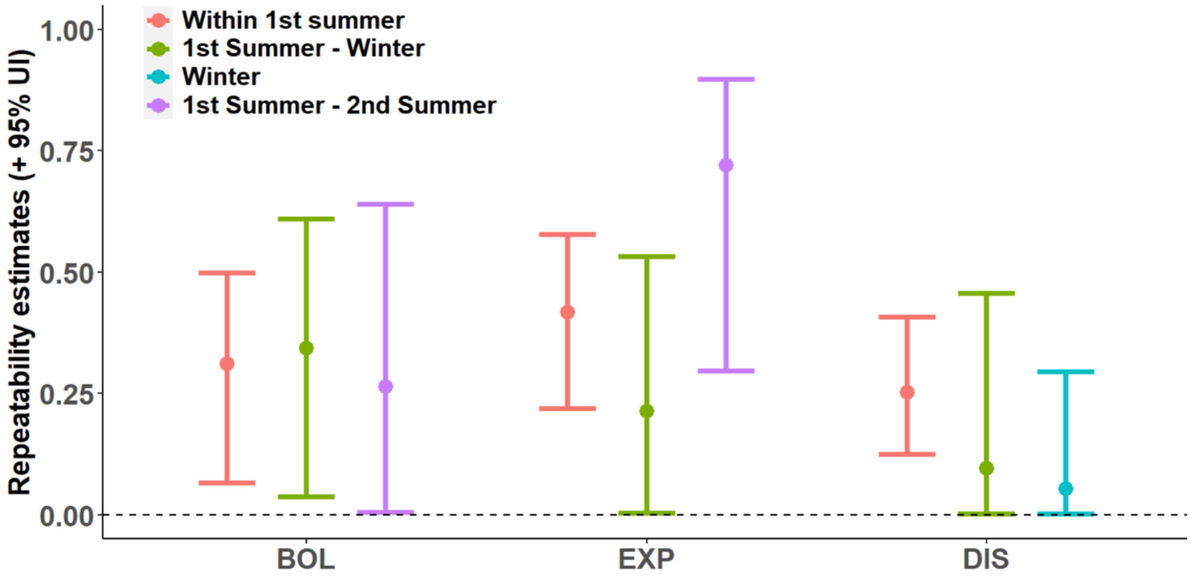

Figure 4. Repeatabilities of boldness (BOL), exploration (EXP) and space use (DIS) in Arctic charr within the 1st summer of study (red), between 1st summer and winter (green), winter (blue) and between the 1st and 2nd summer of study (purple). Dashed line indicates 0.

RQ2: The relation between laboratory measurements and initial travel distance in the field.

A trend was visible that the ‘stable’ exploration score (median = 0.01, range=[-0.52 – 1.49]) influenced initial travel distance, where more explorative individuals had a higher initial travel distance (median = 0.21, range=[-0.08 – 0.50]), while ‘stable’ boldness score (median = -0.05, range=[-1.02 – 1.30]) did not influence initial travel distance (median = -0.02, range=[-0.29 – 0.27]); Fig. 5), nor did sex (median = -0.23, UI95 %=[-0.85-0.37]) or length (median = 0.17, UI95 %=[-0.10-0.43]).

