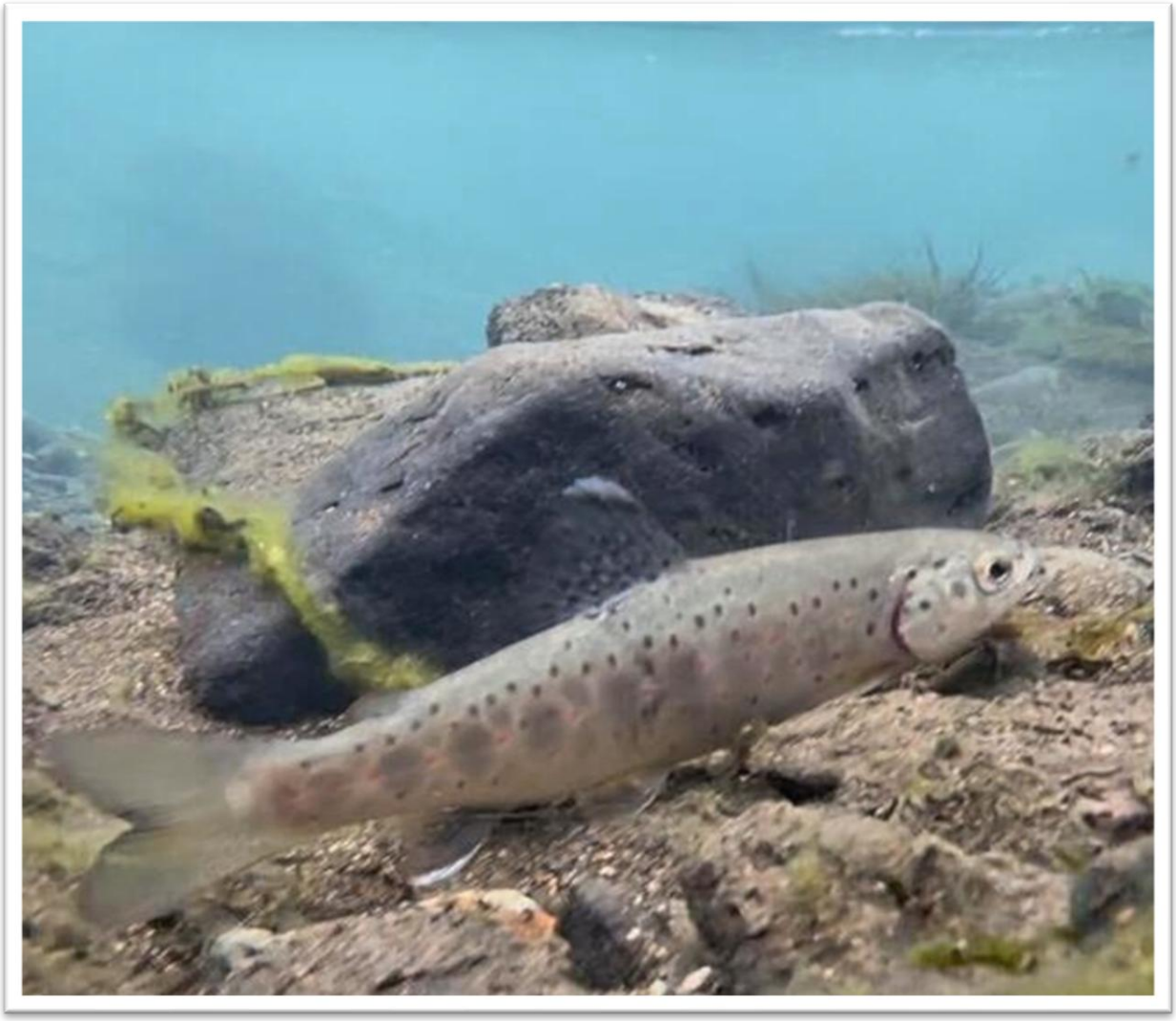
# Metabolic Drivers of Salmonid Growth and Survival in a Warming World



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School of Life Sciences

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*“Journey before destination”*

*Brandon Sanderson*

## i. Abstract

Global warming is altering aquatic environments worldwide, with important consequences for ectotherms whose metabolism is directly influenced by temperature. Although metabolic responses to temperature are well studied in laboratory settings, much less is known about how metabolism affects fitness in wild populations. This thesis develops and applies approaches to understand how environmental conditions associated with climate change, particularly increased temperature and thermal variability, shape metabolism and its consequences for fitness in salmonids, a taxonomic group of major ecological, cultural, and economic importance.

Chapter 1 introduces salmonid ecology and the role of metabolism in shaping individual performance. Chapter 2 develops and validates a novel method for measuring fish metabolic rates in the field against laboratory-based intermittent-flow respirometry (the current gold standard). Chapter 3 applies this approach to show that exposure to greater thermal variability produces more thermally sensitive metabolic rates and associated fitness traits, suggesting increased phenotypic plasticity. Chapter 4 expands this work across the latitudinal range of Atlantic salmon, showing that thermal regimes influence how metabolic rate affects fitness traits. Chapter 5 addresses management by presenting a conceptual framework for applying emerging chemical tracers to reconstruct fish movements and growth histories. In the final chapter these findings are synthesised to demonstrate that thermal environments shape both metabolic phenotypes and their fitness consequences in wild salmonids, providing new insights into how populations may respond to ongoing climate change and highlighting priorities for future research and conservation.

## ii. Contributing Statement

I declare that the chapters within this thesis and all associated publications are the work of myself. My supervisory team (Drs Eoin O'Gorman, Anna Sturrock, Thomas Cameron, Colin Bull, and Rasmus Lauridsen) provided guidance on approach, methodology, and editorial feedback on many drafts. External collaborators (Drs Neil Metcalfe, Shaun Killen, Rachel Paterson, Coralie Moccetti, Alexia González-Ferreras, José Barquín, and Tor Næsje) alongside Astrid Tonstad all provided advice throughout different stages of the thesis, contributing to data collection, methodology, analysis, and providing editorial feedback on draft manuscripts.

## iii. Acknowledgements

I have wanted to do a PhD since I was ten years old, although at the time I imagined it would be in astrophysics. The process and the last four years has been the most enriching and enjoyable thing I have done with my life so far, I have learned so much about both the natural world, myself, and of course salmonids. But I could not have completed it without a swathe of amazing people who have lent their time and knowledge throughout the process, I could not have got here without you all and will not be able to thank you enough here.

To my supervisors Eoin, Anna, Tom, Rasmus, and Colin thank you for your guidance at every stage developing and pushing me to be a better and more independent researcher, thanks for all the feedback, fieldwork, amazing travel opportunities, and even occasionally opening up your homes. It's been a blast, you've all been incredible, and I could not have hoped for a better supervisory team.

To all the collaborators and helpers on different parts of this project (Shaun, Neil, Rachel, Astrid, Tor, Alexia, Pepe, Luke, Will, Bill, Sophie, Jessica, the teams at the GWCT, AST, and Tweed commission, Russ, John, Joe, and so many others) Thank you for giving me your time and expertise, so much of this work would have been impossible without you. Thanks also to my funders ARIES and the AST without whom none of this would have been possible.

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To the fish, thanks for being part of this, I hope you continue to fill our rivers.

To my family, Fiona, Nick, and Ren, I owe you endless thanks for inspiring my love of learning, nurturing both my curiosity about our blue speck and my desire to protect it and supporting me through every triumph and setback along the way. I could never be here without you and owe you so so much.

To the light at the end of the tunnel, here's to the future!

And finally, to me for putting up with every hurdle, redraft, and failure, what's the next mountain to climb?!

## iv. Ethics

Much of the work in this thesis involved experimental work on wild animals, generally in situ, at every stage effort was made to maximise wellbeing, minimise any distress, and follow the 3R's of reduce, replace, and refine.

All of the procedures in Chapter 2 were licensed under the UK Home Office Animals (Scientific Procedures) Act, project licence number: PP6899400 and under ethics approved by the University of Essex ethics committee: ETH2324-192, with all work carried out by trained and licenced personal.

Chapters 3 and 4 were approved by the GWCT Animal Welfare and Ethical Review Body and the University of Essex: ETH2324-192 and were carried out by licensed personnel under a UK Home Office ASPA project licence: PP9506723.

Finally Chapter 5 was approved by the University of Essex ethics committee (ETH2627-0160). While sampling was authorised by the County Governor of Trøndelag (Statsforvalteren i Trøndelag; permit no. 2021/1934).

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# Chapter 1. General Introduction

## 1.1 Executive Introduction Summary

This introduction aims to introduce the key concepts and literature underpinning this thesis, namely how changes in metabolism in a warming world may affect the growth, migratory strategy, and survival of salmonids.

First, it will outline the life history and ecology of European salmonids, primarily Atlantic salmon and brown trout. It will then examine how they are threatened and what conservation work has been done alongside remaining research gaps. In the next section it will then go on to explore metabolism, how it varies, and how it can be measured. While the third section will bring these two concepts together to see how metabolism intersects with the ecology and life history of salmonids to influence their growth and survival, highlighting what key knowledge gaps remain impeding successful conservation. Finally, the introduction will lay out the aims of this thesis to fill some of the identified knowledge gaps.

## 1.2 Salmonids

Fish represent the most diverse and widely distributed group of vertebrates on Earth, occupying nearly every aquatic habitat from high-altitude streams to the deepest ocean trenches. With over 34,000 described species, they comprise more than half of all extant vertebrate diversity and play critical ecological roles as both predators and prey in aquatic food webs (Fricke et al., 2022; Helfman et al., 2009; Nelson et al., 2016). Fish exhibit extraordinary evolutionary and physiological diversity, encompassing a wide range of morphologies, life histories, and metabolic strategies that enable persistence across extreme gradients of temperature, salinity, and oxygen availability (Clark et al., 2013; Somero, 2010). Beyond their ecological significance, fish underpin global food security and economies providing nearly 20% of the world’s animal protein intake and supporting highly valuable industries worldwide (FAO, 2020). Among these, Salmonidae stand out for their ecological, cultural, and economic importance, as well as their remarkable migratory life cycles and sensitivity to environmental change (Jonsson and Jonsson, 2011; Klemetsen et al., 2003).

Salmonidae are a family of ray finned fish within the order Salmoniformes containing well over 200 species and can be broken down into three subfamilies: Coregoninae or freshwater whitefish, Thymallinae or grayling, and Salmoninae, see Fig. 1.1 (Fricke et al., 2022). Salmoninae can further be separated into two tribes: Oncorhynchini containing Pacific salmon and Pacific trout, and Salmonini including Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), and char (*Salvelinus* spp.), which will henceforth be referred to as salmonids (Fricke et al., 2022). Salmonids are characterised by having pelvic fins towards the rear of the fish and an adipose fin near the end of the spine (Nelson et al., 2016). This family includes many members with heightened tolerance of both freshwater and seawater, with these members being fully or partially anadromous, meaning they undergo a marine migration (Royce, 1996).

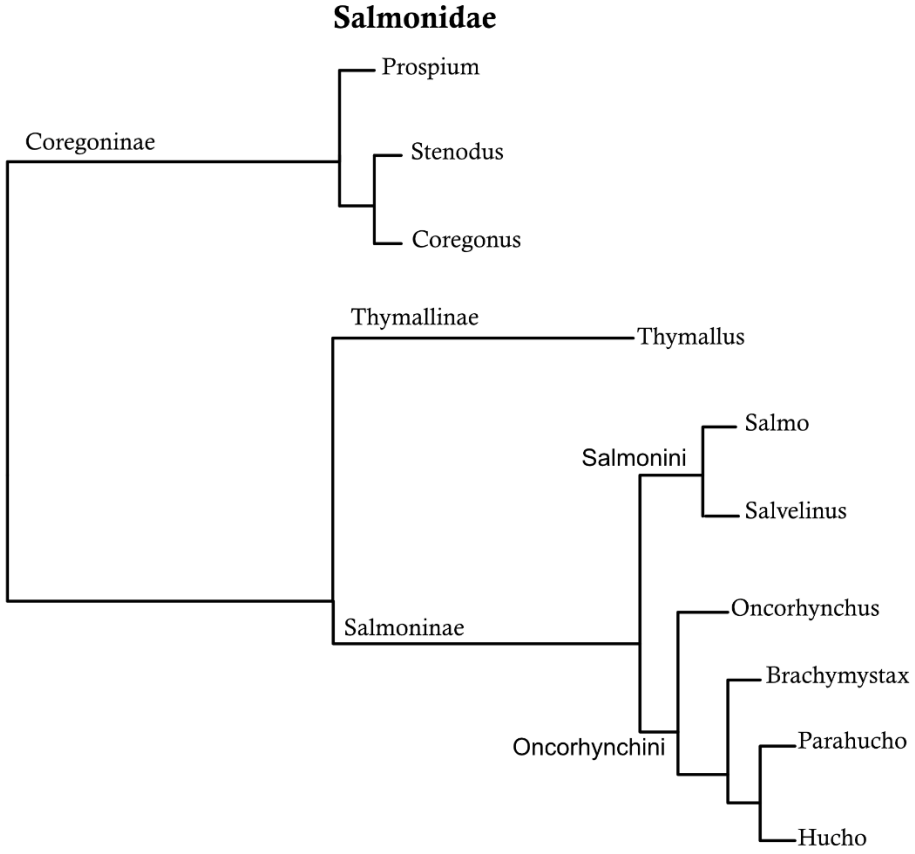



**Figure 1.1** - Phylogeny of Salmonidae see Crête-Lafrenière et al., 2012).

Salmonids are charismatic species with strong cultural and historical roots across Europe and North America (Kochalski et al., 2022). But are also a key ecological link between freshwater, terrestrial, and marine ecosystems (Walsh et al., 2020), and

can provide sustenance to land mammals, birds, and marine predators such as whales and tuna (Strøm et al., 2023; Walsh et al., 2020). Furthermore, individuals that die post-spawning after their return migration up their natal river deposit a large quantity of marine-derived nutrients into the freshwater environment (Schindler et al., 2003). For example, Pacific salmon release over 170 tons of phosphorous in Lake Illiamna and provide 25% of the organic nitrogen for tree growth in Alaskan rivers (Rahr, 2016; Schindler et al., 2003; Walsh et al., 2020), while Atlantic salmon carcasses can lead to a five-fold increase in stream macroinvertebrate biomass, contributing to increased juvenile salmon growth (McLennan et al., 2019).

Beyond their ecological impacts salmon also provide a range of valuable ecosystem services. Recreational salmon fishing contributed £109 million to the UK economy in 2008 (NASCO, 2008). Across the Baltic recreational Salmon fishing is worth €6 – 25 million and is estimated to provide social and cultural impacts of even greater value (Kulmala et al., 2013). While Pacific salmon populations in Alaska and Russia have not suffered the same declines as Atlantic salmon in Europe and so are particularly lucrative for recreational fishing. Indeed, Pacific salmon catch in Alaska bay is worth $500 million each year, whilst 80% of the local economy in several regions of Russia are dependent on salmon (Rahr, 2016). This high value potential has led in part to large investment in European research leading to the formation of a range of projects such as the SAMARCH (SAlmonid MAnagement Round the Channel), improving our understanding of salmon mortality, connectivity and stock assessment, while the West Coast Tracking Project aims to reveal marine and coastal migratory distribution of Scottish wild salmon (Samarch, 2023; The Atlantic Salmon Trust, 2023). Much of this research has focussed on how best to restore and manage stocks of wild salmon, though this can be confounded by their complex life history.

### 1.2.1 Atlantic Salmon Life history

As an anadromous species salmon exhibit a complex life history: juvenile salmon or alevin hatch in spring from excavated depressions called redds in rivers (Sedgwick, 1982). The timing of hatching is determined by local water temperatures, with higher temperatures speeding development, until mortality and deformity begin to occur with increasing frequency at 12°C, reaching total mortality by 16°C (Lightfoot and Solomon, 2008; Sedgwick, 1982). Development from fertilisation until emergence from the gravel of the redd takes around 800 “degree days” thus the eggs would

develop in 80 days at 10°C or 160 days at 5°C temperatures (Hendry and Cragg-Hine, 2003; Koss, 1994; Musialak et al., 2025). Flow over the gravel of the redd and therefore fresh oxygen is also key for development, with survival rates increasing with discharge, though particularly high flows may scour the redd and kill any eggs (Gibson and Myers, 1988; Hendry and Cragg-Hine, 2003). Furthermore in lowland populations fine sediment can clog redd pores reducing egg survival (Heywood and Walling, 2007). Once hatched, alevin (~2.5 cm) draw energy from their yolk sack while developing the capacity to hunt for themselves. Once they can sustain themselves, they are known as fry (Hendry and Cragg-Hine, 2003) (~3 cm), which feed primarily upon aquatic insect larvae such as stonefly and mayfly, supplementing this with terrestrial insects caught on the surface (Hendry and Cragg-Hine, 2003). This is the first major pinch point in salmonid life history with few fry surviving, see Fig. 1.2.

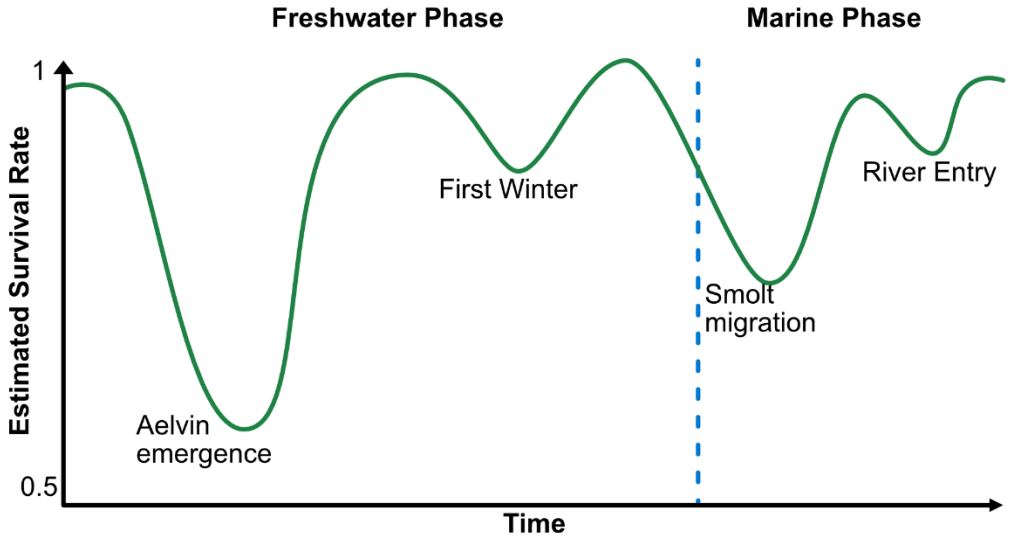



**Figure 1.2** – Conceptual figure showing the major pinch points in salmonid survival throughout their life history (Elliott et al., 2026).

As growth continues, salmon develop bands along their sides and are now referred to as parr (5 -15 cm), shown in Fig. 1.3. Parr are highly territorial and feed by intercepting particles and prey drifting in currents as well as foraging in the surrounding substrate (Mills, 1989; Stradmeyer and Thorpe, 1987). Come midsummer, many slower growing fish reduce their feeding and remain within the river for another year, while faster growers retain high feeding rates and will likely smoltify the following spring (Metcalfe et al., 1988). Fish also show daily rhythms preferring deeper water in the day and shallower water at night with this exacerbated by low flow (Riley et al., 2009). By autumn, some salmon leave the riffles and move to deeper pools where they become nocturnal and remain throughout winter before returning to the riffles when the temperatures rise again in spring (Mills, 1989). Co-occupancy of deeper pools by salmon and trout can lead to resource partitioning, whereby salmon change microhabitat moving to shallower water or staying more active in the day (Harwood et al., 2002; Mills, 1989).

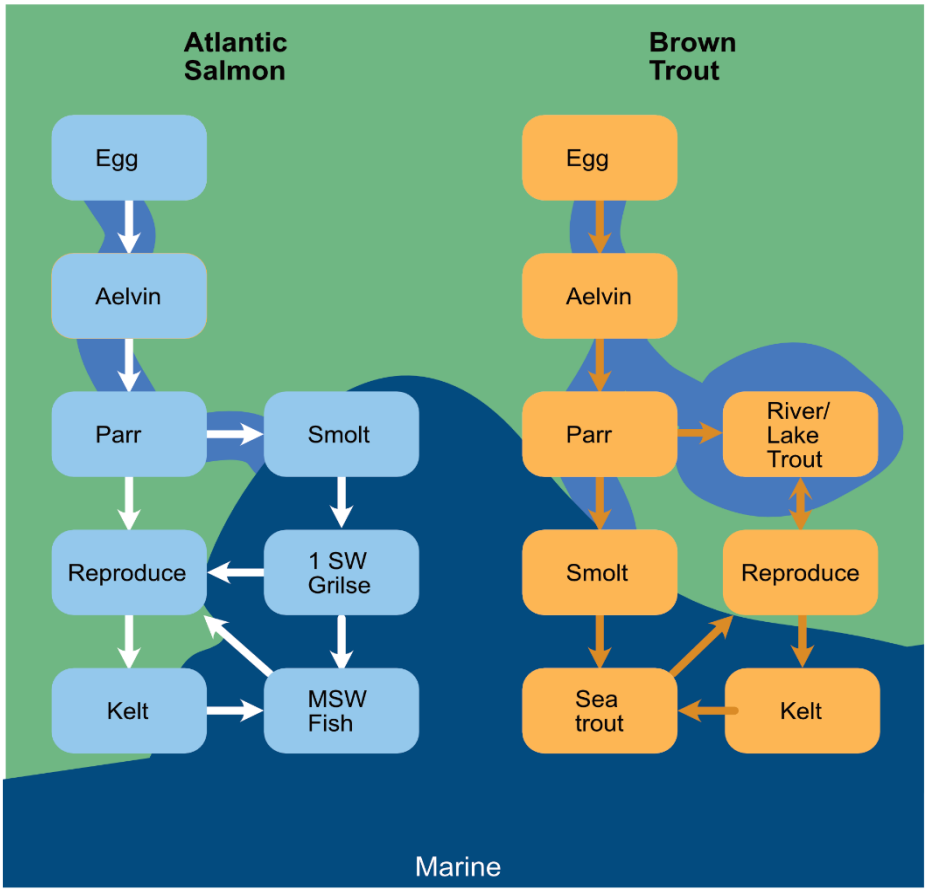



**Figure 1.3** – The life stages of Atlantic salmon and brown trout, it should be noted some trout will be born and remain resident within a lake.

Resource partitioning can also be seen in streams with deciduous riparian canopy, where trout and salmon vertically stratify (Dineen et al., 2007). The typically larger trout occupy the upper water column and feed on the larger terrestrial invertebrates while the smaller salmon feed on benthic invertebrates (Dineen et al., 2007).

After 1 – 5 years, most parr will undergo smoltification, with faster growing parr smolting earlier (Økland et al., 1993), smolting involves a major reorganisation of the osmoregulatory organs (kidneys, gut, and gills) to allow the fish to tolerate seawater (Hoar, 1988). The smolt (typically >12 cm), as it is now called, will migrate to sea in spring, generally between April and June (Hendry and Cragg-Hine, 2003). However, some pre-smolts have been observed making an autumn shift downstream though not into marine waters with one study seeing this more commonly in fish closer to the estuary (Aarestrup et al., 2018; Ibbotson et al., 2013; Riley et al., 2008). At sea salmon feed upon herring, sprat, stickleback, and other fish, while they grow quickly before returning to spawn in their stream of birth (Hansen and Quinn, 1998). Survival at sea is thus essential for the salmon to reproduce and smolt size is thought to be a key determinant of this, with larger smolts generally shown to have higher return rates and higher mating success (Gregory et al., 2019; Jonsson et al., 2017; Koenings et al., 1993; Mobley et al., 2020). The length of time the salmon spend in freshwater and later at sea is highly variable and much of this variation is attributed to genetics and specifically the *vgll3* locus, with the (early) and (late) alleles determining the effect (Barson et al., 2015; Mobley et al., 2020). Younger freshwater age and older sea age relates to increased reproductive fitness in females, with larger individuals producing more eggs, but not males since individuals of all sizes can attempt opportunistic fertilisation (Mobley et al., 2020). This leads to a tug of war between the early allele of *vgll3* which increases female fitness and the late allele which increases male fitness, often presenting as increased migration activity and thus earlier migration in females (Mobley et al., 2020; Niemelä et al., 2022). Furthermore maturation is a interplay between environment and growth, with growth in the first six months at sea a strong driver of whether the fish stay at sea another year or return (Tréhin et al., 2024). Time spent in the marine phase ranges from 1 - 3+ years, with an inverse relationship between time spent in freshwater and time spent at sea often observed (Erkinaro et al., 2019; Klemetsen et al., 2003).

During the first few months at sea, mortality risk is highest when the salmon are both smallest and still adjusting to the new conditions and this marks the second major pinch point in survival (Hansen and Quinn, 1998). After a growing period at sea the fish return to their home river to reproduce, though the size at which they do this may be declining, and larger fish often migrate back earlier in the year (Klemetsen et al., 2003; Valiente et al., 2011). This is in part driven by the trade-off between the increased risk of predation at sea and the greater size and higher fecundity gained by staying and feeding, with the average 2SW (2 sea winter) female laying twice as many eggs as a 1SW female and thus dominating the gene pool of the next generation (Hansen and Quinn, 1998). Fish that only spend one winter at sea are referred to as grilse while fish that spend longer are MSW (multiple sea winter) salmon (Hendry and Cragg-Hine, 2003). Salmon begin migrating back to freshwater in April, reaching a peak in July, though this does vary spatially with latitude and population and larger fish may preferentially migrate earlier (Foldvik et al., 2024; Økland et al., 2001). The rate of return is affected by a variety of factors, including discharge, temperature, and light (Erkinaro et al., 1999; Jonsson and Jonsson, 2009). Increased discharge leads to an earlier upstream migration especially in larger salmon, indicating a higher water level and thus fewer physical barriers. Higher temperatures have the same effect, likely as salmon try to avoid migration in the possibly higher and more stressful late spring temperatures, though they will not return during temperature extremes (Jonsson and Jonsson, 2009; Valiente et al., 2011).

Salmonid return migrations consist of three phases: (1) migration upriver close to the location of their own spawning, (2) a searching phase where they move up and downstream to find their own spawning area, and (3) a holding phase, where they remain in this location without feeding until spawning occurs in Autumn or Winter (Finstad et al., 2005; Økland et al., 2001). Salmon generally return to the site of their birth though straying does occur at a rate of around 3% (Stabell, 1984), evidence from hatcheries suggests that basin size, and temperatures may play a role in mediating this rate (Westley et al., 2025). Once it is time to spawn, salmon dig depressions in gravel substrate called redds to shield the eggs from extreme flows and predators (Hendry and Cragg-Hine, 2003). A typical female produces around 1,100 eggs per kilogram of mass, which are fertilised by dominant males (Mills,

1989). However, some smaller males will attempt to opportunistically fertilise redds and some parr will mature before going to sea, reducing growth rates but thereby able to attempt fertilisation of eggs pre-migration (Saunders et al., 1982). Females will then move downstream while males may attempt to fertilise more eggs, whereby most redds will have eggs fertilised by up to 16 different males (Weir et al., 2010). This process of upstream migration and fertilisation is incredibly taxing with an observed 60 - 70% decline in body mass of males and females over the spawning period, alongside a higher daily fat loss in females (Hendry and Beall, 2004; Jonsson et al., 1997). The salmon are now referred to as kelt and 95% will not survive to spawn again, though this varies substantially among river, sex, and age (Hubley et al., 2008; Persson et al., 2023). Fish that survive spawning will return to sea in spring after overwintering in riverine pools to feed before potentially returning to spawn again in later years (Hubley et al., 2008).

### 1.2.2 Brown Trout Life history

Brown trout display a very similar life history to salmon with some key differences. Generally, all Atlantic salmon smoltify and migrate to sea with the notable exceptions of landlocked populations (Berg, 1985), however many trout spend their entire life cycle in freshwater (Klemetsen et al., 2003). Trout are generally born in small natal streams or inlets, as they grow, some become river resident trout while others migrate to lakes (lacustrine trout) or the sea (sea trout) though this may still involve some time resident within a lake (Ferguson et al., 2019; Klemetsen et al., 2003). Unlike salmon, trout make greater use of lakes, and many trout stay resident to their natal lake or stream (Klemetsen et al., 2003). Brown trout have a great range of genetically and physiologically distinct morphs within each of the resident, lacustrine, and sea groups, often exhibiting different feeding behaviours and habitat preferences reducing intraspecific competition (Mangel and Abrahams, 2001; Piggott et al., 2018). These differences are driven by a range of spatial and environmental factors including distance, oxygen demand, and habitat (Rodger et al., 2025). The variety of morphs of brown trout illustrates their plasticity and capacity to adapt to variable environments (Jensen et al., 2008; Rodger et al., 2025).

The decision of brown trout to migrate is heavily influenced by the fish’s energy state, which acts as a cue and is likely controlled by the environment, competition, and/or genetics (Ferguson et al., 2019). This cue must overcome a genetically

419 determined threshold controlling whether the trout will migrate or mature in
420 freshwater (Ferguson et al., 2019). This cue can be influenced by elevated egg
421 incubation temperatures which increase rates of smolting alongside metabolic rates
422 and aggressiveness (Sloat and Reeves, 2014). Higher individual growth may also
423 increase freshwater maturation rates, suggesting competitive freshwater fish may
424 choose to remain in the environment in which they have been successful, while less
425 competitive fish will risk smolting despite their smaller size reducing marine survival
426 (Sloat and Reeves, 2014). Another hypothesis suggests that increased energy
427 demand from the larger size can only be met by the increased feeding opportunities
428 at sea. To test this the relative energy consumption or metabolism of fish would need
429 to be known in combination with their migratory history something which has not
430 been done before. However, there are a range of other factors including sex that are
431 likely to impact the life history choice to smolt and understanding the relative
432 importance of these is key to identifying what drives success in salmonids (Olsen et
433 al., 2006).

434 Many migratory brown trout may only stay at sea for a short period over summer
435 when productivity and thus growth is highest (Klemetsen et al., 2003; Olsen et al.,
436 2006). Though some trout also overwinter at sea, potentially in an attempt to
437 increase winter survival in the more stable marine habitat with less competition from
438 other trout (Thorstad et al., 2016). Despite the higher growth rates in the marine
439 environment, mortality is greater due to increased predation at sea and threats from
440 the migration itself including salmon lice and pollution, threats also faced by Atlantic
441 salmon (Jonsson, 1989; Paterson et al., 2021). Female brown trout exhibit a much
442 larger tendency to migrate than males, as the number of eggs produced is directly
443 related to body size and they are better able to acquire high value territory to form
444 their redds (Berghe and Gross, 1989; Campbell, 1977; Jonsson et al., 1997). As
445 trout age at sea, marine growth declines and they eventually return to freshwater
446 normally to spawn (Kennedy et al., 2022). Sea trout also display increased rates of
447 straying with rates as high as 36% observed in some populations, suggesting less
448 genetic separation between populations (Källo et al., 2022).

449 Returning sea trout are generally larger than the resident trout, with more energy
450 diverted to gonadal development increasing fecundity (Elliott, 1995; Jonsson et al.,
451 1997). During reproduction, larger males will often outcompete the smaller males to

fertilise the eggs within a redd (Jonsson, 1985). However, smaller males can hide near females and dart in to fertilise their eggs when they are ovipositing, a particularly successful strategy when larger anadromous males are absent (Gross, 1985; Jonsson, 1985).

After spawning, trout have a much higher survival rate than salmon, with up to 90% surviving virgin spawning and repeated spawners observed surviving (Berg et al., 1998). Trout have also been observed to be more aggressive than salmon within their home streams and may outcompete salmon for preferred niches (deeper pools) (Stradmeyer et al., 2008). This forces salmon into fast flowing riffles or shallower waters, for which they are better adapted (Harwood et al., 2002).

### 1.2.3 Salmonid Habitat

Juvenile salmonids have specific habitat requirements, with substrate, water depth, velocity, and macrophyte cover all considered key factors (Heggenes, 1990). Smaller parr prefer gravel substrate (1.6 - 6.4 cm) while larger parr prefer boulders and cobbles (Danie et al., 1984). Ideal water depth is generally 15 – 40 cm with salmon preferring fast riffles (>30 cm/s) and trout favouring slower moving water, with salmon generally holding station closer to the substrate than trout (Addo et al., 2025; Armstrong et al., 2003; Morantz et al., 1987). Both species select microhabitat with easy access to vegetation cover, with macrophyte species e.g. *Ranunculus* supporting greater fish abundance as it creates shelter for both salmonids and their prey while mediating flows (Marsh et al., 2020). The heterogeneous nature of riverine habitat can lead to drastic changes in salmonid habitat suitability over a few metres. Temperature also significantly affects habitat suitability with ideal conditions generally sitting between 13 - 16°C with upper lethal limits at 29.5°C and lower limits just above freezing point (Lightfoot and Solomon, 2008). Salmonids have a wide geographical range covering from the Iberian Peninsula to the Arctic, see Fig. 1.4 (Jonsson and Jonsson, 2009).

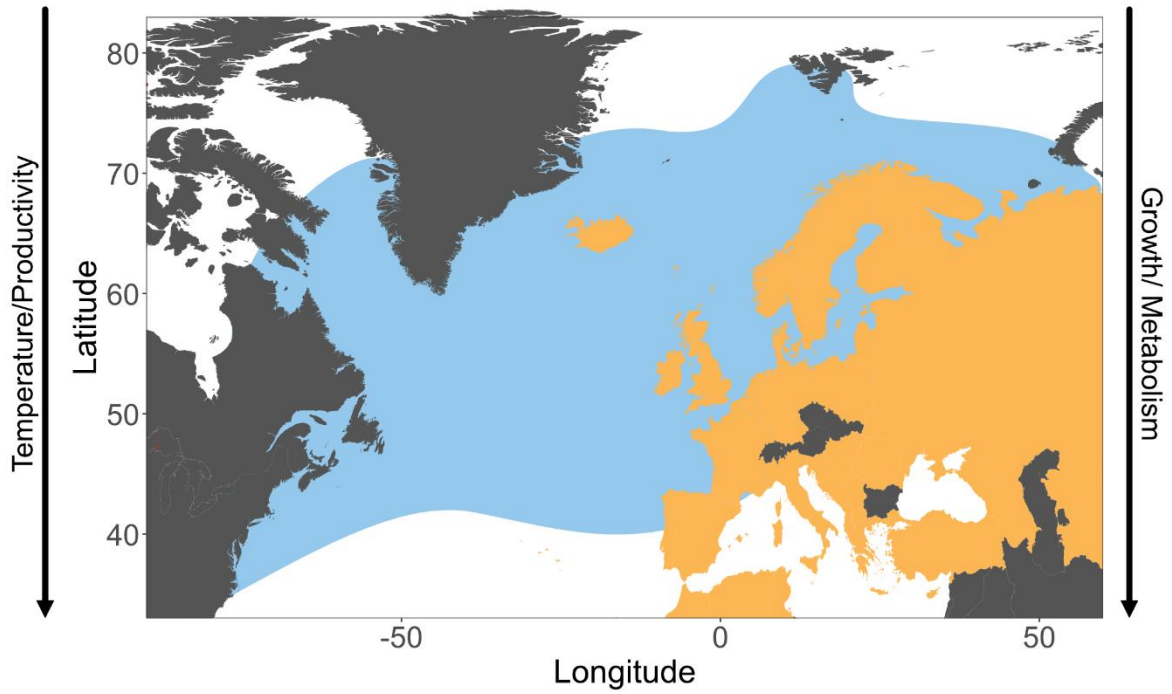



**Figure 1.4** – Conceptual figure showing the range of Atlantic salmon (blue) and native brown trout (yellow), also showing how key environmental (left) and biological rates (right) vary spatially (OSPAR, 2022).

Across this range habitat characteristics vary between each river however there is some broad regional grouping of rivers that display similar characteristics (Elliott et al., 1998). The northern islands (Iceland and Greenland are characterised by short rivers, spring freshets, short growing seasons constrained by limited light availability and day length, low temperatures, and limited riparian cover (Petersen et al., 1995). Scandinavia and Russia by contrast has longer rivers, winter and spring freshets, somewhat warmer temperatures, highly oxygenated water, and boreal forest cover (Elliott et al., 1998; Petersen et al., 1995). Finally Western Europe exhibits highly variable river length, winter freshets, warmer temperatures, longest growing seasons, and mixed forest cover though with much forest clearance and urbanisation (Elliott et al., 1998). All these differences in environment will affect salmonid ecology leading to differences in life history and strategy across catchments and regions (Jonsson and Jonsson, 2009). One of the most pervasive is temperature change with latitude, which influences growth rate, body size, and generation timing in ectotherms (Conover, 1992; Heibo et al., 2005; Trip et al., 2014).

### 1.2.4 Threats and Exploitation

Salmon have been a key part of European fisheries for thousands of years, with cave paintings depicting salmon fishing from 20,000 BCE, and they have been exploited in some form ever since (Goldhahn, 2021). Salmonids have traditionally faced a range of threats from predation to interspecific competition leading to a variable mortality rate throughout their life (Strøm et al., 2019). However anthropogenic impacts have placed additional stressors upon these species (Bull et al., 2022). Since the 1980s, populations have declined drastically alongside a number of freshwater spawning fish, a pattern also seen in America and across the world in freshwater populations (Deinet et al., 2020; NASCO, 2019a). This decline has continued in recent years with mortality before reaching 1SW doubling between 1990 and 2007 (NASCO, 2019a). Furthermore, stock status in only 14% of rivers across the population are at sustainable levels and only one river in England (River Tyne) is classed as “not at risk” despite extensive conservation efforts (CEFAS, 2022; NASCO, 2019a). Not only are less salmon returning but those that do are often smaller on both sides of the Atlantic, leading to less fecund populations (Atlantic Salmon Federation, 2020; Curd et al., 2010). One of the primary anthropogenic stressors in the latter half of the 20$^{th}$ century was exploitation, with over 400,000 wild fish taken per year in Scotland alone (The Scottish Government, 2020). In the 21$^{st}$ century, 474 tonnes or ~100,000 are caught each year within the EU with 61% of this occurring in Norway while many other nations such as Denmark and France take ~10 tonnes a year (Myrvold et al., 2019). Recreational fisheries are still open in the UK, with declared net catch in 2024 36% below the average of the last 5 years, while rod catch is down 22% compared to the five-year average (EA, 2025). Understanding the extent of the damage to salmon fisheries is confounded by shifting baselines, whereby there is no data on population size before human exploitation and therefore do not have a reliable baseline to compare to modern fisheries (Schijns and Pauly, 2022). This suggests that we may be overestimating the health of fisheries and populations may be at higher risk than previously believed (Schijns and Pauly, 2022). This makes identifying the underlying causes of salmonid population decline of great import.

There are a variety of local anthropogenic stressors currently contributing to the decline of salmonids. For example, habitat alteration in the form of dam construction

(e.g. for hydroelectric power) can limit or prevent salmon returning to their natal river to spawn by physically blocking migration (Forseth et al., 2017). Similarly, river widening can alter discharge, water temperature, and river morphology, whilst nutrient leaching can affect water quality, all of which can impact parr and smolt development alongside the olfactory cues used by returning adults (Forseth et al., 2017; Hendry and Cragg-Hine, 2003). Salmon farming often promotes disease and the prevalence of sea lice, which can proliferate through a fish farm before entering a wild river population (Johansen et al., 2011; Skaala et al., 2012). Consequently, increasing mortality and reducing the fitness of infected wild salmon and trout (Fjelldal et al., 2020; Middlemas et al., 2013). Indeed, wild trout may change their life history strategies when infected with lice, staying in freshwater rather than migrating to sea (Halttunen et al., 2018). This protects them from lice as many species cannot withstand the low salinities but reduces growth, which may increase their predation risk and reduce fecundity in the long term (Halttunen et al., 2018; Wright et al., 2016). Escapees from fish farms also breed with wild populations, with the offspring found to have reduced sea survival and return rates (Skaala et al., 2012). Furthermore, hazardous substances and heavy metals can be released from industry and mining with effects ranging from reduced gonadal development to increased mortality (Forseth et al., 2017).

Salmonids populations are also influenced by global stressors, the most pressing of which is climate warming increasing the thermal stress placed on salmonids. The thermal limit of Atlantic salmon varies with adaptation and acclimation but sits at around 23°C (Hvas et al., 2017; Strøm et al., 2020). Where this limit is exceeded, mortality will rapidly rise while measures of performance and fitness such as growth and burst swim speed will decline (Hvas et al., 2017; Strøm et al., 2020). These thermal limits are now regularly exceeded during summer at the southern limit of the salmonid distribution, reducing the performance of these populations and this is only predicted to intensify with time (Forseth et al., 2017; Jonsson and Jonsson, 2009). Rising temperatures may lead to habitats exceeding salmonids thermal limits in summer, excluding them from key foraging areas both at sea and within less thermally stable freshwater systems, exacerbating population declines (Isaak et al., 2018; Welch et al., 1998). Furthermore, high summer temperatures may delay return migrations till cooler autumnal temperatures thereby partially excluding migratory

564 salmon and trout from the gene pool (Baisez et al., 2011). Rising temperatures in
565 winter especially in the southern portions of the range may also lead to increased
566 egg mortality (Jonsson and Greenberg, 2022; Koss, 1994). Rising temperatures are
567 also predicted to decrease body size across a range of species (Baudron et al.,
568 2014). This shift in body size may be exacerbated by an increased pace of life (i.e.
569 metabolism) driven by rising temperatures, whereby salmonids will reach maturity
570 earlier and smaller (Londoño et al., 2015). Changes in size may have severe
571 consequences in salmonids where body size is key for determining reproductive
572 output, mortality at sea, and return rates (Gregory et al., 2019; Pörtner et al., 2017).
573 However, in areas where salmonids sit below their thermal optima rising
574 temperatures may be beneficial and lead to increased growth and production in both
575 the ecosystem and the fish (O'Gorman et al., 2016). Indeed, this may lead to a shift
576 of salmon population further north (Bilous and Dunmall, 2020; Nielsen et al., 2013;
577 Shelton et al., 2021).

578 Another widespread threat is ocean acidification, the decreasing pH of sea water due
579 to rising $CO_2$ (Doney et al., 2009). While in freshwater deposition of sulphur and
580 nitric acids from acid rain can lower pH and release toxic aluminium, which can
581 cause mortality, or elicit sub lethal effects in freshwater that may become lethal
582 during smolting (Forseth et al., 2017). Acidification is thought to be influencing
583 salmon with the commercial salmon catch in Norway falling in regions with extensive
584 acidification (Hestagen and Hansen, 1991). Additionally, acidification may decrease
585 how salmon brains process scent which is a key sense used to return to their natal
586 stream thereby affecting reproduction (Williams et al., 2019), though this has been
587 the topic of recent controversy (Sundin, 2023). Acidification is also predicted to
588 negatively impact lower trophic levels of marine temperate food webs, this could lead
589 to indirect effects on the resource supply (Haigh et al., 2015) upon which salmonids
590 rely to sustain a high feeding and growth rate at sea. Furthermore, acidification
591 impacts may be compounded by global warming and other climatic changes, though
592 the interactive effects of these multiple stressors are poorly understood (Haigh et al.,
593 2015).