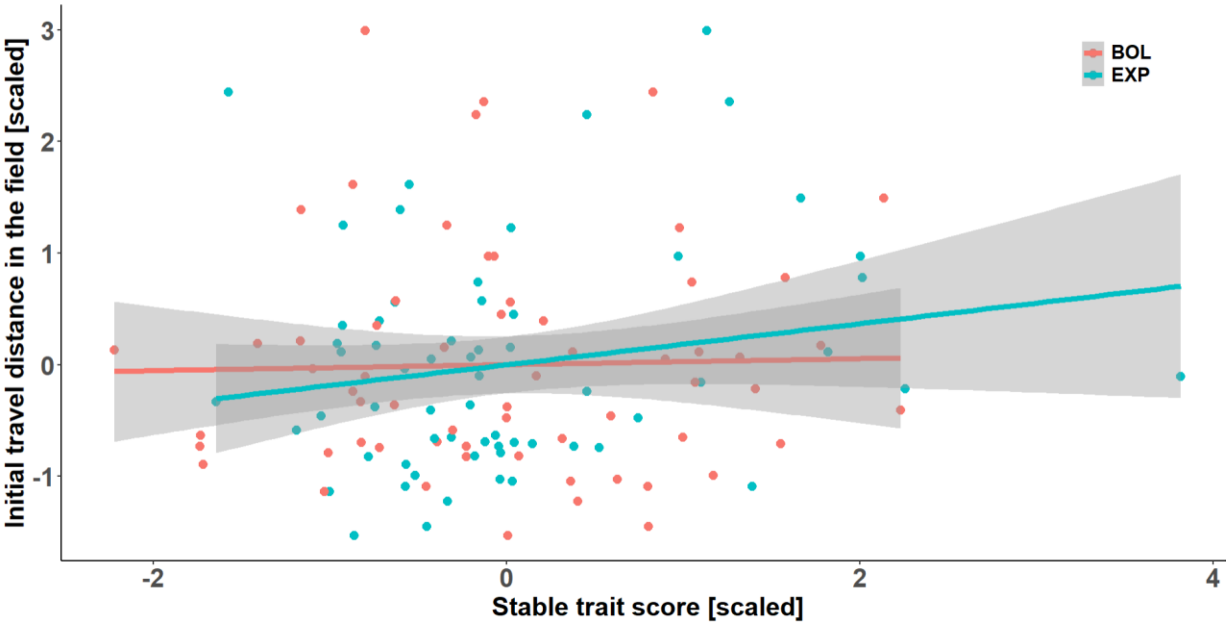

Figure 5. Linear regression between the stable exploration (blue) and boldness (red) tendency derived from the laboratory and the initial travel distance in the field. Grey area indicates 95%UI.

RQ3: Repeatability of weekly consecutive distances between GPS points within and between seasons

Weekly consecutive distances between GPS points (as a proxy for space use) were repeatable within summer (R=0.25; UI95 %=[0.12, 0.41], but not within winter (R=0.05; UI95 %=[0.00, 0.29]), nor between summer and winter (R=0.10; UI95 %=[0.00, 0.46]; Fig 4). This was mainly caused by substantial variation between individuals in summer, while this was absent in the winter (Table S1). Furthermore, within-individual variation was lower in summer than in winter. Median distances between weekly consecutive GPS positions did not differ between seasons (median winter = -0.04, UI95 %=[-0.19-0.11]). Length, sex, and the number of detections did not influence space use in summer, or in winter (Table S1). A post-analysis of only the fish that were present in both samples revealed similar results.

RQ4: The relationship between laboratory estimates, initial travel distance from release, and consecutive distances between GPS points in the field

Neither summer laboratory exploration and boldness, nor initial travel distance explained space use in the field (median = 0.29, UI95 %=[-0.31 – 0.89], median = -0.26, UI95 %=[-0.68-0.17], median = -0.01, UI95 %=[-0.17 – 0.17] respectively).

Discussion

In this study, we investigated (i) seasonal, long-term (up to a year) exploration and boldness estimates in the laboratory, (ii) seasonal space use in the field, and (iii) the correlation between these estimates. Specifically, we collected data from a natural population of stream Arctic charr, which we subjected to a shelter and open field test in the laboratory in two summers and intervening winter. Between the laboratory measurements, the study fish roamed freely in their stream of origin, where we collected weekly GPS locations in summer and early winter. Exploration was repeatable within and between summers, but not between summer and winter, whereas boldness was repeatable within summer and marginally between summer and winter, but not between summers. In the field, space use was only repeatable in summer, but not in winter and not between summer and winter, while the mean population exploration and boldness estimates did not differ between seasons. Finally, exploration measured in the laboratory explained exploration in the field marginally, but neither boldness nor exploration explained space use in the field. We discuss these findings below.

RQ1: Are laboratory estimates of boldness and exploration repeatable and correlated between seasons?