594 **1.2.5 Conservation**

595 Conserving and rebuilding stocks is key to maximising their economic and ecological
596 value and a variety of conservation strategies have been implemented in response to

declining populations and the myriad threats outlined above. Firstly, salmon total allowable catch has been reduced across the EU, falling to zero in many sea fisheries, while recreational angling has refocussed on catch-and-release in an effort to minimise direct removal of salmon (Morris et al., 2022; The European Commission, 2021). Furthermore, salmon ladders have been installed in a number of rivers across Europe and America to prevent dams blocking migration upriver, and research continues to improve their efficiency at allowing salmon to return to their spawning site (Williams et al., 2012). Measures have also been taken to remove these in some cases increasing river connectivity. Supplementary stocking, which is the process of adding hatchery raised “wild” fish to a wild population, has been attempted to increase population sizes (Perrier et al., 2016) and remains a controversial issue see Harrison and Berseth, (2024). However, there is little evidence to indicate this is successful in the long term due to the lower survival rates and limited reproductive success of stocked fish (Morris et al., 2022; Perrier et al., 2016). Habitat restoration has been undertaken to reduce the damage of human interference such as pollution, eutrophication, and channelization, which disrupt ecosystem function and connectivity, by creating deleterious conditions (Tummers et al., 2016). Thereby reducing eutrophication and leaching from pesticides all of which reduce water quality (Tummers et al., 2016). Restoration can take many forms, river re-meandering increases the volume of the river while also limiting the scouring potential of high flows, with other restoration measures also taken to better control flow rates (Costaz-Puyou et al., 2025). While tree planting has also been used to both increase terrestrial subsidies and shade streams, reducing variability and extremes (Lee et al., 2012). These measures can be taken from reach to catchment scale but are generally most effective though also most expensive across catchment (Tummers et al., 2016).

However, most of these restoration efforts fail to create a self-sufficient population despite large amounts of stakeholder money, highlighting the importance of conserving any remaining “healthy” salmon rivers (Lennox et al., 2021). In order to better understand where mortality is occurring large tracking arrays using Passive Integrated Transponder (PIT) tags have been installed in many rivers. This has highlighted that much mortality occurs at sea (Chaput, 2012). However, these systems cannot be used to track small fish below taggable size, creating a gap in the

knowledge of fish movements in many river systems. An aspect this thesis will aim in part to address. Another reason for the failure of restoration is likely rising temperatures and our limited understanding of the optimum “thermal habitat” for wild salmonids limiting the development of future “healthy” salmon rivers (Jonsson, 2023). While much literature exists on absolute thermal limits, fitness will be limited at much lower temperatures, and different populations will have adapted different optima (Jonsson, 2023). Understanding this may be key to predicting and shielding remaining healthy populations from climate change and is something else this thesis will seek to address. However, to do this requires an understanding of metabolism, a primary driver of life history decisions, and fitness, but that is influenced directly by temperature (Brown et al., 2004).

## 1.3 Metabolic Ecology

### 1.3.1 Overview

Metabolism is the process by which organisms convert biological resources consumed from the environment into energy, influencing a range of ecological features within every organism (e.g. growth, feeding, reproduction), and the ecosystems they comprise (Brown et al., 2004; Gillooly et al., 2001). The pace at which that processing occurs is the metabolic rate, which is typically measured as a rate of energy expenditure, with multiple metrics for different rates. Standard metabolic rate (SMR) is the cost of self-maintenance, without any energy allocated for growth, reproduction, or other key drivers of performance such as foraging (McNab, 1997). This includes the summation of many background processes from immune response to maintenance and will vary with life stage (Darveau et al., 2002; Killen et al., 2010; Rosenfeld et al., 2015). Routine metabolic rate (RMR) is the energy used by unfed fish or SMR with the addition of routine movement and can fall anywhere between the SMR or maximum energy a fish can expend (Chabot et al., 2016a; Fry, 1971). Field metabolic rate (FMR) is the average energy expenditure of an organism as it interacts with its environment, including daily maintenance tasks such as foraging and digesting (Treberg et al., 2016; Warham, 1996). Finally, MMR is the maximum metabolic rate an organism can sustain, though generally only for short periods of activity (Biro and Stamps, 2010; Careau et al., 2008). The difference between SMR and MMR is called the aerobic scope, this is a measure of an organism’s ability to increase metabolic rate, required for activities such as sustained

swimming, growth, and performance (Eliason and Farrell, 2016). It is also the capacity of a fish to cope with environmental stressors such as warming, a larger scope granting a greater buffer against factors that may change energy expenditures from fitness related activities (Clark et al., 2013; Eliason and Farrell, 2016). These factors can all be demonstrated by thermal performance curves which show how a given rate changes with increasing temperatures see Fig. 1.5. Increasing temperatures increase reaction rates but will have differing effects on each metric of metabolism due to the differing components of each metric, which will be explored in later sections.

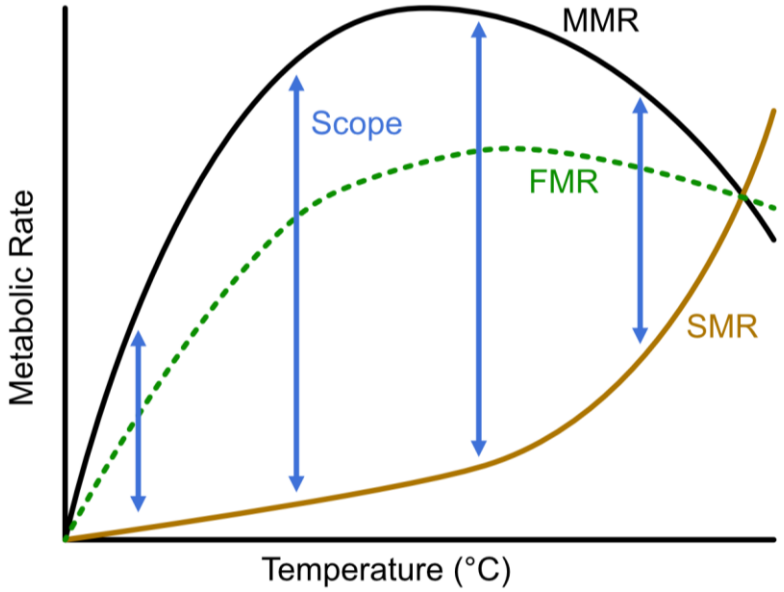



**Figure 1.5** – Typical thermal performance curves of SMR (brown), FMR (green), MMR (black), and demonstrating the aerobic scope between SMR and MMR (blue arrows).

Metabolism is primarily driven by aerobic respiration and is therefore dependant on the creation of ATP. Oxygen is the final electron acceptor in this process, with ATP then used for maintenance, activity, or growth of organisms (Rich, 2003). Anaerobic respiration is only rarely used for burst swimming and salmonids can reach 80% of their maximum swim speed purely aerobically (Jones, 1982). Thus, metabolic rates in fish are generally measured as oxygen consumption per unit time. Maintaining a given metabolic rate requires energy expenditure, fuelled by a rate of energy intake to match demand. However, a mismatch can arise when environmental factors affect these rates differently, such as temperature causing a larger increase in basal

metabolic rates than feeding rates reducing energy available for non-basal tasks such as growth (Brown et al., 2004; Byström et al., 2006; Vucic-Pestic et al., 2011). Capacity to increase metabolic rate scales with RMR, which can be seen as the "idling cost" of a "metabolic engine", with higher costs facilitating higher FMR and MMR (Biro and Stamps, 2010; Careau et al., 2008). Metabolism is influenced by a wide variety of factors, but two of the most important are thought to be body size and environmental temperature (Gillooly et al., 2001).

### 1.3.2 Metabolic Theory of Ecology

The predictable scaling of metabolism with body size and temperature has been summarised in the metabolic theory of ecology (MTE) in an attempt to scale the physiological effects on individual organisms to the structure and function of entire ecosystems (Brown et al., 2004). To sustain their metabolism, organisms uptake and transform materials from the environment, while maximising their fitness (Brown et al., 2004). Metabolic rate underpins rates fundamental to the ecology of all organisms, ranging from growth to reproduction, while ecosystem process such as carbon cycling and gross primary product are effectively controlled by the sum of metabolic rates within the ecosystem (Brown et al., 2004). This allows predictions using metabolic rate to scale from the individual right up to population and community levels (Brown et al., 2004; Schramski et al., 2015).

MTE predicts metabolism increases with body mass following a scaling exponent of 0.75 (Brown et al., 2004), meaning that larger organisms will have a lower mass-specific metabolic rate. The underlying logic for this three-quarter scaling is based on the requirements of a transport system to deliver the raw materials for metabolism (West et al., 1997). This network would need to be branching, fractal, terminate in a size invariant unit and, minimise energy requirements for transport, thus the 0.75 exponent is modelled to arise from the geometric constraints of these three requirements (Brown et al., 2004; West et al., 1997). The MTE further posits that metabolism increases with temperature by increasing the kinetic energy of the cell and thus the energy available for reaction following the Arrhenius equation, until higher temperatures begin to damage the cell slowing rates (Brown et al., 2004). The activation energy of metabolism (the minimum energy required for the reaction to begin) is 0.60–0.70 eV, which is within a similar range to an array of biological rates

from population growth to life span suggesting metabolism is a key underlying driver of ecology (Gillooly et al., 2001; Savage et al., 2004).

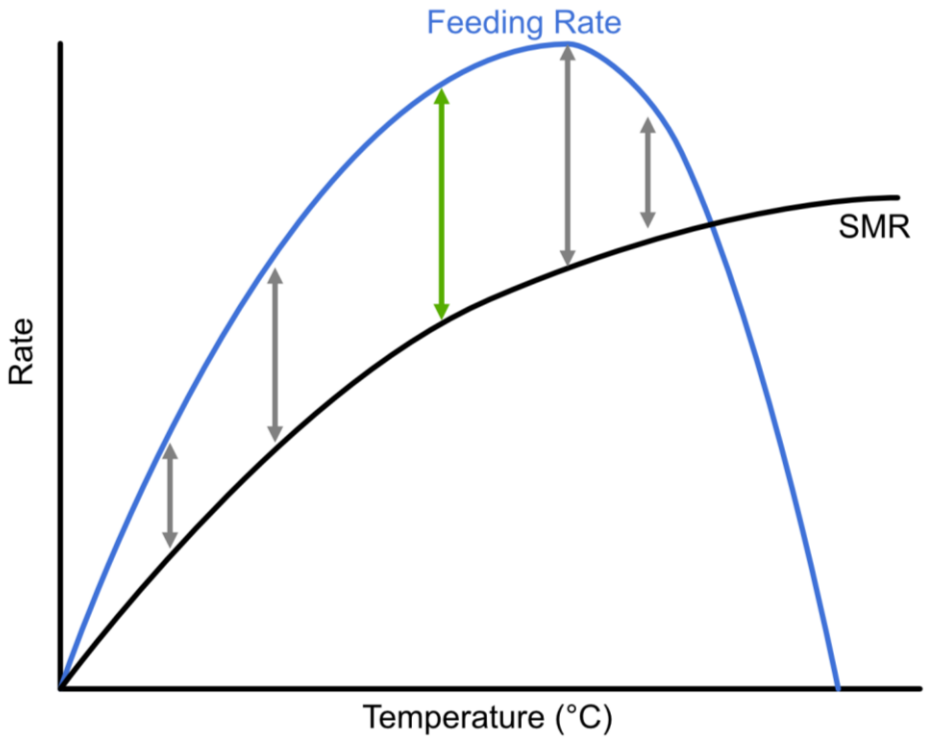
The values of the mass scaling exponent outlined above, and its drivers have been subject to long debate (Clarke, 2004; Killen et al., 2010; White and Marshall, 2023). For example, the metabolic boundaries hypothesis proposes that the exponent governing the relationship between metabolism and size will decline as metabolic rate increases before increasing as MMR is approached forming a U-shape (Glazier, 2010; Killen et al., 2010). The hypothesis assumes two key boundaries on metabolism: surface area limits on exchange of metabolic resources and mass limits on tissue power production and maintenance costs during activity and rest (Glazier, 2010), with the relative importance of these factors during rest and exercise changing the mass scaling exponent of metabolism (Killen et al., 2010). Other theories such as the cell metabolism hypothesis instead argue larger cells will have a depressed metabolic rate due to their lower surface area to volume ratio, therefore the exponent should be 1 for large cells of fixed mass and decline to 0.67 in smaller cells with more variable masses (Kozłowski et al., 2003; Luo et al., 2015).

Furthermore, there is contention over the relationship between temperature and metabolism (Clarke, 2004). While thermodynamics drive the temperature relationship, the complexity and number of reactions within organisms means simple thermodynamics cannot be directly applied to model them (Clarke, 2004; O'Connor et al., 2007). Debate over the MTE continues, however it has been used to successfully predict metabolic rates, standing stock of biomass, and macroecological patterns such as species richness gradients using temperature–richness relationships (Algar et al., 2007; Hechinger et al., 2019; Luo et al., 2015; Sears et al., 2012). While the exact exponents and mechanisms behind them may require further work, the MTE none-the-less provides a powerful basis to understand underlying ecological mechanics (Price et al., 2012). This is particularly true as the exponents can be calculated individually for any population or group, thereby allowing the MTE to be used to mass- and temperature-correct metabolic data.

### 1.3.3 Metabolic Ecology and Temperature

Temperature primarily influences metabolism by changing reaction rates (Clarke and Fraser, 2004). Generally chemical reaction rates increase with temperature, but

749 different processes can have different relationships or increase at differing rates.
750 These relationships are demonstrated by thermal performance curves (Fig. 1.6),
751 which show how different measures of metabolism and performance change with
752 temperature (Condon et al., 2010). Activities such as burst swimming and foraging
753 have an optimum temperature however these optima may not align. Where basal
754 maintenance costs increase at different rates to foraging and energy acquisition
755 there will be an optimum temperature beyond which foraging will be less effective
756 and overall performance is reduced (Condon et al., 2010). These rates will vary with
757 seasonal and life history changes in behaviour and therefore thermal optima will
758 change throughout an organism's life (Pettersen et al., 2018; Riek et al., 2017).




759

760 **Figure 1.6** – TPC showing that when energy uptake or feeding rate (blue curve)
761 scales with temperature at a lower rate than minimum energy expenditure or SMR
762 (black curve), this leads to a thermal optimum that maximises energy available
763 (green arrow) below the thermal optima of both feeding rate and SMR.

764 Differing rates of increase between metabolic rates with temperature can also
765 influence fitness. Evidence shows RMR increases with warming while MMR
766 becomes limited at higher temperatures due to maximum heart rate impairing
767 function and oxygen transport (Farrell et al., 2009; Norin et al., 2013; Pörtner et al.,

2017). This leads to a declining aerobic scope and smaller energy budget, constraining life history choices (Pörtner et al., 2017). However, other evidence suggests that maximum attained metabolic rate can increase with temperature and indeed may increase more than SMR up to the thermal limit of a species, making the aerobic scope highest at a temperature far above the current environment and thermal niche of the fish (Norin et al., 2013). This suggests that other factors such as feeding rate are a more likely source of thermal limitation than aerobic scope. Therefore, understanding the adaptation of a species to its thermal habitat and how this varies across its range is key to predicting the effect of rising global temperatures, and how these may vary across populations. However this is currently constrained by poor and limited methods for measuring metabolism *in-situ*, a research gap this thesis will seek in part to address (Treberg et al., 2016). While limits may be constrained SMR will increase following the Arrhenius equation until cell damage creates limits, other rates such as FMR and RMR will undergo a combination of thermodynamic increases with temperature will still having a constrained ceiling (Farrell et al., 2009; Norin and Clark, 2016; Sandblom et al., 2016). However, RMR and FMR, will also have an added behaviour and movement component that may be modified to change the rate under differing thermal conditions (Treberg et al., 2016). All these rates also have the capacity to plastically vary to differing degrees as well as adapt to differing conditions over generations (DeWitt et al., 1998; Morgan et al., 2022).

Temperatures also influence oxygen saturation in water, a fundamental component of metabolism (Rich, 2003), and so oxygen saturation can limit metabolism in both freshwater and marine environments. This is concerning as rising water temperatures resulting from climate change will decrease the concentration of dissolved oxygen, which may have pronounced effects on metabolic rate in warmer low latitude regions (Genner et al., 2017). Declining oxygen saturation can constrain metabolic rate and the size of an organism's energy budget and therefore potentially thermal tolerance range as warmer waters become too limiting (Chabot et al., 2016a; Chabot and Claireaux, 2018; Deutsch et al., 2020). Furthermore, gill size may be allometrically constrained, meaning gill oxygen uptake will not scale with size and therefore as fish grow and oxygen saturation falls, oxygen uptake could become more limited (Pauly, 2021), forcing fish to be smaller or operate with a smaller

energy budget (Pauly, 2019). While this mechanism is debated, there is little doubt that declining oxygen saturation will affect fish metabolism, potentially forcing them to move to cooler waters with a higher oxygen content (Deutsch et al., 2020; Lefevre et al., 2017). This potential to move is particularly pertinent in freshwater and marine environments where thermal refugia are rarer than on land, often requiring significant migration in order to maintain preferred temperatures (Pinsky et al., 2019). There is particular concern over how already declining salmonids may respond to rising temperatures, especially for species displaying anadromy and a preference for spawning in their natal rivers which reduces the capacity for natural range shifts (Chaput, 2012; Hendry and Cragg-Hine, 2003).

## 1.4 Ecological Drivers in Salmonids

### 1.4.1 Size and Growth

Early growth is key to success in salmonids as faster growing parr are larger in the spring and more likely to smolt and migrate to sea (Metcalfe and Thorpe, 1992). Once at sea, larger salmonids tend to be more successful and are more likely to survive the return migration to reproduce (Gregory et al., 2019). This trend of larger fish being more successful starts early as the first salmon to hatch are more likely to become dominant and therefore grow faster and become larger (Sigourney et al., 2013). There is debate over whether dominance actually leads to increased growth, however, and this will be explored in more detail below, especially in streams containing trout as they will routinely outcompete the most competitive salmon parr (Harwood et al., 2002; Metcalfe and Thorpe, 1992). Growth starts slow and homogeneous, but variance increases as spring approaches due to increasing food availability (Sigourney et al., 2013). Body size can be a key driver of variance in growth with larger fish competing for better territory (Sigourney et al., 2013). This divides the population into large, fast growers which will migrate at an earlier age than small, slow growers (Thorpe et al., 1998). The larger fish retain a high metabolism throughout winter, helping to drive greater foraging and growth, while the smaller fish suppress their metabolism (Thorpe et al., 1998). Larger, fast-growing fish are more prone to aggressive attacks by other large fish and predation risk, especially over winter, and suffer from increased mortality (Nicieza and Metcalfe, 1999). As spring and thus migration nears, a compensatory effect is seen whereby the smaller growth-suppressing fish undergo compensatory increased rates of

834 growth as they increase feeding rates (Sigourney et al., 2013). This can allow some
835 of these growth-suppressing fish to reach a large enough size to migrate in that year,
836 resulting in three key strategies for growing smolt: grow fast early, grow fast late, or
837 defer migration (Sigourney et al., 2013). Thus, growth and the factors that affect it
838 can drive the number of smolts and the timing of their migration. Growth can also be
839 affected by diet, with higher biomass prey promoting faster growth (Ward et al.,
840 2009). Prey availability and species vary across the natural range of salmonids.
841 Furthermore size is positively influenced by both maternal provisioning, e.g. egg
842 size, and genetics from both parents, and this can further influence metabolism, with
843 larger eggs exhibiting larger metabolic rates (Iritani et al., 2025; Legacki et al., 2025).

844 **1.4.2 Metabolism**

845 RMR varies widely within salmonids and is expected to have a variety of fitness
846 consequences from increased aggressiveness and risk taking to higher productivity
847 (Biro and Stamps, 2010; Killen et al., 2012). Higher RMR increases the basic cost of
848 living while potentially decreasing growth and fitness (Fry, 1947). But it also
849 correlates with metabolic scope for activity, rate of food acquisition, and digestion,
850 alongside maintaining the capacity for a higher MMR (Fry, 1947; Millidine et al.,
851 2009). An increased rate of intake is seen in salmon with a higher RMR offsetting the
852 higher basal costs and allowing increased growth, so long as these increased rates
853 of intake can be maintained (Millidine et al., 2009). However, whether this will be the
854 case as rivers warm is not yet known. Growth is a salmonid's primary aim during its
855 early life history, however, the relationship between metabolic rate (measured as
856 SMR) and growth is highly context-dependant as will be explored below (Archer et
857 al., 2021).

858 **1.4.2.1 Growth**

859 Laboratory experiments have shown that juvenile salmon with higher SMR exhibit
860 more aggressive behaviour and thus control the best feeding locations, leading to
861 faster growth (Fausch, 1984). However, this is not necessarily the case in the wild,
862 where the highest growth is seen in those with the lowest SMR required to achieve
863 dominance and control beneficial feeding areas (Metcalfe et al., 1995; Reid et al.,
864 2011). Here growth becomes a function of population density and aggressiveness,
865 with optimum SMR increasing as population and intraspecific competition increases
866 (Reid et al., 2011). Suggesting that in more productive dense rivers a higher

867 metabolism, may be more beneficial than in less densely populated rivers.
868 Additionally, increased unpredictability of food weakens the relationship between
869 SMR and growth and combines with increased visual complexity to break the
870 relationship between SMR and dominance as the optimum territory is both hard to
871 track and changing unpredictably (Reid et al., 2012).

872 This complex relationship between SMR and growth is also seen in trout with SMR
873 either having no effect on growth or a negative one, suggesting the cost of a higher
874 SMR and the dominance this infers may not result in sufficient additional feeding
875 opportunities to be worth the costs (Álvarez and Nicieza, 2005). Interestingly, these
876 results were observed in streams with high environmental variability, which is
877 associated with a more negative relationship, suggesting thermal variability may
878 favour fish with a lower SMR due to their increased efficiency and capacity to retain
879 a larger scope (Álvarez and Nicieza, 2005). Movement and activity are also key
880 contributors to growth and success, especially in variable habitats, and these factors
881 do not necessarily scale with SMR (Martin-Smith and Armstrong, 2002).

882 One issue of comparing measured values of SMR and its influence on growth in
883 juveniles is that the synthesis of new tissues as a fish grows will raise SMR even
884 when the fish is resting (Van Leeuwen et al., 2012). Additionally, SMR does not
885 reflect the metabolism of fish interacting with and competing in their environment,
886 which is encapsulated by FMR (Treberg et al., 2016). These two rates are
887 connected, whereby FMR is larger than but increases with SMR, but the rate of
888 increase especially when including the influence of temperature and body size has
889 been observed to vary among individuals and among taxa (Chung et al., 2019; Nagy,
890 1987; Niven and Scharlemann, 2005). This may also mean that the aforementioned
891 relationships between SMR, temperature, and behaviour may not hold for FMR. This
892 is an area of research that requires future development; understanding the
893 contributions of behaviour to observed metabolic rates.

894 The complex relationship between metabolic rate and growth also interacts with
895 habitat complexity (Enders and Boisclair, 2016). Increased complexity can provide
896 refuge from high water speeds and predators, and even mitigate extreme
897 temperatures (Cunjak, 1988; Greenwood and Metcalfe, 1998; Rimmer et al., 1984).
898 All these factors can increase metabolism, therefore salmonids within vegetation or

cobble cover can operate at a lower metabolic rate, increasing the energy available for growth (Enders and Boisclair, 2016; Metcalfe et al., 1987; Rimmer et al., 1984). Furthermore the reduced visual contact with conspecifics can reduce the metabolic cost of defending territory (Kalleberg, 1958). A higher SMR also increases performance in more structurally complex habitats, as individuals with higher SMR and thus energy demand have an increased willingness to take risk (Bull et al., 1996). These individuals then feed in adjacent structurally simple habitats and rest in the complex habitat, profiting from the higher prey densities and decreased competition as lower SMR individuals remain in the complex habitat (Finstad et al., 2007). In simpler habitats, however, higher SMR leads to increased metabolic costs without any increase in energy intake, thus reducing growth rate (Finstad et al., 2007). Salmonids compete for cover as it provides shelter from predation and strong currents, making the aggressiveness of individual salmonids a key factor in their development (Kalleberg, 1958; Kemp et al., 2005). Lack of access to cover leads to increased stress and thus metabolism, reducing the excess energy available for growth (Enders and Boisclair, 2016). Therefore competition, habitat, and metabolism all interact to affect growth.

#### 1.4.2.2 Thermal change and variability

As outlined above, temperature effects on metabolism are a fundamental driver of ectotherm ecology. Basal metabolic rates will increase with temperature, however, chronic exposure to high temperatures may limit this increase (Brown et al., 2004; Sandblom et al., 2016). But chronic exposure does not have this effect on MMR, leading to a lower aerobic scope which can reduce the energy available for growth (Sandblom et al., 2016). This flexibility in SMR is also seen between salmonids raised in high or low temperatures, with the relationship between growth and SMR changing between regimes (Archer et al., 2021). Growth increases with SMR in water below the thermal optima, after which growth declines, and the converse relationship is observed with MMR (Archer et al., 2021). This suggests that a wider aerobic scope increases growth above the optimum temperature, but that growth is maximised below this temperature by minimising SMR and consequently reducing the capacity for MMR (Archer et al., 2021; Millidine et al., 2009).

The effect of temperature on metabolism is typically quantified as the average temperature over an experimental period, but stream temperature can be highly

variable, depending on the volumes of groundwater, surface run-off, solar radiation, and air temperature (Caissie, 2006; Enders and Boisclair, 2016). River temperatures can vary diurnally by up to 15°C and over 20°C annually (Caissie, 2006). Parr can respond to increased diurnal variance by increasing SMR (Beauregard et al., 2013). Furthermore, stream temperature and range of diurnal variance relative to ideal growth conditions is also important with fish experiencing variable temperatures in waters bellow the growth optimum showing reduced SMR (Oligny-Hébert et al., 2015). For fish occupying waters close to their thermal limit, increased thermal variance led to increased SMR as the highest stream temperatures exceeded their critical thermal maximum, causing heat stress and damage to cells (Oligny-Hébert et al., 2015).

Terrestrial insects exposed to the highest range of temperatures showed the greatest metabolic plasticity in the face of warming and the greatest suppression of their metabolic rate (Fleming et al., 2021; Williams et al., 2012). Furthermore, water fleas reared at more variable temperatures had the highest thermal tolerance after six generations, indicating that evolutionary adaptation may increase the scope for adjusting metabolic rates to match the local thermal environment (Chen and Stillman, 2012). How thermal variance impacts thermal tolerance in salmonid populations that have historically been exposed to these conditions is unknown and is something this thesis will seek to explore. However metabolic plasticity of fish exposed to stable conditions declines over generations (Morgan et al., 2022). Furthermore, intertidal gobies which are adapted to a wide and rapidly varying temperature range display wide performance breaths that can be maintained in high temperatures, suggesting this relationship may be present in marine ectotherms such as salmonids (Silva et al., 2019). However, this adaptation may be limited by the physiological cost of maintaining the capacity to perform at a range of temperatures which may suppress this response in rivers which do not experience regular thermal variability (Semsar-kazerouni and Verberk, 2018). The idea of a cost to metabolic and phenotypic plasticity is also unclear and a subject of debate (Auld et al., 2010; Buskirk and Steiner, 2009). Rivers across the geographical distribution of Atlantic salmon and brown trout experience great thermal variability (Caissie, 2006). Therefore, it may be of great importance to understand if fish from rivers

experiencing a greater range of temperatures will be more resilient to global warming, a research question this thesis will seek to answer.

## 1.5 Thesis Outline

This thesis integrates methodological innovation with ecological application to investigate how climate change, specifically how increasing temperature and thermal variability, affects the metabolism, growth, and survival of salmonids. A central challenge in predicting climate responses is the limited understanding of how metabolic processes measured under controlled conditions translate to natural environments, and how these scale to influence fitness across populations. To address this, the thesis develops and validates *in situ* metabolic approaches, applies them across environmental gradients, and links metabolic variation to key life-history traits. Collectively, this work provides both mechanistic insight and practical tools to improve conservation and management under climate change.

**Chapter 2** develops and validates a novel *in situ* method for measuring fish metabolic rates using closed chambers combined with high-resolution temperature and oxygen sensors. Metabolic estimates derived from this approach are directly compared with conventional respirometry to assess accuracy, reliability, and ecological relevance. This chapter establishes whether metabolism can be reliably quantified under field conditions using closed chambers, addressing a limitation in current experimental approaches.

**Chapter 3** applies the validated method across contrasting thermal environments, comparing fish from thermally stable spring systems and highly variable stream habitats. This chapter tests how exposure to differing thermal variability regimes influences the thermal sensitivity of metabolism and its relationship with fitness-related traits. In doing so, it evaluates whether thermal variability alters population-level resilience to warming and how increased variability in the future may influence resilience.

**Chapter 4** extends this framework across a broad latitudinal gradient, from southern to northern Europe, encompassing populations adapted to distinct thermal and productivity regimes. It examines how metabolic traits vary among populations and how these interact with environmental temperature to influence growth, migration timing, and survival. By leveraging this natural gradient, the chapter generates

predictions of responses to future warming and identifies potential thermal optima and constraints.

**Chapter 5** translates these insights into an applied context by developing a framework for tracking movement and growth without reliance on physical tagging. Using chemical tracers, including stable isotopes and elemental signatures, this chapter provides an accessible methodology for reconstructing life-history trajectories. This approach enables improved identification of critical habitats, such as nursery and feeding areas, thereby supporting more effective management of threatened salmonid populations.

**Chapter 6** provides a synthesis of the knowledge gained in the previous chapters, puts them into the context of what we already know of the ecophysiology of salmonids, as well as identifying where future research should focus to improve conservation efforts for this charismatic species.

Through these chapters the thesis has four main aims:

1. Continue the development of a new method of measuring metabolism *in situ* and validate these measurements against current standard respirometry metrics.
   *Hypothesis:* There will be a positive relationship between field measures of metabolism and laboratory respirometry measures.

2. Quantify how thermal variability within a freshwater system impacts the thermal sensitivity and growth in salmonids that reside there, and the broader role of thermal variability on metabolic rate in a warming world.
   *Hypothesis:* Salmonids in rivers with high thermal variability will have higher fitness in warmer conditions relative to conspecifics.

3. Determine the key drivers of growth and migration in salmonids, how these are reflected in metabolic rate and, how these relationships vary with temperature and latitude.
   *Hypothesis:* Higher metabolic rates will improve growth rate throughout life history and correlate with an earlier migration period in Salmon and a marine migration in Trout. It is further expected that the relationship between routine

metabolic rate and growth will intensify in fish acclimated to lower temperatures and weaken in fish acclimated to higher temperatures due to the increased thermal plasticity of basal rates compared to maximal rates.

4. Develop a framework for using chemical tools to better track salmonid movements without intensive tagging infrastructure using retrospective chemical tracers
   *Hypothesis:* Chemical tracers will be able to reconstruct both within river and marine movements as well as infer growth.

# Chapter 2. Low-cost field respirometry for wild fish: validation of a rapid closed-chamber approach

*Under review at Methods in Ecology and Evolution*

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**Abstract**

Metabolism underpins growth, reproduction, and survival, and is strongly temperature dependent; accurate estimates are therefore essential for understanding growth dynamics and predicting how environmental change will affect fish production and persistence.

Traditional methods, such as intermittent flow respirometry, are time-intensive, laboratory-based, and require animal transport, limiting their application in wild populations. *In situ* closed-chamber respirometry provides a rapid alternative for measuring metabolism under natural conditions, yet its comparability with laboratory-derived estimates remains uncertain.

We compared metabolic rates of individuals from three fish species measured using both field-based closed chambers and laboratory intermittent flow respirometry. Field-derived routine metabolic rates were positively correlated with laboratory estimates of standard and routine metabolic rate and were significantly repeatable across species.

Adoption of this approach would facilitate large-scale evaluation of links among metabolism, fitness, and environmental variation, improving predictions of fish energetics and population persistence under climate change.

## 2.1 Introduction

Metabolism comprises the chemical reactions through which organisms convert nutrients into energy and biological material, with metabolic rate influencing processes from cells to ecosystems (Brown et al., 2004; Schramski et al., 2015). Since metabolic rate increases predictably with body mass and temperature, climate warming is expected to alter organismal energy demands (Brown et al., 2004; Pinsky et al., 2019). Rising temperatures elevate maintenance metabolic costs, potentially reducing fitness and survival when energetic demands cannot be matched by increased energy acquisition or when temperatures exceed physiological thresholds (Brijs et al., 2025; Payne et al., 2021). Consequently, accurately quantifying metabolic responses to natural thermal variation is critical for predicting the effects of climate change on fish growth, survival, and biomass production (Carozza et al., 2019; Lefort et al., 2015).

Fish metabolic rates can be estimated using physiological, biochemical, and modelling approaches (Treberg et al., 2016). In fish, the most frequently used technique is respirometry, which directly quantifies individual aerobic metabolic rate. Respirometry typically measures three different rates, the standard metabolic rate (SMR), routine metabolic rate (RMR), or maximum metabolic rate (MMR) (Brett, 1964; Chabot et al., 2016a). SMR is the cost of maintenance, without any energy allocated for growth, reproduction, or other drivers of performance and is standardised for a given temperature (McNab, 1997). MMR is the maximum metabolic rate an organism can sustain, though generally only for short periods of activity (Biro and Stamps, 2010; Careau et al., 2008). RMR is the energy used by unfed but normally active organisms and can fall anywhere between SMR and MMR (Chabot et al., 2016b; Fry, 1971). All these respirometry measures exclude specific dynamic action, the increase in metabolism after feeding (Secor, 2009).

There are three primary respirometry methods used to measure these various rates in fish: closed-system, continuous flow, and intermittent flow (Svendsen et al., 2016). Closed-system respirometry measures oxygen depletion in a sealed chamber but can cause hypoxia and waste accumulation over time (Steffensen, 1989). Continuous-flow respirometry avoids these issues by continuously flushing water through the chamber and estimating oxygen consumption from inflow–outflow differences, although inaccurate flow rates can create mixing errors (Eriksen, 2002; Svendsen et al., 2016).

Intermittent-flow respirometry combines both approaches by alternating closed measurement periods with flushing phases to maintain high oxygen levels and remove waste (Svendsen et al., 2016).

However, traditional respirometry is limited by long acclimation times, low throughput, and laboratory conditions that may not accurately reflect metabolism in wild fish (Auer et al., 2016; Svendsen et al., 2016). Extended capture and holding periods can also raise welfare concerns (Huntingford et al., 2006), driving interest in field-based approaches (Treberg et al., 2016). Although field respirometry using swim tunnels or intermittent-flow systems can produce laboratory-comparable measurements, these methods often require extensive equipment and long measurement periods (Durhack, 2020; Mochnacz et al., 2017). Simpler field-based closed-chamber methods reduce equipment needs and handling time, but their relationship with standard laboratory metabolic metrics remains unclear (Alexia M. González-Ferreras et al., 2023; Rasmussen et al., 2012). Here, we demonstrate a low-cost and high-throughput field-based closed-chamber respirometry approach and compare the measures of metabolism that it generates in the field with laboratory-measured intermittent flow measures of SMR, RMR, and MMR in the same individuals. We conducted these experiments on three freshwater fish species and demonstrated the repeatability of field-based closed-chamber respirometry by measuring metabolism multiple times in the same individuals to test for consistency.

## 2.2 Methods

### 2.2.1 Subjects and Husbandry

Wild fish belonging to three species of freshwater fish were captured from rivers near the University of Glasgow, UK in early spring 2024. European minnows (*Phoxinus phoxinus,* Linnaeus 1758; *n* = 20; length = 36 - 70 mm) and three-spined sticklebacks (*Gasterosteus aculeatus,* Linnaeus 1758; *n* = 19; length = 39 - 58 mm) were collected from the River Kelvin using hand nets. Juvenile brown trout (*Salmo trutta,* Linnaeus 1758; *n* = 16; length = 99 - 131 mm) were captured by electrofishing as part of a fish rescue from a drained section of the Brock Burn flowing into Balgray Reservoir, East Renfrewshire. It was not possible to measure SMR immediately after capture due to both quarantine requirements and the need to ensure fish were fully acclimated to laboratory conditions, consistent with standard SMR measurement protocols. This

acclimation is necessary to obtain unstressed and comparable estimates using intermittent-flow respirometry.

Therefore, all fish were first transferred to laboratory aquarium facilities at the University of Glasgow, where the minnows were held together in a single 42 L tank at 14°C, while the sticklebacks were kept in individual 10 L tanks at 12°C and the trout individually in 4 L compartments separated by mesh within a recirculating stream system at 14°C. All the tank temperatures were broadly similar to those at the capture locations at the time of collection. Fish were kept in these tanks for approximately 2 months to allow time to acclimate to the lab setting prior to the experiment, exposed to a 12:12h light:dark cycle, and fed bloodworms twice a day *ad libitum* (Jenkins et al., 2014).

### 2.2.2 Lab Respirometry

Laboratory derived SMR, RMR, and $MMR_{recovery}$ (hereafter referred to as MMR) were obtained in (mg $O_2$ $h^{-1}$) using standard methods following the approaches of (Chabot et al., 2016b; Norin and Clark, 2016). At the start of each laboratory respirometry experimental run, up to 15 fish of one species were fasted for 24 hours before transfer to individual intermittent flow respirometry chambers (details in appendix Table S4). Fish were left in the respirometry chambers overnight for ~16 h, then subjected to cycles of 2-4 min of flushing with oxygenated water followed by 6-8 min of no water circulation ('closed phases'), depending on the species (detailed in Table S5). In each experimental run there were approximately 90 closed phases, during which the slope of oxygen was calculated (Svendsen et al., 2016), resulting in ~90 estimates of oxygen consumption per fish, to be used in the calculation of SMR and RMR (henceforth referred to as $RMR_L$; see below). Once an experimental run concluded, fish were removed in turn and chased around a 15 L tank until exhaustion (mean chase time = 93s). They were then immediately transferred back into a respirometry chamber for a 10-minute closed phase, or until oxygen depleted below 5 $mgL^{-1}$, to obtain an estimate of $MMR_{recovery}$, hereafter referred to as MMR (Chrétien et al., 2021; Norin and Clark, 2016). Background oxygen consumption rates (e.g. from microbial respiration within the system) were measured before and after the fish experiments in every respirometry chamber while no fish were present.

SMR was calculated using the respR package (Harianto et al., 2019) in R v4.3.1 (R Core Team, 2024) as the lower 20$^{th}$ percentile of overnight (before 7:30am) oxygen consumption rate measurements (Chabot et al., 2016b). Slopes with an $r^2$ below 0.8 were excluded following Schaal et al., (2022). This was to remove non-linear slopes. Sensitivity analyses conducted with a higher $r^2$ of 0.9 showed this lower threshold decreased SMR by 1%, suggesting this lower threshold is not significantly influencing the results (Chabot et al., 2021). $RMR_L$ was calculated using the respR package as the mean of all oxygen consumption rate slopes with $r^2 > 0.8$, measured between 7:30am and the end of the experiment at approximately 10:30am (Harianto et al., 2019; Killen et al., 2021). Finally, MMR was calculated using the chaseR package as the maximum slope from rolling regressions of 30s over the 10-min closed phase following the chase protocol, with this length of rolling regression selected to ensure $r^2$ exceeded 0.8 (Killen, 2024). Note that in all of these measurements, the value for oxygen consumption rates (mg $O_2$ $h^{-1}$) was calculated by multiplying the slope of oxygen depletion by the volume of water (i.e. the volume of the respirometry chamber and tubing minus the volume of the fish, which was assumed to be equivalent to its mass), and finally subtracting background respiration which was modelled linearly using the before and after control measurements.

### 2.2.3 Field Respirometry

Immediately after each laboratory respirometry trial, each fish was individually transferred into a 7.2-L sealed plastic tub containing water at the same temperature as during the trial and transported approximately 45 minutes by car to a tributary stream that enters the River Endrick at Drumtian, near Killearn. All three fish species are native to the River Endrick and have previously been found within 200 m of the site of the field trials (Maitland, 1965). The stream was approximately 1 m wide; trials were run when there had been no significant recent rain so that the stream was at near baseline flows, with water depths of 15 - 50 cm depending on location. Once at the stream, circular, airtight transparent plastic chambers (32 cm diameter) were filled with filtered river water using a 250 µm sieve, ensuring that there were no visible air bubbles (Fig. 2.1). A single fish was added to each chamber, along with a probe (miniDOT, Precision Measurements Engineering “PME”, accurate to 0.01 $mgL^{-1}$ ± 5%) to measure water oxygen concentrations and temperature every minute, and an underwater motor (Underwater motor: 7350, Playmobil, UK) to circulate the water at

0.06 m $s^{-1}$ (note that this flow rate varied around the chamber, the probe provided some refuge from the flow, and fish were not observed actively swimming against this current). The miniDOT logger measures dissolved oxygen using light: oxygen in the water changes how a light-sensitive coating on the sensor glows, and the logger converts this signal into an oxygen reading, adjusting for water temperature. It also assumes that salinity, temperature, and air pressure were measured accurately and that conditions did not change much during a trial.

One additional chamber containing filtered river water and only a probe and underwater motor (i.e. no fish) was used as a control each day to estimate background rates of oxygen consumption caused by other biological activity. Chambers were placed into the stream in shallow areas just deep enough to cover the chamber, with a rock on top to prevent movement. The chambers were then left undisturbed for approximately 90 minutes; the lowest $O_2$ levels reached over this period were 7.41 $mgL^{-1}$ (well within natural levels). These field experiments began around midday (approximately two hours after the laboratory respirometry had finished) and concluded by 2pm.

The first 30 minutes of data from each field trial were excluded as a settling period, after which time 20-minute rolling linear regressions of oxygen against time were run across all remaining data. The mean of the lowest 20% of these slopes with $r^2 > 0.8$ was used in the calculation of field routine metabolic rates using a modified approach from González-Ferreras et al., (2023). However, due to a low signal to noise ratio in the smaller fish (minnows and sticklebacks) all slopes with an $r^2 > 0.5$ were visually inspected and those with a non-linear depletion were excluded ($n$ = 2) (Chabot et al., 2021). The oxygen consumption rate (mg $O_2$ $h^{-1}$) was calculated by multiplying each of the final slope values by the volume of the water (i.e. the volume of the chamber minus the volumes of the miniDOT, motor, and fish) and subtracting background respiration, which was modelled linearly over the duration of the experiment in the control chamber. The calculated metabolic rates are henceforth referred to as $RMR_F$ and represent the metabolism of unfed but normally active organisms (RMR) with the addition of field stresses. Following the field respirometry experiment, the fish's fork length and wet weight was recorded. Due to equipment failure some minnows could not be weighed, instead mass was calculated using the length: weight relationship of

the remaining minnows. All of the above experimental procedures were licensed under the UK Home Office Animals (Scientific Procedures) Act, licence number: PP6899400.