Boldness and exploration were short-term repeatable within summer, which was already shown and discussed in Beukeboom (2023). The current study shows additionally that boldness was marginally repeatable between summer and winter, but not between two consecutive summers. The opposite was found for exploration, which was not repeatable between summer and winter, but highly repeatable between the two consecutive summers. Long-term repeatable exploration behaviour has been found in other fish species, (e.g. Beukeboom et al., 2023; Polverino et al., 2016) which corresponds with findings of other studies summarized in Bell et al. (2009) and Stuber et al. (2022). Our findings demonstrate that exploration, but not boldness, can also be repeatable for an even longer-term interval (i.e. one year), but that long-term repeatability may depend on seasonal (environmental) conditions, even though the mean population exploration rate did not differ between the long-term trials. Although sample size can influence repeatability and numbers decreased between our measurements (2.5-fold in October and fivefold in the 2nd summer compared to the 1st summer; Bell et al., 2009), repeatability did not follow the opposite trend, so it is unlikely that the changing repeatability between seasons was simply caused by the decrease in sample size. To our knowledge, this is the first study in fish that found long-term, season-dependent repeatability of exploration behaviour in the laboratory. Finally, we found no correlation between exploration and boldness in either the short- or the long-term models. Data on other fish species are incongruent (summarized in Conrad et al., 2011). The absence of correlation is most likely because the traits evolved separately which is due to independent functional roles (Sih, Bell, Johnson, et al., 2004).

RQ2: Can laboratory exploration explain natural exploration (i.e. initial travel distance) in the field?

A trend was visible that more explorative, but not bolder Arctic charr in the laboratory, travelled bigger distances during the first week after release in the stream. Correlations between laboratory exploration and initial travel distance in the field have been found in three similar studies on this topic (Kobler et al., 2009; Yokota et al., 2007; Závorka et al., 2015). However, the strength of this correlation may have been weakened by several factors. Firstly, the small-scale, constrained open field test may indicate a ‘stable’ exploration tendency, exploration in the field is likely not just determined by this predisposition as it is unconstrained and across a much larger area, and may therefore be hindered by individual physical abilities as well as the environment. For example, condition-dependent swimming speed, food availability, stream flow, and competition absent in the laboratory may likely influence dispersal abilities, either by a decrease in initial travel distance when encountering high habitat quality and low competition, or by an increase resulting from low food quality and competition (Bégué et al., 2023; Larranaga, 2016; Martínez et al., 2004; Nelson et al., 2008; Schoener, 1974; Sih & Bell, 2008, p. 30). Secondly, in the three mentioned studies fish were released in a novel stream. In the current study, fish were not released at the point where they were caught, as they were not identified until in the laboratory, but they were returned to the same stream section (i.e. the enclosures were in the stream section where they were caught). The 'initial travel distance' measured here, may have captured the return to familiar habitats or home ranges where they were initially caught i.e. 'homing', (e.g. Miller & Menzel, 1986), which could explain the weak correlation between the two exploration measurements.

RQ3: Is space use in the field repeatable and stable within seasons?