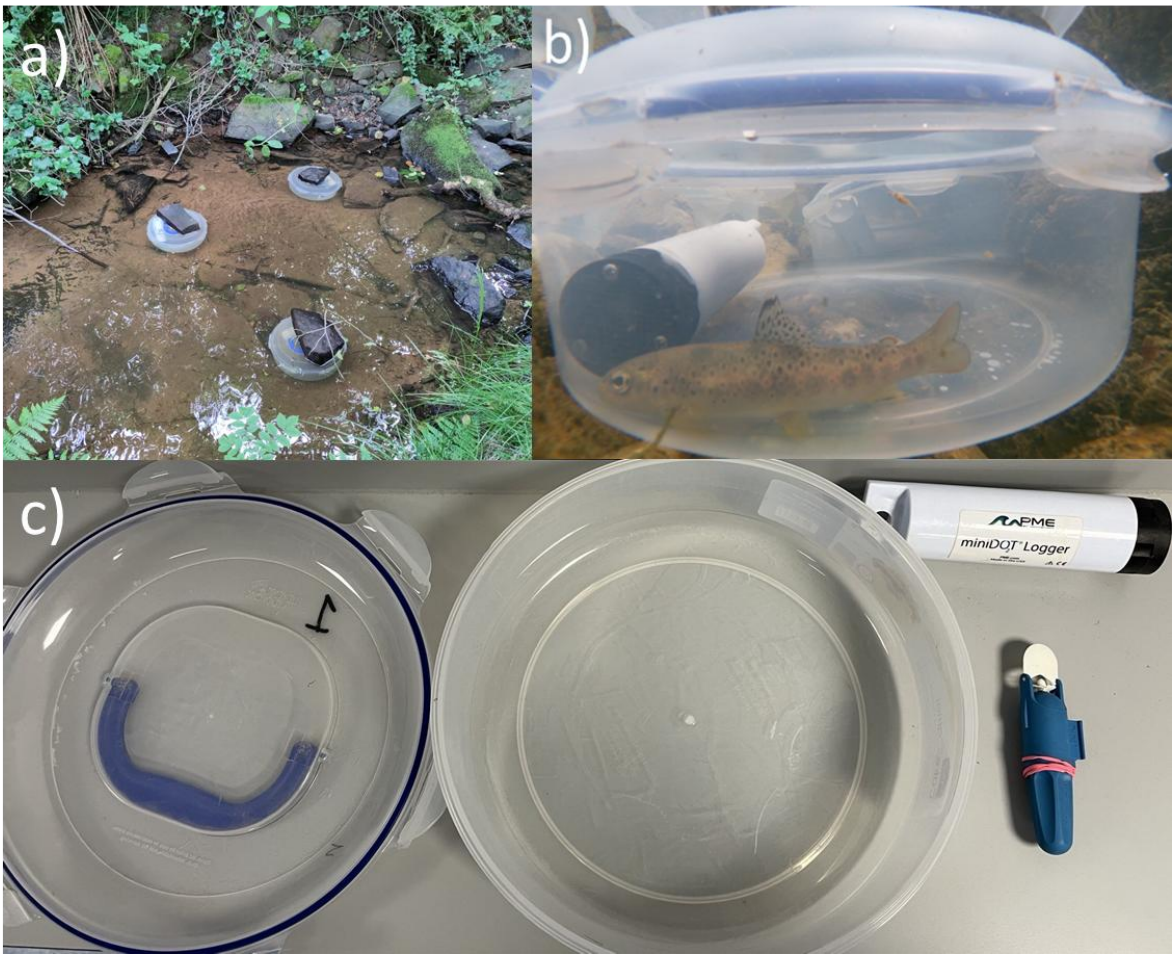



**Figure 2.1** - Closed-chamber field respirometry setup showing a) multiple chambers in the field, b) a brown trout during an experiment, and c) the closed-chamber equipment, including plastic chamber and lid, dissolved oxygen logger, and underwater motor.

### 2.2.4 Field Repeatability

Time constraints meant that repeating the Glasgow-based field experiments multiple times was not possible. However, a dataset on brown trout collected previously from two streams in Spain provides an opportunity to explore how consistent the measurements of $RMR_F$ are in the field. This allowed us to compare these estimates of repeatability to those quantified during each closed-chamber period of the intermittent-flow laboratory experiments described in Supplementary Text S2.1. In this separate experiment, brown trout were captured by electrofishing at two streams in Asturias, Spain in September 2023: Arroyo de Farfada, ($n$ = 40, TL = 78 - 194 mm,

average water temperature at the time of capture = 8.8 °C) and Fuente Dé ($n$ = 40, TL = 55 - 206 mm average water temperature = 10.2 °C). Each fish was then subjected to four consecutive 90-min runs of the field respirometry methodology (as described above) between the hours of 8am and 6pm. Each time that the experiment was repeated, the fish was removed from the chamber, which was refilled with fresh stream water before sealing the fish back inside and returning to the stream. Oxygen consumption rates from each of the four experimental runs on each fish were calculated as described above for the field respirometry.

### 2.2.5 Statistical Analysis

Metabolism was corrected for fish body mass by plotting ln metabolism against ln mass for each method and taking the slope: (SMR = 0.91, $RMR_L$ = 0.85, $RMR_F$ = 0.76, MMR = 0.74, see Table S2.1 for full details). These slopes were then used as scaling exponents to mass-correct the metabolic rates observed under each method.

The relationship between lab and field methods was then analysed using linear regression. All possible combinations of the model including ln $RMR_F$ as the explanatory variable and main and interactive effects of species identity and ln metabolic rate in the lab (either SMR, $RMR_L$, or MMR) were explored, with the most parsimonious model chosen using Akaike Information Criterion. To further analyse the compatibility of the lab and field-based measurements, Spearman's rank correlation tests were conducted within each species to compare the rank order of each individual in terms of their measured metabolic rates in the lab and field.

The differences among SMR, $RMR_L$, MMR, and $RMR_F$ were examined using a mixed effects model from the nlme package (Pinheiro et al., 2023). Here ln mass-corrected oxygen consumption rate (mg $O_2$ $g^{-b}$ $h^{-1}$, where b is given by Table S2.1) was the response variable with main and interactive effects of species identity and metabolic rate type (SMR, $RMR_L$, MMR, and $RMR_F$) included as explanatory variables. Fish individual identity was included as a random effect to account for the estimation of multiple metabolic rate types from the same individual. The varIdent variance weighting structure was used to account for heterogeneity of variance among different metabolic rate types.

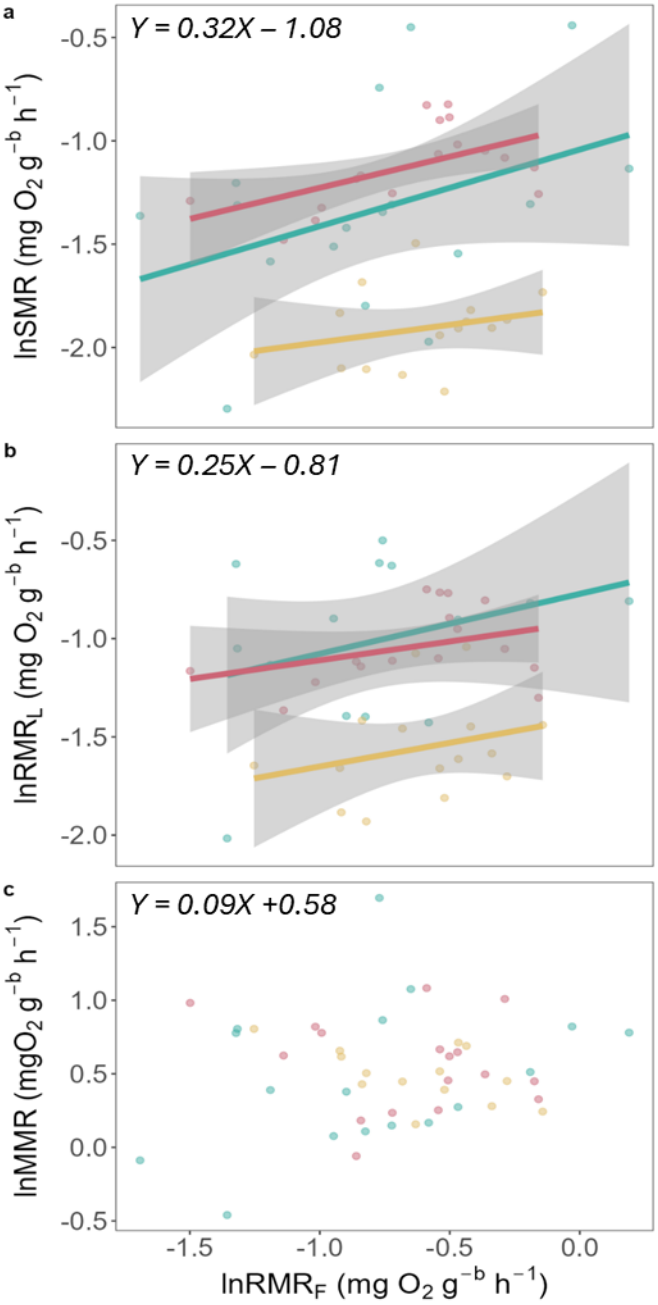
Finally, repeatability was examined using GLS to model the coefficient of variation for each repeated measure of $RMR_F$ in the Spanish fish and compare it to repeated

measures of $RMR_L$ in the Glasgow fish in the laboratory. The varIdent variance weighting structure was again used to account for heterogeneity of variance among metabolic rate types. The repeatability of $RMR_F$ was calculated using rptR (Stoffel et al., 2017) with a mixed effects model including main effects of ln mass, temperature, experimental run, and stream and a random effect of fish ID. This was compared to the repeatability of $RMR_L$ using mixed effects model in rptR including ln mass and a random effect of fish ID. To inform sample sizes for future studies, a power analysis was performed using the standard deviation observed among field repeats. Required sample sizes were estimated for detecting biologically moderate and strong effects, corresponding to standardised effect sizes of 0.5 and 0.8 standard deviations respectively, following conventional benchmarks proposed by (Cohen, 1988). Larger effect sizes require smaller sample sizes to detect because the biological signal is greater relative to background variation.

## 2.3 Results

### 2.3.1 Respirometry Comparisons

The most parsimonious models relating ln mass-corrected $RMR_F$ to lab-based metrics of ln mass-corrected metabolism showed a significant positive relationship between $RMR_F$ and both lab-derived SMR ($F_{3,45}$ = 21.79, $p$ = 0.007, Fig. 2.2a) and $RMR_L$ ($F_{3,41}$ = 12.56, $p$ = 0.044, Fig. 2.2b), but not MMR ($F_{1,46}$ = 0.48, $p$ = 0.493, Fig. 2.2c). There was a significant main effect of species identity for both SMR and $RMR_L$, but no interactive effects in any model (see Table S2.2). However, there was no significant correlation in rank order of metabolic rates between $RMR_F$ and any lab rates (see Table S2.3). Mass-specific relationships of metabolic rate are shown in Fig. S2.1.




1319

1320 **Figure 2.2** - Laboratory-derived metabolic rates for a) SMR, b) $RMR_L$, and c) MMR
1321 plotted against $RMR_F$. All rates are mass corrected (where mass exponent *b* is given
1322 by Table S2.1) and then natural logged, with species denoted by colour (blue for
1323 minnows, red for sticklebacks, and yellow for brown trout). Regression lines are only
1324 plotted for significant relationships, with these relationships given as equations when
1325 significant (see Table S2.2).

1326 $RMR_F$ was significantly higher than either SMR or $RMR_L$, while MMR was higher still
1327 (Fig. 2.3). There was an effect of both species and individual identity on the differences
1328 between metabolic rate measurements for all measures of metabolic rate. Grouping

across all species, $RMR_F$ was 2.2-fold higher than SMR and 70% lower than MMR, while MMR was 7.2-fold higher than SMR. The factorial difference between SMR and $RMR_F$ ($RMR_F$ / SMR) was greatest in trout (3.7) and smallest in sticklebacks (1.6), while the difference between MMR and $RMR_F$ was greatest in sticklebacks (0.42) and smallest in trout (0.28). The standard error was lowest in trout (0.338) and highest in sticklebacks (0.418), while standard error of each method increased from SMR (0.001) through $RMR_L$ (0.014) and $RMR_F$ (0.033) peaking with MMR (0.100). Mass-specific plots of unlogged metabolic rate are shown in Fig. S2.2.

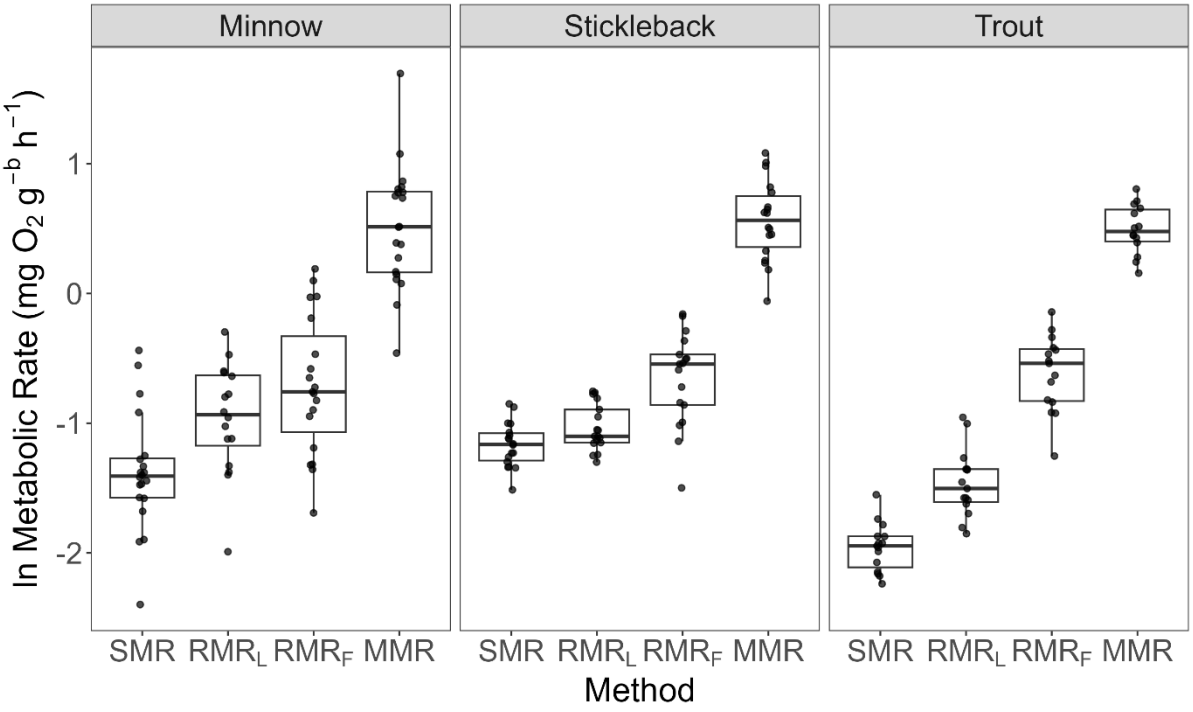



**Figure 2.3** - Boxplots of ln mass-corrected metabolic rate measurements (where *b* is given in Table S2.2) using each method (SMR, $RMR_L$, $RMR_F$, MMR) for each species.

### 2.3.2 Respirometry Repeatability

The coefficient of variation for repeated measurements of $RMR_L$ on brown trout in the lab was significantly lower than the repeated measurements of $RMR_F$ from brown trout in the field in Spain (GLS: Model = Coef ~ Method, $t$ = -2.288, $p$ = 0.025, Fig. 2.4). However, it should be noted that the lab measurements were not true technical repeats but were instead successive measurements in the same chamber without removal and reintroduction of the fish. The $RMR_F$ measurements from the trout in Glasgow could not be used as there was only one true linear depletion per fish. Mixed effect repeatability models on the Spanish trout showed that field measurements were

significantly repeatable ($R$ = 0.36, 95% CI = 0.23 - 0.49, $p$ < 0.001), with the variability within measures of a single fish's metabolism being lower than the variability among different fish. Furthermore, the repeatability of these $RMR_F$ measurements had overlapping confidence intervals with the repeatability of $RMR_L$ ($R$ = 0.428, 95% CI = 0.15 - 0.625, $p$ < 0.001). Based on the observed variance among field repeats, approximately n = 25 and n = 63 individuals per group would be required to detect strong (0.8 standard deviations) and moderate (0.5 standard deviations) effects respectively.

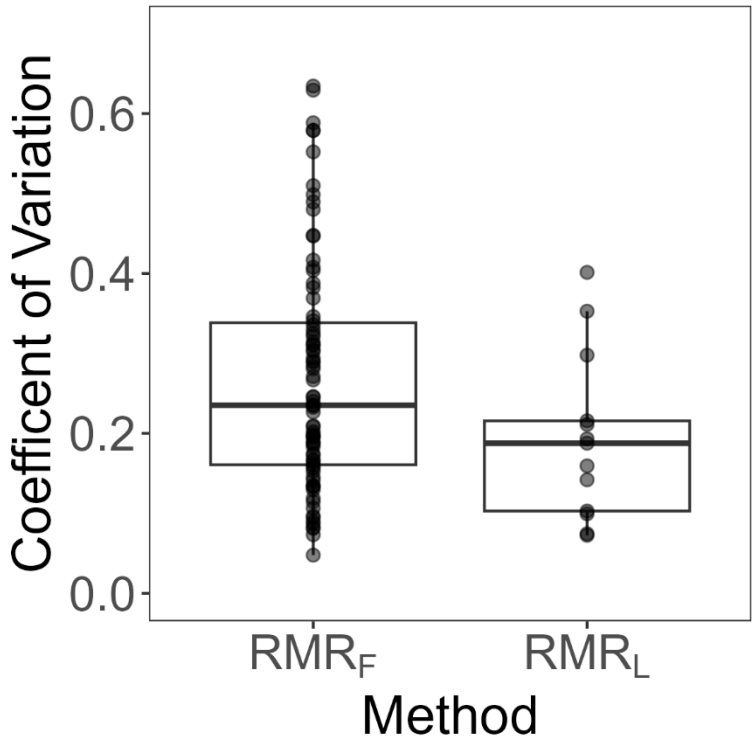



**Figure 2.4** - Coefficients of variation for repeated measurements of $RMR_L$ ($n$ = 16) taken from the brown trout measured in Glasgow and $RMR_F$ taken in Spanish brown trout ($n$ = 79).

## 2.4 Discussion

Our results demonstrate that short-duration field-based closed-chamber measurements of metabolism are positively and consistently related to laboratory-based measurements of SMR and $RMR_L$ (Fig. 2.2), suggesting this method can be used to assess the metabolism of wild fish *in situ*. These $RMR_F$ measures fell between $RMR_L$ and MMR as would be expected by a field rate and this trend held across species. This suggests broad applicability in use on a range of fish species

and size classes despite species-level differences in metabolism arising from different allometry and behavioural responses in the lab vs field (Killen et al., 2010). We show that these field measures are repeatable i.e. the variability among fish is greater than the variability of individual measures of an organism's metabolism. Thus, despite the inherent variability in $RMR_F$ (e.g. due to individual and temporal variation in activity levels), closed-chamber respirometry could be used to distinguish effects of environmental change on individual metabolism in wild settings and these field measures linked back to laboratory measures. However, while closed-chamber respirometry is positively related to laboratory rates, both the precision and consistency of these measurements is lower than laboratory approaches. This is unsurprising given the increased variability and behavioural costs inherent to field settings and the lack of many repeated measurements (Treberg et al., 2016).

Our measured field rates were expected to fall well above SMR and $RMR_L$ but below MMR. This was generally the case, with $RMR_F$ being on average 2.2x SMR and 1.6x $RMR_L$ but well below MMR. While few studies have successfully measured FMR in freshwater fish, it has been measured in juvenile cod (*Gadus morhua,* Linnaeus 1758*)* as being in the range 0.7-2x literature estimates of SMR, placing it within the same range as $RMR_F$ in our study (Chung et al., 2019). Despite $RMR_F$ and $RMR_L$ both being measurements of routine metabolic rate, $RMR_F$ was expected to be higher due to the stress associated with handling and transportation to the field site (Iversen et al., 1998), coupled with a shorter settling time prior to measurement. Additionally the presence of visual and auditory cues associated with a wild environment, other fish, and the greater capacity to move may all increase metabolism, with the flow rates potentially stimulating the smaller fish to swim against the current (though this was not observed) (Fausch, 1984; Hall and Clark, 2016). It should be noted that such field experiments would normally not involve stress due to transportation, potentially reducing some of the variability associated with the measure here. However, in this case it was necessary for logistical reasons to measure metabolic rates in the laboratory first then transport the fish directly to the field due to quarantine protocols and to provide a direct comparison. It is also important to consider that while $RMR_F$ may capture more of the vagaries of metabolism in the field (e.g. greater movement, visual cues etc) it is not a true measure of FMR since it does not represent a freely moving individual exhibiting

normal behaviour (feeding, reproducing, resting, growing etc) over an extended period of weeks to months (Treberg et al., 2016).

Through the repeatability experiment in Spain, we observed significant repeatability of $RMR_F$, which was also shown to have overlapping confidence intervals with repeated measures of $RMR_L$. However, these $RMR_L$ measures were not true technical replicates as the fish had not been removed and placed back into the chamber each time. Instead, this serves as a benchmark to demonstrate the variability of $RMR_F$ measurements as comparable to that of laboratory-based metrics. While the variability associated with measurements of $RMR_F$ was higher than that of $RMR_L$ (Fig. 2.4), we suspect this is due to the uncontrolled field environment introducing multiple factors that influence metabolism. These factors include environmental cues such as time of day, light intensity, and temperature variability, all of which are strictly controlled in the laboratory (Helfman, 1986; Portz et al., 2006). These may also contribute to the low Spearman's rank correlations between laboratory and field measurements. Furthermore, there may be a systematic decline in SDA, whereby digestion declines over the course of the experiment as the fish can no longer hunt and consume prey once captured though this was likely minimal as no systematic decline was observed (Secor, 2009). The release of waste into the chambers may have led to an increase in within-chamber respiration over the course of each experiment as bacterial respiration increased (Keys, 1930). These factors will only have been the case for the repeatability experiment as guts were given time to clear before SMR for the direct comparison. Furthermore, we did not observe any systematic increase in metabolic rate and our approach for estimating $RMR_F$ used the mean of the lowest 20% of slopes, reducing the likelihood that transiently elevated rates influenced the results.

For all species, both MMR and $RMR_F$ exhibited higher among-individual variation than SMR and $RMR_L$ estimates (Fig. 2.2). This may be because SMR and $RMR_L$ both exclude more components of metabolism (e.g. movement, visual cues etc) thus reducing sources of variability, whereas MMR and $RMR_F$ include contributions to metabolism from activity which will vary more as a function of behaviour. For example, fish that show less response to chasing may exhibit less frantic swimming behaviour and thus a lower MMR. This increased variability and unreliability in response may also explain the lack of relationship between MMR and $RMR_F$, despite

the positive correlations between MMR and both SMR and $RMR_L$ which would be expected (Fig. S2.3) (Hillman et al., 2013). The lack of correlation between MMR and $RMR_F$ may arise from individual fish showing inconsistent behavioural responses to stressors such as being placed in a new environment or being chased (Hillman et al., 2013; Treberg et al., 2016).

Closed-chamber respirometry approaches in the wild have a number of advantages, such as facilitating a rapid assessment of metabolism *in situ* without needing to transport fish or introduce additional stressors. Furthermore, this may present a more ethical option for minimising stress associated with handling, transportation, and holding (Iversen et al., 1998; Portz et al., 2006). We propose that this short-duration method, while enclosing the fish in a chamber, does not expose the individual animal to conditions that vary significantly from field experience; it is therefore a candidate method for measuring metabolism in wild fish or indeed other aquatic organisms with less regulatory burden, reducing one barrier for research on wild fish. This approach could be useful for studying adaptation, or long-term acclimation to local environmental conditions (e.g. local pollution or elevated temperatures), which would require long-term maintenance of fish in an artificial laboratory environment and may not require high precision. Furthermore, closed-chamber respirometry is particularly suited to remote locations where the low tech and non-invasive nature of the methodology allow sampling of fish more rapidly than would be possible with traditional laboratory-based respirometry techniques, and with no requirement to remove them from their natural habitat which may be hard to access. However, application may require higher sample sizes due to the coarse nature and large component of individual variation observed. Additionally, an index of activity could be used to ensure observed differences are due to metabolism and not activity, though due to the paired nature of this study activity and metabolism links are likely consistent. Where a higher precision approach is preferable, field-based intermittent flow respirometry may instead be a more suitable approach (Mochnacz et al., 2017).

We suggest that for common usage of our closed-chamber approach, fish are placed in the field respirometer immediately after capture from the wild. $RMR_F$ can then be measured within 30 mins of capture (and while SDA is still at natural levels, assuming the fish have been feeding normally). Though this added biological realism will also increase noise, alternately fish could be held in the field for 24 hours to allow

guts to clear before measuring $RMR_F$, allowing SDA to be eliminated (O'Gorman et al., 2026). We also suggest a ratio of 400-800 between fish mass (g) and available chamber volume (mL) though this can vary depending on experiment length, and activity. Overall, these closed-chamber respirometry field measurements provide a rapid, field-based, lower-stress approach for assessing how wild populations energetically respond to their environment and global change.

## 2.5 Supplementary Material

### 2.5.1 Supplementary Tables

**Table S2.1** – Mass correction slopes and associated error for each method using the most parsimonious model.

| **Method** | **Model** | **Estimate** | **Std. Error** | ***p*-value** | ***Adj r²*** |
|---|---|---|---|---|---|
| SMR | log(SMR)~log(Weight) + Species | 0.910 | 0.104 | >0.001 | 0.867 |
| $RMR_L$ | log($RMR_L$)~log(Weight) + Species | 0.848 | 0.104 | >0.001 | 0.884 |
| MMR | log(MMR)~log(Weight) + Species | 0.735 | 0.117 | >0.001 | 0.850 |
| $RMR_F$ | log($RMR_F$)~log(Weight) | 0.760 | 0.049 | >0.001 | 0.830 |

**Table S2.2** - Model structure and output of the effect of mass-corrected $RMR_F$ and species on mass-corrected SMR, $RMR_L$ or MMR. The bottom model considers the effect of method of measuring metabolism (SMR, $RMR_L$, MMR or $RMR_F$) on the rate of (mass-corrected) oxygen consumption (metabolism) with an interactive effect of species. All measures of metabolic rate were natural logged in all models and the most parsimonious model chosen using Akaike Information Criterion is shown in all cases.

| **Model Structure** | **Model Outputs** | | | | | |
|---|---|---|---|---|---|---|
| | **Fixed Effects** | **Estimate** | **Std Error** | **t** | **P** | **Adj $r^2$** |
| **lm: ln(SMR) ~ ln($RMR_F$) + Species** | Intercept | -1.085 | 0.115 | -9.439 | <0.001 | 0.57 |
| | $RMR_F$ | 0.317 | 0.112 | 2.842 | 0.007 | |
| | Stickleback | 0.169 | 0.104 | 1.624 | 0.111 | |
| | Trout | -0.630 | 0.108 | -5.812 | <0.001 | |
| **lm: ln($RMR_L$) ~ ln($RMR_F$) + Species** | Intercept | -0.813 | 0.124 | -6.577 | <0.001 | 0.44 |
| | $RMR_F$ | 0.252 | 0.121 | 2.081 | 0.044 | |
| | Stickleback | -0.066 | 0.108 | -0.611 | 0.544 | |
| | Trout | -0.589 | 0.110 | -5.35 | <0.001 | |
| **lm: ln(MMR) ~ ln($RMR_F$)** | Intercept | 0.582 | 0.108 | 5.391 | <0.001 | -0.01 |
| | $RMR_F$ | 0.093 | 0.135 | 0.692 | 0.493 | |
| | | **numDF** | **denDF** | **F** | **P** | |
| **lmm: ln(Metabolism) ~ Method * Species** | Intercept | 1 | 137 | 804.37 | <0.001 | 0.87 |
| | Method | 3 | 137 | 607.08 | <0.001 | |
| | Species | 2 | 48 | 19.51 | <0.001 | |
| | Method:Species | 6 | 137 | 17.29 | <0.001 | |

**Table S2.3** – Spearman's Rank Correlation outputs of mass corrected $RMR_L$ vs $RMR_F$ for each species.

| Species | *S* | *p*-value | ρ |
|---|---|---|---|
| Trout | 406 | 0.320 | 0.275 |
| Minnow | 328 | 0.333 | 0.279 |
| Stickleback | 472 | 0.249 | 0.306 |

**Table S2.4** - Full information of the intermittent-flow respirometry set-up and measurements of maximum metabolic rate (MMR), standard metabolic rate (SMR), and routine metabolic rate in the laboratory ($RMR_L$) of fish, list from Killen et al., (2021).

| Number | Criterion and Category | Response |
|---|---|---|
| | **EQUIPMENT, MATERIALS, AND SETUP** | |
| **1** | Body mass of animals at time of respirometry | 0.5 - 22.38 grams |
| **2** | Volume of empty respirometers | 80 – 138 mL (Depending on the size of fish) |
| **3** | How chamber mixing was achieved | Peristaltic pump |
| **4** | Ratio of net respirometer volume (plus any associated tubing in mixing circuit) to animal body mass | 6.6 - 235 |
| **5** | Material of tubing used in any mixing circuit | Tygon gas-impermeable tubing |
| **6** | Volume of tubing in any mixing circuit | 10.3 - 12.5 |
| **7** | Confirm volume of tubing in any mixing circuit was included in calculations of oxygen uptake | Yes |
| **8** | Material of respirometer (e.g. glass, acrylic, etc.) | Glass |
| **9** | Type of oxygen probe and data recording | FireStingO2; Pyro Science GmbH, Aachen, Germany |
| **10** | Sampling frequency of water dissolved oxygen | 2s |
| **11** | Describe placement of oxygen probe (in mixing circuit or directly in chamber) | In recirculation circuit |
| **12** | Flow rate during flushing and recirculation, or confirm that chamber returned to normoxia during flushing | About one chamber volume/min; chambers returned to normoxia during flushing |
| **13** | Timing of flush/closed cycles | See table S2 |
| **14** | Wait (delay) time excluded from closed measurement cycles | 60s |
| **15** | Frequency and method of probe calibration (for both 0 and 100% calibrations) | 0% at start of experiment and 100% before each run's measurement day |
| **16** | State whether software temperature compensation was used during recording of water oxygen concentration | No |

| | | |
|---|---|---|
| | **MEASUREMENT CONDITIONS** | |
| **17** | Temperature during respirometry | 12ºC for Sticklebacks, 14ºC for Trout and Minnows |
| **18** | How temperature was controlled | Thermostat (TMP-REG; Loligo Systems, Viborg, Denmark) controlled a pump that directed water through a heat exchange coil within a cooled water reserve whenever temperature within the bath dropped below the setpoint. |
| **19** | Photoperiod during respirometry | ~10:14 (light:dark) |
| **20** | If (and how) ambient water bath was cleaned and aerated during measurement of oxygen uptake (e.g. filtration, periodic or continuous water changes) | Continuously aerated during measurement via airstone in the bath. |
| **21** | Total volume of ambient water bath and any associated reservoirs | 40L |
| **22** | Minimum water oxygen dissolved oxygen reached during closed phases | Mean minimum across all SMR measurements was 8.33 $mgL^{-1}$ and MMR exceptionally reached 4.93 $mgL^{-1}$ |
| **23** | State whether chambers were visually shielded from external disturbance | Yes, shielded with dividers around each chamber |
| **24** | How many animals were measured during a given respirometry trial (i.e. how many animals were in the same water bath) | 2 - 15 |
| **25** | If multiple animals were measured simultaneously, state whether they were able to see each other during measurements | No, dividers shielded each tube |
| **26** | Duration of animal fasting before placement in respirometer | 24h |
| **27** | Duration of all trials combined (number of days to measure all animals in the study) | 9 days |
| **28** | Acclimation time to the laboratory (or time since capture for field studies) before respirometry measurements | ~2 months |
| | **BACKGROUND RESPIRATION** | |
| **29** | State whether background microbial respiration was measured and accounted for, and if so, method used (e.g. parallel measures with empty respirometry chamber, measurements before and after for all chambers while empty, both) | Before SMR and after MMR with each chamber |
| **30** | State if background respiration was measured at beginning and/or end, state how many slopes and for what duration | 3 slopes before fish went in for SMR and 3 slopes after MMR |
| **31** | State how changes in background respiration were modelled over time (e.g. linear, exponential, parallel measures) | Linearly |
| **32** | Level of background respiration (e.g. as a percentage of SMR) | 6.2% |
| **33** | Method and frequency of system cleaning (e.g. system bleached between each trial, UV lamp) | The system was cleaned with bleach after every respirometry trial and water continuously cleaned with ultraviolet (UV) lamps during trials. |

| | | |
|---|---|---|
| | **STANDARD OR ROUTINE METABOLIC RATE** | |
| **34** | Acclimation time after transfer to chamber, or alternatively, time to reach beginning of metabolic rate measurements after introduction to chamber | 3 hours |
| **35** | Time period, within a trial, over which oxygen uptake was measured (e.g. number of hours) | SMR: ~16 hours. RMR: 3 hours |
| **36** | Value taken as SMR/RMR (e.g. quantile, mean of lowest 10 percent, mean of all values) | SMR: Lowest 20$^{th}$ percentile. RMR: Mean of all slopes with $r^2 > 0.8$, measured between 7:30am and the end of the experiment at approximately 10:30am |
| **37** | Total number of slopes measured and used to derive metabolic rate (e.g. how much data were used to calculate quantiles) | SMR: ~90 Slopes. RMR: ~20 Slopes |
| **38** | Whether any time periods were removed from calculations of SMR/RMR (e.g. data during acclimation, periods of high activity [e.g. daytime]) | Daytime (7:30am onwards) was excluded from SMR measurements, Nighttime (before 7:30am) was excluded from RMR measurements. |
| **39** | $r^2$ threshold for slopes used for SMR/RMR (or mean) | 0.80 |
| **40** | Proportion of data removed due to being outliers below r-squared threshold | 1.8% |
| | **MAXIMUM METABOLIC RATE** | |
| **41** | When MMR was measured in relation to SMR (i.e. before or after) | After |
| **42** | Method used (e.g. critical swimming speed respirometry, swim to exhaustion in swim tunnel, or chase to exhaustion) | Chase to exhaustion |
| **43** | Value taken as MMR (e.g. the highest rate of oxygen uptake value after transfer, average of highest values) | Highest rate after transfer |
| **44** | If MMR measured post-exhaustion, length of activity challenge or chase (e.g. 2 min, until exhaustion, etc.) | Until exhaustion |
| **45** | If MMR measured post-exhaustion, state whether further air-exposure was added after exercise | No air exposure |
| **46** | If MMR measured post-exhaustion, time until transfer to chamber after exhaustion or time to start of oxygen uptake recording | ~10s |
| **47** | Duration of slopes used to calculate MMR (e.g. 1 min, 5 min, etc.) | 30s |
| **48** | Slope estimation method for MMR (e.g. rolling regression, sequential discrete time frames) | Rolling regression. |
| **49** | How absolute aerobic scope and/or factorial aerobic scope is calculated (i.e. using raw SMR and MMR, allometrically mass-adjusted SMR and MMR, or allometrically mass-adjusting aerobic scope itself) | Allometrically mass-adjusted |
| | **DATA HANDLING AND STATISTICS** | |
| **50** | Sample size | 54 |
| **51** | How oxygen uptake rates were calculated (software or script, equation, units, etc.) | RespR R package (Harianto et al., 2019) |
| **52** | Confirm that volume (mass) of animal was subtracted from respirometer volume when calculating oxygen uptake rates | Yes |

| | | |
|---|---|---|
| **53** | State whether analyses accounted for variation in body mass and describe any allometric mass-corrections or adjustments | Metabolic rate was adjusted for by body mass by calculating scaling exponents for each metabolic rate measurement with body mass and adjusting by these (see methods). |

**Table S2.5** - Length of flush/ closed phases and species numbers for each day of the intermittent flow experiments.

| Day | Flush/Closed Time (min) | Species |
|---|---|---|
| 1 | 2/8 | N=15 (Minnow) |
| 2 | 3/7 | N=1 (Trout) and N=5 (Minnow) |
| 3 | 3/7 | N=2 (Trout) and N= 12 (Stickleback) |
| 4 | 4/6 | N=2 (Trout) |
| 5 | 4/6 | N=2 (Trout) and N=5 (Stickleback) |
| 6 | 4/6 | N=2 (Trout) and N=1 (Stickleback) |
| 7 | 4/6 | N=2 (Trout) |
| 8 | 4/6 | N=2 (Trout) |
| 9 | 4/6 | N=2 (Trout) |

### 2.5.2 Supplementary Figures

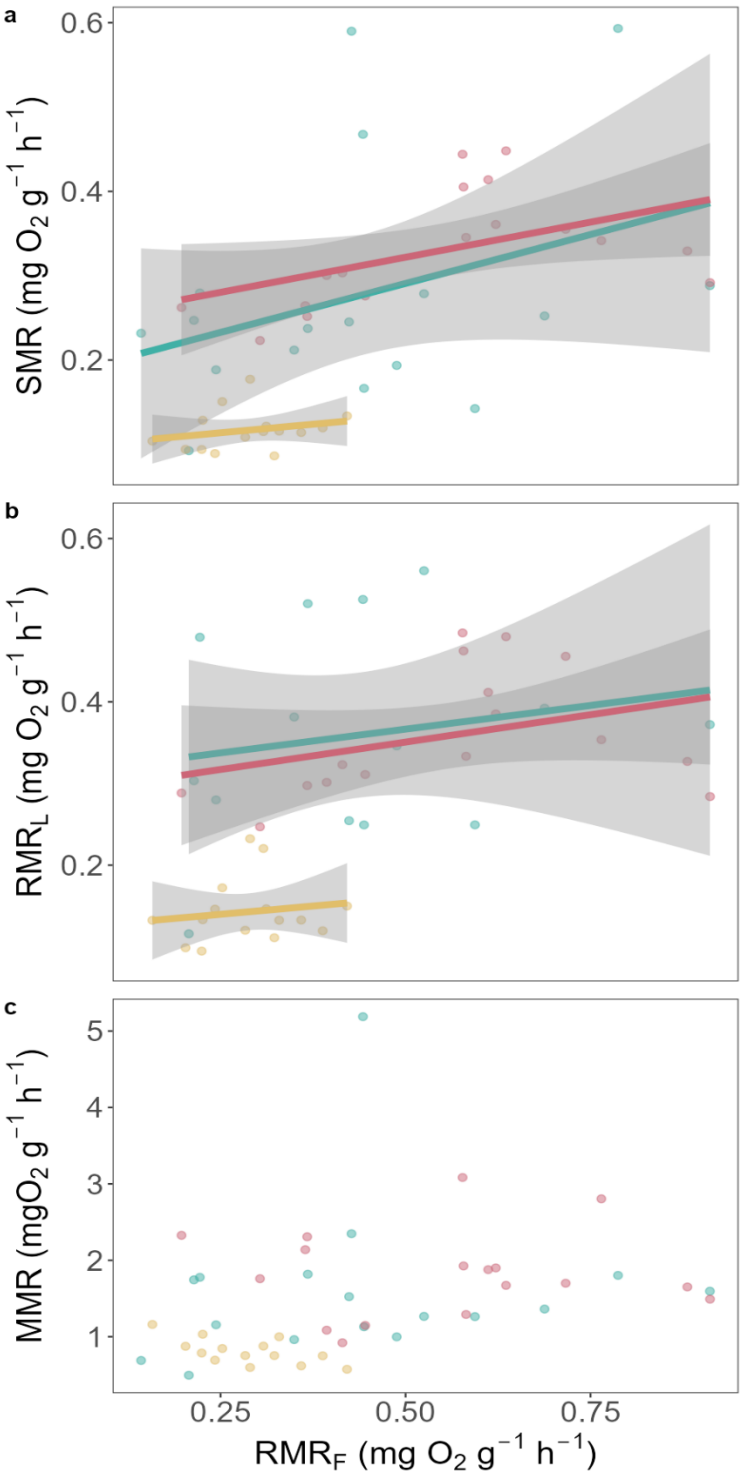



**Figure S2.1** – Uncorrected metabolic rates for a) SMR, b) $RMR_L$, and c) MMR plotted against $RMR_F$. Species is denoted by colour (red for sticklebacks, blue for minnows, and brown for brown trout), regression lines are only plotted for significant relationships.

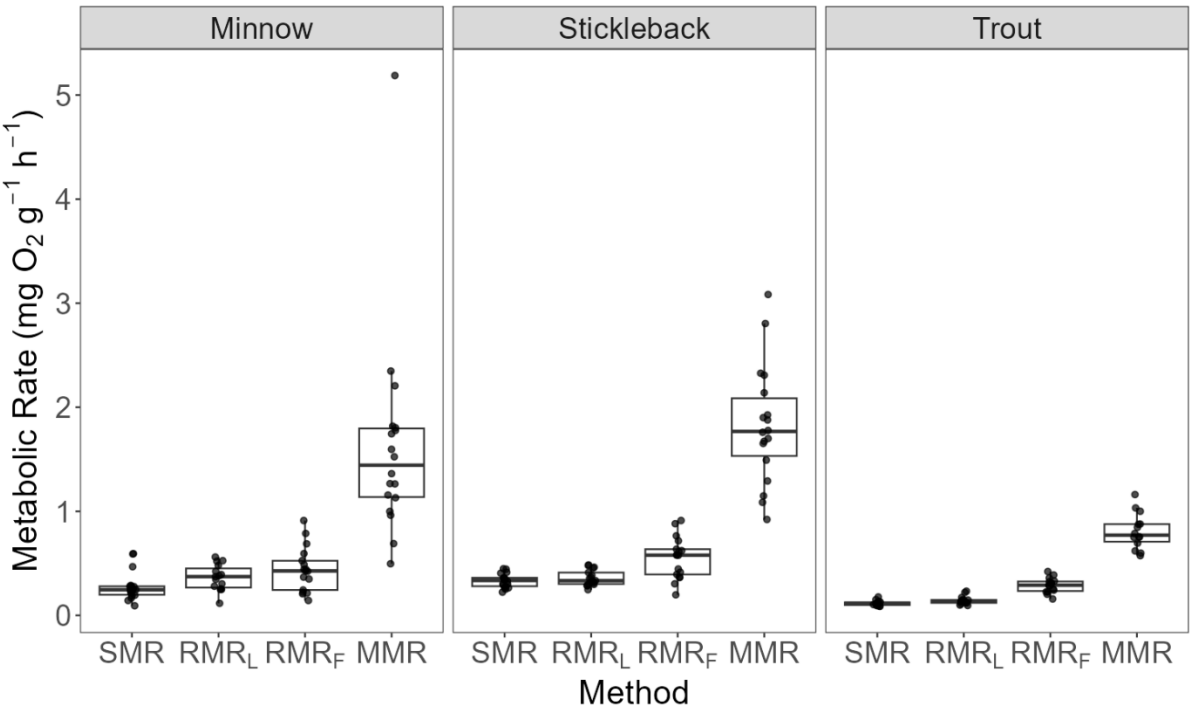



**Figure S2.2** – Boxplots of metabolic rate measurements using each method (SMR, $RMR_L$, $RMR_F$, MMR) for each species.

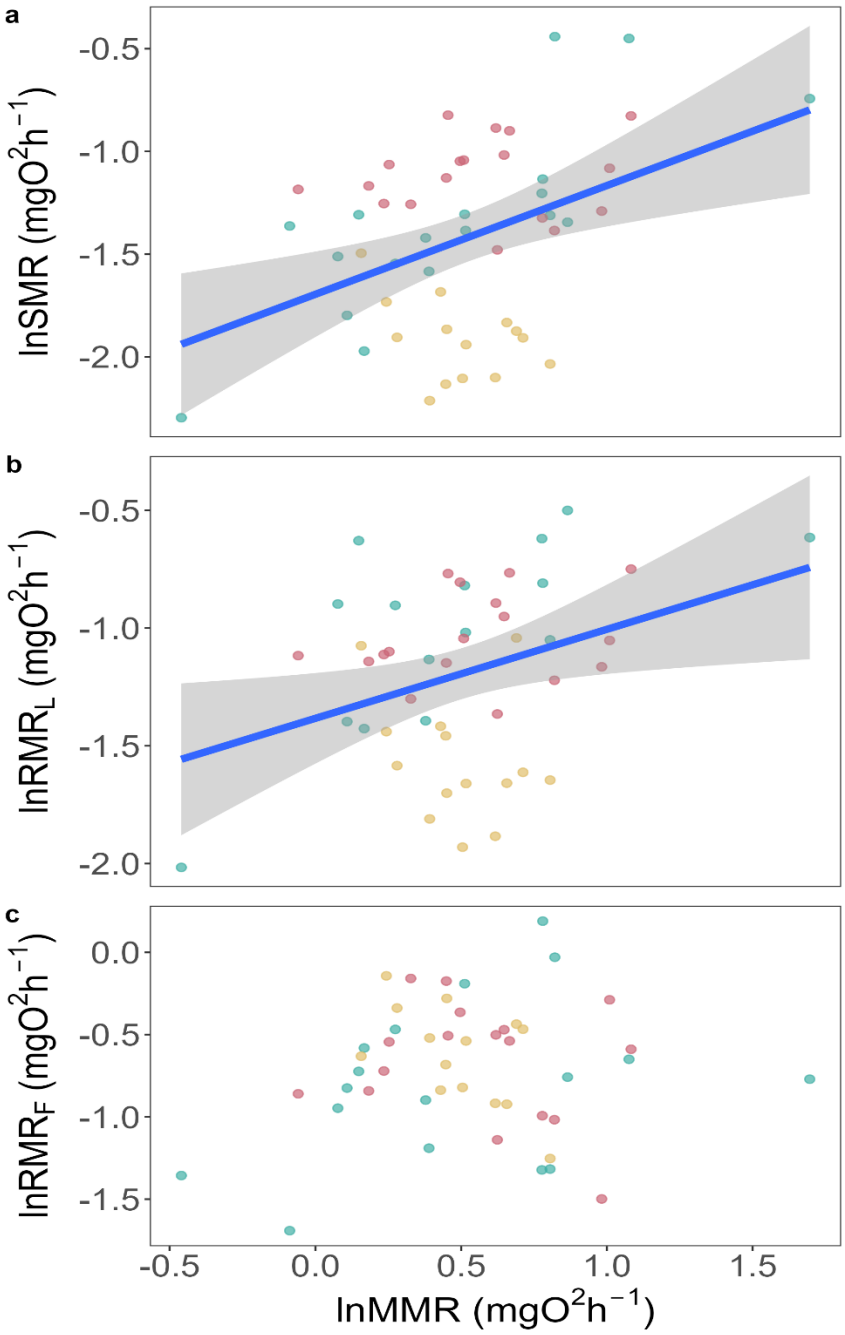



**Figure S2.3** - Metabolic rates for a) SMR, b) $RMR_L$, and c) $RMR_F$ plotted against MMR. All rates are mass corrected and then logged with species denoted by colour (red for sticklebacks, blue for minnows, and brown for brown trout), regression lines are only plotted for significant relationships.

# Chapter 3. Thermal variability can increase the thermal sensitivity of metabolism, growth, and condition in brown trout (*Salmo trutta*)

*In prep for Global Change Biology*

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**Abstract**

Climate change is increasing both the mean and variability of temperatures, with larger and more frequent fluctuations predicted globally. For ectotherms such as fish, thermal variability may be particularly challenging because fluctuating conditions require greater physiological plasticity. If fish can change their energy use allowing them to adjust efficiently to ambient conditions, they will be more resilient to a changing climate. However, it remains unclear whether exposure to different levels of thermal variability result in differences in plasticity, and how this ultimately influences fitness in the wild. Here, we compared the thermal sensitivity (inferred by a steeper relationship with temperature) of metabolism, growth, and condition factor in brown trout (*Salmo trutta*) from six Spanish streams exhibiting contrasting thermal regimes. Fish from variable streams exhibited greater thermal sensitivity in all three traits than conspecifics from thermally stable streams. Growth was faster in thermally variable streams at low temperatures but declined sharply in the warmest site; while condition in these fish was lower than that of stable conspecifics at low temperatures but increased at high temperatures. Together, these results suggest that long-term exposure to thermal variability can promote a more plastic phenotype capable of adjusting physiological performance and energy allocation in response to changing temperatures. This plasticity may enhance performance in variable climates, although its benefits appeared constrained at upper limits. Further work disentangling adaptive and acclimatised responses and across a broader range of temperatures and taxa is needed to determine the generality of these responses and their implications for resilience to climate change.

## 3.1 Introduction

Although global mean air temperature is projected to rise by 1.5–4.4 °C by 2100, some of the most acute biological challenges are expected to arise from extreme events like heatwaves and cold snaps (IPCC, 2023). Such events generate rapid and pronounced departures from baseline temperatures, exceeding the magnitude and threat of mean warming (Vasseur et al., 2014). These events are of particular concern for freshwater fish, a third of which are already at risk of extinction (Sayer et al., 2025). Furthermore, in the near future freshwater fish may have half of their present-day range exposed to climatic extremes beyond modern levels (Barbarossa et al., 2021). These temperature spikes are expected to have a range of direct impacts on freshwater fish, including reduced oxygen availability, elevated metabolic rates, and habitat loss via reduced water levels (Clarke, 2004; Dudgeon et al., 2006; Limburg et al., 2020). Consequently, the influence of thermal variability on physiological performance has been highlighted as crucial to predicting the impacts of climate change (Morash et al., 2018).

One mechanism by which organisms may cope with increased thermal variability may be greater trait plasticity, which is the capacity of individual organisms to alter their physiology, behaviour, or life history expression in response to environmental change (McKechnie, 2008). Notably, studies have shown that fish exposed to stable conditions over generations show reduced plasticity, suggesting the converse could be true (Morgan et al., 2022). Furthermore, higher plasticity is thought to increase resilience to climate change as organisms can better optimise for the current conditions and is evolutionarily favoured in variable conditions where the variation is predictable via cues. Acclimation is linked to plasticity, whereby acute responses to environmental perturbations decline over the lifetime of the organism. Plasticity can maximise fitness and minimise unnecessary costs by altering traits such as metabolic rate in response to stimuli (e.g. temperature or food availability) (Affinito et al., 2024; Auer et al., 2015; Cavieres and Sabat, 2008). Plasticity may involve metabolic or survival costs, especially given it is not retained without selection pressure, but evidence of these costs is mixed (Auld et al., 2010; Buskirk and Steiner, 2009; DeWitt et al., 1998).

Metabolism is the sum of all energetic reactions within an organism, and is strongly governed by both body mass and temperature (Brown et al., 2004). There are

several common metrics of metabolism, such as standard metabolic rate (SMR) the cost of self-maintenance and routine metabolic rate (RMR) which is SMR plus the addition of routine movement (Fry, 1971; McNab, 1997). Rising temperatures will increase metabolism, raising baseline energy requirements while also enabling faster physiological processes such as food acquisition and digestion (Brown et al., 2004; Volkoff and Rønnestad, 2020). When prey are abundant enough to meet these higher demands, fish may exhibit accelerated growth and earlier maturation driven by faster developmental rates, potentially also resulting in a smaller size at maturity (Brett, 1971; Ikpewe et al., 2021; Neuheimer et al., 2011). Thermal sensitivity describes the rate at which metabolism increases with temperature. Lower thermal sensitivity is often interpreted as evidence of thermal compensation, whereby ectotherms maintain more stable metabolic rates across temperatures and may therefore be more resilient to warming (Schulte, 2015; Seebacher et al., 2015). Many biological rates (e.g. metabolism and growth) follow characteristic thermal performance curves (TPC's) (Elliott and Elliott, 2010). In TPC's the rate increases with temperature to a thermal optima beyond which the rising cost of maintenance can exceed the ability to increase cardiac output and food intake, constraining growth, fitness, and ultimately resulting in death (Neubauer and Andersen, 2019; Neuheimer et al., 2011). The relationship between metabolism of an individual and growth is complex, with higher metabolic rate individuals associated with dominance and faster growth in laboratory environments (Fausch, 1984). While in the wild, the highest growth can be achieved with the lowest SMR required to dominate the best feeding areas (Metcalfe et al., 1995; Reid et al., 2011). However, a higher metabolic rate will also constrain growth during poor feeding conditions, when feeding cannot subsidise the high SMR (Zeng et al., 2017).

Given the fitness implications of metabolism, it is no surprise that fish routinely exposed to high temperatures over multiple generations may adaptively suppress their metabolic rate and/or evolve greater tolerance to thermal extremes, mitigating some of the effects outlined above (McGaughran et al., 2021; Pilakouta et al., 2020). However, while research has often focussed on the responses to mean and also extreme warming, limited studies have investigated the influence of thermal variability, and whether long-term exposure to temperature fluctuations may result in organisms becoming better adapted to a changing climate. This is of particular note

as the magnitude of thermal variability is predicted to increase rapidly over coming decades (IPCC, 2023).

Freshwater streams can experience substantial thermal variability, undergoing daily variations of up to 15°C and seasonal fluctuations of over 20 °C due to their reliance on fresh water inputs and low volumes (Caissie, 2006). However, a strong influence of cold ground water can buffer this variation (Constantz, 1998; Kaandorp et al., 2019), creating a range of variability across natural streams. Organisms exposed to more variable temperatures over generations can become more thermally tolerant, as seen across distinct taxa, ranging from insects to gobies (Chen and Stillman, 2012; Silva et al., 2019). Therefore, fish from more variable environments are likely to exhibit different responses to temperature than stable adapted conspecifics and this may increase resilience to climate change. In this study, we exploited a series of streams in Northern Spain characterised by contrasting levels of temperature variation at the southern (native) range margin of brown trout (*Salmo trutta*). Several streams have experienced much more stable thermal ecology due to a stronger groundwater influence than streams with a variable thermal regime, making this an ideal model system to test how the thermal sensitivity of biological traits compare for fish that are inhabiting streams with low thermal variability (LTV) or high thermal variability (HTV).

We hypothesise that wild fish from HTV streams will exhibit a more buffered and therefore lower thermal sensitivity of metabolism, but a more plastic and flexible fitness response to differing temperatures than fish from LTV streams, as indicated by their growth, and condition factor.

## 3.2 Methods

### 3.2.1 Sites

Six streams were selected within the Picos de Europa national park, Spain (Fig. 3.1), three of which were groundwater fed and showed low annual thermal variation and thus categorized as LTV and three which were not and thus categorized as HTV (Constantz, 1998). Each LTV site had a nearby paired HTV site within 5 km to reduce potential confounding factors of the surrounding landscape. Measurements of stream temperatures were taken every five minutes over periods ranging from a week to a month from 2015 to 2024 (Table S3.1). The mean of all these temperature

records for each stream between June 1 and September 1 was used to represent each stream's mean summer temperature. Note that temperature data for one stream (Ponga Ermita) were not available thus temperatures were collected from 500 m downstream in the main Ponga river. However, these temperatures may have diverged from the true temperatures experienced by the fish thus all analyses were repeated excluding this point to ensure the same directionality in model terms was observed.

All streams were narrow (<2 m width), shallow (<1 m depth), and shaded by riparian vegetation. To assess similarity in broad habitat features among sites, Normalised Difference Vegetation Index (NDVI) of the surrounding landscape was calculated, with higher values indicating healthier, denser vegetation (Table S3.1). NDVI was obtained from the MODIS MOD13Q1 product (250 m resolution, 16-day composites) using the MODISTools R package (Hufkens, 2013). For each site, NDVI values were extracted from the MODIS pixel or pixels within 250 m of each site and averaged across the 12 months preceding the sampling month (following Jackson et al., 2024).

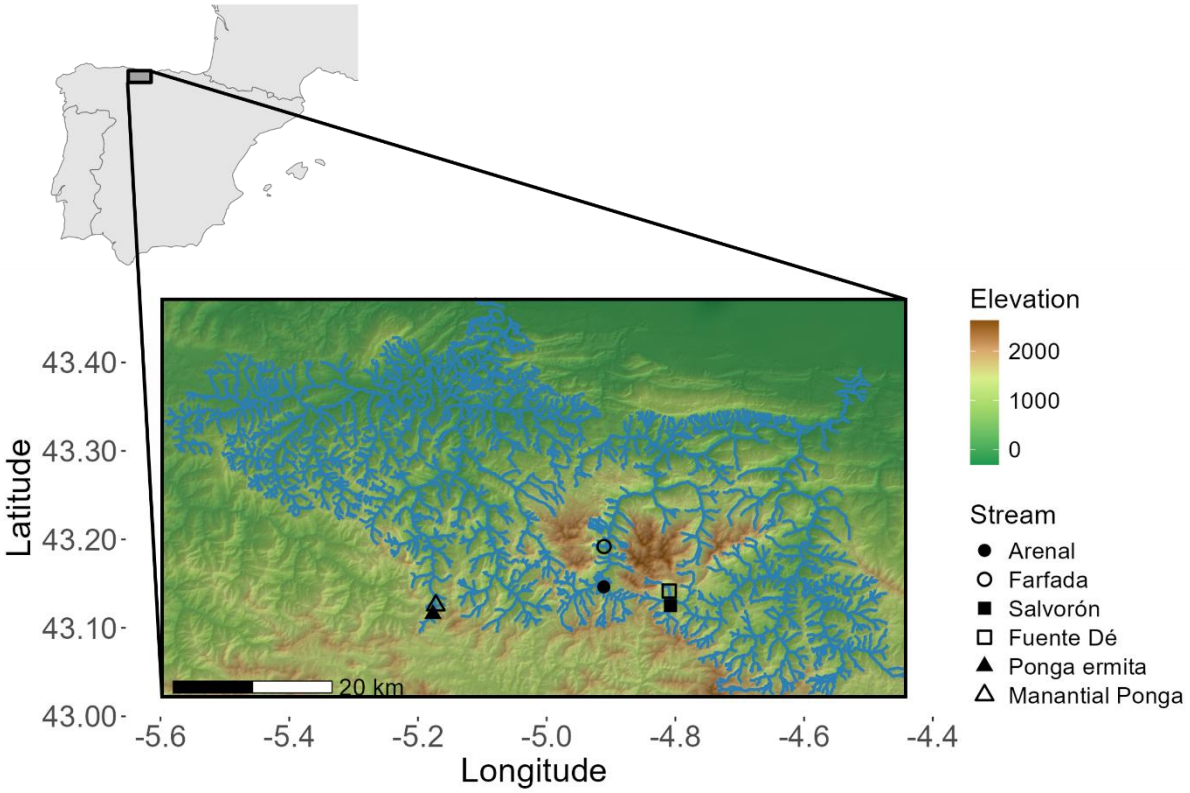



**Figure 3.1** - Map of Spain with the sampling region highlighted and an inset showing all stream sites within the river network (blue) of the Picos de Europa national park.

Filled and open symbols represent high and low thermal variability streams, respectively.

### 3.2.2 Sampling

At each site, 24-38 brown trout (fork length [FL] = 129±35 mm, age = 1+ - 4+) were captured via single pass electrofishing (Table S3.1). Each fish was individually transferred into a 7.2 L chamber, filled with water filtered through a 250 µm sieve to remove any small plant or animal matter. Each chamber also contained a probe (miniDOT, Precision Measurements Engineering “PME”, accurate 0.01 mg/L ± 5%) to continuously log temperature and dissolved oxygen concentrations every minute, and an underwater motor (Model no. 7350, Playmobil) to circulate the water. Chambers were sealed and checked for air bubbles before being submerged in the river at a depth of 5-20 cm where they were left for 90 minutes. An additional chamber without a fish was used as a control to calculate the background respiration rate over each trial. After the 90-minute experiment, each fish was transferred into clove oil anaesthetic until reaching surgical anaesthesia, characterised by unconsciousness and loss of responsiveness, then their fork length and total weight measured, and approximately five scale samples collected. This was all carried out under ethics approved by the University of Essex ethics committee (ETH2324-192). Fish were then placed into a recovery bucket of fresh stream water before being released back at the location from which they had been caught.

### 3.2.3 Metabolic Rate

The first 30 minutes of each experiment was considered as habituation time for the fish with the remaining 60 minutes used to calculate the routine metabolic rate in the field, henceforth referred to as $RMR_F$, representing unfed but normally active organisms with the addition of field stresses (Chabot et al., 2016b; Treberg et al., 2016). Oxygen consumption rates were calculated by running 20-minute rolling linear regressions of dissolved oxygen against time, with the mean of the lowest 20% of these slopes with $r^2 > 0.8$ used to calculate $RMR_F$. A metabolic rate was not calculated if all slopes were below this $r^2$ threshold, which occurred in 1.4% of cases. $RMR_F$ (mg $O_2$ $h^{-1}$) was calculated by dividing each of the accepted slope values by the volume of the water (i.e. the volume of the chamber minus the volumes of the miniDOT, motor, and fish) and subtracting background respiration, which was modelled linearly over the duration of the experiment in the control chamber.

### 3.2.4 Scale Aging and Growth

3-5 scales from each fish were individually imaged with the best condition scale used to estimate the age of the fish by counting winter checks (Chilton and Beamish, 1982). Size at first and second winter check was then estimated using the Fraiser-Lee method of linear back-calculation based on size-at-capture, here assuming a fork length at first scale formation of 30 mm (Heidarsson et al., 2006; Jensen and Johnsen, 1982; Lea, 1910). Size at first winter was used as a proxy for early growth rate, to minimise ontogenetic effects and maximise sample size, as many fish were <2 years old, but all were >1 years old. Their size at first winter check was then divided by the days between hatch (assumed to be 15$^{th}$ March) and the end of the active growing season (assumed to be 6$^{th}$ December, where temperatures first dropped to 0% growth potential, see Chapter 4 methods) in order to estimate an average daily growth rate per fish in the first year of its life, hereafter referred to as growth (Bal et al., 2011; Lobón-Cerviá, 2007).

### 3.2.5 Condition Factor

Fulton's condition factor, $K$, was calculated for each fish as $K = 100 \times W / L^3$, where $W$ is the weight (g) and $L$ is the length (mm) of the fish (Ricker, 1975). In addition, we used a historic database of brown trout length and weight data (caught from the same sites and months; August – October) using the same methods between 2012 and 2025; ($n$=2606, FL = 110±44, Table S3.2), to facilitate comparisons of condition factor between stable and variable streams over an extended time period.

### 3.2.6 Statistical Analysis

All statistical analysis was carried out in R and Rstudio (R Core Team, 2024). First, metabolic rates were mass corrected as follows:

$$I_M = \frac{I}{M^b} \quad (1)$$

Where $I_M$ is mass-corrected metabolism, $I$ is whole organism metabolic rate, $M$ is mass of the organism, and $b$ is the allometric scaling exponent which for our data was 0.86 (Brown et al., 2004). $I_M$ was then temperature corrected as follows:

$$I_{MT} = \frac{I_M}{e^{E_A \frac{T-T_0}{kTT_0}}} \quad (2)$$

Where $E_A$ is the activation energy in electron volts (eV) (i.e., the slope of the relationship between metabolic rate and Arrhenius temperature, which was 0.24 across all fish), $T$ is temperature in kelvin, $T_0$ is the mean temperature of all chambers in the study over the measurement period, and $k$ is the Boltzmann constant ($8.617 \times 10^{-5} eVK^{-1}$) (Brown et al., 2004).

To examine the effect of thermal variability on the thermal sensitivity of metabolism, a linear model was run with log-transformed metabolism (mass corrected) as the response variable and the main and interactive effects of experimental temperature (continuous) and thermal variability (two levels: high and low) as the explanatory variables. Temperature varied little within streams and was primarily driven by differences among streams, whilst the high variability streams were also warmer than the low variability streams at the time of sampling (Fig. S3.1). To facilitate comparisons between thermal variability levels, temperature was centred by subtracting the mean temperature for each variability group from the temperature of each stream. This approach allowed a more direct comparison of fish responses to temperatures experienced within their naturally occurring range across all plots and models.

To assess the effect of thermal variability on growth, both a linear and second order polynomial model were run with growth rate as the response variable and all possible main and interactive effects of mean summer temperature (centred as above), thermal variability, log-transformed mass- and temperature-corrected metabolism, and condition factor as explanatory variables. This followed expectation that growth would exhibit a linear or quadratic response typical to a TPC. The optimal model from all combinations of terms (including linear and second-order polynomial variants) using the '*dredge*' function within '*MuMin*' was selected by Akaike Information Criterion (AIC) where there was no difference in AIC greater than two the simplest model was used (Burnham and Anderson, 2002; Bartoń, 2025).

Finally, the extended dataset gathered over 13 years was used to test for an association between thermal variability and condition factor via a linear and second order polynomial mixed effects model using the *'lmer'* function within the *'lme4'* R package (Bates et al., 2015). This included main and interactive effects of thermal variability and centred mean summer temperature, alongside random effects of

sampling month nested within sampling year nested within sampling site. The optimal model from all combinations of terms was selected as above by AIC.

## 3.3 Results

### 3.3.1 Thermal Variability and Metabolism

Overall fish in this study exhibited a significant log-linear increase in metabolism with increasing temperature across all streams ($t$ = 2.932, $p$ = 0.004; full model adjusted $r^2$ = 0.09), while thermal variability level had no significant effect on metabolism ($t$ = 0.652, $p$ = 0.515). However, there was a significant interaction with variability level, with fish found in HTV streams having a significantly higher thermal sensitivity of metabolism than those found in LTV streams ($t$ = 2.128, $p$ = 0.035, Fig. 3.2). Thus, the metabolic rate of HTV stream fish was greater at higher temperatures but less than LTV stream fish at lower temperatures (Fig. 3.2). The range of temperatures experienced over the course of the experiment in variable streams was narrower and higher than stable streams, showing the opposite trend than the annual temperature range (see Fig. S3.1). Note when the model was rerun without Ponga Ermita the same directionality in all model terms was observed (see Table S3.3).

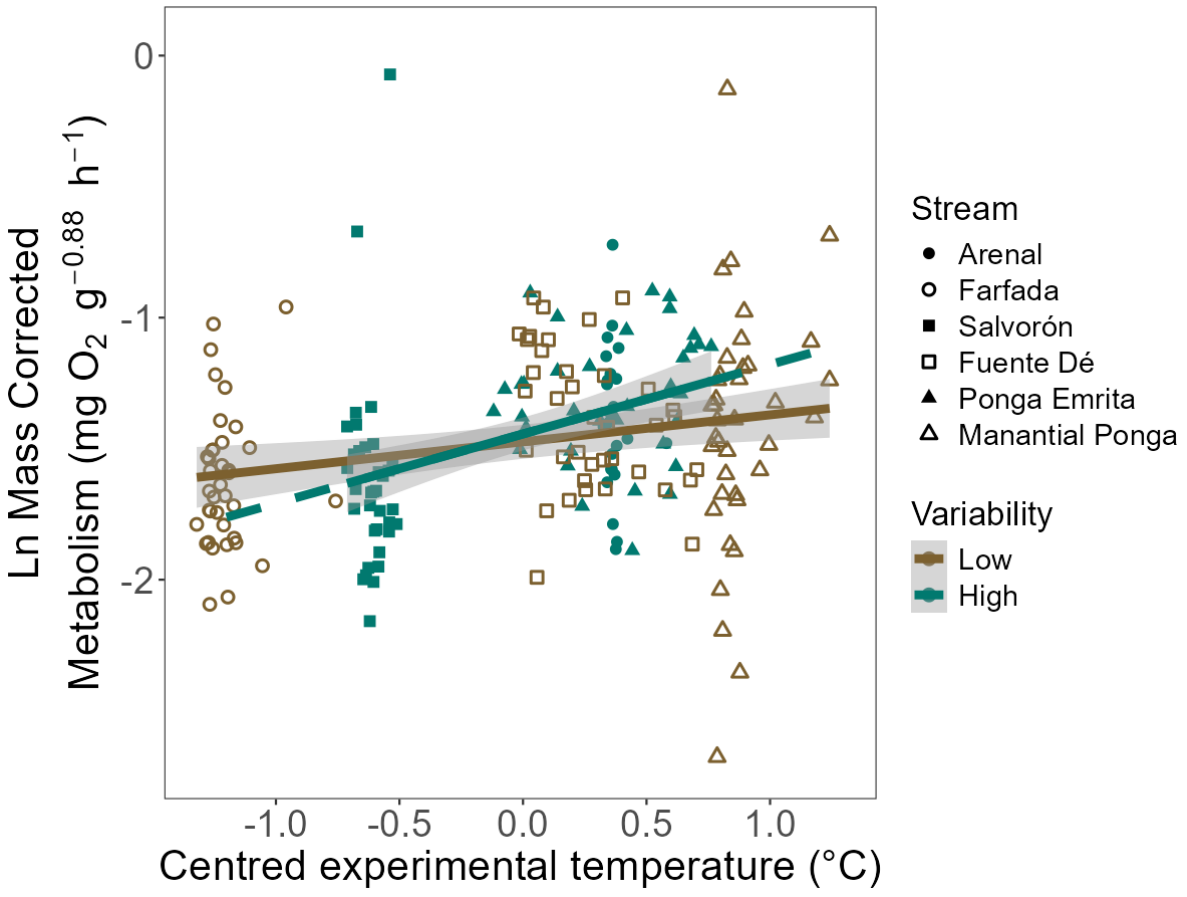


**Figure 3.2** – The effect of centred temperature measured during the experiment on the log-transformed metabolic rate of fish captured from high variability streams (filled symbols) or low variability streams (open symbols). Lines and shaded areas represent model predictions and 95% confidence intervals, respectively (Low variability: $y = -1.47+0.10x$; high variability: $y = -1.44+0.26x$), with the dotted line showing predictions beyond the measured temperature range. Note that metabolic rate was mass-corrected to account for the different sizes of fish in the experiment, whilst temperature was centred within each thermal variability level for a more direct comparison between the two. See Fig. S3.1 for the same plot using raw temperature data and see Table S3.4 for full model outputs.

### 3.3.2 Thermal Sensitivity of Growth

The best fitting model for growth (adjusted $r^2 = 0.25$) in the first year included a non-significant linear positive effect of temperature on growth in the LTV streams ($t = 1.376$, $p = 0.171$), and no polynomial temperature influence on growth ($t = -0.580$, $p = 0.563$). However, there was an interaction between variability and temperature resulting in a significant polynomial effect of temperature on growth in the HTV streams with an initial increase in growth followed by up to a 52% reduction from 0.33 mm/day to 0.17 mm/day at higher temperatures ($t = -3.240$, $p = 0.014$, Fig. 3.3). There was a significant increase in growth between the HTV and LTV streams ($t = 2.633$, $p = 0.009$) though this was mediated by temperature as above. Note that neither metabolism nor condition was included as a co-variate in the best-fitting model. The same relationship was also found for the growth of trout in their second year, albeit with fewer data points, as many fish were less than two years of age (Fig. S3.2). When the model was rerun without Ponga Ermita, the same directionality in all model terms was observed (Table S3.3). See Table S3.5 for all candidate models within 2 AIC.

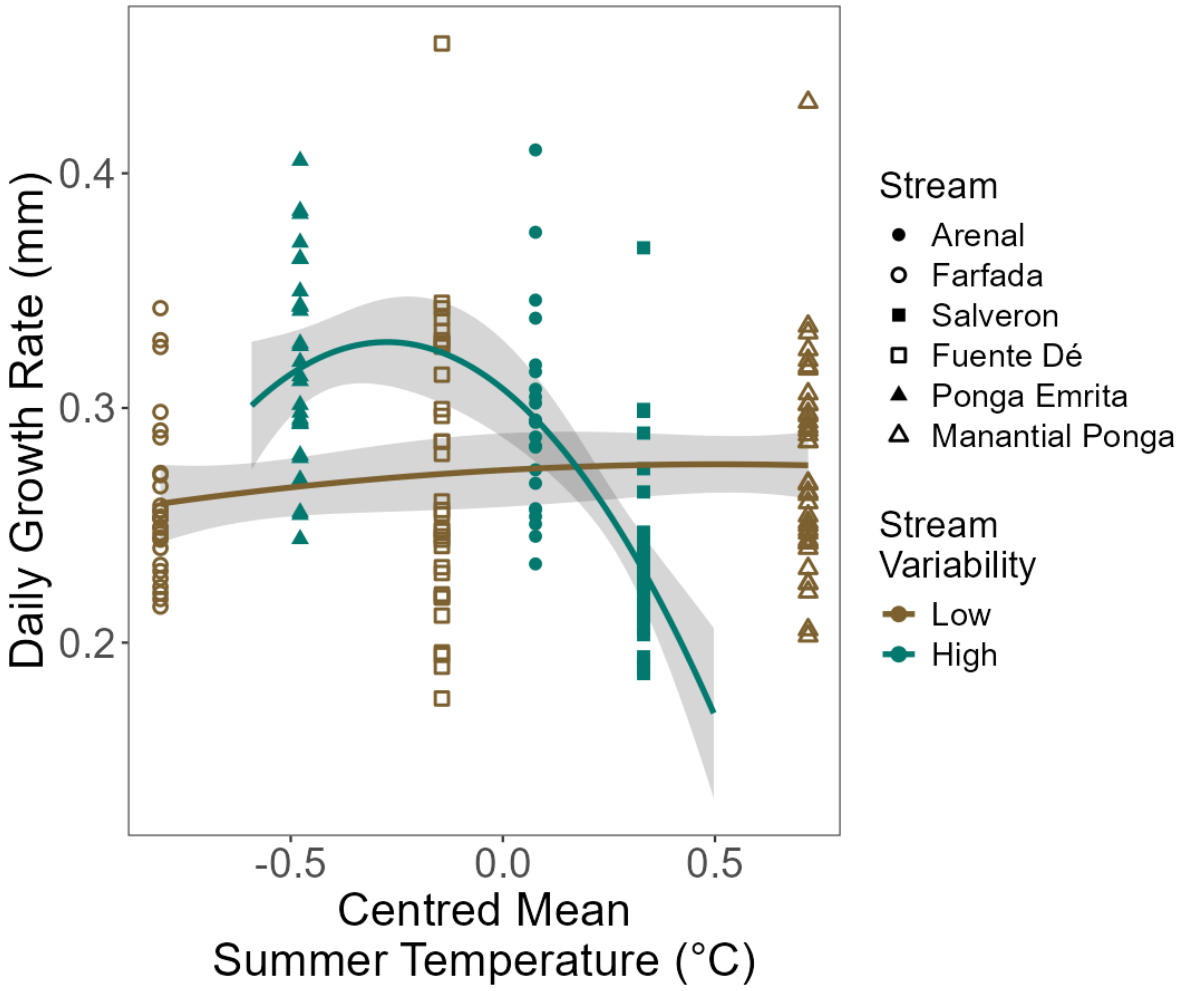



**Figure 3.3** - Growth over the first year against centred mean summer temperature for fish caught from high thermal variability streams (green, filled symbols) and low thermal variability streams (brown, open symbols). Lines and shaded areas represent model predictions and 95% confidence intervals, respectively (Low variability: $y = 0.274+0.001x–0.001x^2$; high variability: $y = 0.311–0.146x–0.266x^2$). See Table S3.6 for full model output and Fig. S3.3 for the same plot using raw temperature data.

### 3.3.3 Thermal Sensitivity of Condition

The best fitting model (Model conditional $r^2 = 0.11$) was a linear model which showed no difference in body condition with summer temperature ($t = -0.705$, $p = 0.483$). Furthermore, high variability led to decreased condition ($t = -2.089$, $p = 0.042$). However, there was a significant interaction between variability and temperature ($t = 2.728$, $p = 0.009$), such that HTV fish had a poorer condition than LTV fish at low temperatures but a higher condition at high temperatures ($t = -2.089$, $p = 0.042$).

Thus, lower summer temperatures appear to be associated with lower condition of fish in variable streams but not in stable ones. When the model was rerun without Ponga Ermita the same directionality in all model terms was observed (Table S3.3).

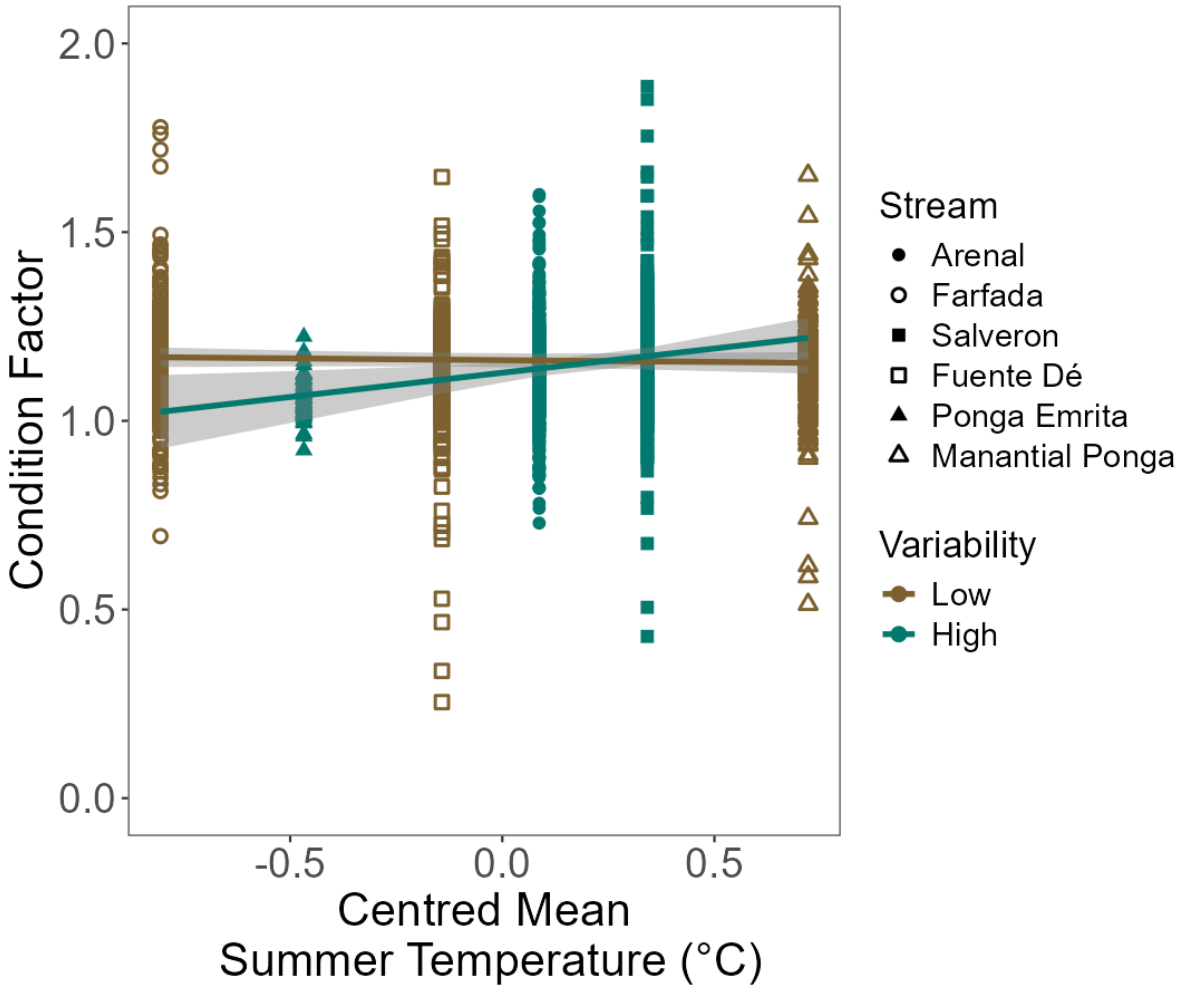



**Figure 3.4** – Condition of historically sampled fish against centred mean summer temperature for fish caught from high thermal variability streams (green, filled symbols) and low thermal variability streams (brown, open symbols). Lines and shaded areas represent model predictions and 95% confidence intervals respectively (Low variability y = 1.16 -0.01x; high variability: y = 1.13+0.10x. See Fig. S3.4 for the same plot using raw temperature data and see Table S3.7 for full model outputs.

## 3.4 Discussion

Our results indicate that brown trout originating from streams with increased thermal variability exhibit greater thermal sensitivity of metabolism, growth, and condition than conspecifics from thermally stable streams. Our findings are consistent with local adaptation of phenotypic plasticity capable of adjusting performance to

changing environmental conditions in HTV streams. This also suggests a cost as this plasticity is not selected for or retained in the LTV environments. Here we consider plasticity to be the capacity of the population to alter their physiology, behaviour, or life history expression in response to environmental change, rather than individual phenotypic flexibility (McKechnie, 2008).

While thermal sensitivity of metabolism is expected in ectotherms (Clarke, 2004), the stronger response observed in HTV streams suggests increased physiological plasticity, i.e. the capacity to elevate their metabolism more at higher temperatures than fish from LTV streams. Higher thermal sensitivity of metabolism is often indicative of poor thermal resilience (Seebacher et al., 2015) and was hypothesised to be lower in HTV streams. However, where these fish are operating within natural temperature ranges and well below thermal limits we argue that thermal sensitivity of $RMR_F$ can facilitate more flexible energetic behaviour potentially maximising efficiency and growth potential depending on the thermal regime (Dijk et al., 2002). Our interpretation is that this increased thermal sensitivity may be indicative of metabolic plasticity with the fish changing their metabolic rate more to maximise fitness opportunities, resulting in the increased growth observed. Fish from HTV streams also exhibited greater thermal sensitivity of growth, condition, and differing allocations between the two with temperature, indicating that thermal variability influences multiple physiological and fitness-related traits rather than metabolism alone.

We observed generally higher growth rates in the fish from HTV streams at lower centred temperatures, suggesting that fish may utilise a more variable metabolism to maximise growth (Mooij et al., 2008; Rountrey et al., 2014). However, growth in the warmest HTV stream was lower than that observed in the LTV streams. While the availability of temperature data only allowed us to estimate mean summer temperatures across multiple years, we expect the HTV streams to experience larger swings in temperature, and speculate that this reduction in growth in the warmest stream could reflect costs associated with more frequent high stress events such as heatwaves and cold snaps that will limit fish performance and growth (Alfonso et al., 2021; Neuheimer et al., 2011). We saw no direct relationship between metabolic rate and growth, suggesting that a high metabolic rate is not necessarily advantageous

for growth as other laboratory studies have suggested for complex, field environments (Reid et al., 2012, 2011).

Where the HTV streams are exposed to warmer summers and cooler winters, the higher growth rates during the first growing season may be the result of fish decreasing their metabolic costs in cooler conditions and then increasing their feeding when in-stream production increases. This is supported by the absolute temperatures observed during the experiments, which averaged 3 °C higher in HTV than LTV streams. A similar mechanism has been observed in starved roach and Sockeye salmon, which selected warmer conditions in the day to maximise feeding and cooler conditions at night to minimise costs (Chen et al., 2019; Dijk et al., 2002; Volkoff and Rønnestad, 2020). Alternatively, increased fat storage in cooler conditions may facilitate survival while waiting for a warm pulse to increase growth opportunities. This has been suggested to occur in other fish experiencing variable water level and feeding opportunities (Junk, 1985), with high condition factor correlating with survival through cold, low-feeding winters (Sogard and Olla, 2000). It is interesting that the LTV streams exhibited lower growth at the lower temperatures (though not overall) despite more stable and thus predictable conditions. This may be the result of a more continuous feeding strategy, though this should be investigated using behavioural studies accompanied by more regular growth measurements throughout the year.

We noted that condition factor was lower in HTV fish at low centred temperatures but higher than LTV fish at higher centred temperatures, showing almost the opposite trend to growth. This may indicate that fish acclimated and adapted to variable conditions show a plastic response in energy allocation shifting allocation from growth in length in cool conditions to fat storage and increased condition factor in warmer conditions. This may be as condition and fat storage is more important than length in environmental extremes and indeed increased condition and falling growth efficiency with temperature has been observed in Atlantic salmon (Dwyer and Piper, 1987; Sogard and Olla, 2000). These differing responses may be the result of LTV fish being able to predict stable future feeding opportunities and thus invest equally in condition and growth, while HTV fish require a more variable plastic strategy to take advantage of differing the conditions (Piersma and Drent, 2003).

While we may expect some fitness or metabolic cost to plasticity we observed no clear metabolic costs, while fitness costs appear temperature dependant (Auld et al., 2010; DeWitt et al., 1998). Measuring metabolic costs was not something our experimental design set out to do, and indeed reproductive success may be a more reliable measure of cost. Nevertheless, the lack of difference in metabolism at the same temperature may be because $RMR_F$ has significant behavioural and movement components that may mask any differences in basal metabolic costs associated with maintaining plasticity. Alternatively, this may be because the plasticity is in the behaviour rather than baseline metabolic costs. Indeed, the fact that there appears to be less plasticity in the LTV streams suggests that there is some cost or it would be retained (Morgan et al., 2022).

The mechanism underlying the different thermal responses observed is likely a combination of acclimation and local adaptation. Brown trout in the Cantabrian Mountains are generally resident (i.e. non-anadromous) and show high site fidelity, completing their life cycles in small stream reaches with few local movements (Lagerspetz, 2006; Lobón-Cerviá, 2009). The fish in more variable conditions should then have acclimated and adapted to the range of temperatures and the trade-offs between basal costs and potential for increased feeding rates selecting a more plastic rate, as has been seen in other organisms both seasonally and annually (Boratyński et al., 2016; Versteegh et al., 2012). Further, fish are more likely to remain resident and reproduce in their natal stream than move (Ferguson et al., 2019; Lobón-Cerviá, 2009), thus facilitating local adaptation.

Our results are consistent with the idea that organisms may increase the plasticity of their traits as Earth's climate becomes more variable (IPCC, 2023; Magozzi and Calosi, 2015; Reed et al., 2011). Organisms acclimated and adapted to HTV may fare better under the increased environmental fluctuations predicted by climate models (McGaughran et al., 2021). However, theoretical models suggest that these benefits are contingent on environmental cues remaining sufficiently reliable to enable adaptive plastic responses, something that may break down with increasing global change (Reed et al., 2010). Longer term resilience to rising thermal extremes may require genetic adaptation, but the pressure to adapt may be weaker in organisms with plastic traits, such as behaviourally avoiding higher temperatures (Buckley and Kingsolver, 2021). However adaptive plasticity may allow more time for

genetic adaption or increased plasticity selected for (Chevin et al., 2010). These more plastic fish may be better able to alter their energetic costs via behaviour and underlying metabolic shifts to optimise performance for a given set of conditions (Affinito et al., 2024; Auer et al., 2015).

However, we cannot disentangle the behavioural and basal SMR components contributing to $RMR_F$ here and so these rates may not be behaviourally moderated and driven solely by an increase in underlying SMR. This in turn would mean that the $RMR_F$ of fish exposed to more variable conditions could become unsustainably high under pronounced warming, making them more vulnerable than the less thermally sensitive, LTV fish. Furthermore, we do see that growth in HTV fish declines at higher temperatures, therefore climate resilience may only extend to increased variability and not mean warming. Future research should seek to better disentangle these relationships.

It should be noted that the fish were only observed over narrow natural thermal gradients experienced on the day of sampling, spanning just 1.5 - 2.5°C within the low and high variability streams. Whilst this is more representative of changing climatic conditions, it provides a very narrow window from which to observe thermal sensitivity. While we cannot rule out the possibility that differences in thermal sensitivity of metabolism between HTV and LTV streams may be due to the absolute differences in temperature, existing literature suggests that over this narrow increase and on log scale we would expect a linear trend especially well below thermal limits relationship (Clarke and Fraser, 2004; Clarke and Johnston, 1999). Though it should be noted that the relationships between metabolism and temperature follow an exponential relationship (Clarke and Fraser, 2004; Clarke and Johnston, 1999). Interestingly the variation of the HTV streams over the measured days was lower than that of the LTV, though this is an artifacts of weather and conditions on the given week. Importantly, our growth and condition analyses show effects of thermal variability taking an average summer temperature over many years of sampling, demonstrating longer term effects that are independent of absolute temperature differences. The low number of sample sites increases the possibility that relationships may be driven by uncontrolled characteristics of any individual stream or stream population, however, the streams were all paired to minimise geographical differences and found to have similar levels of surrounding productivity (Table S3.1).

Additionally, the measured temperatures from one stream (Ponga Ermita) showed reduced variability than would be expected from a HTV stream. This is likely because there were no temperatures available for this stream so a site on the Ponga river downstream was used instead, and this will be less variable than the experimental stream due to the larger volume of water. However, to ensure this did not unduly influence results, all analyses were repeated with this stream excluded and the same directionality was found in all model terms.

In summary, our findings show that long-term exposure to thermal variability is associated with greater thermal sensitivity of metabolism, growth, and condition, consistent with a more plastic phenotype that adopts different energy allocation strategies across temperatures. Further research is needed to disentangle the contributions of selective mortality, genetic differentiation, and phenotypic plasticity to the patterns observed here, all of which may have important implications for species vulnerability to future warming and increasing thermal variability. Although thermal variability was associated with higher growth at low and intermediate temperatures, its generality and limits should be tested across broader thermal, temporal, and taxonomic scales. Deeper understanding of the mechanisms underpinning these responses, particularly the relative contributions of behavioural activity and basal metabolic upregulation to $RMR_F$, will improve predictions of how fish respond to climate change. This could be achieved through complementary laboratory and field studies combining measurements of SMR, $RMR_F$, and behaviour.