For the space used in the field, similar patterns were found as in the laboratory: space use was repeatable within summer, but not in winter, nor between summer and winter. The finding that distances between weekly consecutive GPS locations of Arctic charr were repeatable in summer, but not in winter may be mainly because individuals behaved more similarly in the winter compared to the summer. This could be caused by an exponential positive relationship between temperature and metabolic rate which directly acts on movement behaviour and thereby decreases variation (Killen et al., 2013; Nakayama et al., 2016). At the same time, individuals were more consistent in their behaviour in summer. A study of the effect of water temperature on within- and between-individual variation in swimming activity in perch also found an increase in population behavioural variation with increasing temperature but also an increase in within-individual variance, which is contrary to our study (Nakayama et al., 2016). An explanation for this discrepancy and the lower plasticity in the summer compared to the winter could be the group of fish that was usually residing near the side-stream inlet with presumably, unmeasured favoured conditions (e.g. temperature, food availability) in summer accounting for a substantial amount of 'non-moving', thereby creating 'pseudo repeatability', where an environmental influence is only experienced by a part of the population (Niemelä & Dingemanse, 2017). Interestingly, although we expected that average space use would decrease in winter, we found no differences between seasons, which corresponds with a study on juvenile Atlantic Salmon (Roy et al., 2013). This result, in combination with the reduced between-individual variation in winter, indicates that fish that were on both sides of the movement spectrum changed their space use pattern to more average space use, rather than stop moving completely. The decrease in temperatures and daylight hours may have caused the most mobile fish to reduce their movement in the winter compared to the summer as an energy-saving strategy (Mulder et al., 2018), while at the same time, the pool at the side stream inlet might have lost its attractiveness with decreasing temperature (e.g. decreasing food availability or oxygen levels), forcing the least mobile fish residing in this pool to search for a better habitat, thereby increasing their space use. Additionally, one might argue that the decrease in behavioural variation could be the result of fish on the edges of the movement spectrum leaving the field site and no longer being represented in our sample. However, the post-analysis of only the fish that were present in both samples indicated that this was not the case. Finally, we do acknowledge that the natural space use presented here might be lower than the actual space use as movements within the weekly scanning points were not captured in the data. However, with the repeated space use measurements, we intended to decrease the influence of such extreme movements and rather capture an overall, and non-autocorrelated measurement of space use. Additionally, study fish that used the most space were likely to be detected less if they moved out of the study stream (Porter & Dooley Jr., 1993).

An additional explanation for the findings from the laboratory and the field is that exploration and space use were short-term repeatable within seasons, but that personality changed between seasons, may be that of spawning behaviour. A study on largemouth bass found repeatable swimming performance within all seasons, except in the spawning season (Hanson et al., 2010). Interestingly, spawning affects movement behaviour in other freshwater fish too (Knaepkens et al., 2004). Consequently, spawning-related movement behaviour may partly explain why exploration behaviour was not repeatable, as we observed sexually mature individuals during electrofishing in October, which represented our winter (Fig. 2). Although spawning of Arctic charr in the study stream has not been studied, lake-dwelling population of Arctic charr exhibit two spawning tactics for males: the ones that intensively guard females and males that sneak onto guarded females (Brattli et al., 2018). Sneaking males may be more explorative and active in locating females in the spawning season whereas the movement behaviour of guarding males may be determined by the movement behaviour of the guarded female. This may result in changes in behavioural hierarchies between males specifically and thereby influence repeatability. Although females were not present in the laboratory, underlying factors influencing spawning behaviour, such as hormones, might have still influenced the behaviour measured in the laboratory environment. Such a scenario will not necessarily result in differences between males and females, which we also did not find to influence the traits. As we did not collect data on the sexual maturity of individual fish, this remains a topic for further investigation.

RQ4: Can laboratory estimates and/or natural estimates explain space use in the field?

Neither laboratory estimates of exploration and boldness, nor field estimates of exploration explained space use in the field. A study on wild burbot also found that initial travel distance occurred independently from space use in the field (Harrison et al., 2015). Although we discussed in RQ2 the differences between the laboratory environment and the natural environment that may be responsible for a lack of correlation between the laboratory and natural environment, in this case, the lack of correlation may also be explained by differences in underlying motivation (Hughes, 1997). Exploration and initial travel distances may function to find a suitable habitat (i.e. movement in an unknown environment), while when found, a more general level of activity or 'routine movement' might take over that is, for example, driven by metabolic rate (Careau et al., 2008), i.e. the movement patterns we found in a known environment (Réale et al., 2007; Van Dyck & Baguette, 2005). If we interpret general space use in the field as a measure of general activity, this may be the reason why we found no correlation between exploration and activity, as exploration and activity have been found to be distinct and not necessarily correlated personality traits in fish in the laboratory (Beukeboom et al., 2022). Alternatively, it is possible that distance between weekly consecutive GPS positions rather captured data on home ranges relocation instead of space use. In this case, these measurements may represent multiple exploration distances (e.g. (Rodríguez, 2002). However, in that case, we would expect to find a correlation between initial travel distance and space use (i.e. later exploration distances), which we did not find.