## 3.5 Supplementary Material

### 3.5.1 Supplementary Tables

**Table S3.1** – Full information on individual stream temperatures sampled (11/09/2023-14/09/2023) (including categorical type, summer mean, and summer variability measured as standard deviation, SD), productivity inferred via NDVI, and number of fish sampled (*n*).

| Stream name | Type | Longitude, Latitude | Summer mean temperature (°C) | Summer temperature SD | NDVI | *n* | FL |
|---|---|---|---|---|---|---|---|
| Arenal | Variable | -4.911, 43.146 | 12.3 | 1.53 | 0.65 | 24 | 108-215 |
| Farfada | Stable | -4.911, 43.191 | 8.7 | 0.82 | 0.71 | 37 | 100-185 |
| Salvorón | Variable | -4.808, 43.125 | 12.5 | 1.63 | 0.66 | 35 | 89-220 |
| Manantial Ponga | Stable | -5.176, 43.123 | 10.2 | 0.77 | 0.61 | 38 | 87-245 |
| Ponga Ermita | Variable | -5.177, 43.116 | 11.7 | 0.70 | 0.60 | 36 | 106-215 |
| Fuente De | Stable | -4.810, 43.142 | 9.3 | 0.51 | 0.65 | 38 | 84-203 |

**Table S3.2** – Historic sampling numbers for each stream in the condition factor analysis.

| Year | Arenal | Farfada | Salvorón | Manantial Ponga | Ponga Ermita | Fuente De |
|---|---|---|---|---|---|---|
| 2012 | 91 | 35 | 125 | 10 | - | - |
| 2013 | 33 | 45 | 64 | 25 | - | - |
| 2014 | 11 | 24 | 44 | 0 | - | - |
| 2015 | 6 | 14 | 34 | 20 | - | - |
| 2016 | 17 | 3 | 20 | 17 | - | - |
| 2017 | 24 | 8 | 20 | 5 | - | - |
| 2018 | 17 | 40 | 94 | 24 | - | - |
| 2019 | 11 | 27 | 34 | 21 | - | - |
| 2020 | 62 | 9 | 46 | 19 | - | 30 |
| 2021 | 52 | 34 | 68 | 14 | - | 51 |
| 2022 | 50 | 0 | 68 | 9 | - | 30 |
| 2023 | 77 | 24 | 79 | 33 | - | 86 |
| 2024 | 211 | 33 | 65 | 7 | - | 61 |
| 2025 | 188 | 94 | 55 | 20 | 62 | 6 |
| **Total** | **850** | **390** | **816** | **224** | **62** | **264** |

**Table S3.3** - Sensitivity analysis model outputs for all models excluding ponga Ermita, the Poly(Temperature)2 * HTV is NA as with only two sites a polynomial is impossible to calculate.

| Model Structure | Main Effects | Estimate | Std Error | t value | p value |
|---|---|---|---|---|---|
| **Lm: Metabolism ~ Temperature * Variability** | Intercept | -1.475 | 0.033 | -45.38 | <0.001 |
| | Temperature | 0.103 | 0.037 | 2.803 | 0.006 |
| | HTV | -0.045 | 0.059 | -0.076 | 0.940 |
| | Temperature * HTV | 0.120 | 0.100 | 1.204 | 0.230 |
| **Lm: Growth ~ poly(Temperature) * Variability + Condition** | Intercept | 0.274 | 0.008 | 34.30 | <0.001 |
| | Poly(Temperature) 1 | 0.010 | 0.007 | 1.37 | 0.173 |
| | Ploy(Temperature)2 | -0.010 | 0.017 | -0.58 | 0.565 |
| | HTV | 0.041 | 0.015 | 2.76 | 0.006 |
| | Poly(Temperature) 1 * HTV | -0.260 | 0.048 | -5.40 | <0.001 |
| | Ploy(Temperature)2 * HTV | NA | NA | NA | NA |
| | Intercept | 1.152 | 0.009 | 123.401 | <0.001 |
| **Lmer: Condition ~ Temperature * Variability** | LTV | 0.011 | 0.013 | 0.804 | 0.425 |
| | Temperature | 0.117 | 0.071 | 1.643 | 0.107 |
| | LTV * Temperature | -0.126 | 0.072 | -1.746 | 0.087 |

**Table S3.4** – Model structure and output for the effect of experimental temperature, and variability on mass corrected metabolism.

| Model Structure | Model Outputs Fixed Effects | Estimate | Std Error | t value | p value |
|---|---|---|---|---|---|
| **Lm: Growth ~ poly(Temperature, 2) * Variability + Condition**) | Intercept | -1.474 | 0.031 | -47.44 | <0.001 |
| | Temperature | 0.103 | 0.035 | 2.93 | 0.004 |
| | High Variability | 0.030 | 0.046 | 0.65 | 0.515 |
| | Temperature * High Variability | 0.162 | 0.076 | 2.13 | 0.035 |

**Table S3.5** - All candidate growth models within 2 AIC of the lowest AIC model

| Model Structure | df | AIC |
|---|---|---|
| Lmer: Growth ~ poly(Temperature, 2)*Var + Condition | 8 | -620.0 |
| Lmer: Growth ~ poly(Temperature, 2)*Var + poly(Temperature, 2)*Condition | 10 | -619.6 |
| Lmer: Growth ~ poly(Temperature, 2)*Var + Condition + Metabolism | 9 | -619.3 |
| Lmer: Growth ~ poly(Temperature, 2)*Var + poly(Temperature, 2)*Condition + Metabolism | 11 | -619.2 |
| Lmer: Growth ~ poly(Temperature, 2)*Var + Condition*Var | 9 | -618.5 |
| Lmer: Growth ~ poly(Temperature, 2)*Var | 7 | -618.5 |
| Lmer: Growth ~ poly(Temperature, 2)*Var + poly(Temperature, 2)*Condition + Conditon*Var | 11 | -618.2 |

**Table S3.6** – Model structure and output for the effect of centred temperature, variability, and condition on growth in the first year.

| Model Structure | Model Outputs Fixed Effects | Estimate | Std Error | t value | p value |
|---|---|---|---|---|---|
| **Lm: Growth ~ poly(Temperature, 2) * Variability + Condition**) | Intercept | 0.274 | 0.008 | 34.489 | <0.001 |
| | Poly (Temperature)1 | 0.010 | 0.007 | 1.38 | 0.171 |
| | Poly (Temperature)2 | -0.010 | 0.017 | -0.58 | 0.563 |
| | High Variability | 0.035 | 0.013 | 2.63 | 0.009 |
| | Poly (Temperature)1 * High Variability | -0.156 | 0.020 | -7.63 | <0.001 |
| | Poly (Temperature)2 * High Variability | -0.257 | 0.079 | -3.24 | 0.001 |

**Table S3.7** – Model structure and output for the effect of centred temperature and variability on condition factor in an additional dataset of fish.

| Model Structure | Model Outputs Fixed Effects | Estimate | Std Error | t value | p value |
|---|---|---|---|---|---|
| **Lmer: Condition ~ Temperature * Variability +1\|Site: Year/Month**) | Intercept | 1.161 | 0.009 | 124.6 | <0.001 |
| | High Variability | -0.033 | 0.016 | -2.09 | 0.042 |
| | Temperature | -0.010 | 0.014 | -0.71 | 0.483 |
| | Temperature*High Variability | -0.138 | 0.051 | -2.73 | 0.009 |

### 3.5.2 Supplementary Figures

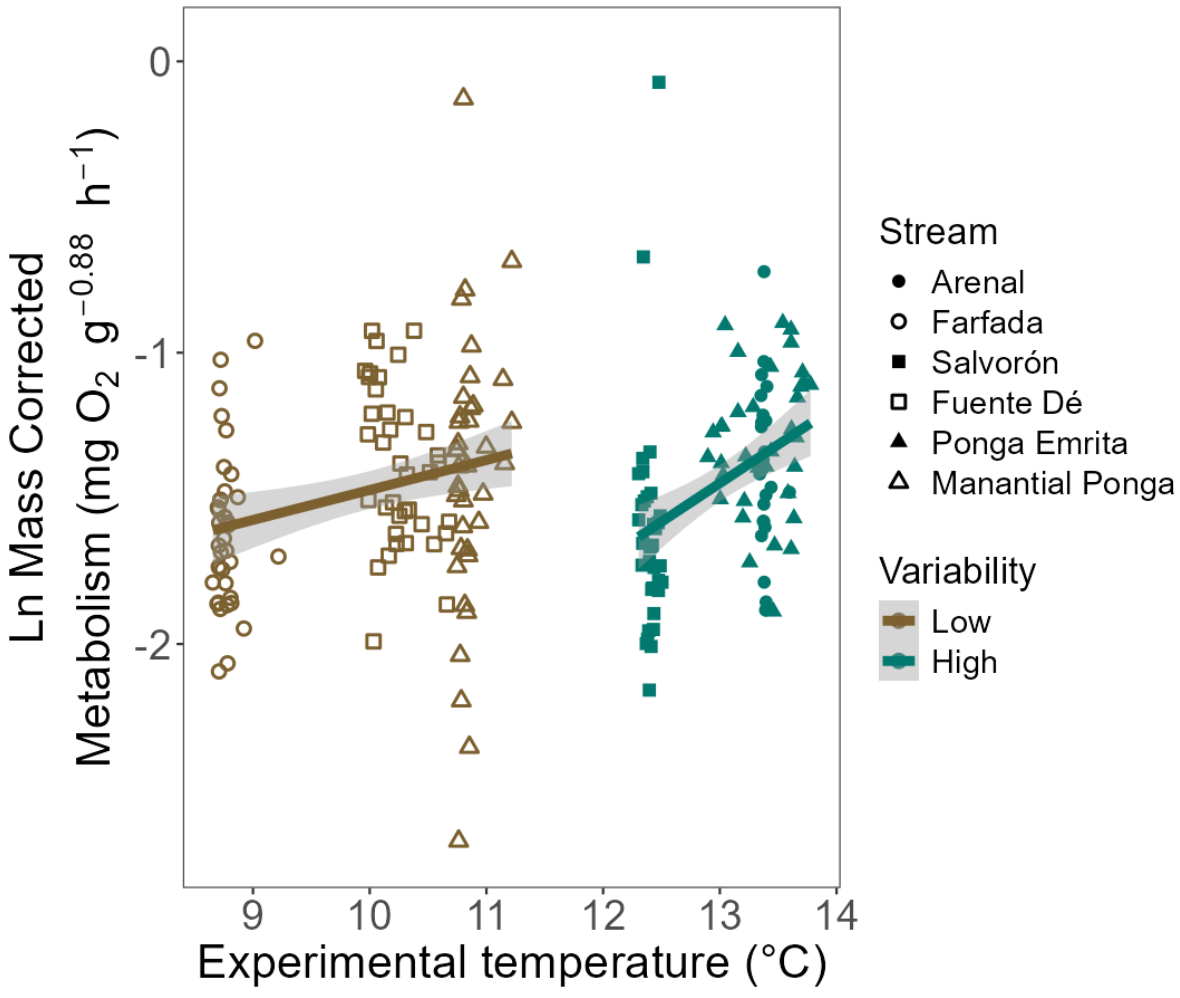



**Figure S3.1** – The effect of temperature on the ln metabolic rate of fish captured from thermally variable streams (full shape) or thermally stable streams (hollow shape). Note that metabolic rate was mass-corrected to account for differences in size of fish in the experiment.

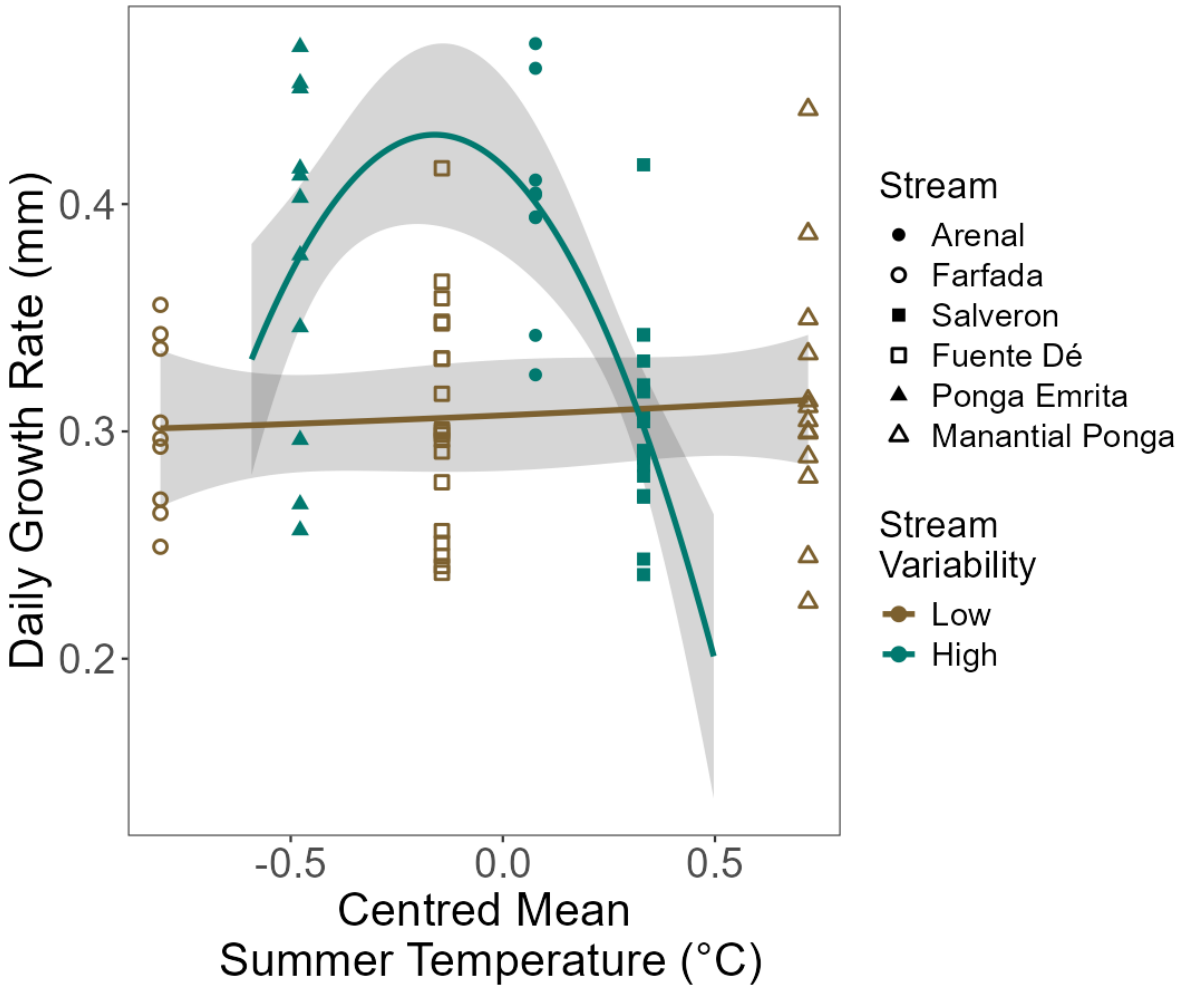



**Figure S3.2** – Daily growth over the second year against centred mean summer temperature for fish from thermally variable streams (full shape) or thermally stable streams (hollow shape), with the lines and confidence intervals given by the predictions of the same model structure as used for the first-year growth.

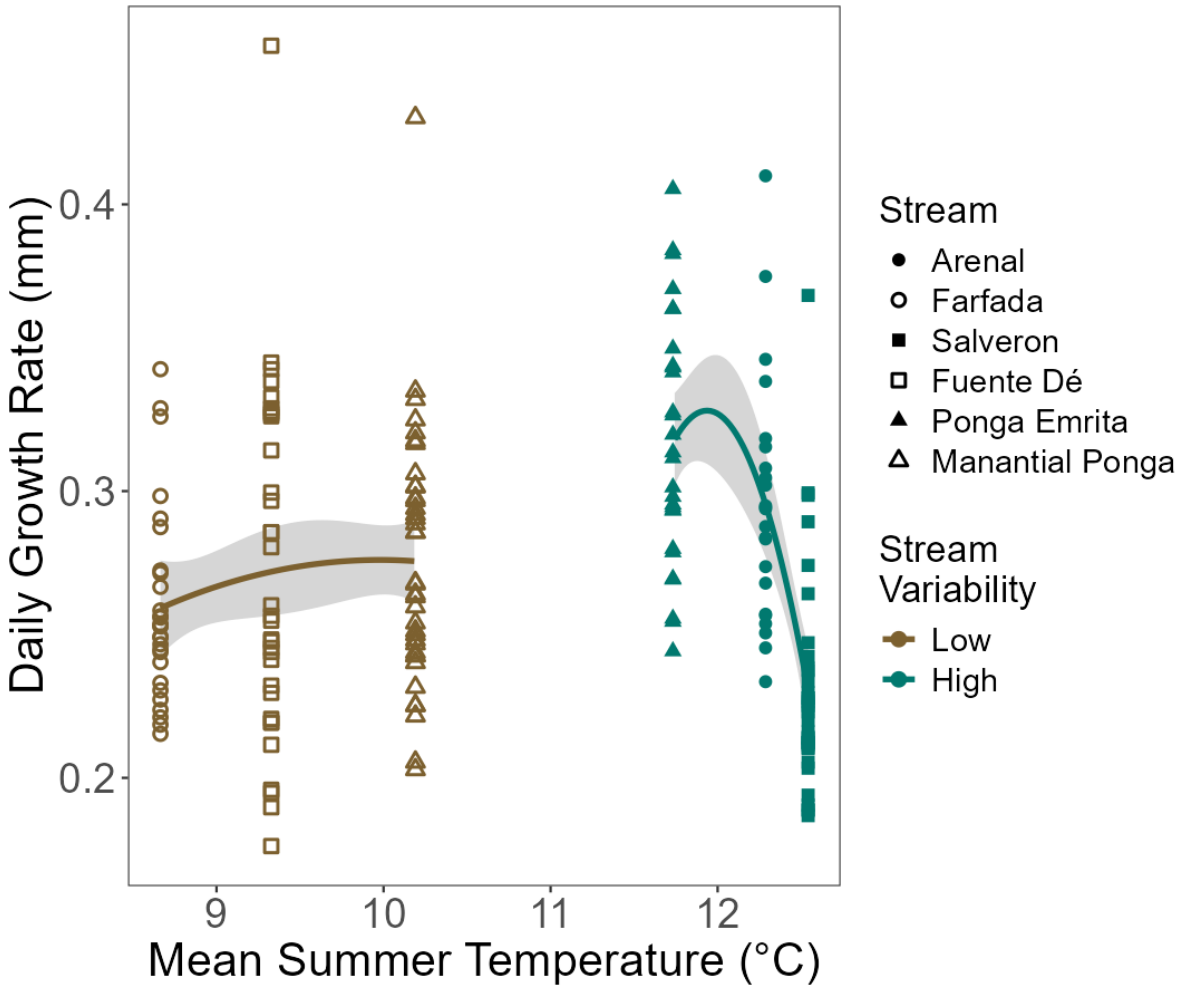



**Figure S3.3** - Daily growth over the first year against uncentred mean summer temperature for fish from thermally variable streams (full shape) or thermally stable streams (hollow shape), with the lines and confidence intervals given by the predictions of the same model structure as used for the first-year growth.

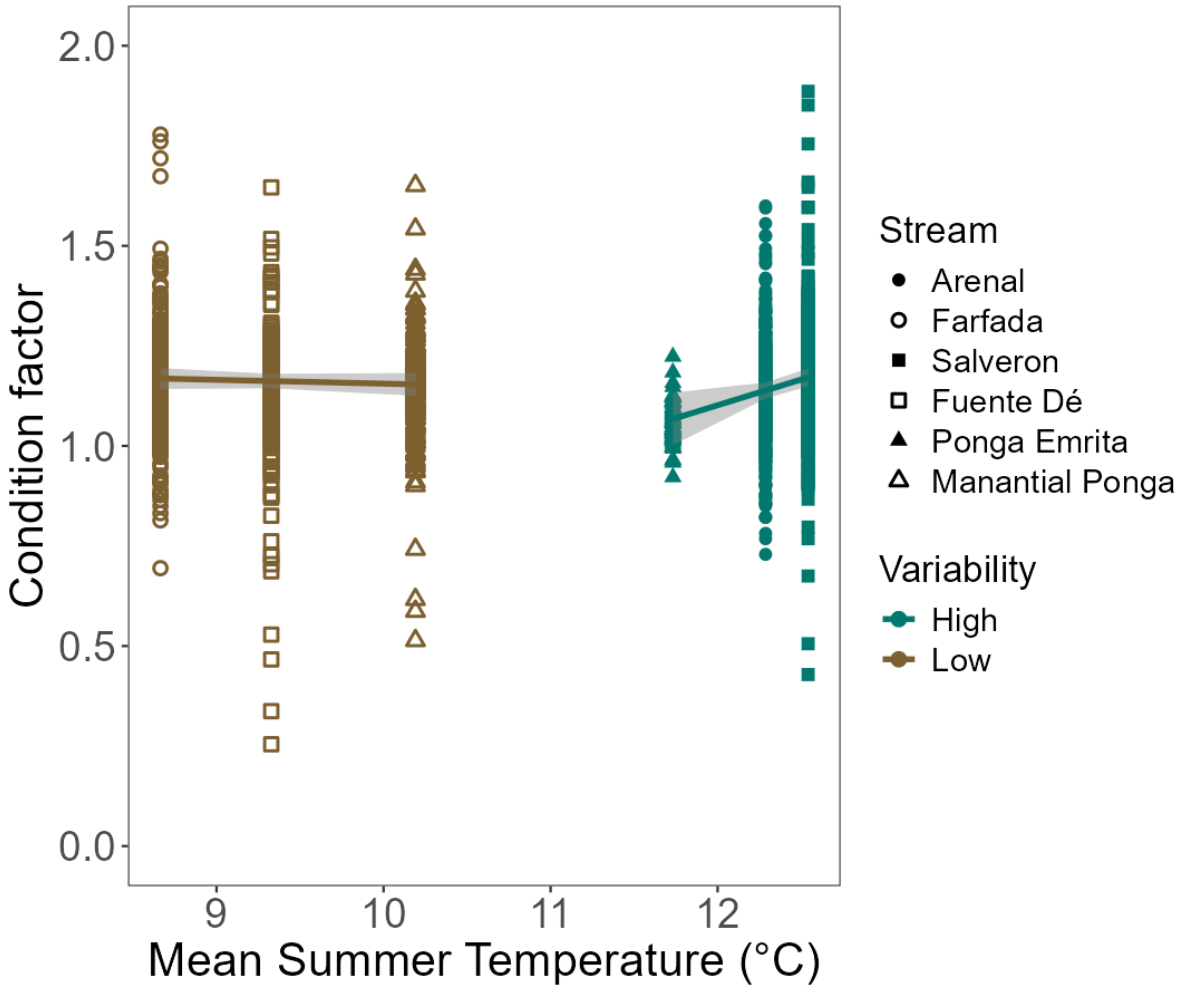



**Figure S3.4** - Condition of historically sampled fish against mean summer temperature for fish caught from HTV streams (full shape) or LTV streams (hollow shape), with the lines and 95% confidence intervals given by the predictions of the best fitting model.

# Chapter 4. Thermal regime shapes metabolic effects on growth, survival, and migration in salmonid fish

*In prep for Nature Ecology & Evolution*

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**Abstract**

Climate warming is reshaping freshwater ecosystems, yet how temperature modifies the ecological consequences of metabolic variation in wild populations remains poorly understood. Here, we quantified *in situ* routine metabolic rate, growth rate, migration timing, and survival in juvenile salmonids across a broad latitudinal gradient spanning rivers from Spain to Iceland. Metabolic rate increased consistently with temperature across populations, but its relationship with daily growth depended strongly on thermal regime. Individuals with elevated metabolic rates grew faster in warmer rivers but more slowly in colder rivers, indicating that the fitness consequences of metabolism reverse across thermal environments. Higher metabolic rates were also associated with reduced survival and earlier migration timing, suggesting a trade-off between rapid growth and long-term energetic sustainability. Daily summer growth rates were highest at both warm and cold range extremes, implying distinct mechanisms underpinning performance across latitudes. Together, these results demonstrate that thermal regime alters how metabolic phenotype translates into growth, survival, and migration timing in wild fish populations. Climate warming may therefore restructure salmonid populations, not only through direct thermal stress, but also by shifting the balance between energetic demand, resource acquisition, and seasonal energy limitation.

## 4.1 Introduction

Climate warming is restructuring ecosystems worldwide, but predicting biological responses requires understanding not only thermal limits, but how temperature alters the energetic mechanisms underlying growth, survival, and life-history variation (Gallagher et al., 2022; Grimm et al., 2013; Magozzi and Calosi, 2015). Freshwater ecosystems are particularly vulnerable because warming is accompanied by altered hydrology, reduced habitat connectivity, and constrained opportunities for range shifts within fragmented river networks (Barbarossa et al., 2021; Fausch et al., 2002). Salmonids are especially sensitive to these changes owing to their complex life histories (Jonsson and Jonsson, 2009), with Atlantic salmon (*Salmo salar*) populations declining throughout much of their native range (CEFAS, 2022; NASCO, 2019b).

The ecological impacts of warming may emerge well before organisms approach upper thermal limits, because temperatures that maximise fitness are often considerably lower than those inducing acute physiological stress (Holt and Jørgensen, 2015). Understanding how warming reshapes the energetic basis of performance is therefore central to predicting future population dynamics. One of the primary ways temperature influences ectotherm performance is through metabolism, which governs organismal energy demand and allocation (Brown et al., 2004). As temperatures rise, metabolic maintenance costs increase, elevating energetic demand even in the absence of growth or reproduction (Chabot et al., 2016a; Clarke and Fraser, 2004). Higher costs can constrain performance and reduce survival likelihood if energy acquisition does not increase proportionally (Bochdansky et al., 2005). However, elevated metabolic rates may also confer ecological advantages due to increased activity, digestion and absorption rates, and thus greater resource acquisition (Killen et al., 2012, 2011; Reid et al., 2012; Volkoff and Rønnestad, 2020). Metabolic phenotype may therefore either enhance or reduce fitness depending on the balance between energetic demand and energetic gain, but this is likely to vary across thermal environments.

In cold, strongly seasonal systems, elevated metabolic costs may be difficult to sustain because feeding opportunities and digestion rates are constrained by low temperature and long winters (O'Connor et al., 2000; Volkoff and Rønnestad, 2020). Conversely, in warmer and more productive environments, elevated metabolic rates

may support greater activity, dominance, and resource acquisition, promoting faster growth and earlier life-history transitions such as migration to sea (Metcalfe et al., 2016; Metcalfe and Thorpe, 1992). However, as temperatures approach thermal optima, maintenance demands may rise faster than energy intake, suppressing growth and survival (Baudron et al., 2014; Jutfelt et al., 2021). Thermal regime may therefore fundamentally alter whether elevated metabolism is advantageous or costly. Yet despite growing recognition that metabolism mediates responses to climate change, few studies have quantified how its fitness consequences vary across natural thermal gradients.

In salmonids, these energetic trade-offs have major consequences for life history. Faster juvenile growth is associated with earlier migration and improved marine survival, while warming is already linked to altered migration timing and reduced age at sea (Dempson et al., 2017; Gregory et al., 2019; Kallio-Nyberg et al., 2020). Warming-associated declines in growth and distribution have also been documented in brown trout (*Salmo trutta*), particularly near southern range limits (Borgwardt et al., 2020). Metabolic phenotype may therefore shape not only somatic growth, but also migration timing and survival across contrasting environments (Metcalfe and Thorpe, 1992).

Here, we tested whether thermal regime modifies the ecological consequences of metabolic phenotype in wild salmonid populations. We combined *in situ* measurements of routine metabolic rate with growth reconstruction from scale annuli and tagging-based estimates of migration timing and apparent survival of Atlantic salmon and brown trout across a broad latitudinal gradient from Spain to Iceland. We hypothesised that: (H1) Metabolic rate increases consistently with temperature across the latitudinal gradient; (H2) Thermal regime mediates metabolic effects on growth, such that elevated metabolic rates enhance growth at intermediate temperatures but suppress growth at thermal extremes; (H3) Elevated metabolic rates lead to earlier migration but reduce survival irrespective of thermal regime, reflecting consistent maintenance costs.

## 4.2 Methods

### 4.2.1 Sites

Six river systems were selected along the latitudinal range of Atlantic salmon and brown trout, from the Iberian Peninsula to Iceland (Fig. 4.1). The selected rivers included: the Cares, Frome, Tweed, Deveron, Vesturdalsá, and Sunnudalsá (Table S4.1). All rivers contained fixed Passive Integrated Transponder (PIT) antennas to allow tracking of both downstream and returning migrations with the exception of the Cares and Sunnudalsá. Sampling for all rivers occurred in late summer of 2023 or 2024, with each river sampled over a week, with up to 4 experimental runs per day comprising 21 - 41 fish per run (see Table S4.1 for full sampling details).

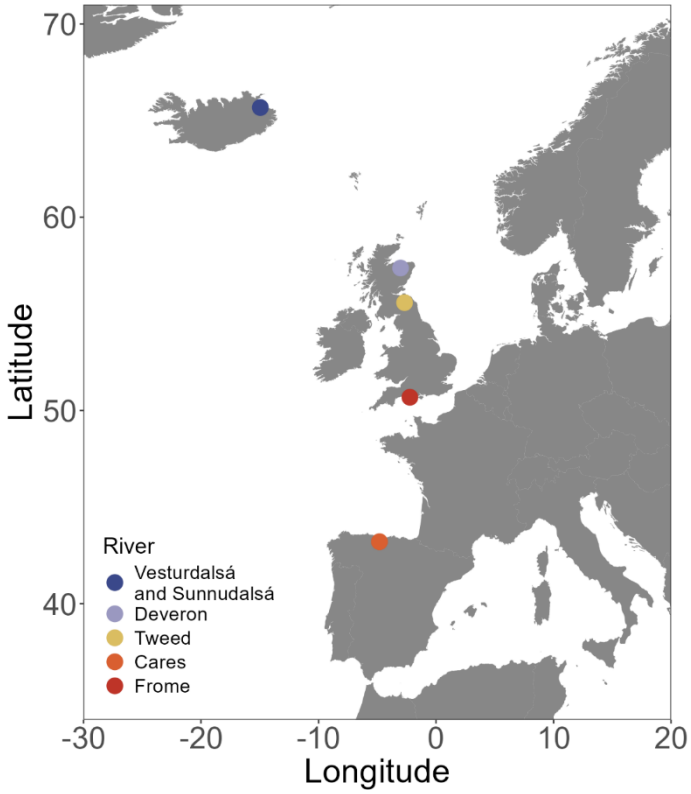



**Figure 4.1** – Map of all sampled rivers ordered and coloured by temperature gradient blue (low to red (high).

The River Frome is an English lowland chalk stream which flows downstream through highly braided channels and is equipped with nine detection antennae distributed between 50.7167, -2.3539 and 50.6814, -2.2082. The River Cares is a steep, high-gradient mountain river in northern Spain that rises in the Picos de Europa and flows through a deeply incised limestone gorge with confined channels,

coarse cobble-boulder substrate, and highly variable discharge regimes. While this river is more southernly it exhibits a lower productivity and temperature than the Frome as it is montane. The River Tweed is a gravel-bed river that rises in the Southern Uplands on the border between Scotland and England and flows east through a broad alluvial valley to the North Sea, equipped with two PIT antenna deployed during April and May at 55.6212, -2.8159. The River Deveron is a spate-driven upland river that rises in the Grampian foothills in Scotland, with a PIT array at 57.5081, -2.7814. The Vesturdalsá is a short, high-gradient subarctic river in Iceland flowing through confined bedrock and coarse cobble–boulder channels with step-pool morphology, equipped with three arrays between 65.6834, -15.0543 and 65.7390, -14.9248. Finally, the Sunnudalsá is a small subarctic river in northeast Iceland characterised by cold, groundwater-influenced flows, confined channels, and coarse cobble–boulder substrate with alternating riffle–run habitat.

To characterise the water temperatures experienced by the subject animals, we used continuous water temperature records over their lifetime where available (Frome, Tweed, Vesturdalsá, Sunnudalsá), and for 2016-2021 for the Deveron. For the Cares, we only had daily water temperatures for August 2014-August 2015. In all cases, water temperature loggers were located within 5 km of the sample sites. We then calculated mean annual water temperature using all available complete years of data for all rivers (Table S4.1), this is referred to as mean river temperature hereafter.

An index of productivity was calculated for each sampling site using Normalized Difference Vegetation Index (NDVI), with higher values indicating healthier, denser vegetation. NDVI was obtained from the MODIS MOD13Q1 product (250 m resolution, 16-day composites) using the MODISTools R package (Hufkens, 2013). Specifically, for each site, NDVI values were extracted from the MODIS pixel or pixels within 250m of each site and averaged across the 12 months preceding the sampling month (following Jackson et al., 2024). The climate of each system was broadly characterised using local air temperature from all monthly averages of surface temperature (°C) for 1981-2010 from the CRU TS (v. 4.06) dataset (see Table S4.1). Photoperiod was calculated from site latitude and day of year using astronomical equations implemented in the R package geosphere (Hijmans, 2026). The Cares while being the most southerly sampling point did not exhibit the highest

temperature. However, where it exhibited temperatures, and productivity more indicative of a mid-latitude site (Table S4.1) it is still a valuable part of this study's temperature and productivity gradient. Minimum, maximum, and annual range in daylength were extracted for each site to quantify photoperiod seasonality (see Table S4.1).

### 4.2.2 Sampling Regime

For each experimental run, fish were caught by single pass electrofishing until enough fish for an experimental run were captured. Fish were weighed on site and their fork length measured. A total of 1041 fish were sampled (Table S4.1), excluding fish >50g and >4 years old to keep size and age consistent among rivers. Fish were individually transferred into a 7.2L closed respirometer, which was filled with river water filtered through a 250 µm sieve to remove any detritus. Each chamber also contained a probe (miniDOT, Precision Measurements Engineering "PME", accurate to 0.01mg/L ± 5%) to measure dissolved oxygen concentrations and experimental temperature every minute, and an underwater motor (Underwater motor: 7350, Playmobil) to circulate the water. Chambers were sealed and checked for air bubbles before being submerged in the river to a depth of 1-20 cm from the lid. Each chamber was then left for approximately 90 minutes over which the oxygen consumption rate was measured. Each run also contained a "control" chamber without a fish to measure background respiration. Thus, the oxygen consumption and a short term "experimental temperature" of each fish was measured for each run within each day. One chamber was left overly exposed to sunlight and thus increased in temperature substantially over the course of the run and was excluded.

After metabolic measurements, fish were individually transferred into either clove oil or 2-phenoxyethanol anaesthetic. Once fish were under anaesthesia, they were identified to species level, had their stomachs flushed, and length and weight were measured. An 11 x 1.5 mm PIT tag was then surgically implanted in the coelomic cavity, after which a scale sample was taken from each fish's dorsal flank and transferred to a dry scale packet. Fish were then transferred to a recovery holding chamber and released back into the river when they had fully recovered. Animal handling and processing procedures were approved by the GWCT Animal Welfare and Ethical Review Body and the University of Essex (ETH2324-192) and were

carried out by licensed personnel under a UK Home Office ASPA licence (PPL PP9506723).

### 4.2.3 Metabolic Rate

To calculate routine metabolic rate in the field ($RMR_F$), a 30-minute habituation period was excluded from all experiments, then 20-minute rolling linear regressions of dissolved oxygen concentration against time were performed across all remaining data. The mean of the lowest 20% of these slopes with $r^2 > 0.8$ was used in the calculation of $RMR_F$ (following a modified version of González-Ferreras et al., 2023 approach) and no metabolic rate was calculated if there were no slopes with an $r^2$ exceeding this threshold (as occurred in 2% of cases). The oxygen consumption rate of the organism (mg $O_2$ $h^{-1}$) was calculated by multiplying each of the accepted slope values by the volume of the water (i.e. the volume of the chamber minus the volumes of the miniDOT, motor, and fish) and subtracting background respiration, which was modelled linearly over the duration of the experiment in the control chamber.

### 4.2.4 Growth Estimates

3-5 scales from each individual were, gently cleaned in water and mounted on glass slides before being photographed and the scale in the best condition was used to estimate the age of the fish by counting winter checks (Chilton and Beamish, 1982, see Table S4.2). Fish can grow replacement scales if they are lost through damage or injury, but these scales will grow at a different rate and not contain winter checks from previous years (Broussonet, 1786; Chilton and Beamish, 1982). Thus, if all imaged scales were replacement scales, then that individual was excluded from further analysis. Size (fork length) at their first winter check was estimated using the Fraser-Lee method of linear back-calculation based on size-at-capture, and length of scale at winter check, assuming a size at first scale formation of 30 mm (Heidarsson et al., 2006; Jensen and Johnsen, 1982; Lea, 1910). This size at first winter check was then converted into growth in mm per day over the growing period (spring – late autumn) by dividing by the estimated number of growing days between emergence and the formation of each fish's first winter check. This required estimating an average spawn and first feeding for each river, and to estimate the slowest period of growth.

Spawning was assumed to be 1st November in the Icelandic rivers (Ísaksson, 1985), 14th November in the Scottish rivers (J. Hunt, personal communication, March 18, 2026), 1st December in the Cares (García-Vega et al., 2017), and 1st January on the Frome (Marsh et al., 2021). Brown trout are known to generally spawn earlier than salmon and so where we did not have a specific spawn date for trout they were assumed to spawn 15 days earlier than the salmon (following Heggberget et al., 1988). Note that these estimates followed the established temperature gradient of spawning, i.e. lower temperatures result in earlier spawning (Heggberget, 1988; Jonsson and Jonsson, 2009; Webb and McLay, 1996).

Average daily river temperature data was used to calculate the most likely fry emergence date for each river. Fry emergence was estimated using a temperature-dependent developmental model in which daily river temperatures were converted to relative developmental units ($\tau_s$), following Gorodilov (1996). These units were cumulatively summed from the spawning date, and emergence was defined as the date at which embryos reached ~450 $\tau_s$, corresponding to emergence from the gravel and first exogenous feeding. This used river temperature for the year of emergence where possible (Frome, Vesturdalsá, Sunnudalsá, and Tweed), or else the average daily temperature from the available data (Deveron and Cares). Finally, the winter check was estimated to form when growth potential for salmonids reached zero, which was assumed to be approximately 5.2°C (a temperature experienced by all rivers) (Bal et al., 2011; Forseth et al., 2001; Jonsson and Jonsson, 2009). Thus, average daily growth over the year was calculated and is henceforth referred to as growth rate. Size at first winter was used to minimise ontogenetic effects and maximise our sample size, as many fish were sampled at <2 years old.

### 4.2.5 PIT Tagging

In total, 783 fish were tagged across the four rivers with PIT tag receivers (Table 4.1). Detections of tagged fish from each river were processed and the species, size, timing, frequency, and direction of detection were all used to determine smolt periods. Migration date was estimated as the last detection of each fish meeting these criteria, following an approach modified from Gillson et al., (2025). A total of 88 fish were detected out-migrating from freshwater (11% of the total tagged), this is in line with observed annual juvenile survival rates of 7 - 18% (Elliott et al., 2026). All outmigration events were for Atlantic salmon, so trout were excluded from all

analyses of movement and survival. Detections were monitored until November 2025, at which point salmon that were not detected out-migrating were assumed to have died. This assumption probably holds true for the warmer low latitude rivers where fish migrate within 1-2 years, but may be weaker for the Icelandic rivers where fish typically remain for one to five years (Olafsson et al., 2016).

**Table 4.1** – Number of fish by species that were sampled and PIT tagged in each river. The fraction of salmon that were detected out-migrating is also shown.

| River | N Total | N Tagged | N Trout | N Salmon | N Salmon detected out-migrating |
|---|---|---|---|---|---|
| Cares | 171 | 0 | 171 | 0 | - |
| Frome | 184 | 183 | 88 | 97 | 8 (8%) |
| Tweed | 176 | 165 | 28 | 149 | 11 (6%) |
| Deveron | 188 | 186 | 6 | 181 | 46 (25%) |
| Vesturdalsá | 249 | 249 | 0 | 249 | 22 (9%) |
| Sunnudalsá | 72 | 0 | 0 | 72 | - |
| Total | 1041 | 783 | 293 | 748 | 88 (11%) |

### 4.2.6 Statistics

Before all analyses, $RMR_F$ was first mass-corrected by modelling ln metabolism against ln mass for every fish, including an effect of Arrhenius temperature and a random effect of run nested within sampling day nested within with system. The slope of this relationship was then used to allometrically correct for body mass following equation 1 (derived from Brown et al., 2004):

$$I_M = \frac{I}{M^b} \quad (1)$$

Where $I_M$ is mass-corrected metabolism, $I$ is whole organism metabolic rate, $M$ is mass of the organism, and $b$ is the allometric scaling exponent (0.86 in this study).

To determine how metabolism varied *in situ* with temperature across the dataset, ln mass-corrected metabolism was modelled as a function of all main and two-way interactive combinations of experimental water temperature, river, age, and species, including a random effect of sampling run nested within sampling day using the '*lmer*' function in the '*lme4*' package and a type 2 ANOVA to test significance (Bates *et al.*,

2015). Three-way interactions were excluded for parsimony and to aid interpretation as 3-way interactions may lack ecological meaning and this approach was taken for all subsequent modelling. We then applied stepwise model simplification removing non-significant terms until the most parsimonious remained.

$I_M$ was then temperature-corrected as follows for all subsequent analyses (following Brown et al., 2004):

$$I_{MT} = \frac{I_M}{e^{E_A \frac{T-T_0}{kTT_0}}} \quad (2)$$

Where $E_A$ is the activation energy in electron volts (eV) (i.e. slope of the relationship between metabolic rate and Arrhenius temperature, which was 0.36 across all fish), $T$ is temperature in kelvin, $T_0$ is the mean temperature of all chambers in the study over the measurement period, and $k$ is the Boltzmann constant ($8.617 \times 10^{-5} eVK^{-1}$). This mass and temperature corrected metabolism is typically termed metabolism within this study.

Growth was then modelled as a function of all possible two-way interactions of ln metabolism, mean annual water temperature, and species, including a random effect for experimental run nested within sampling day nested within river and a random effect of age class nested within river. Mass was excluded due to expected covariation with both age and mass at the end of the first year, i.e. growth. We then undertook backward stepwise model selection removing non-significant terms until the most parsimonious model remained. The main model included a random effect for age class nested within river as different age classes will have undergone different conditions in their first year of growth. To ensure results from this model were not due to 0+ fish (born that calendar year) exhibiting higher daily growth or biases in rivers exhibiting more 0+ fish, the model was also run excluding all 0+ individuals. These were then visualised using by calculating the partial residuals these being the model residuals with the addition of all main effects thereby, correcting for the random effects of sampling run nested within sampling day nested within river and age class nested within river. While an index productivity was also measured for all rivers this showed high co-variation with temperature and was thus dropped from all modelling.

To illustrate growth rate differences between rivers, growth was corrected using a random effect from the same model of age class not nested within rivers. Age class corrected growth between rivers was then compared with a linear model again these were then visualised using the model partial residuals as above.

To determine whether metabolism is associated with survival probability in tagged salmon, a binomial GLMM was modelled using the '*glmer'* function in the '*lme4*' package (Bates et al., 2015). The full model included all independent terms deemed to influence survival including the main effects of age, ln mass, mean annual river temperature, and ln metabolism with a random effect for river. All possible two-way combinations of these factors were examined before applying backward stepwise model selection removing non-significant terms until the most parsimonious model remained. Given that fish may defer migration in the high latitude streams and therefore not migrate but still survive within our measurement window, this model was also rerun excluding all high latitude (Icelandic fish).

Finally, a relationship between metabolism and migration timing in surviving salmon was explored using the 'coxme' function in the 'Cox' and 'survival' packages (Therneau, 2024a, 2024b). Migration timing was normalised, so each river had the same start day, while age was normalised within river and mass was normalised within river and age class. The full model included ln metabolism, mean annual river temperature, normalised ln mass, and normalised age, alongside a random effect for river. All possible two-way combinations of these factors were examined before applying backward stepwise model selection removing non-significant terms until the most parsimonious model remained. Hazard ratios output by the model were then used to infer if the factor resulted in earlier or later migration. Hazard ratios qualify how the event rate changes with a predictor, whereby values >1 signify the event occurring sooner than average and values <1 signify later than average. A hazard ratio of 1.5 represents an increase in migration probability per day of 50% compared to an average value.

## 4.3 Results

### 4.3.1 Metabolism and Growth

The most parsimonious model (conditional $r^2$ = 0.65; Table S4.3) determining the factors influencing mass-corrected metabolism included only the significant main effects of experimental temperature ($X^2$ = 7.21, $p$ = 0.007, Fig. 4.2) and river ($X^2$ = 175.89, $p$ <0.001). This indicated a consistent slope of the relationship between temperature and metabolism across sites, in support of H1. River intercepts were generally similar, except for the Deveron which had a significantly lower metabolism than all other sites ($p$ < 0.001). Interestingly, neither species nor age were included in the final model.

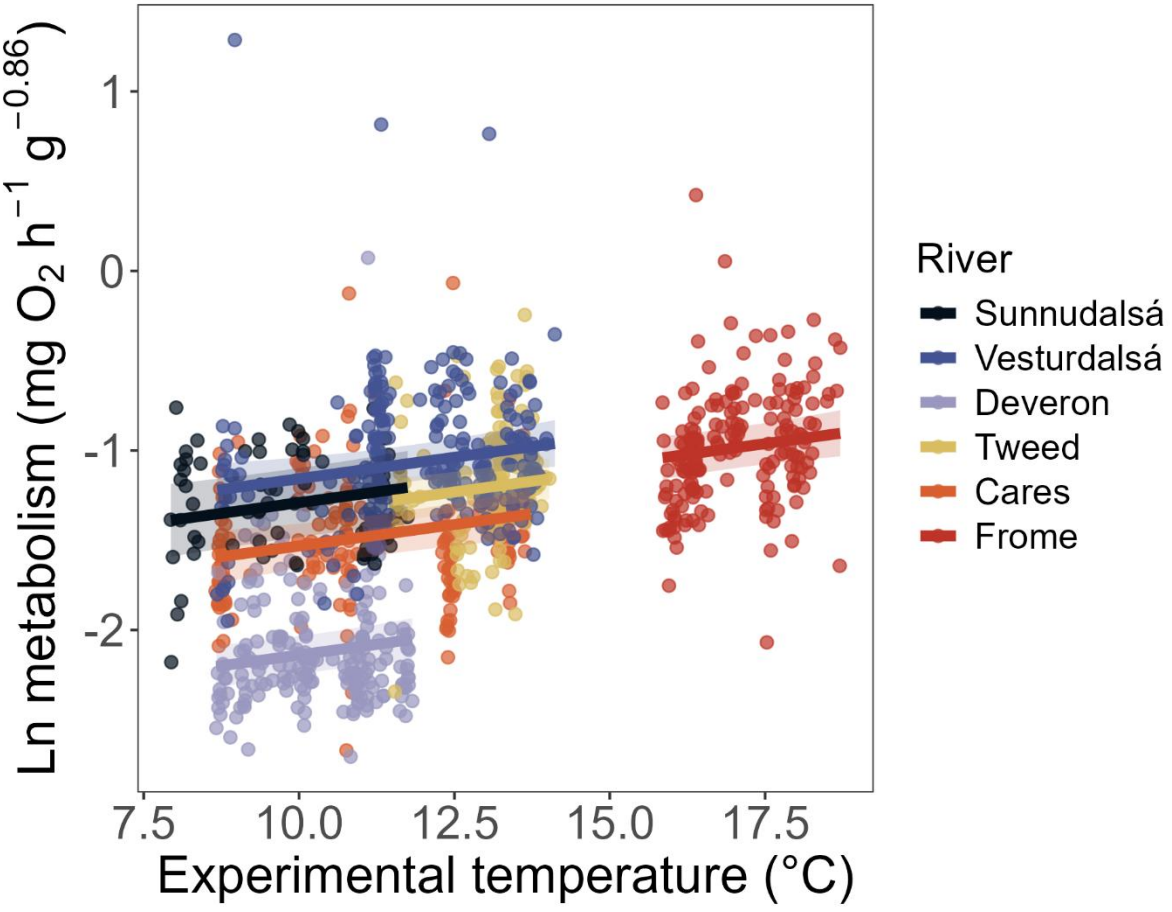



**Figure 4.2** – The relationship between ln mass-corrected metabolism and experimental temperature within each river. Lines show the predictions for each river based on the fixed and random effects (see Table S4.3) with 95% confidence intervals for the model predictions around each line. Note that metabolism is mass corrected with the allometric exponent b given by 0.86 (see methods).

The most parsimonious model determining the factors influencing growth in the first year included main effects of mean annual river temperature, metabolism, and species, as well as interactions between metabolism and both mean annual temperature and species (conditional $r^2$ = 0.77; Fig. 4.3, Table S4.4). Temperature had a marginally non-significant positive effect on growth ($t$ = 1.98, $p$ = 0.062), whilst metabolism had a negative effect on growth ($t$ = -3.09, $p$ = 0.002). However, temperature and metabolism interacted such that fish with higher metabolic rates grew faster under warmer conditions, whereas individuals with lower metabolic rates grew better in cooler environments ($t$ = 3.47, $p$ <0.001; Fig. 4.3a), supporting H2. Brown trout exhibited a more negative relationship between metabolism and growth than Atlantic salmon, with a lower growth rate in higher metabolic rate fish ($t$ = -3.36, $p$ <0.001; Fig. S4.1). Thus, only in the warmest waters did high metabolic rate led to positive growth in trout (Fig. S4.1b). The same directionality and significance of terms were observed when excluding all that hatched that year: termed (0+) fish (Fig. S4.2). These were excluded as they had not yet completed a year of growth and therefore may show different daily growth rates when averaged over their life so far. There was a significant effect of river on age-class-corrected growth (F = 78.4, $p$ <0.001; Fig. 4.3b), with growth rates significantly higher at the range extremes (Sunnudalsá = 0.327, Vesturdalsá = 0.229, Frome = 0.228 mm day$^{-1}$) than at intermediate temperatures (Tweed = 0.206, Cares = 0.212, Deveron = 0.198 mm day$^{-1}$; $p$ < 0.03).

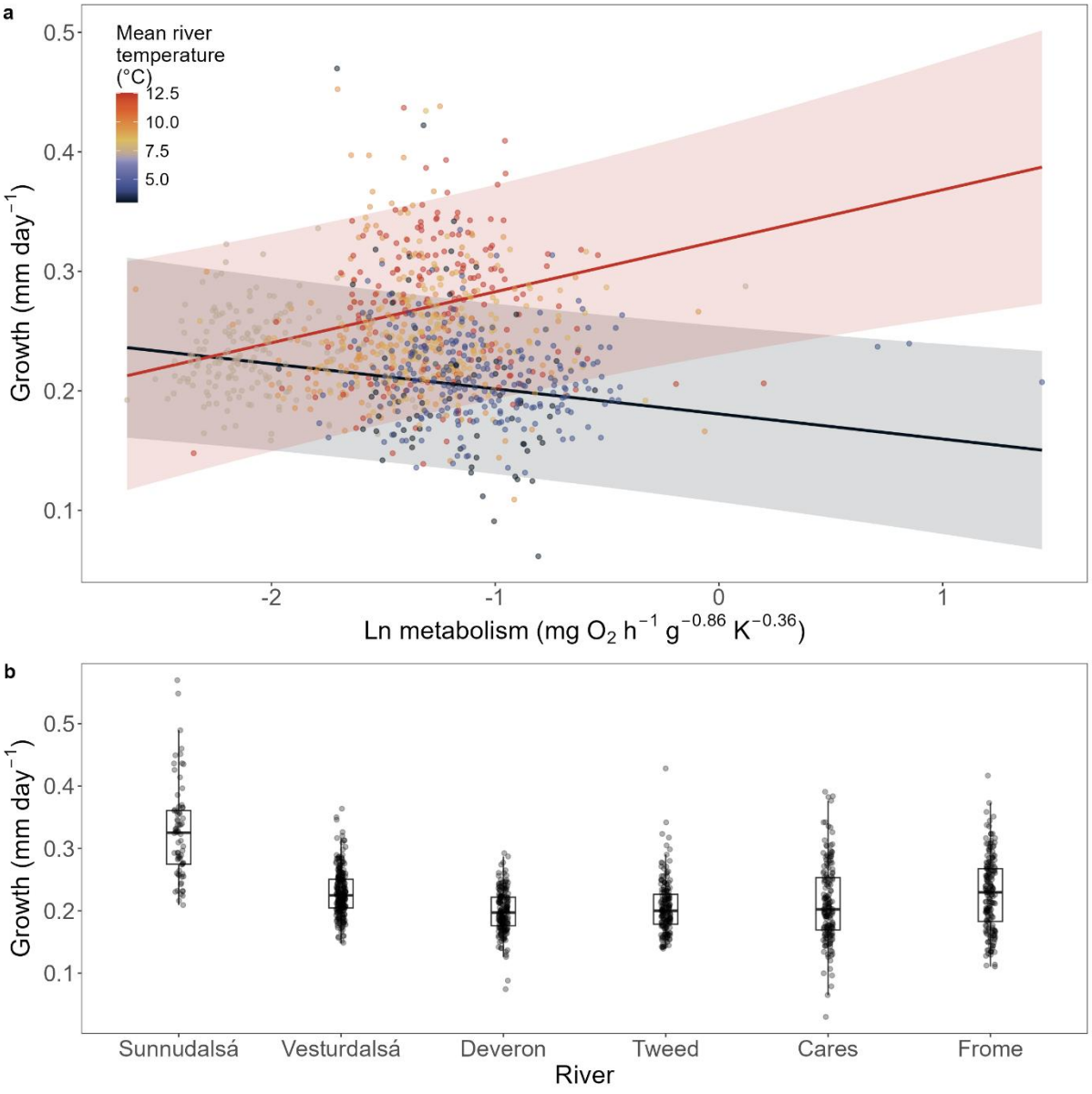
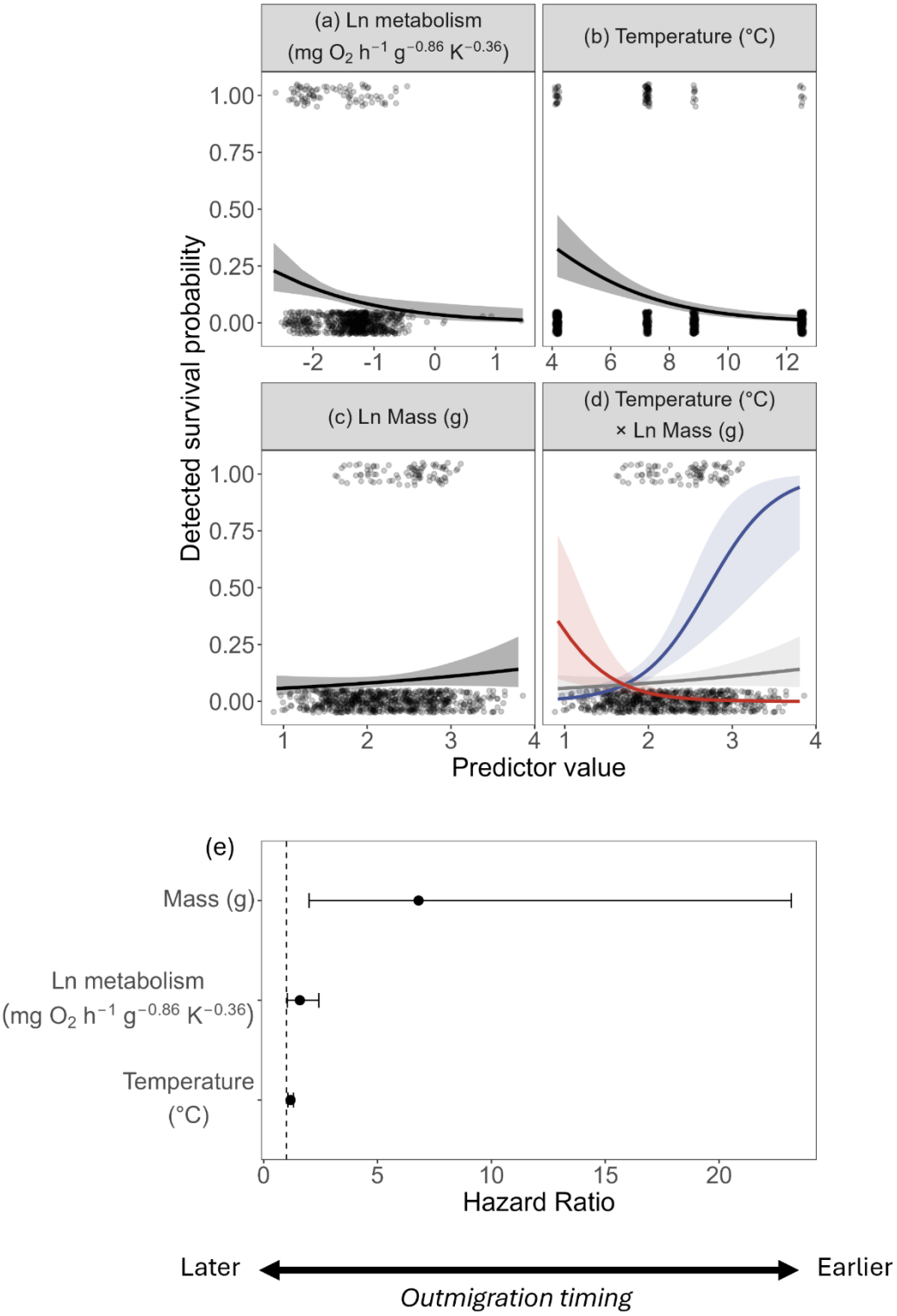



**Figure 4.3** – Variation in growth due to metabolism, river temperature, fish species, and river systems. Growth in the first year against mass- and temperature-corrected metabolism (the allometric exponent is 0.86 and the activation energy is 0.36, see methods) with model predictions (lines) and 95% confidence intervals given for (a) min (3.0 °C) and max (12.5 °C) mean annual river temperatures (see Fig. S4.3 for raw growth data). (b) Differences in age-class-corrected growth rate between the rivers, ordered by river temperature.

### 4.3.2 Salmon Survival and Migration

The most parsimonious model for determining the factors influencing salmon survival included the main effects of mean annual river temperature, metabolism, body mass, and an interaction between temperature and body mass (marginal $r^2$=0.239; Fig.

4.4a-d). Survival probability was negatively related to metabolic rate in support of H3 (z = –2.69, $p$ = 0.007; Fig. 4.4a), but positively related to temperature (z = 3.70, $p$ <0.001; Fig. 4.4b) and body mass (z = 4.494, $p$ <0.001; Fig. 4.4c). There was also a significant interactive effect of temperature and body mass (z = -4.274, $p$ <0.001, Fig. 4.4d) whereby large individuals at high temperatures suffered reduced survival, whereas larger size increased survival at lower temperatures. Finally, the most parsimonious mixed effects cox model determining the factors influencing migration timing included the main effects of mean annual river temperature, metabolism, and body mass. There was a significant positive effect of temperature (z = 3.09, $p$ = 0.002), metabolism (z = 2.15, $p$ = 0.032), and body mass (z = 3.06, $p$ = 0.002), with high values resulting in earlier migration, in support of H3 (Fig. 4.4e).




2495

2496 **Figure 4.4** – Model-predicted survival probability and migration timing. Survival
2497 probability curves are shown for (a) ln mass- and temperature-corrected metabolism
2498 (with an allometric exponent of 0.86 and an activation energy of 0.36, see Methods),
2499 (b) mean river temperature, (c) ln body mass, and (d) the interactions between mass
2500 and temperature with blue representing the minimum temperature (4.2°C) and red

representing the maximum (12.5°C), with raw binomial data plotted. For a-c, all other model factors are held at mean levels, whilst survival probability is visualised at minimum, mean, and maximum temperatures in d. (e) Predicted hazard ratios with 95% confidence intervals of the significant factors affecting migration timing. Hazard ratios >1 signify earlier outmigration as that variable increases while those below one signify later outmigration.

## 4.4 Discussion

Across a broad latitudinal gradient, we show that the ecological consequences of metabolic phenotype are strongly dependent on thermal environment. Elevated metabolic rates promoted growth in warmer rivers but constrained growth in colder systems, demonstrating that metabolism does not exert universally positive or negative fitness effects. Instead, the balance between energetic demand and energy acquisition shifts across thermal regimes, providing a framework for understanding how warming may restructure populations across their geographic range.

Higher metabolic phenotypes are often associated with increased activity, dominance, and resource acquisition under controlled conditions (Metcalfe et al., 2016; Reid et al., 2011). Our findings suggest that these advantages translate into enhanced growth only where energetic demands can be subsidised by sufficient resource availability. In warmer and more productive rivers, elevated metabolic rates may support higher feeding rates and sustained growth across longer growing seasons. In contrast, in colder and more seasonal systems, the energetic costs associated with elevated metabolism appear to outweigh these benefits. Low temperatures may constrain feeding opportunity and digestive processing, while prolonged winters likely increase the importance of maximising energetic efficiency and overwinter persistence (Hvas et al., 2020; Volkoff and Rønnestad, 2020). Under such conditions, lower metabolic phenotypes may be favoured because reduced maintenance lowers cumulative energetic costs across the annual cycle.

These findings align with laboratory evidence showing that relationships between metabolism and growth vary across thermal environments (Archer et al., 2021), but extend these patterns into wild populations spanning a large natural climatic gradient. Interestingly, Archer et al. (2021) found the same relationship between maximum metabolic rate, growth, and temperature, but the opposite in standard

metabolic rate, suggesting activity and behaviour may be driving our observation more than basal rates. Our results indicate that growth optimisation depends not simply on temperature or metabolism, but on the interaction between metabolic demand, seasonal energy budgets, and environmental productivity. The fitness consequences of metabolism should therefore be interpreted within broader seasonal or annual energy contexts rather than instantaneous thermal conditions alone.

Daily growth rates were highest at both warm and cold extremes of the latitudinal gradient, suggesting that distinct ecological mechanisms may support rapid growth in different environments. Higher temperatures and productivity in southern rivers may permit sustained growth throughout extended growing seasons, whereas rapid growth in Icelandic systems may reflect compensation for short growing seasons through extremely long summer photoperiods, which can extend feeding opportunities (Imsland et al., 2014; Saunders et al., 1985). This may allow for very high daily growth, though still resulting in smaller overall size at the end of the year (given the short growing season). These contrasting pathways highlight that similar growth outcomes may emerge through different energetic strategies across latitudes.

We also found that brown trout exhibited a more negative relationship between metabolism and growth, such that higher metabolic rates were associated with positive growth only in the warmest rivers. This contrasting pattern may reflect interspecific differences in life history, physiology, and thermal niche breadth, as brown trout generally occupy and tolerate warmer thermal environments than Atlantic salmon (Elliott and Elliott, 2010; Jonsson and Jonsson, 2011). Consequently, trout may be better able to offset the elevated energetic costs associated with higher metabolic rates under warmer conditions.

Although the relationship between metabolism and growth was strongly context dependent, elevated metabolic rate was consistently associated with reduced survival. This suggests that the energetic costs of maintaining higher metabolism may impose a persistent burden across environments, potentially increasing vulnerability during periods of reduced food availability or seasonal energetic stress (Álvarez and Nicieza, 2005; Killen et al., 2011). Temperature was also negatively associated with survival, consistent with broader evidence that warming can reduce

salmonid persistence across freshwater systems, though this was moderated by mass as is explored below (Nicola et al., 2018). Taken together, our findings suggest that elevated metabolism may promote rapid growth under favourable conditions while simultaneously increasing long-term energetic risk, reflecting a trade-off between resource acquisition and survival.

Body size positively influenced survival, consistent with previous work linking larger juvenile size to reduced predation risk and improved marine performance (Koenings et al., 1993; Saloniemi et al., 2004). However, temperature and body size interacted to favour larger fish in cold conditions and smaller fish in warm conditions, following the established temperature size rule and expectation of body size shrinkage as temperatures rise (Atkinson and Sibly, 1997; Trip et al., 2014; Verberk et al., 2021).

Our survival estimates should be interpreted with some caution because non-detection at PIT arrays may reflect imperfect or differential detection rates or delayed migration rather than mortality (Aymes and Rives, 2009; Saboret et al., 2021). This uncertainty is particularly relevant in northern systems where individuals may defer migration to older ages (Ísaksson, 1985). Nevertheless, the same directionality in model terms was observed when all northern (Icelandic) fish are excluded from the analysis (Table S4.5) this suggests confidence in our results.

Metabolic phenotype also influenced migration timing, with higher metabolic rates associated with earlier migration. One explanation is that individuals with elevated energetic demands transition earlier to marine habitats where feeding opportunities and growth potential are greater (Berg and Jonsson, 1990). Larger fish also migrated earlier, consistent with previous studies linking body size to smolt readiness and marine survival (Eldøy et al., 2021; Gillson et al., 2025). Finally, warmer rivers generally had more fish migrate earlier within their observed migration window, consistent with studies showing earlier migration in warmer years (Keefer et al., 2008; Quinn et al., 1997).

Metabolic rates and their relationship with temperature were broadly similar among rivers despite the large geographic range encompassed by the study, suggesting relatively conserved thermal sensitivity across populations. The exception was the Deveron, which exhibited consistently lower metabolic values and may reflect population-specific energetic strategies. The thermal sensitivity of $RMR_F$ was much

lower (0.36 eV) than that generally expected of basal rates (0.65 eV), albeit measured over a narrow temperature range, suggesting that the thermal sensitivity of fish in their natural habitats may be much lower than expected (Clarke, 2004; Clarke and Fraser, 2004). Interestingly, some of the highest metabolic rates occurred in the coldest rivers, consistent with hypotheses predicting compensatory metabolic elevation in cold-adapted populations (White et al., 2012). However, inference regarding adaptive divergence remains limited because temperature ranges within individual rivers only partially overlapped.

Projected climate warming is expected to elevate temperatures throughout much of the salmonid range (IPCC, 2023), increasing metabolic demand across populations. However, increases in energetic expenditure are unlikely to be matched universally by equivalent increases in resource availability or growing-season opportunity. This mismatch may be particularly important in highly seasonal northern systems where photoperiod remains fixed despite warmer winters (Karlsson et al., 2005). Under these conditions, elevated maintenance costs could increase cumulative energetic deficits, reduce survival, and weaken the advantage of high metabolic phenotypes despite potentially faster summer growth, although earlier springs may increase growth (Gudbergsson and Bardarson, 2023). In contrast, warmer southern systems may increasingly approach physiological optima where aerobic capacity and feeding performance decline while maintenance demands continue to rise (Jutfelt et al., 2021). Our results suggest that warming may therefore simultaneously alter growth, survival, and migration strategies by shifting the balance between energetic demand and resource acquisition across environments. Elevated metabolic phenotypes may initially gain growth advantages and migrate earlier under warmer conditions, but this could lead to mismatch with marine prey (Cushing, 1990; Gotceitas et al., 1996). Furthermore, these benefits may be offset by reduced survival if energetic costs cannot be sustained across the annual cycle. Climate warming may consequently restructure salmonid populations not only through direct thermal stress, but by altering the energetic trade-offs linking metabolism, growth, survival, and life-history timing across latitudes.

Future work should directly evaluate the mechanisms inferred here by quantifying seasonal energy balance and its ecological drivers. Continuous measurement of overwinter metabolic expenditure, coupled with estimates of food availability and

predator pressure, would allow explicit tests of whether maintenance demand versus energy acquisition governs growth and survival across thermal regimes. Refining survival inference will also be critical; integrating multi-array detection frameworks, independent estimates of detection probability, and complementary mark–recapture approaches would reduce uncertainty associated with non-detection and delayed migration. A priority is to partition metabolic phenotype in the field into its constituent components. Independent estimation of standard metabolic rate (SMR), maximum metabolic rate (MMR), and field or routine metabolic rate (FMR/RMR) in wild individuals would allow mechanistic linkage between energetic capacity, maintenance demand, and realised performance. This is particularly relevant where our $RMR_F$ measurement integrates behaviour and physiological components (Chabot et al., 2016a). Coupling these measurements with longitudinal growth trajectories and habitat-specific resource measurements would clarify how different components of the energy budget translate into life-history variation.

Collectively, our findings demonstrate that the fitness consequences of metabolic phenotype emerge from interactions between temperature, seasonality, and energetic opportunity. Elevated metabolism promoted growth under warmer conditions but constrained performance in colder systems, while simultaneously imposing an apparent survival cost across environments. These results suggest that climate warming may restructure salmonid populations not only through direct thermal stress, but by altering the energetic trade-offs linking metabolism, growth, survival, and migration. Where warming increases metabolic demand without proportional increases in resource availability, populations may experience reduced survival and shifts in the distribution of favourable metabolic phenotypes. Such processes may contribute to ongoing declines in salmonids across both warm and highly seasonal regions.

## 4.5 Supplementary Information

### 4.5.1 Supplementary Tables

**Table S4.1** – Information regarding each river sampled, including characteristics, temperatures, photoperiod, productivity, site locations, and fish per site. Experimental water temperature represents the water measured in each closed respirometer. NDVI stands for Normalized Difference Vegetation Index. Mean air temperature taken from monthly air temperatures between 1981-2010 Rivers ordered by latitude

| River | Fish sampling month and year | River Length (km) | Catchment area ($km^2$) | Mean experimental water temperature (°C) | Mean annual water temperature (°C) | Mean air temperature (°C) | NDVI | Min Photoperiod (h) | Max Photoperiod (h) | Site longitude | Site latitude | N fish |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Cares | 09/2023 | 54 | 1,200 $km^2$ | 11.2 | 9.7 | 10.5 | 0.647 | 9.0 | 15.4 | -4.91121 | 43.14637 | 2 16 |
| | | | | | | | | | | -4.80955 | 43.14164 | 2 34 |
| | | | | | | | | | | -4.80757 | 43.12525 | 2 37 |
| | | | | | | | | | | -4.91084 | 43.19192 | 2 27 |
| | | | | | | | | | | -5.17671 | 43.11562 | 2 34 |
| | | | | | | | | | | -5.17222 | 43.12551 | 2 33 |
| Frome | 08/2024 | 48 | 454 | 17.0 | 12.5 | 10.3 | 0.724 | 8.0 | 16.4 | -2.41949 | 50.71741 | 3 62 |
| | | | | | | | | | | -2.23646 | 50.68615 | 4 62 |
| | | | | | | | | | | -2.34441 | 50.71499 | 3 63 |
| Tweed | 09/2024 | 156 | 5000 | 13.1 | 9.0 | 8.1 | 0.664 | 7.0 | 17.5 | -2.87166 | 55.6544 | 3 54 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | -2.8869 | 55.72044 | 4 72 |
| | | | | | | | | | -3.06877 | 55.67267 | 3 55 |
| Deveron | 09/2023 | 97 | 1266 | 10.0 | 7.2 | 7.7 | 0.603 | 6.6 | 18.0 | -2.95534 | 57.42493 | 4 81 |
| | | | | | | | | | -3.02891 | 57.32819 | 4 80 |
| | | | | | | | | | -3.02769 | 57.34213 | 3 61 |
| Sunnudalsá | 07/2024 | 32 | 218 | 9.9 | 3.0 | 1.3 | 0.240 | 3.0 | 23.7 | -14.9494 | 65.72222 | 13 84 |
| Vesturdalsá | 07/2024 | 38 | 182 | 11.9 | 4.2 | 1.3 | 0.238 | 3.0 | 23.7 | -14.9886 | 65.64092 | 2 56 |

2662

**Table S4.2** – Number of fish from each age class in each river. Rivers ordered by latitude

| River | 0+ | 1+ | 2+ | 3+ |
|---|---|---|---|---|
| Cares | 19 | 106 | 46 | 0 |
| Frome | 184 | 0 | 0 | 0 |
| Tweed | 54 | 121 | 1 | 0 |
| Deveron | 4 | 176 | 8 | 0 |
| Sunnudalsá | 0 | 2 | 54 | 16 |
| Vesturdalsá | 0 | 44 | 162 | 46 |

**Table S4.3** – Model structure and outputs on the effect of temperature and river on ln mass corrected metabolism including a random effect of experimental run nested within sampling day nested within river.

| Model Structure | Model Outputs | | | | |
|---|---|---|---|---|---|
| | Fixed Effects | Estimate | Std Error | t value | p value |
| **Lmer: ln(Metabolism) ~ Temperature + River +(1 \| River:Day/Run)** | Intercept | -2.01 | 0.21 | -9.49 | <0.001 |
| | Temperature | 0.05 | 0.02 | 2.69 | 0.0101 |
| | Deveron | -0.61 | 0.08 | -7.47 | <0.001 |
| | Frome | 0.21 | 0.13 | 1.66 | 0.107 |
| | Sunnudalsá | 0.24 | 0.12 | 2.05 | 0.059 |
| | Tweed | 0.18 | 0.09 | 2.11 | 0.047 |
| | Vesturdalsá | 0.37 | 0.08 | 4.82 | <0.001 |

**Table S4.4** - Model structure and outputs on the effect of ln mass and temperature corrected metabolism, mean annual temperature, and species on growth in the first year including a random effect of experimental run nested within sampling day nested within river and age nested within river.

| **Model Structure** | **Model Outputs** | | | | |
|---|---|---|---|---|---|
| | **Fixed Effects** | **Estimate** | **Std Error** | **t value** | ***p* value** |
| **Lme: Growth ~ ln (Metabolism) * Temperature + Age + Species + Condition +(1 \| River/Day/Run)** | Intercept | 0.135 | 0.058 | 2.34 | 0.031 |
| | Ln (Metabolism) | -0.041 | 0.013 | -3.09 | 0.002 |
| | Annual mean temperature | 0.015 | 0.008 | 1.98 | 0.062 |
| | Trout | -0.055 | 0.016 | -3.43 | <0.001 |
| | Ln (Metabolism) * Temperature | 0.007 | 0.002 | 3.47 | <0.001 |
| | Ln (Metabolism) * Trout | -0.039 | 0.012 | -3.36 | <0.001 |

**Table S4.5** - Model structure and outputs on the effect of ln mass, annual mean temperature, and metabolism on survival including a random effect of river, excluding all Icelandic rivers.

| **Model Structure** | **Model Outputs** | | | | |
|---|---|---|---|---|---|
| | **Fixed Effects** | **Estimate** | **Std Error** | **t value** | ***p* value** |
| **Glmer: Survival ~ ln (Metabolism) + Temperature * ln(Mass) +(1 \| River)** | Intercept | -4.72 | 4.129 | -1.14 | 0.25 |
| | Ln (Metabolism) | -1.11 | 0.454 | -2.45 | 0.01 |
| | Temperature | 0.22 | 0.448 | 0.49 | 0.62 |
| | Ln (Mass) | 1.53 | 1.857 | 0.83 | 0.41 |
| | Ln (Mass) * Temperature | -0.23 | 0.213 | -1.08 | 0.28 |

### 4.5.2 Supplementary Figures

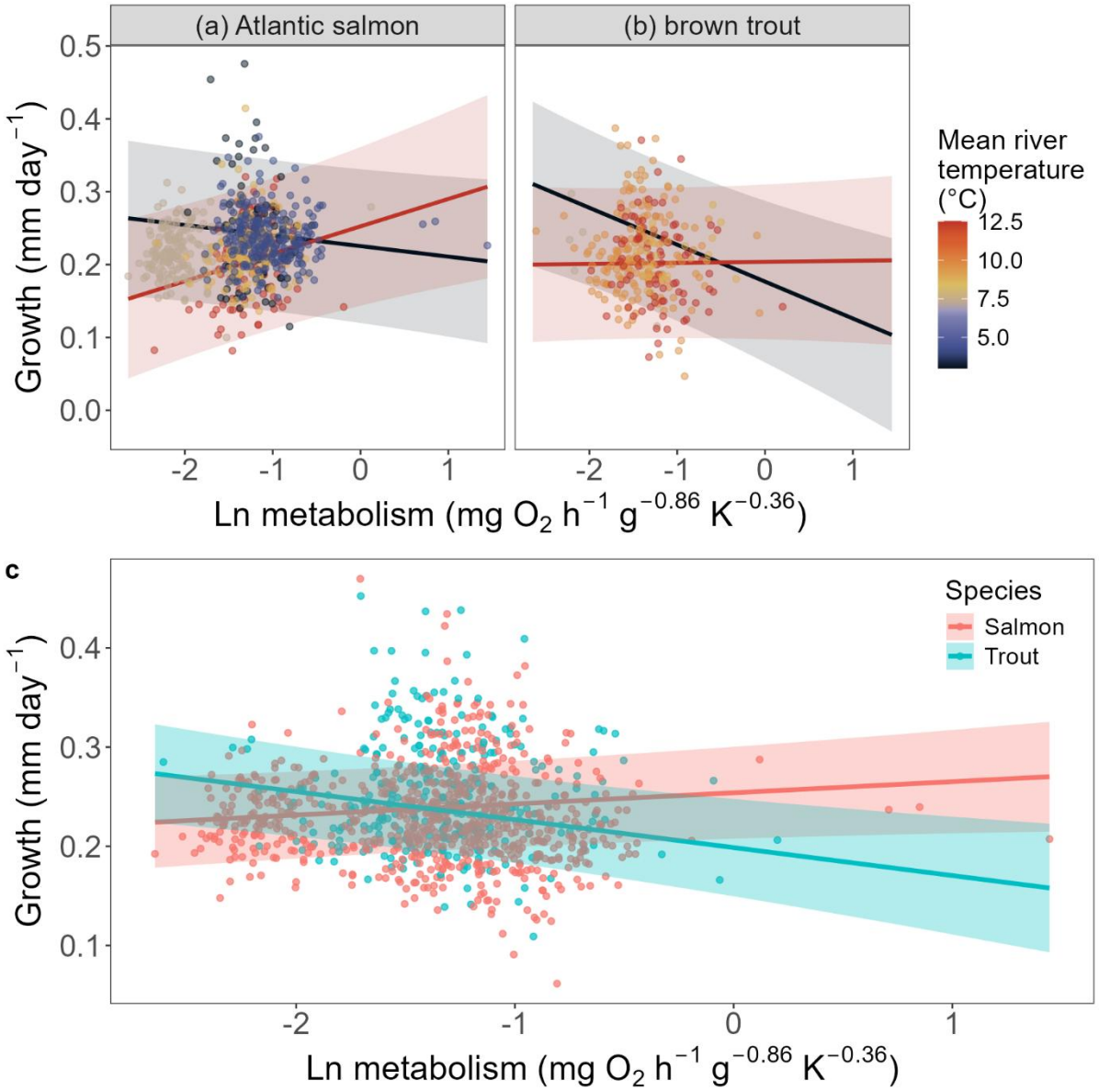



**Figure S4.1** – Variation in growth due to metabolism, river temperature, fish species, and river systems. Growth in the first year against mass- and temperature-corrected metabolism (the allometric exponent is 0.86 and the activation energy is 0.36, see methods) with model predictions (lines) and 95% confidence intervals given for (a-b) min (3.0 °C) and max (12.5 °C) mean annual river temperatures for (a) Atlantic salmon, (b) brown trout two and (c) the difference in slope between salmonid species, with data points visualised as the partial residuals of the model (see Fig. S4.3 for raw growth data).

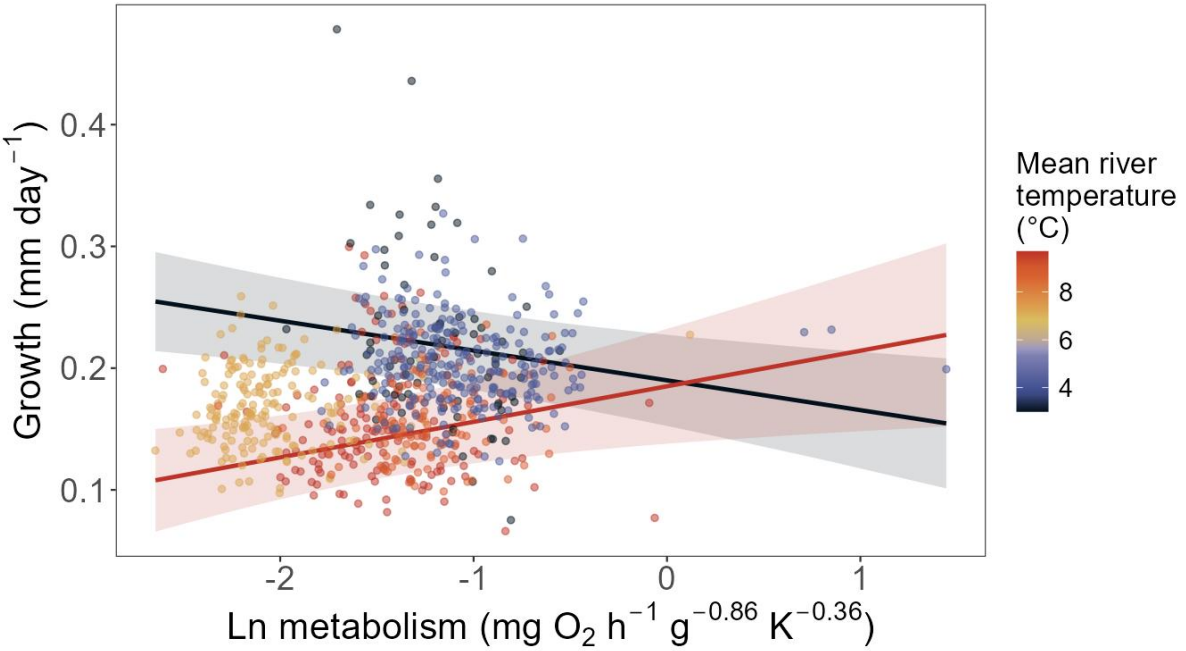
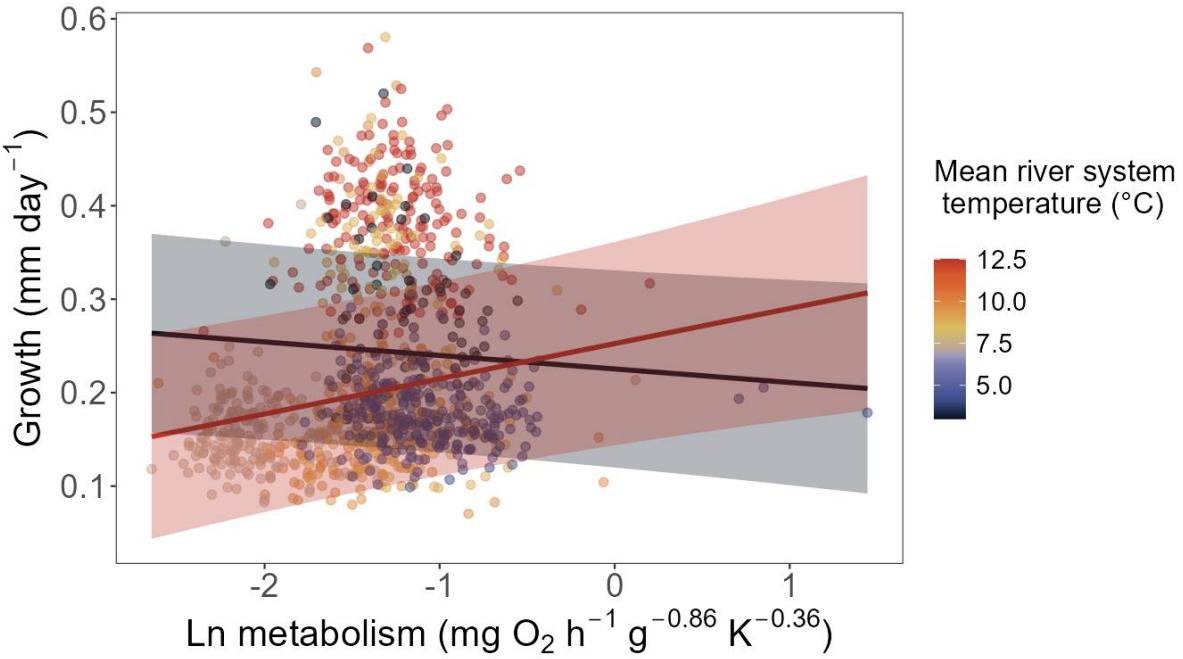



**Figure S4.2** – Showing the growth model outputs with all 0+ fish excluded, with the model predictions (lines) for growth in the first year under max (3.0) and min (12.5) mean river temperature regimes with 95% confidence intervals. These predictions are plotted over the partial residuals of the model, these being the model residuals with the addition of all main effects thereby, correcting for the random effects of sampling run nested within sampling day nested within river and age class nested within river.




2731

2732 **Figure S4.3** – Showing the growth model predictions (lines) with 95% confidence
2733 intervals for summer daily growth in the first year under max (3.0) and min (12.5)
2734 mean river temperature regimes, plotted over the raw data and coloured by
2735 temperature.

# Chapter 5. A framework for using tissue chemistry and biochronologies to reconstruct fish habitat use and growth

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**Abstract**

Understanding fish habitat use, migration patterns, and growth is fundamental for effective fisheries management and conservation, yet reconstructing individual life histories in variable environments remains challenging.

Recent advances in tissue chemical tracers have provided novel tools to retrospectively ascertain habitat use, however these approaches are often deemed inaccessible to individuals without chemistry backgrounds, or applied inconsistently between studies, often without clear rationale. Here, we present a framework for using chemical tracers from archival tissues to reconstruct the lifetime habitat use and growth histories of fish.

We demonstrate the utility of the framework by applying it to brown trout (*Salmo trutta*) in a Norwegian system of interconnected lake, river, and marine habitats. We describe the extent to which adult trout used two freshwater lakes as juveniles and explore variation in out-migration timing and growth rates between anadromous and resident forms. We illustrate that chemical tracers can provide novel and valuable information when applied correctly.

Practical Implication: This framework offers a clear, transferable tool for using chemical tracers to reconstruct habitat use and growth across diverse fish species. This enables both researchers and managers to deliver key insights into lifetime habitat use and growth in both freshwater and marine environments.

## 5.1 Introduction

The use of natural chemical tracers recorded in organism tissues has increased markedly over recent decades, particularly in the fields of behavioural ecology, food traceability and archaeology (Krahn et al., 2007; Lichtfouse, 2000). Most of these applications rely on the principle that geographic variation in local environmental chemistry and diet will generate chemical differences in the tissues of organisms living there, mediated by factors such as temperature, trophic level, and physiology (Hüssy et al., 2021a; Trueman and Glew, 2019). Given the challenges and costs associated with handling and tagging aquatic animals or performing laboratory experiments, natural chemical tracers such as tissue isotope ratios and element concentrations are increasingly used to reconstruct fish habitat use (Tabouret et al., 2010), ontogenetic niche shifts (McMahon et al., 2011), metabolic phenotypes (Trueman et al., 2023), and thermal histories (Holden et al., 2022). These studies often utilize tissues that grow incrementally through the lifetime of the animal -so called archival tissues- such as otoliths (earstones), eye lenses, vertebrae, fin rays, and scales (Campana, 1999; Tzadik et al., 2017). These techniques can be used in combination to identify natal habitats contributing most to mixed populations and habitats supporting higher growth, allowing targeted restoration or protection of those habitats that contribute most to supporting a population.