Conclusion

Our findings suggest that personality exists in movement-related behaviours in the laboratory as well as in natural situations, but can change between seasons, even though they are stable in the long-term within the same season. If these differences are heritable and induce fitness differences, it may provide a mechanism for the co-existence of multiple personality types within the population (Dingemanse & Wolf, 2010), which could be a topic for further research. Additionally, measuring personality in one season may not show the full picture and multiple seasons should ideally be included in future studies. Our results also suggest that correlations between the laboratory and the field are not obvious. Future research should therefore continue these first steps made in recent years to combine laboratory with field observations (e.g. Adriaenssens & Johnsson, 2011, 2013; Kobler et al., 2009; Wilson & McLaughlin, 2007; Yokota et al., 2007; Závorka et al., 2015) as well as continuing studying the effect of seasons on consistent individual differences (e.g. Eccard & Herde, 2013; Hanson et al., 2010; Nakayama et al., 2016) to increase our knowledge of these topics.

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Paper V - Supplementary materials

Table S1. Model outputs of the three models run in the laboratory. Bold indicates medians away from zero and non-zero overlapping 95%UI, italic indicates a trend.

	Within summer			***Summer – Winter***			***Within winter***	***Between summers***	
Predictor	*BOL*	*EXP*	*DIS*	*BOL*	*EXP*	*DIS*	*DIS*	*BOL*	*EXP*
ID-level									
Between-individual	*0.29* *(0.06 – 0.54)*	**0.40** **(0.19 – 0.66)**	**0.26** **(0.12 – 0.49)**	*0.33* *(0.03 – 0.79)*	*0.23* *(0.00 – 0.75)*	0.00 (0.00 – 0.04)	0.06 (0.00 – 0.38)	0.26 (0 – 1.1)	**0.78** **(0.25 – 2.11)**
Length	*0.26* *(0.06 – 0.45)*	*0.17* *(-0.04 – 0.38)*	*0.09* *(-0.08-0.26)*	*0.38* *(-0.00 – 0.74)*	0.10 (-0.29 – 0.48)		-0.02 (-0.26-0.21)	-0.05 (-0.54 – 0.43)	-0.18 (-0.69 – 0.33)
Sex (male)	0.02 (-0.31 – 0.35)	0.21 (-0.14 – 0.56)	0.19 (-0.18 – 0.55)	0.19 (-0.35 – 0.74)	0.20 (-0.36 – 0.74)		0.09 (-0.37 – 0.55)	-0.11 (-0.99 – 0.73)	-0.76 (-1.82 – 0.28)
Trial	**-0.05** **(-0.29 – -0.19)**	*0.24* *(0.03 – 0.46)*		-0.34 (-0.92 – 0.27)	-0.50 (-1.15 – 0.17)			-0.13 (-1.35 – 1.08)	-0.21 (-1.01 – 1.41)
Test order (OFT first)	**-0.44** **(-0.76 – -0.11)**	*-0.41* *(-0.75 – -0.07)*		-0.44 (-1.00 – 0.11)	-0.26 (-0.85 – 0.30)			-0.57 (-1.44 – 0.33)	-0.42 (-1.53 – 0.62)
# Observations			0.02 (-0.09 – 0.12)				0.02 (-0.10 – 0.14)		
Correlation	0.06 (-0.08 – 0.22)			-0.03 (-0.22 – 0.22)				*0.31* *(-0.04 – 1.11)*	
Residual-level									
Within-individual	**0.64** **(0.48 – 0.90)**	**0.56** **(0.42 – 0.77)**	**0.77** **(0.64 – 0.94)**	**0.63** **(0.40 – 1.01)**	**0.84** **(0.53 – 1.34)**	0.08 (0.00 – 0.11)	**0.99** **(0.75 – 1.35)**	**0.74** **(0.41 – 1.42)**	**0.32** **(0.16 – 0.78)**
Correlation	*0.12* *(0.00 – 0.27)*			**0.40** **(0.18 – 0.70)**				*0.13* *(-0.08 – 0.49)*	