However, despite widespread applicability, often low-cost relative to telemetry, and unique suitability to smaller-bodied life stages and species, the use of chemical tracers to track fish movements is rarely utilised by managers and not consistently applied between studies (Benjamin et al., 2014; Munroe et al., 2018). Studies using chemical tracers often fail to follow a clear and logical approach, which is key to reproducibility and transferring best practices across species, studies, and systems. As the complexity of research questions increases, more decisions and assumptions are required to answer them, and a transparent and consistent methodological framework becomes increasingly important (Elsdon et al., 2008). As such, we have developed a logical framework for managers and researchers to follow when considering and applying chemical tracers to reconstruct fish habitat use in their system. This framework will help to select the appropriate tool(s) for a given study system, species, or question (or to confirm if none are available). First, we outline each step (Fig. 5.1) along with their justification and context, providing additional

detail for associated statistical and chemical analyses, which tend to be the most complex and daunting for new practitioners entering this field. Second, we use brown trout (*Salmo trutta*) as a model species to apply the framework to, given its diversity in movement behaviour and growth (Jonsson and Jonsson, 2011). We focus on a trout population inhabiting a Norwegian coastal catchment where both anadromous 'sea trout' and freshwater 'residents' coexist. In the Methods, we apply the framework to address two key questions around variation in (1) freshwater nursery habitat use and (2) growth rates among migratory forms, highlighting the cost-benefits of our approach, and ways we attempted to reduce uncertainty along the pipeline. In the Results and Discussion, we use the outputs to discuss what we observed and the advantages and disadvantages of different techniques and potential refinements that could be considered.

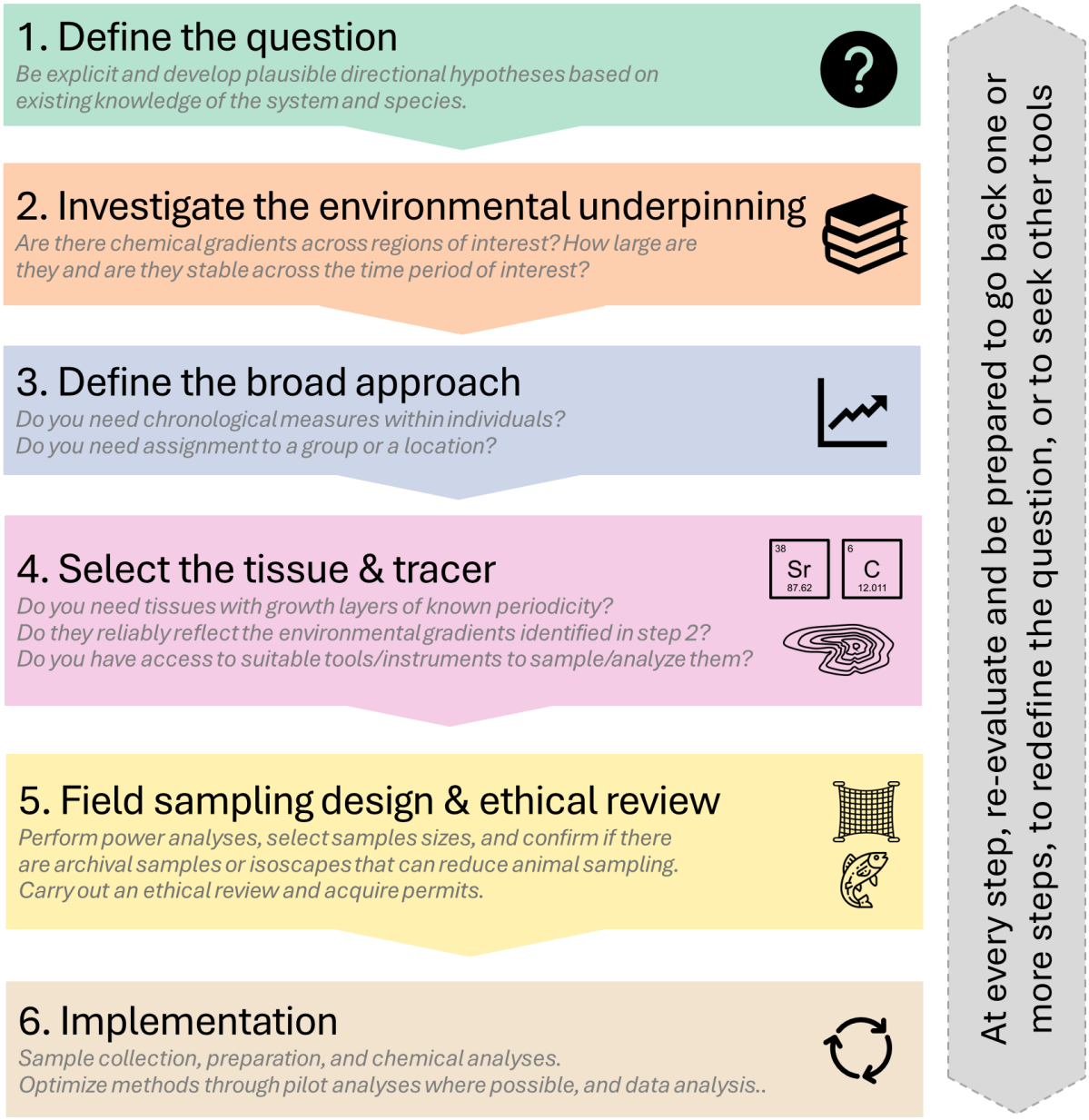



**Figure 5.1** - A framework for using chemical tracers in fish tissues for addressing ecological questions, with a primary focus on habitat use and movement reconstruction.

**A framework for using tissue chemical tracers to infer fish habitat use**

**Step 1. Define the question.** Be explicit about the spatiotemporal scales of interest. Identify whether it is important to resolve to site or region level, or whether geographic location is less important (e.g. if interested in habitat type or stock membership). The temporal scale could be for a single time point (e.g. recent, natal, juvenile; (Johnson et al., 2008)) or span a time series of individual movements (e.g. sequential geolocations (Tanaka et al., 2010)).

**Step 2. Investigate the environmental underpinning.** Review the literature, maps, and datasets to assess if environmental gradients may exist across the region of interest. Tracers may vary as a function of salinity, temperature, geology, pollution, local biogeochemical processes such as hypoxia, or physicochemical features such as ocean fronts (Sturrock et al., 2012). Environmental gradients can also be created by differences in local food webs relating to energy sources and habitat types that might be inferred from stomach contents and stable isotope data, which are often presented and analysed in the form of 'isoscapes' (Trueman and Glew, 2019). Consider whether spatial gradients remain stable over the study period, whether their magnitude outweighs seasonal or interannual variability, or whether global change may modify them (e.g. the Suess effect causing a global shift in $\delta^{13}C$ (Keeling, 1979)).

**Step 3. Define the broad approach.** Decide between a single time point or repeated measures and select a statistical approach. Four main approaches include:

(a) Continuous isoscapes (isotopic maps): Interpolate isotope values and environmental covariates to predict origin based on tissue isotopic measurements. This requires known tracer-tissue relationships, with most applications using organic $\delta^{13}C$ and $\delta^{15}N$ (Trueman et al., 2017), otolith $\delta^{18}O$ (Sakamoto, 2024) or otolith $^{87}Sr/^{86}Sr$ (Brennan et al., 2019). Given the complex structure of dendritic riverscapes, water $^{87}Sr/^{86}Sr$ isoscapes require more complex modelling techniques such as Spatial Stream Network Modelling (Brennan et al., 2016).

(b) Nominal assignment: Classifies individuals into predefined groups using models like discriminant function analysis or random forest (Wang et al., 2018). Does not require tracer-tissue relationships but needs extensive, tissue- and context-matched reference libraries, hampering transferability.

(c) Unsupervised clustering: Groups individuals by similar chemical signatures (e.g. stocks or migratory types) using methods such as Bayesian mixture models. A disadvantage is that geographic resolution is often unclear (Hobbs et al., 2019; Wang et al., 2018)

(d) Movement reconstruction: Typically uses time-series chemical tracer data recorded in sequential growth bands of archival tissues to infer individual movements via zoning, change-point analysis, or recursive partitioning (Hedger et al., 2008; Vignon, 2015)

**Step 4. Select the tissue and tracer.** This step is the most complex, with multiple tissues from a single individual and/or multiple tracers in the same tissue potentially required to answer a given question. See Text S5.1 for additional details.

Tissue: In teleost fish, archival tissues such as otoliths and eye lenses are well-suited to movement reconstruction as they are metabolically inert, and therefore tracers should be retained in growth layers permanently; however, they can only be lethally sampled (Campana and Thorrold, 2001; Quaeck-Davies et al., 2018). Non-lethally sampled tissues such as fin clips (single time point), scales or fin rays (chronological) may be suitable, depending on the question, tracer type, movement timing and tissue turnover rate (Jovičić et al., 2023), but post-depositional chemical alterations need to be carefully considered (Tray et al., 2022).

Tracer: Variations in water chemistry are generally better reflected in inorganic matrices (e.g. otolith calcium carbonate). Conversely, dietary differences generally manifest in protein rich tissues (e.g. muscle, liver, eye lenses), although organic material can be isolated from calcified structures (McMahon et al., 2011). Common tracers in fish movement research include:

(a) Elemental concentrations in otoliths and other calcified structures are widely used due to the ease of measuring multiple elements at fine temporal resolution via Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICP-MS). While some elements (e.g. Sr, Ba, Mn) reflect environmental conditions, most have complex or weak relationships with ambient concentrations (Sturrock et al., 2015). Beyond salinity-driven movement (inferred via Sr, Ba), elemental data are most often used for nominal assignment, where physiology enhances population differences (Sturrock et al., 2012). Elements like Zn, Mg, and P are also used for age estimation

and to create chemical chronologies for movement reconstructions (Hüssy et al., 2021a).

(b) Stable isotope analysis (SIA) of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ in organic tissues (e.g. muscle, fin, eye lens) via Isotope Ratio Mass Spectrometry (IRMS) is often used to infer food web dynamics and past habitat use (Bell-Tilcock et al., 2021; Post, 2002), however temporal resolution is heavily influenced by soft tissue turnover rates (relatively short for blood and liver, longer for muscle and fins/skin). Tissue $\delta^{13}C$ and $\delta^{34}S$ values of low trophic level prey items also vary with salinity, serving as tracers of marine-freshwater movement and estuarine residency (Moore et al., 2016). Compound-specific SIA offers finer resolution for movement but is costly and time-intensive (Harada et al., 2022).

(c) Isotope ratios in the inorganic phase of calcified structures: Otolith $\delta^{18}O$ and $^{87}Sr/^{86}Sr$ broadly reflect geographic variation in water $\delta^{18}O$ (and salinity), temperature and bedrock geology, aiding movement reconstruction in aquatic systems (Brennan et al., 2015; Sakamoto, 2024). A key challenge is being able to sample the otolith at fine enough temporal resolution, although secondary ion mass spectrometry and multi-collector LA-ICP-MS can help to address this (Hanson et al., 2010). While used less for movement reconstruction, otolith $\delta^{18}C$ is often measured alongside carbonate $\delta^{18}O$, providing additional information about individual metabolic rate (Chung et al., 2019).

**Step 5. Field sampling design and ethical review.** Where possible, a power analysis should be conducted using pilot data or data from the literature, ideally for the same species and system (Kemal, 2020). The results should be used to inform a sampling plan that will give sufficient power for the proposed statistical approach. An ethical review should then be conducted that considers sample sizes relative to the population size, and how to minimise lethal take or animal suffering (e.g. using non-animal alternatives or existing tissue archives), and how to minimise potential habitat damage caused by the sampling (Bennett et al., 2016). Finally, sampling permits, and local permissions should be obtained.

**Step 6. Implementation.** Perform pilot analyses to check that the planned instrument and tissue sampling methods can measure the chosen tracer(s) at the required temporal resolution and detection levels. If required, perform method

development to optimise the approach. Fieldwork, sampling, and tissue analyses should then be carried out and the statistical approaches identified in Step 3 used to analyse the data and answer the research question. Throughout this framework, it is important to constantly re-evaluate and revisit previous steps or even stopping altogether and exploring other tools if the selected tracer does not vary as expected or falls below detection limits in specific tissues.

## 5.2 Methods: Norwegian trout case study

In 2021, we sampled 53 trout from two lakes in Trondheim, Norway, with the goal of answering the following questions: (1) What fraction of brown trout used each of the two lakes along the river network as nursery habitat? and (2) At what age do sea trout first leave freshwater, and do their growth rates differ to resident trout before and/or after their first seaward migration? We used the framework to design our methods, as outlined below and in Table 5.1.

The two freshwater lakes, Storvatnet (upstream) and Litjvatnet (downstream; Fig. 5.2) are 2.92km$^2$ and 0.47km$^2$, respectively, and known from tagging studies and fish surveys to be frequently used by juvenile trout. To ensure good representation of all lake habitats and a wide spread of size classes, trout were sampled by gill nets using a broad range of mesh sizes (5 - 55mm) that were left overnight across a range of habitats. Total sample sizes for each lake were 10 reference fish (mean FL = 167mm, range = 104-241mm) and 17 adults (mean FL = 496mm, range = 450-562mm) for Litjvatnet, and 19 reference fish (mean FL = 181mm, range = 108-234mm) and 7 adults (mean FL = 482mm, range = 403-576mm) from Storvatnet. Based on the timings and sizes of tagged trout that performed marine migrations (Paterson et al., 2021), we were confident that our immature reference fish (fork lengths (FL) <250mm) had never been to sea and were thus used as lake and freshwater ‘reference samples’ (Table 5.1). Conversely, the adults (>400mm FL) had unknown migration histories. Sampling was authorised by the County Governor of Trøndelag (Statsforvalteren i Trøndelag; permit no. 2021/1934).

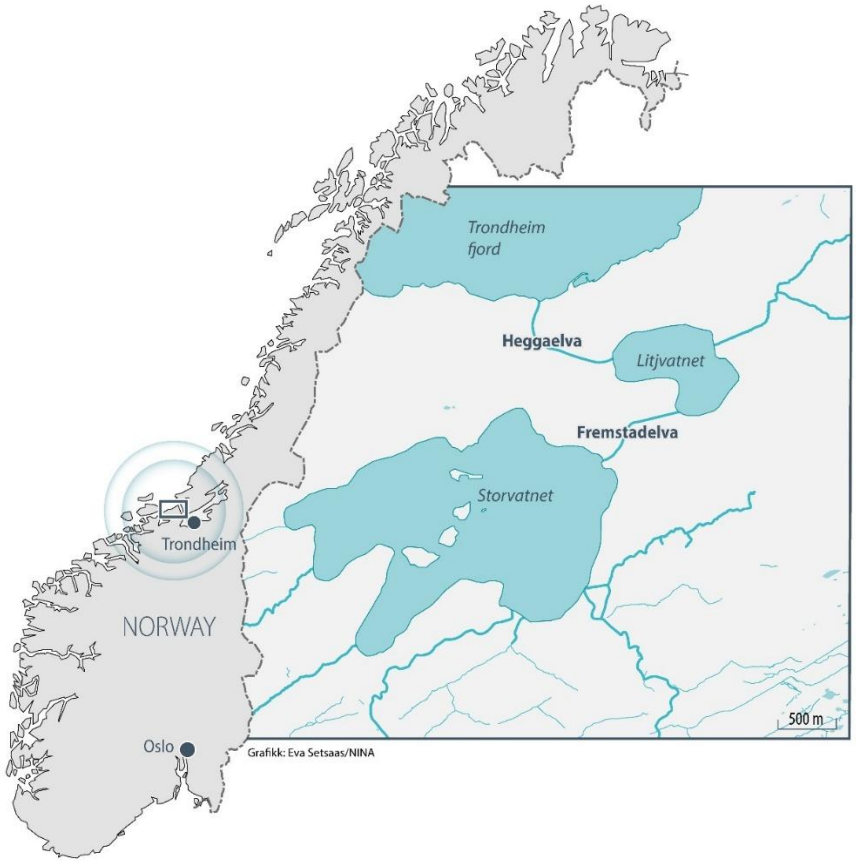



**Figure 5.2** - Map of the Fremstad catchment in central Norway, with the inset map showing the two focus lakes and their connection to the Trondheim fjord and sea.

Fish were euthanised and their eye lenses and sagittal otoliths extracted. Eye lenses were stored frozen and otoliths stored dry. To investigate each fish's trophic history (and thus habitat use), the lenses were thawed then sequential laminae dissected, air-dried then encapsulated in tin cups using the methods of Bell-Tilcock et al., (2021). Lens laminae were then analysed for bulk $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ (excluding the core ~600µm diameter, as it was below the instrument's minimum mass requirements). Using Elemental Analyzer-Isotope Ratio Mass Spectrometry via a vario PYRO cube elemental analyser (CN mode) coupled with visION isotope ratio mass spectrometer. Both fish muscle standard ERM-BB422 (sample no. 0487 certified reference material fish muscle, European Commission, JRC, Geel, Belgium) and Sulfanilamide were used as standards. Isotope ratios are reported in delta (δ) notation relative to VPDB (C), AIR (N), and VCDT (S), analytical precision based on repeated measurements of internal standards, was ±0.06‰ for $\delta^{13}C$, ±0.09‰ for $\delta^{15}N$, and ±0.33‰ for $\delta^{34}S$ (1 SD). Otoliths were ground and polished on the sagittal

plane following, Sturrock et al., (2015), then analysed for element concentrations ($^{7}$Li, $^{23}$Na, $^{24}$Mg, $^{31}$P, $^{39}$K, $^{43}$Ca, $^{52}$Cr, $^{55}$Mn, $^{56}$Fe, $^{59}$Co, $^{60}$Ni, $^{63}$Cu, $^{66}$Zn, $^{85}$Rb, $^{88}$Sr, $^{107}$Ag, $^{111}$Cd, $^{138}$Ba and $^{208}$Pb) from the core to the dorsal edge using LA-ICP-MS via an ESI NWR193 laser ablation unit coupled to an Agilent 7900 ICP-MS (see Text S5.2 for full details). Prior to finalising the laser ablation settings, we performed a series of trials to identify the optimal settings and beam diameter that would allow us to meet detection limits for low level elements for among-lake habitat discrimination while maximising temporal resolution to determine brief marine excursions. Details of these trials and final instrument conditions for analyses are outlined in Text S5.2, Fig. S5.1, and Table S5.1. Otolith element concentrations were then despiked and smoothed (detailed in Text S.5.3) and elements with >50% of measurements below detection limits or exhibiting high RSD values were excluded (Li, P, Cr, Fe, Co, Ni, Cu, Rb, Ag, Cd, Pb; Table S5.2).

### 5.2.1 Question 1: What fraction of brown trout used each of the two lakes along the river network as nursery habitat?

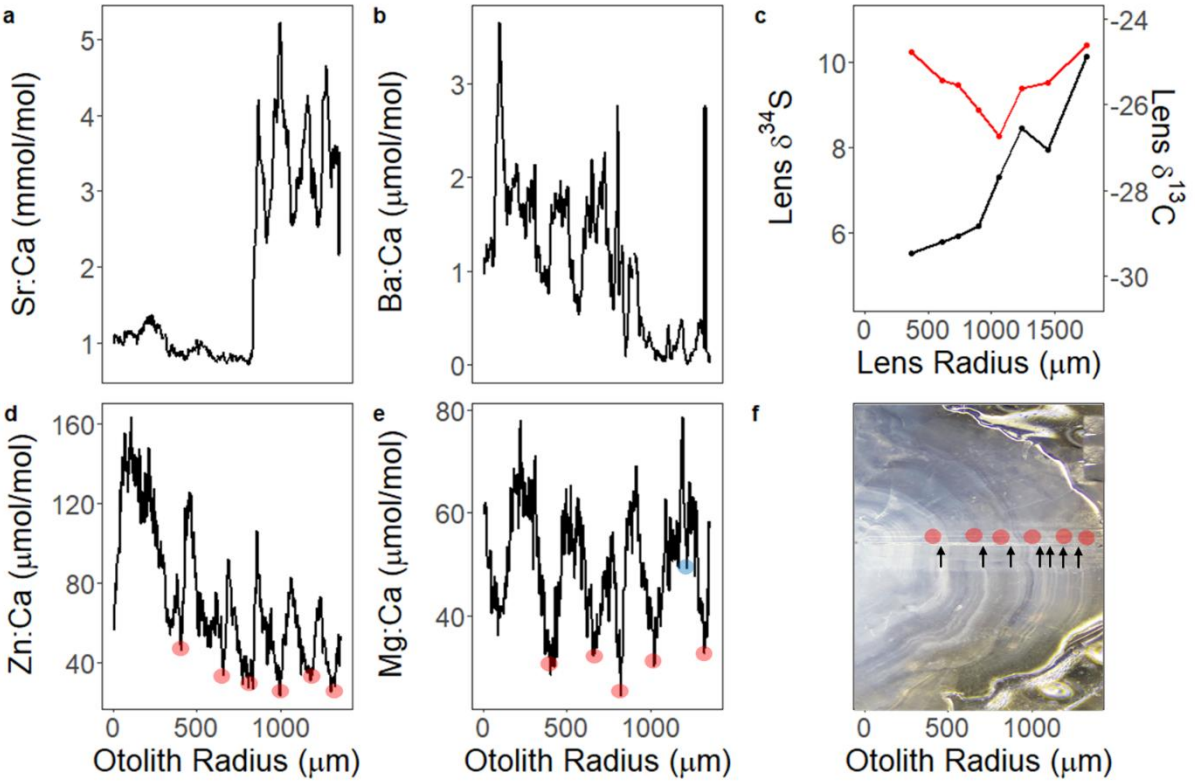
To characterise each lake's signature, we used the outermost material from the eye lenses (outer ~243 ± 43μm of the eye lens, diameter range=1396 - 3182μm) and otoliths (final 20μm of each line scan; radius range = 540-1094μm) from the immature trout, representing the most recent growth. We then targeted the same approximate size and age period in the adult otoliths (radius range = 708 - 7336μm). Eye lens isotope data were not used for the adults for this question, as discussed in the results. Chemical differences between lakes were characterised using the reference samples and Wilcoxon tests as the data did not meet assumptions required for parametric tests, for these tests the element tracers were natural log transformed. Random forest models (from the *caret* R package (Kuhn et al., 2023)) were then trained on 70% or 100% of the reference samples, with their accuracy tested using the remaining 30% (out-of-sample; OOS) or out-of-bag (OOB) approaches, respectively. The model with the highest accuracy was then used to analyse the equivalent size range in the adult fish tissues and assigned each individual to a nursery habitat. To generate 95% confidence intervals (CI) for our predictions, the model was trained on all training data 100 times, and each output model used to predict the adult assignments, with the mean probability used to predict final assignment to either lake. We classified these assignments as 'high

confidence' if their 95% CI did not overlap the 0.5 chance of being assigned to either lake *cf.* 'low confidence' if they did.

### 5.2.2 Question 2: At what age do sea trout first leave freshwater, and do their growth rates differ to resident trout before and/or after their first seaward migration?

The lifetime eye lens $\delta^{13}C$ and $\delta^{34}S$ and otolith Sr:Ca and Ba:Ca chronologies were used to reconstruct marine migrations in the adult trout. The four putative salinity markers showed changes suggestive of movement across the salinity gradient in the predicted directions (Fig. 5.3a-c). However, the lenses could not be sampled at sufficient temporal resolution to detect sub-annual migrations and meet IRMS mass requirements, while otolith Ba:Ca tended to be noisier than otolith Sr:Ca and less effective for identifying freshwater-marine migrations later in life (Fig. 5.3). Therefore, otolith Sr:Ca was selected for detecting anadromy, using a threshold value of 2.42 mmol/mol (equivalent to 2052 ppm) based on the maximum value observed in the freshwater reference samples after excluding the core material (specifically, the first 250μm from the core), given that this would exhibit elevated Sr:Ca if the mother was anadromous (Johnson et al., 2008). This threshold was similar to those used in other salmonid-focused studies (Hart et al., 2015; Mainguy et al., 2023).

Otoliths were both visually and chemically aged, the latter using the minima from Zn:Ca and Mg:Ca cycles drawing confidence among the two tracers when one was noisier, with a second reader aging (n=10 visual and n=8 chemical for comparison) (Fig. 5.3d-f). As among-reader variation was higher for visual reads than chemical reads (Fig. S5.2), chemical ages were selected to estimate fish age and annulus widths. Incomplete annuli at the edge were excluded.




3044

3045 **Figure 5.3** – Example tracer profiles against otolith or eye lens radius from a single
3046 adult trout. Top row shows putative salinity markers, otolith (a) Sr:Ca and (b) Ba:Ca,
3047 and (c) eye lens $\delta^{34}S$ (black) and $\delta^{13}C$ (red). Bottom row shows putative age
3048 markers, otolith (d) Zn:Ca and (e) Mg:Ca, and (f) a photograph of the sagittal otolith
3049 on the dorsal axis under reflected light. Red dots in (d) to (f) denote estimated annuli
3050 based on chemical ageing. The blue dot in (e) denotes an annulus that was placed
3051 based on otolith Zn:Ca cycles despite lack of a clear pattern in otolith Mg:Ca.
3052 Visually identified growth bands in (f) are denoted by black arrows, which were
3053 generally deemed more difficult to read due to false annuli, here resulting in an
3054 additional year of growth compared to chemical ageing.

3055 Given ontogenetic trends in growth rate for all fish, a Generalised Additive Mixed
3056 Model (GAMM) was fitted in *mgcv* R package relating annulus width against age,
3057 excluding ages >7 to ensure good representation across fish and phenotypes
3058 (Ashworth et al., 2017; Vigliola and Meekan, 2009). The GAMM included an
3059 interaction between migratory phenotype and age, so that differences in growth rate
3060 at different ages could be tested for using GAM difference in the *gratia* package
3061 (Simpson, 2019). The model also included a categorical variable for phenotype
3062 (anadromous vs. resident) and habitat (freshwater if the annulus was formed wholly

in freshwater vs. marine if the annulus was at least partially formed while the fish was at sea). Finally, the model included a random effect of fish ID to allow the intercept to vary by fish and allow for individual variation in growth.

## 5.3 Results and Discussion

### 5.3.1 Question 1: What fraction of brown trout used each of the two lakes along the river network as nursery habitat?

Of all chemical tracers examined, only eye lens $\delta^{15}N$ values and ln (otolith Mn:Ca) exhibited significant differences between the lakes (Wilcoxon: W= 148, $p$ = 0.014 and $W$ = 145, $p$ = 0.021, respectively; Table S5.3, Fig. 5.4). Though markers such as ln (otolith Sr:Ca) and ln (otolith Ba:Ca) did show sufficient difference to contribute meaningfully to differentiating between lakes in the multivariate classifier (Fig. S5.3b). Many tracers show a large spread of values and in some cases e.g. ln (otolith Mg:Ca), variance partitioning from ANOVA indicates 99.98% of variance was within lake, and it contributed basically zero explanatory power to the assignment model (Fig. S5.3). This between-individual variation is likely due to differences in physiology, growth rate, and diet, see Hüssy et al., (2021) and Sturrock et al., (2015).

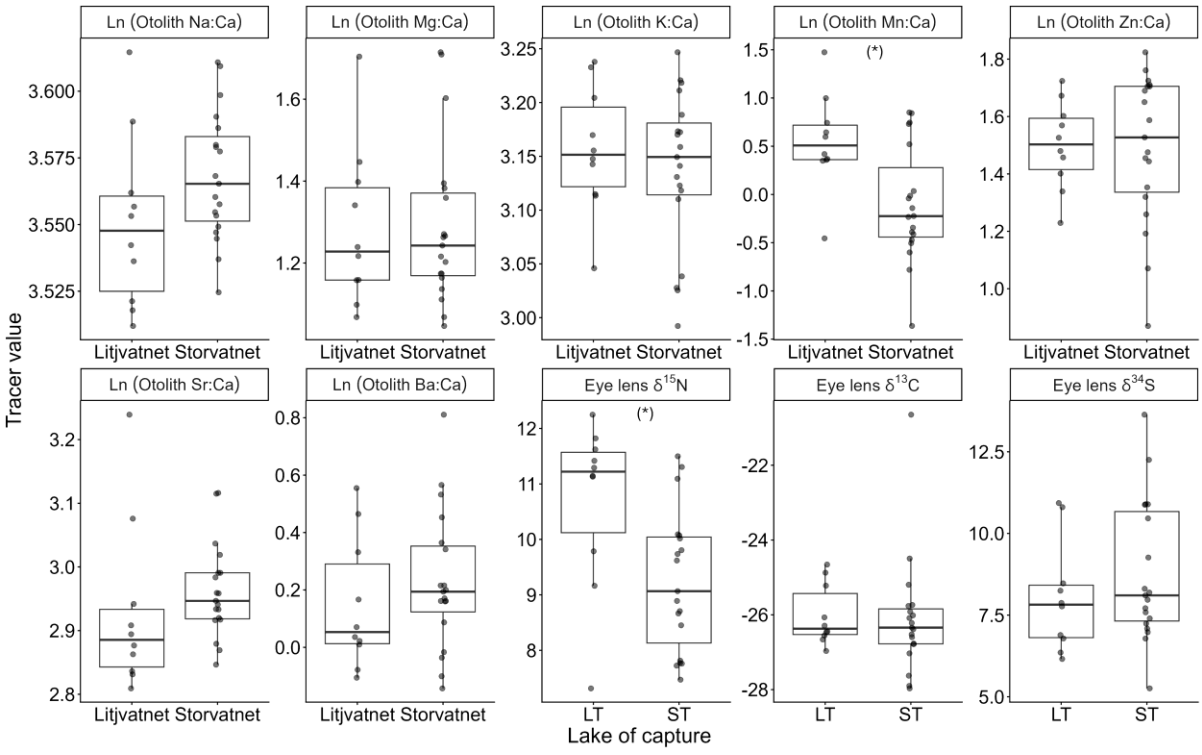


**Figure 5.4** – Differences in tracer values measured in the outer eye-lens lamina (measured δ-isotope values) and at the otolith edge (elemental concentrations expressed as natural log mmol/mol) of immature ('freshwater reference') brown trout captured in Litjvatnet and Storvatnet lakes in Trøndelag, Norway. Asterisks denote significant relationships.

The random forest (RF) models trained on (a) lens isotopes, (b) ln otolith element concentrations or (c) both, exhibited prediction accuracies ranging from 64% to 70% (OOB) and 75% for all three (OOS; Table 5.2). Given the small dataset (resulting in very small test datasets for OOS, Table 5.2), we decided to include all training data to predict the rearing lake used by the adults and thus used the model with the highest OOB accuracy (i.e. the model trained only on otolith elements). This model was driven primarily by among-lake variation in otolith Mn:Ca, with the higher concentrations observed in fish caught from the lower lake (Litjvatnet) characterised by higher levels of agriculture, potentially reflecting periods of hypoxia (Fig. S5.3b) (Limburg et al., 2015). Surprisingly, the model trained on both otolith and eye lens markers exhibited lower OOB accuracy (66%), despite also including lens $\delta^{15}N$ values, which drove discriminatory power in the lens-only model (Fig. S5.3c).

Our model predicted that 21% of the lake-sampled adults had used the lower lake, Litjvatnet, as nursery habitat (4% at high confidence and 17% at low confidence) (Fig. 5.5). Conversely, 79% were predicted to have reared in the upstream lake, Storvatnet (33% at high confidence and 46% at low confidence) (Fig. 5.5). This was expected given that Storvatnet is a larger, less human-impacted lake, fed by multiple spawning streams (i.e., the first large non-natal habitat experienced by downstream migrating fry). The failure to assign many adult fish to one of the two lakes with high confidence may be due to rearing in areas excluded from our baseline (e.g. upstream spawning streams), however previous electrofishing efforts indicated few 2+ trout in nearby spawning streams (R. Paterson, personal communication, March 06, 2025), suggesting that these populations reside mainly in the lakes prior to onset of sexual maturity and potential seaward migration. It may also be due to regular movement of immature fish between the lakes, having lower numbers of reference samples than suggested by our power analysis, and/or interannual variability in water or diet chemistry (Jonsson, 1985). Future studies should consider sampling upstream tributaries and connecting rivers, and cohort-matching reference and adult

samples (Table 5.1). However, of the adults assigned to either lake with high confidence, 67% had developed in the same lake that they were captured in, suggesting high site fidelity (Fig. 5.5).

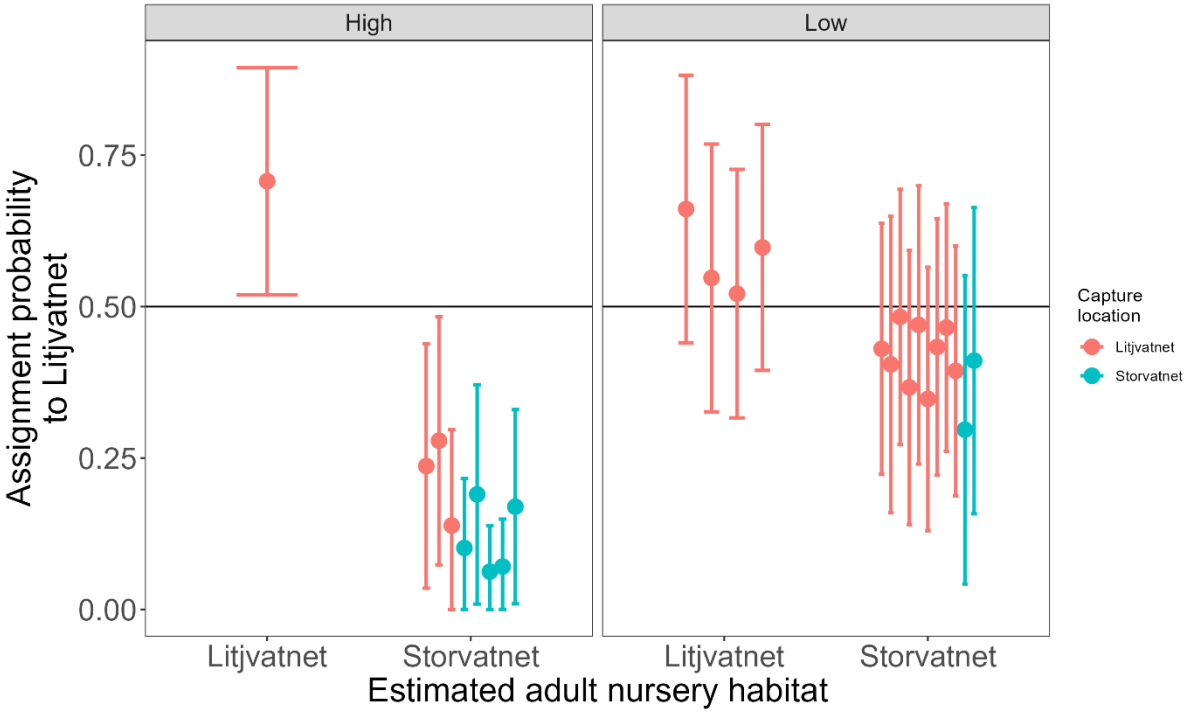



**Figure 5.5** – Mean assignment probability for unknown origin adults to Litjvatnet (assignment probability to Storvatnet is the inverse) using the random forest model trained on otolith elements ±95% CI based on 100 repeat models. Individuals with mean probabilities >0.5 were assigned to Litjvatnet and <0.5 to Storvatnet. The adults are separated between high and low confidence predictions based on their 95% CI overlapping or not overlapping an assignment probability of 0.5, respectively. Colour indicates the lake in which the adult was captured.

### 5.3.2 Question 2: At what age do sea trout first leave freshwater, and do their growth rates differ to resident trout before and/or after their first seaward migration?

Within the 24 adult trout sampled, 70.8% (*n* = 17) were identified as anadromous, 12.5% (n=3) as freshwater residents, and 16.7% (n=4) as having an uncertain migratory history, given otolith Sr:Ca concentrations that increased, but to levels only just above or below the threshold (Fig. 5.6). Many individuals appeared to undertake repeated migrations, and four exhibited a distinct Sr:Ca spike at the core greater than the marine threshold value, suggesting that their mothers were anadromous and feeding at sea during vitellogenesis (Johnson et al., 2008; Volk et al., 2000). Multiple other individuals also exhibited elevated core Sr:Ca concentrations, though below our putative marine threshold. Given difficulties in sampling the absolute core, variation in core Sr values depending on the timing of vitellogenesis and maternal migration patterns (Volk et al., 2000), and thus uncertainty in the appropriate threshold to indicate maternal phenotype, we did not include maternal strategy as one of our research questions. However it is interesting that many of the anadromous adults exhibited completely flat Sr:Ca concentrations at the core, suggesting that they were the offspring of resident mothers and evidencing transgenerational phenotype-switching, a phenomenon that has been confirmed previously for trout using tagging (Berejikian et al., 2014; Dębowskii and Dobosz, 2016), and highlighting the life history diversity of this highly plastic species. In fully marine fish, this variation in otolith Sr:Ca is largely explained by physiology (particularly growth rate), potentially with some influence of temperature (Hüssy et al., 2021a; Sturrock et al., 2012, 2015). For trout, however, a lot of the among-individual variation in otolith Sr peak values is also likely explained by the interaction between otolith growth rate, time spent in marine or freshwater habitats, and the laser beam diameter(Miller, 2011; Sturrock et al., 2015; Vignon et al., 2023). For example, a slow growing fish at sea for a relatively short period (say 1 month) would likely exhibit a lower peak otolith Sr concentration than a fast-growing fish at sea for the same length of time, as the laser beam is overlapping more otolith material deposited in freshwater before and after the excursion in the former. While annual and seasonal changes in water chemistry may influence the strontium concentrations in water, and while some freshwater systems exhibit water Sr concentrations higher than marine, the mixing curves between water Sr:Ca and

salinity tend to be logarithmic, with most of the change in Sr:Ca occurring between 0 and 10ppt (Brown and Severin, 2009; Hicks et al., 2010; Walther and Limburg, 2012). Thus, we are confident that if a trout had migrated from fully fresh to fully marine water, it would exhibit large increases in otolith Sr:Ca which would well exceed our threshold independent of the year, as observed in all anadromous-assigned fish (Fig. 5.6). All fish were captured in freshwater, but not all individuals exhibited "freshwater" Sr:Ca values at the otolith edge. This was likely in part due to the lags and signal averaging mentioned above, but also due to challenges associated with sampling the outer otolith margin, where drops in calcium counts often result in the loss of chemical data from the last few days to weeks of life.

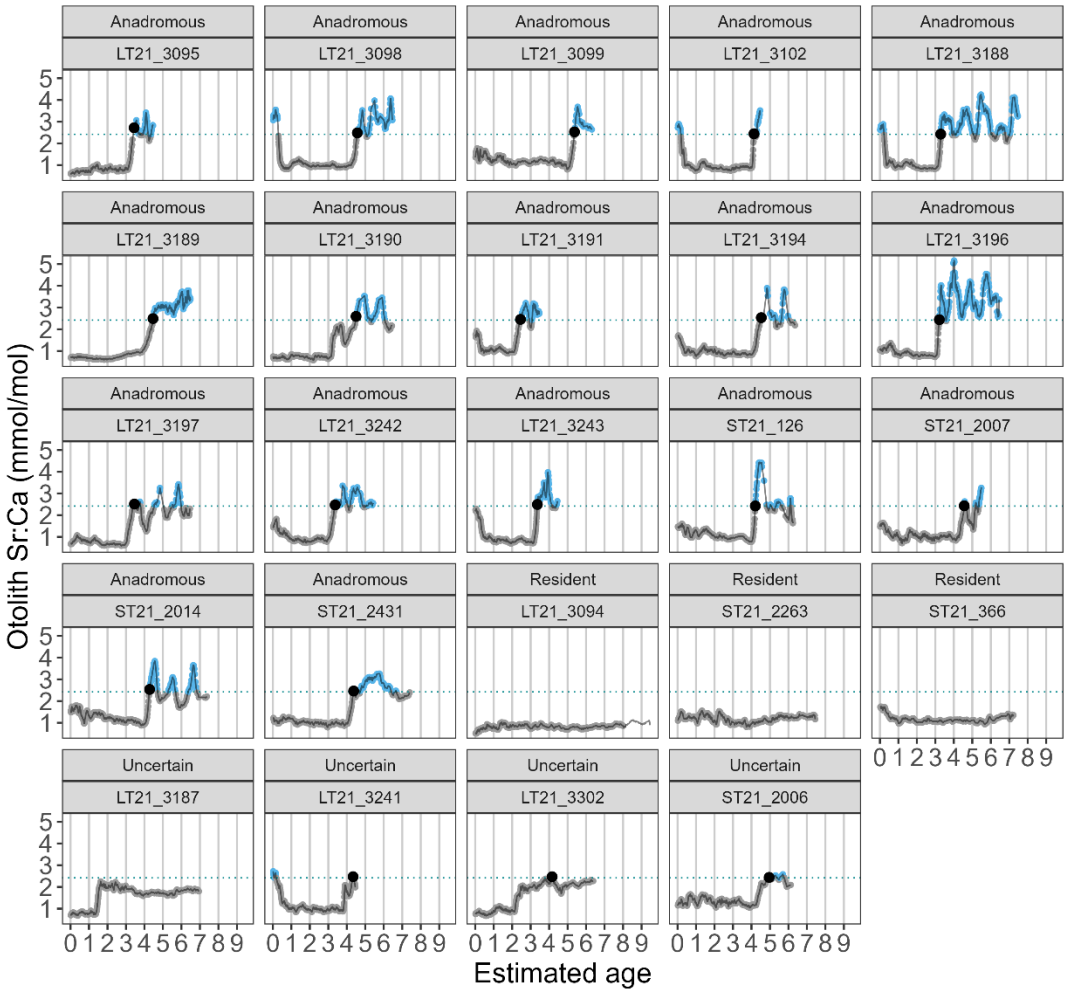



**Figure 5.6** – Otolith Sr:Ca profiles for 24 adult trout, separated into migratory phenotypes identified by otolith Sr concentrations: anadromous, resident, or uncertain given otolith Sr values just above or below the threshold value of 2.42 mmol/mol (dotted line). Periods interpreted as freshwater or sea residence are

indicated in grey and blue, respectively, and age at first outmigration (based purely on the first exceedance of our threshold value outside of the core) is indicated by a black circle. Note that elevated Sr concentrations in the otolith core suggest an anadromous mother, however, difficulties in accurately sampling the core and uncertainty in an appropriate threshold meant that maternal strategy was not reported in this study.

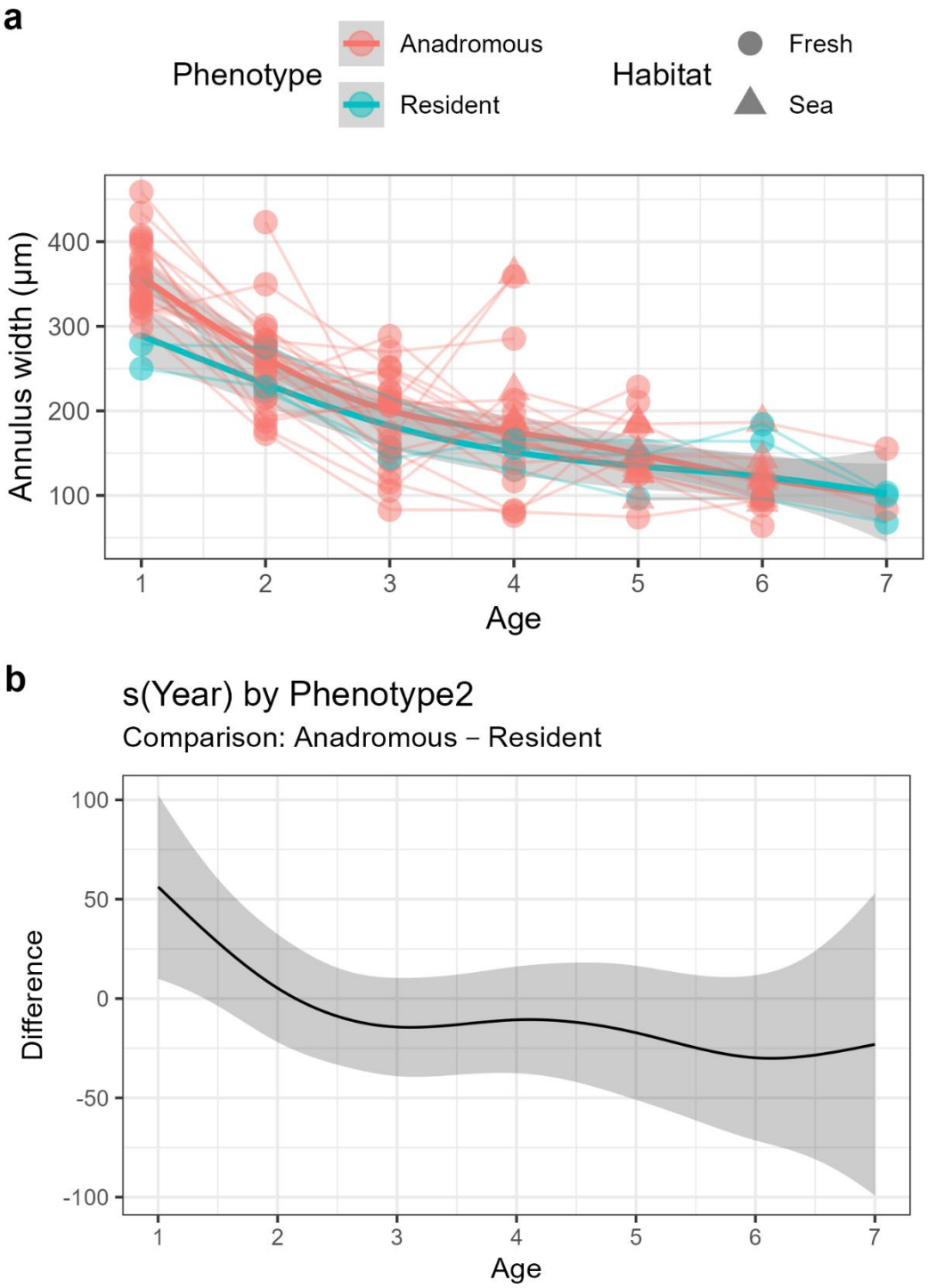
The individuals identified as 'uncertain' exhibited lens $\delta^{34}S$ in outer laminae that tended to be higher than in resident fish (Fig. S5.4). Taken with the intermediate otolith Sr:Ca values, this suggests frequent movements across the salinity gradient or foraging in brackish habitats, and thus these fish were assumed most likely to be anadromous. This highlights the disadvantage of using a static threshold for defining marine migration, as opposed to methods such as zoning algorithms or change point analysis (Walther et al., 2011). Overall, the results suggest a higher proportion of sea trout in this system compared to other Norwegian populations (Jonsson, 1985) and what had been expected based on tagging studies carried out in this system (Paterson et al., 2021). This may be due to the majority of the adults (67%) being sampled from the lower lake, Litjvatnet, which is closer to the sea and smaller in area than Storvatnet, potentially increasing rates of anadromy. It is also likely that our size-based selection criteria to define adult fish (>400mm) biased the sample towards larger, anadromous individuals.

Among the individuals we confidently assigned as anadromous (Fig. 5.6), age at first marine migration occurred between 3 and 7 years old (mean = 3.99 ±0.73 years SD), similar to ages observed in other Norwegian systems, with smolt ages ranging between 2-7 years (Økland et al., 1993). Here, the frequency of return migrations from river to sea varied among individuals, but typically occurred annually, suggesting sub-annual periods at sea (Fig. 5.6). Similarly, in other systems, tagging data have showed many trout overwintering in freshwater and only spending a few months per year at sea (Eldøy et al., 2015; Paterson et al., 2021; Thorstad et al., 2016).

The GAMM explained about 70% of the variance in increment width, with most of this explained by a strong effect of ontogeny ($p < 0.001$ for both phenotypes), with growth generally decreasing with age (Fig. 5.7; Table S5.4). No overall difference in

growth rate was observed among phenotypes ($p$ = 0.168), although the low sample size of resident fish (n=3) would have greatly reduced our ability to resolve any differences. There was also no effect of within-year 'habitat' use on growth rate ($p$ = 0.175). However, the age-phenotype interaction (Fig. 5.7b) suggests that growth rates were significantly higher in marine phenotype fish in the first year (Fig. S5.5). This was consistent whether we assumed the 'uncertain' fish were anadromous (Fig. 5.7b) or excluded them from the analysis (Fig. S5.5).

We posit three potential reasons for the lack of differences in growth among migratory phenotypes, or among years when sea trout had been to sea *vs.* remained in freshwater. First, our sample of freshwater residents was very small (n=3) and likely biased towards faster growing fish, given the size threshold of 400mm used to define 'adults'. Second, due to the high productivity of these coastal lakes, residents may actually grow at similar rates to their anadromous counterparts (Ulsund, 2013; Winnem, 2010). Third, reduced marine growth may occur in this system due to sea lice infestations (*Lepeophtheirus salmonis*) associated with the intensive salmon farming in this region, which can reduce the health and growth of sea trout and lead to premature freshwater return (Bolstad et al., 2025; Gjelland et al., 2014; Thorstad et al., 2015). Sea trout are particularly vulnerable to sea lice infection (compared to other salmonids) due to their marine migrations often concentrating in nearshore areas used for salmon farming (Eldøy et al., 2015).




3232

3233 **Figure 5.7** – Growth rates of anadromous (red) vs. resident (teal) adult trout in this
3234 study (n=24), with (a) showing the raw annulus width data and whether the annulus
3235 was deposited entirely in freshwater (circle) or at least part was formed while the fish
3236 was at sea (triangle). Individual growth trajectories are linked by thin lines in (a), and
3237 GAM smooths were fitted to each phenotype. Plot (b) shows the difference between
3238 the GAM smooths for the relationships between otolith annulus width and age, by

phenotype, suggesting significant differences when confidence intervals do not overlap.

## 5.4 Conclusion

Developing and applying explicit frameworks is vital to ensure reproducible science and to guide new users in the use of emergent methods. We developed such a framework for using tissue chemistry and biochronologies to reconstruct trout habitat use and growth, demonstrating its application in both marine and freshwater settings to investigate fish nursery areas and to explore variation in migratory behaviours and growth rates. Our results suggest that Storvatnet, the upstream lake, plays a disproportionate role in supporting the growth and survival of juvenile trout in this system. Future steps could include additional tagging experiments and targeted fish sampling to better understand the underpinning mechanisms. If the results reflect lower survival rates in the lower lake (*cf.* simply lower movement rates into it), this could guide management actions aiming to increase trout productivity in this system. Our study also supports previous studies illustrating the plasticity of migration patterns exhibited by anadromous trout, an adaptation that has – at least historically - increased their resilience to disturbances across marine and freshwater realms. The results suggest that early life growth rates may influence migratory tendency, and - unlike previous studies - that growth rates were similar among resident vs. anadromous forms. Future work should confirm this result with larger sample sizes and validate otolith reconstructions using tagged fish with known migration histories. One could also compare results from contemporary *vs.* historical otolith samples (e.g. pre-aquaculture or even pre-humans) to explore the influence of anthropogenic influences on trout behaviour and growth. Overall, by using a methodical and transparent approach, we demonstrated how the framework could be used to help researchers and managers decide whether chemical tracers are the best tool for their question, species and system, and how to apply them to answer different questions about fish movement and growth.

## 5.5 Supplementary Material

### 5.5.1 Supplementary Text

**Text S5.1** – Additional information to support new users working through Step 4: Selecting the tissue(s) and tracer(s) for your question

Identifying the best tissue-tracer combination ideally includes both a literature review and pilot analyses, as how you sample the tissue and how well you can measure the tracer in that sample are intrinsically intertwined. Note: you may need to analyse multiple tissues from a single individual and/or multiple tracers on the same tissue (i.e., multiple instruments) to effectively answer your question.

**Tissue:** Based on the previous steps in the framework, does your question require (a) chronological records from a single individual or (b) a single measure of past habitat use? For (a), archival structures allow sampling across their growth layers (i.e., 'through time'). For fish, the most commonly used archival structures are otoliths, eye lenses, scales, fin rays, vertebrae and opercula (Tzadik et al., 2017). These hard structures vary in their relative protein content, the periodicity of growth increments, and potential for reworking post-formation. Otoliths and eye lenses are both metabolically inert and thus most likely to retain a permanent record of the chemical tracer (Campana and Thorrold, 2001; Quaeck-Davies et al., 2018), but differ in their composition comprising mostly inorganic (>99% calcium carbonate crystal lattice) vs. organic (>90% crystallin protein (Mahler et al., 2013; Surguchev and Surguchov, 2010)) matrices, respectively. Both structures can also only be lethally sampled, which is problematic when working with endangered species. For (b), archival tissues are also popular, but soft tissues can retain a chemical record of the habitat used prior to capture, depending on the individual's residence time there vs. the tissue's turnover rate (relatively short for blood and liver, longer for muscle and fins/skin).

**Tracer:** Perform a literature review to identify the tissue-tracer combinations that are most likely to vary as a function of the environmental gradients identified in Step 2. In general, water chemistry and/or temperature differences are better reflected in inorganic matrices (e.g. otolith calcium carbonate), while food web differences are better recorded by protein rich tissues (e.g. muscle, eye lenses), although it can be

possible to isolate the organic fractions of calcified structures (McMahon et al., 2011).

Below, we outline the tracers most commonly used in fish movement research, and their sampling and analysis methods, divided into three categories: (1) Element concentrations in calcified structures, (2) Organic- and (3) Inorganic-hosted isotope ratios.

**(1) Element concentrations in calcified structures:** Strontium (Sr) and barium (Ba) are most frequently used in fish movement studies given their ready substitution for calcium in otoliths in proportion to ambient concentrations (Campana, 1999) and strong relationships with salinity (typically positive and negative, respectively, however see (Brown and Severin, 2009) for exceptions for Sr, and note that Ba concentrations can also peak at mid-salinities, particularly when turbidity is high). Accordingly, many studies have used otolith Sr and Ba concentrations singularly (Limburg, 1995) or in tandem (e.g. Sr/Ba) to track fish movements between fresh and marine waters (Hale and Swearer, 2008; Tabouret et al., 2010). In terms of other useful otolith elements, manganese (Mn) provides a promising tracer of hypoxia experience, while zinc (Zn), magnesium (Mg) and phosphorus (P) can track seasonal changes in metabolic rate and growth, thus providing tools to assess age and growth rate (Hüssy et al., 2021b). Otolith multi-elemental “fingerprints”, typically including 3-10 elements, are often used to assign individuals to a particular group or stock (Arslan and Secor, 2005; Avigliano et al., 2020; Duan et al., 2021; Hüssy et al., 2021b). Particularly for applications attempting to use this method to link these fingerprints to a geographic area, it is important to collect an exhaustive and representative reference library (ideally matching species, tissue, life stage, season and cohort), as the mechanisms driving among-group or -area differences are usually unknown. In reality - such as the case study included in the main text of this paper - the field opportunities to collect such reference libraries are not often limited. Importantly, most otolith elements are not incorporated proportionally to ambient concentrations, and they can be subject to strong ontogenetic, taxonomic and physiological effects (Hüssy et al., 2021b; Sturrock et al., 2015).

**Sampling/analysis methods:** Otoliths are renowned biochronometers, exhibiting daily and annual growth rings that allow movement timings and fish growth rates to

be estimated. However, ring widths decrease with age, often resulting in 'signal averaging' across chemical measurements, and reduced temporal resolution to explore sub-annual movements in adults or slow growing species. For movement reconstruction or provenance assignment using elemental concentrations, otoliths are usually sectioned through or ground down to the core, and sampled by spot, raster or line transects by laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS), which allows for targeted sampling and inclusion of a large range of elements (Sturrock et al., 2012)). For population or stock assignment, otoliths can also be dissolved and analysed by solution-based ICP-MS. Other mass spectrometry methods and elemental mapping approaches (e.g. Synchrotron) are outlined in (Campana, 1999).

**(2) Organic-hosted isotope ratios.** Stable isotopes of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and increasingly also sulphur ($\delta^{34}S$) in organic matrices such as muscle, skin, liver and eye lenses can be used to infer fish habitat use based on differences in the underlying food webs between areas and/or habitat types. Tissue $\delta^{13}C$ varies according to the relative contributions of terrestrial vs. aquatic vs. recycled carbon to the local food web, for example, providing a tracer of pelagic *vs.* benthic habitat use or movements between mangrove and reef habitats (DeNiro and Epstein, 1978; McMahon et al., 2011; Wada et al., 1991). Tissue $\delta^{15}N$ can act as a geographic marker if nitrogen input types and volumes vary between areas, but is most frequently used to determine trophic level, based on diet-consumer fractionation patterns (Caut et al., 2009; Pinnegar and Polunin, 1999; Sweeting et al., 2007). Tissue $\delta^{34}S$ varies with bacterial fractionation of inorganic sulphur compounds and local geology (Fry et al., 1986; Mitchell et al., 2001; Raoult et al., 2024), providing a promising tracer of fish movements from freshwater e.g. (Bell-Tilcock et al., 2021; Young et al., 2022) to marine environments e.g. (Cani et al., 2023). Also, tissue $\delta^{13}C$ and $\delta^{34}S$ typically exhibit positive relationships with salinity, providing additional tracers of marine-freshwater movements and estuary residence times (Moore et al., 2016). For more precise movement reconstructions, compound specific isotope analysis (CSIA) shows great promise, but tends to be more expensive and time consuming, particularly if using extracts from calcified structures (McMahon et al., 2011).

**Sampling/analysis methods:** Soft tissues and eye lens laminae (layers) are usually sampled via dissection, then dried and analysed by Isotope Ratio Mass Spectrometry (IRMS). If C:N ratios in the results are >3.5, $\delta^{13}C$ lipid correction is necessary (DeNiro and Epstein, 1978; Skinner et al., 2016). If analysing multiple lens laminae per fish, particularly if $\delta^{34}S$ is also required, costs can increase dramatically, for example with long-lived fishes sometimes exhibiting >30 laminae per lens. Another major consideration is the mass requirement for your analysis type and instrument, with the dried mass required for combined $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ analysis being >0.6mg on some instruments and <1mg on others. Here, the higher minimum mass requirement resulted in sequential laminae sometimes being combined, reducing temporal resolution. Also, the periodicity of laminae formation is unknown, but lens diameter is usually positively related to fish size (Quaeck-Davies et al., 2018).

**(3) Inorganic-hosted isotope ratios:** Oxygen isotopes ($\delta^{18}O$) in calcified structures vary as a function of water $\delta^{18}O$ and temperature. Ambient $\delta^{18}O$, in turn, varies as a function of evaporation, precipitation, advection, and runoff (Rohling and Bigg, 1998), creating a strong positive relationship with salinity. Otolith $\delta^{18}O$ has thus been used to track fish movements within and between freshwater and marine environments (Gillanders, 2005; Northcote, 1992). While not usually used for habitat reconstructions, otolith carbonate $\delta^{13}C$ (i.e. in the inorganic fraction) is a useful tracer of field metabolic rate, although most easily applied to fish in fully marine settings (Chung et al., 2019). Finally, strontium isotope ratios ($^{87}Sr/^{86}Sr$) often exhibit high levels of variation among freshwater catchments due to heterogeneity in bedrock geology. Unlike other tracers, $^{87}Sr/^{86}Sr$ ratios exhibit basically no fractionation during biomineral incorporation, resulting in a powerful tracer of fish movements within river networks and across salinity gradients (Johnson et al., 2008; Phillis et al., 2018).

**Sampling/analysis methods:** Otoliths tend to be physically sampled by micro-drilling (computer guided or handheld) to obtain sufficient carbonate powder for measuring $\delta^{18}O$ and $\delta^{13}C$ by IRMS. This approach usually provides reliable isotopic measurements, but at the expense of temporal resolution, with sub-annual measurements often difficult to achieve, particularly for adult fish. Conversely, otolith $\delta^{18}O$ can also be measured by secondary ion mass spectrometry (SIMS), which improves the temporal resolution but is more expensive, time consuming (particularly

for sample preparation) and can be confounded by matrix interferences (Leesen et al., 2021).

**Text S5.2** – Laser protocol

All otoliths were ground on the sagittal plane until reaching the core, then analysed for element concentrations at the University of Essex by LA-ICP-MS using an ESI NWR193 laser ablation unit coupled to an Agilent 7900 ICP-MS. Laser settings are provided in Table S1. Otolith concentrations of $^{7}$Li, $^{23}$Na, $^{24}$Mg, $^{31}$P, $^{39}$K, $^{43}$Ca, $^{52}$Cr, $^{55}$Mn, $^{56}$Fe, $^{59}$Co, $^{60}$Ni, $^{63}$Cu, $^{66}$Zn, $^{85}$Rb, $^{88}$Sr, $^{107}$Ag, $^{111}$Cd, $^{137}$Ba and $^{208}$Pb were measured using a continuous line transect from core to dorsal edge. Transects were first pre-ablated to remove potential surface contamination (Davies et al., 2011) using a beam diameter of 45µm, a scan speed of 30µm/s, a frequency of 20Hz, and a laser power of 20%. In some cases where line transects did not reach the edge, new line transects were ablated parallel and overlapping with the original line before merging the data removing the overlap.

To optimize the analysis settings, we carried a series of parallel trial transects on a single otolith from an anadromous trout, modifying beam diameter and scan speed to balance tradeoffs between detecting sub-annual movements and obtaining as many elements above detection limits as possible for lake assignments. Trials used the following settings:

i. Beam diameter: 5µm, Speed: 3µm/s
ii. Beam diameter: 10µm, Speed: 3µm/s
iii. Beam diameter: 30µm, Speed: 3µm/s
iv. Beam diameter: 5µm, Speed: 10µm/s
v. Beam diameter: 10µm, Speed: 10µm/s

At lower scan speeds and beam diameters, finer scale changes in Sr were detected (Fig. S1), with slower speeds also resulting in higher counts and deeper troughs. However, at lower beam diameters, rarer trace elements fell below detection limits more often. Thus, method (iii) was selected for subsequent analyses for maximising the number of elements above detection limits while detecting shorter duration movements in adult life stages.

Specifically, otoliths were ablated using a beam diameter of 30µm, a scan speed of 3µm/s, a repetition rate of 15Hz, and power of 60%, generating a fluence of 6.8

mJ/cm$^2$. Otoliths were analysed in a random order to minimize effects of drift or variable operating conditions, with NIST612 and NIST610 glasses ablated at the start, end, and every hour through the run (Paton et al., 2011). Raw count data were converted into concentrations in Iolite, after background subtraction and internal standardization to Ca, assuming a homogenous concentration of 388,000ppm. Concentrations were calibrated and drift corrected using NIST610 and NIST612. Ideally, we would have also analyzed carbonate certified reference materials such as FEBS-1 or MACS3, but these were unavailable at the time.

**Text S5.3** – Outlier removal and smoothing protocol

Otolith element concentrations were ‘despiked’ then smoothed using the *OCE* package in R (Kelley et al., 2023). Outliers were identified as five times the standard deviation within a moving window of 10 consecutive element concentration measurements, representing an otolith distance of ~28μm. Outliers were then removed and elemental measurements smoothed using a rolling mean and a moving window of five values (Zeileis et al., 2023).

### 5.5.2 Supplementary Tables

**Table S5.1** – Operating conditions of the Agilent 7900 and ESI NWR 193 nm Laser.

| **Instrument parameters** | |
|---|---|
| **Agilent 7900 Quadrupole ICPMS** | |
| Forward power | 1300 W |
| Extraction Lens 1 | 3 V |
| Extraction Lens 2 | neg 180 V |
| Omega Lens | 12 V |
| Analyzer pressure | 0.000227 Pa |
| Cones | Nickel Sampler, Nickel Skimmer |
| Torch depth | 6 mm |
| Detector array | Discrete Dynode Electron Multiplier |
| Detector configuration | Single |
| Gas flows | |
| Coolant gas | 15 L/min |
| Argon makeup gas | 0.8 L/min |
| Helium gas to cell (MFC1) | 0.8 L/min |
| **ESI NWR 193 nm laser** | |
| ArF Excimer | 193 nm |
| HelEx | dual-volume LA cell |
| **Method parameters** | |
| Isotopes analysed | Dwell time (s) |
| $^{7}$Li | 0.01 |
| $^{23}$Na | 0.01 |
| $^{24}$Mg | 0.01 |
| $^{31}$P | 0.01 |
| $^{39}$K | 0.02 |
| $^{43}$Ca | 0.01 |
| $^{52}$Cr | 0.1 |
| $^{55}$Mn | 0.01 |
| $^{56}$Fe | 0.1 |
| $^{59}$Co | 0.1 |
| $^{60}$Ni | 0.05 |
| $^{63}$Cu | 0.05 |
| $^{66}$Zn | 0.01 |
| $^{85}$Rb | 0.01 |
| $^{88}$Sr | 0.03 |
| $^{107}$Ag | 0.1 |
| $^{111}$Cd | 0.1 |
| $^{137}$Ba | 0.01 |
| $^{208}$Pb | 0.1 |
| Cycle time (s) | 0.951 |

**Table S5.2** - Mean limits of detection (LOD), percentage of measurements below detection, range of these elements ppm, range of despiked and smoothed values, and percent relative standard deviation (RSD) based on background counts and repeat measures of NIST 610 and 612 certified reference material, respectively, averaged between the runs.

| Element | LOD (ppm) | % Below LOD | Value Max | Value Min | %RSD (Run 1) NIST 610 | %RSD (Run 1) NIST 612 | %RSD (Run 2) NIST 610 | %RSD (Run 2) NIST 612 | %RSD (Run 3) NIST 610 | %RSD (Run 3) NIST 612 |
|---|---|---|---|---|---|---|---|---|---|---|
| $^{7}$Li | 2.46 | 98.6 | 580 | -73 | 3.17 | 5.09 | 7.80 | 4.99 | 1.59 | 4.28 |
| $^{23}$Na | 5.84 | 0.0 | 8979 | 2833 | 2.66 | 1.76 | 2.46 | 2.10 | 3.82 | 1.25 |
| $^{24}$Mg | 0.65 | 0.0 | 118 | 5 | 2.23 | 4.29 | 7.21 | 3.73 | 2.44 | 3.28 |
| $^{31}$P | 48.0 | 22.9 | 1533 | 1 | 3.55 | 11.90 | 8.01 | 17.10 | 256.33 | 355.99 |
| $^{39}$K | 10.6 | 0.0 | 2652 | 581 | 3.11 | 11.32 | 9.42 | 7.56 | 4.49 | 42.50 |
| $^{52}$Cr | 0.87 | 59.9 | 16 | 0 | 1.33 | 1.68 | 7.28 | 4.06 | 1.89 | 4.96 |
| $^{55}$Mn | 1.31 | 27.0 | 98 | -1 | 2.23 | 2.73 | 7.58 | 3.09 | 1.43 | 4.31 |
| $^{56}$Fe | 6.93 | 98.5 | 299 | -7 | 1.97 | 14.18 | 7.44 | 6.17 | 7.12 | 27.10 |
| $^{59}$Co | 0.78 | 98.8 | 5 | -1 | 2.18 | 5.92 | 7.10 | 2.26 | 1.39 | 2.07 |
| $^{60}$Ni | 0.47 | 98.8 | 8 | -1 | 2.25 | 2.88 | 7.26 | 1.77 | 2.45 | 5.49 |
| $^{63}$Cu | 0.99 | 97.7 | 13 | -0 | 2.68 | 6.69 | 7.65 | 2.48 | 1.22 | 4.52 |
| $^{66}$Zn | 2.36 | 0.1 | 179 | 4 | 2.57 | 7.36 | 7.98 | 6.19 | 3.22 | 6.47 |
| $^{85}$Rb | 0.16 | 31.7 | 11 | 0 | 1.30 | 117.41 | 7.11 | 44.93 | 1.75 | 5.01 |
| $^{88}$Sr | 0.40 | 0.0 | 4382 | 429 | 1.84 | 6.37 | 8.14 | 2.74 | 1.89 | 2.91 |
| $^{107}$Ag | 0.20 | 98.7 | 8 | 0 | 3.27 | 2.42 | 7.53 | 1.67 | 1.13 | 2.90 |
| $^{111}$Cd | 0.25 | 94.1 | 2 | -2 | 2.79 | 3.42 | 7.99 | 4.28 | 3.06 | 6.24 |
| $^{137}$Ba | 0.27 | 0.0 | 22 | 0 | 1.97 | 6.85 | 7.87 | 4.43 | 2.16 | 4.43 |
| $^{208}$Pb | 0.23 | 98.4 | 177 | -2 | 1.93 | 20.95 | 7.81 | 7.24 | 2.51 | 4.16 |

**Table S5.3** - Outputs of Wilcoxon tests comparing the outermost measurements of log otolith elemental concentrations and eye lens stable isotope ratios between immature reference trout sampled from Litjvatnet *vs.* Storvatnet Lake (Fig. 5.1)

| **Structure** | **Tracer** | **w value** | ***p* value** |
|---|---|---|---|
| Eye lens | $\delta^{15}N$ | 148 | 0.014 |
| | $\delta^{13}C$ | 105 | 0.668 |
| | $\delta^{34}S$ | 76 | 0.403 |
| Otolith | Na:Ca | 58 | 0.094 |
| | Mg:Ca | 91 | 0.875 |
| | K:Ca | 104 | 0.701 |
| | Mn:Ca | 145 | 0.021 |
| | Zn:Ca | 89 | 0.804 |
| | Sr:Ca | 54 | 0.062 |
| | Ba:Ca | 73 | 0.330 |

3484 **Table S5.4** - GAM outputs

| **Model Structure** | **Model Outputs** | | | | | |
|---|---|---|---|---|---|---|
| | **Effects** | **Estimate** | **Std Error** | **t** | ***p*** | **Dev Explained** |
| **Annulus width ~ Phenotype + Habitat + *s*(Age, by = Phenotype, k=6) + *s*(Fish_ID, Age, bs = 're')** | Intercept | 212.02 | 6.50 | 32.61 | <0.001 | 73.5% |
| | Phenotype: Resident | -21.738 | 15.676 | -1.387 | 0.168 | |
| | Habitat: Sea | 22.646 | 16.583 | 1.366 | 0.175 | |
| | **Smooth Terms** | **edf** | **Ref.edf** | **F** | ***p*** | |
| | s(Age): Anadromous | 3.442 | 4.082 | 51.566 | <0.001 | |
| | s(Age): Resident | 1.829 | 2.258 | 11.871 | <0.001 | |
| | s(Fish_ID, Age) | 4.954 | 22 | 0.285 | 0.212 | |

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### 5.5.3 Supplementary Figures

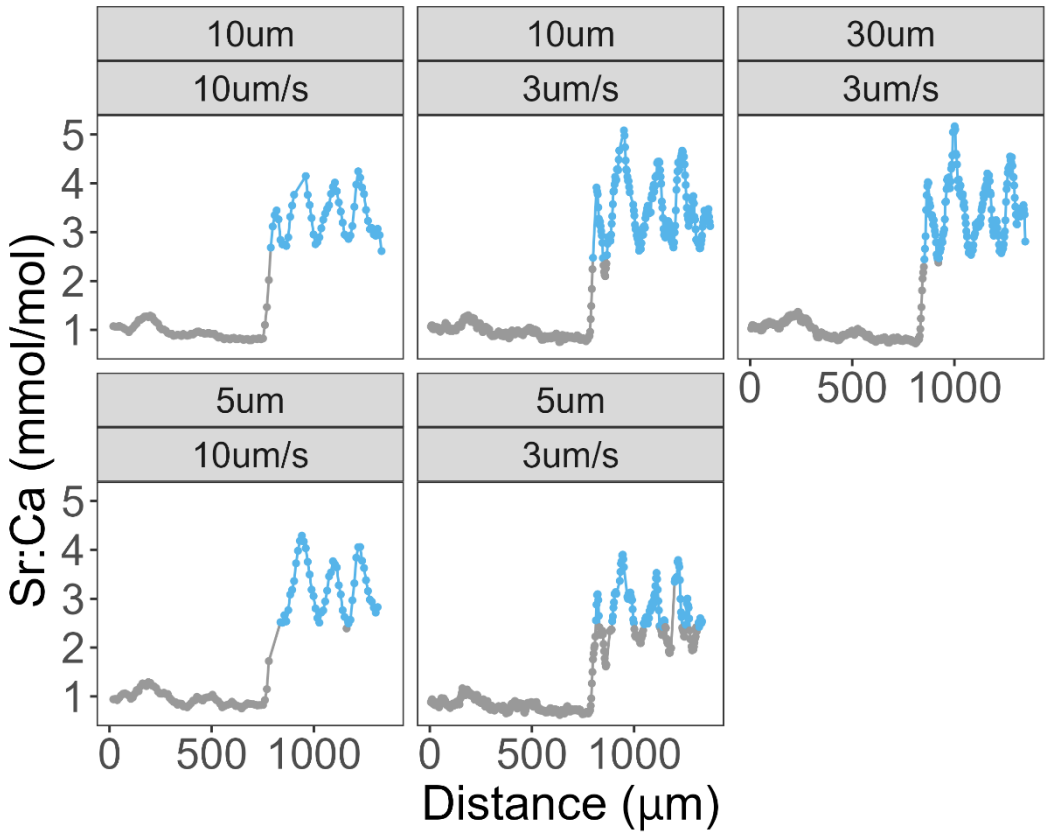



**Figure S5.1** – Otolith Sr:Ca profile from primordia to the dorsal edge of the otolith from an adult anadromous trout, with inferred habitat shown by colour, with grey denoting freshwater and blue denoting marine. For each plot, laser power was at 60%, frequency was 20Hz while beam diameter and speed are as labelled with the top line denoting beam diameter and the bottom-line representing scan speed.

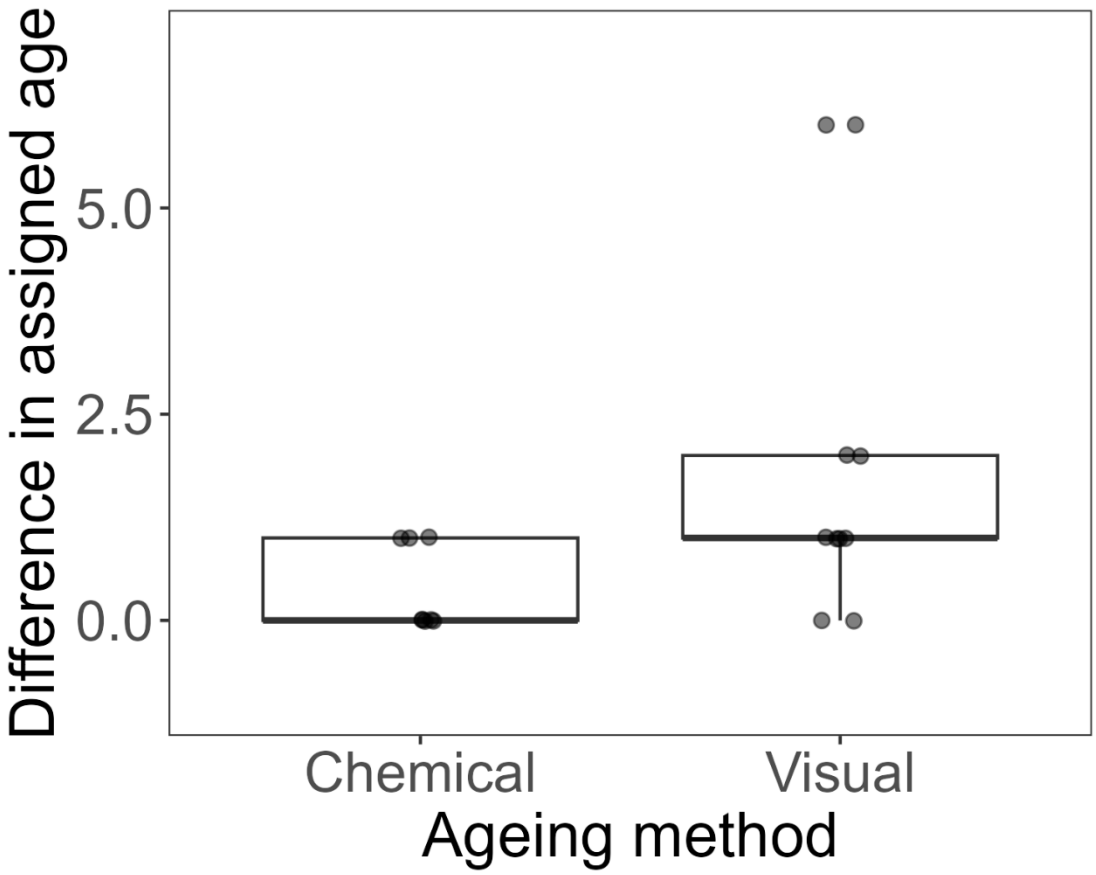



**Figure S5.2** – Boxplots of differences in assigned age between the primary and secondary reader for chemical aging *vs.* visual ageing

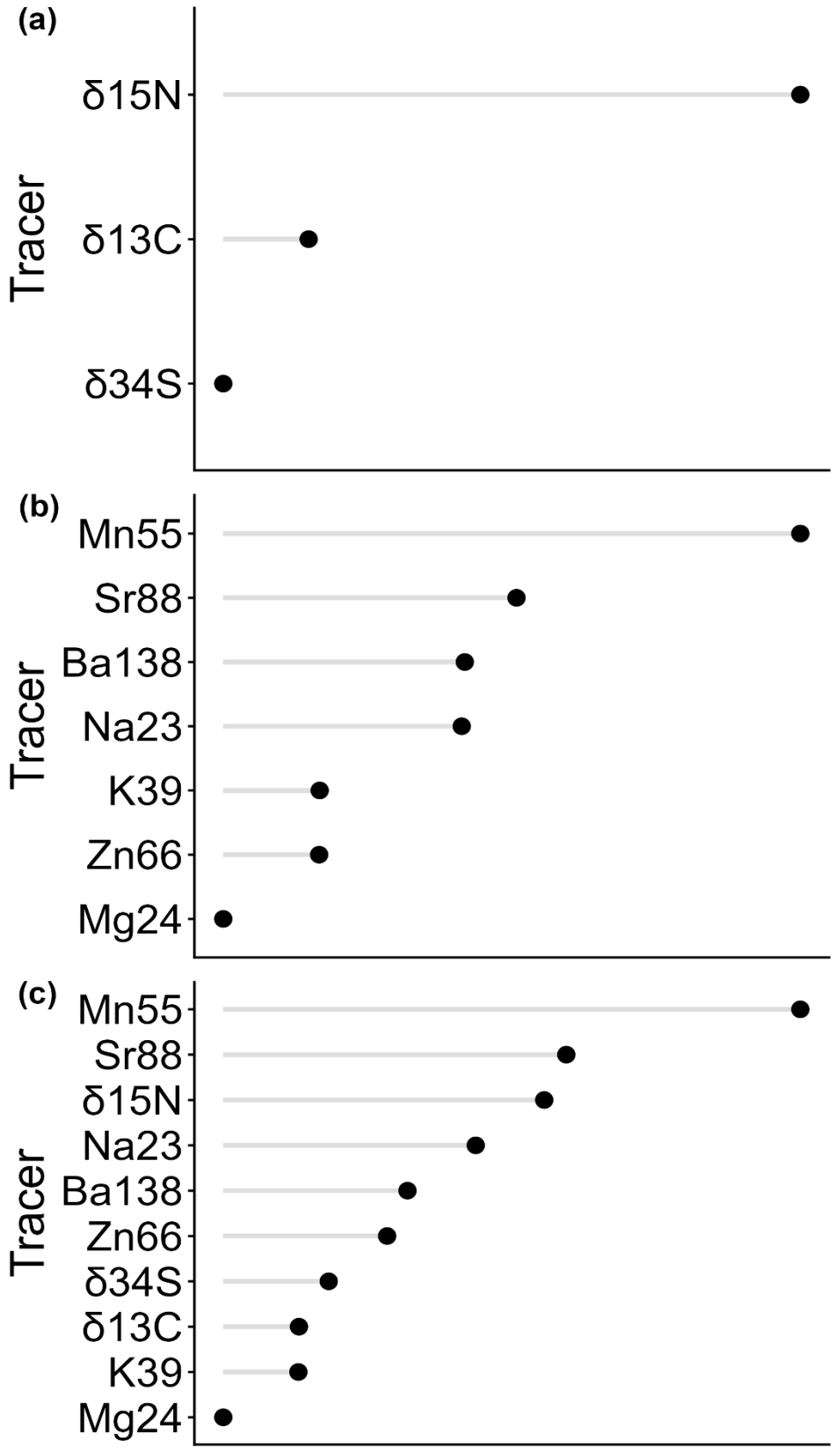



**Figure S5.3** – Showing the Gini based importance of each variable in the assignment of reference fish to one of the two lakes via a random forest model

trained on (a) eye lens stable isotope ratios, (b) otolith element concentrations and (c) both eye lens stable isotopes and otolith element concentrations.

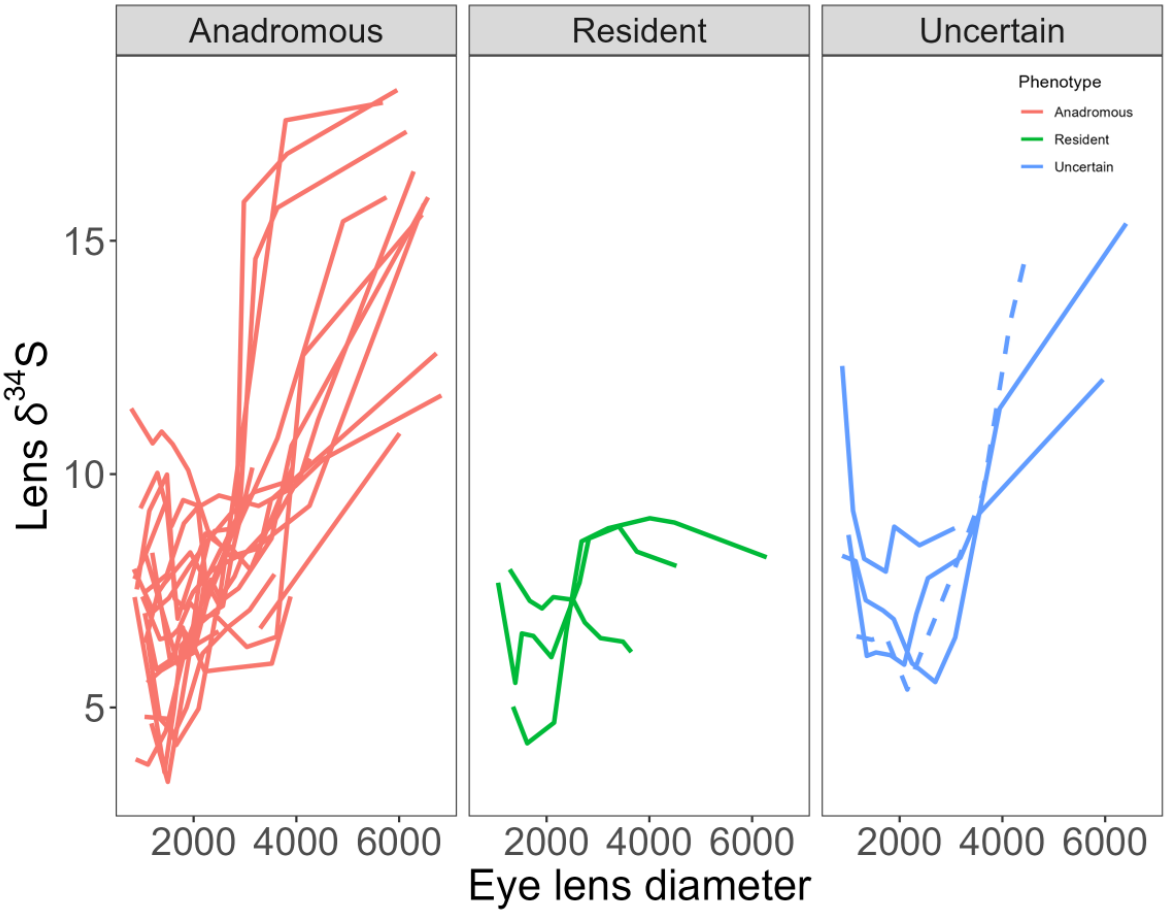
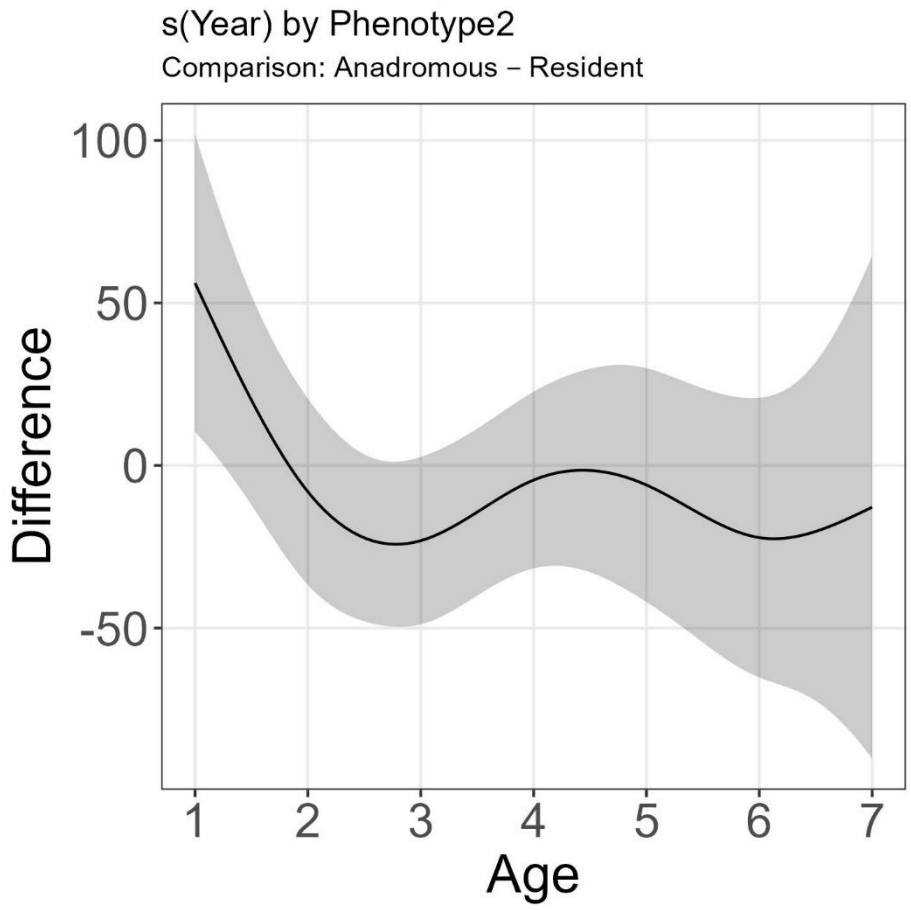



**Figure S5.4** – $\delta^{34}S$ profile from core to edge for each adult trout, with phenotype denoting fish identified in Fig. S6 as anadromous, resident, or 'uncertain' based on otolith Sr concentrations. Fish LT21_3187 (dashed line) exhibited otolith Sr concentrations just below the threshold value, but lens $\delta^{34}S$ values in outer layers >10 and was thus deemed most likely to be anadromous, along with all the other 'uncertain' fish.




3529 **Figure S5.5** – Shows the difference between the GAM smooths for the relationships
3530 between otolith annulus width and age, by phenotype, with the four “uncertain” fish
3531 excluded. Significant differences are suggested when confidence intervals do not
3532 overlap zero.

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# Chapter 6. General discussion

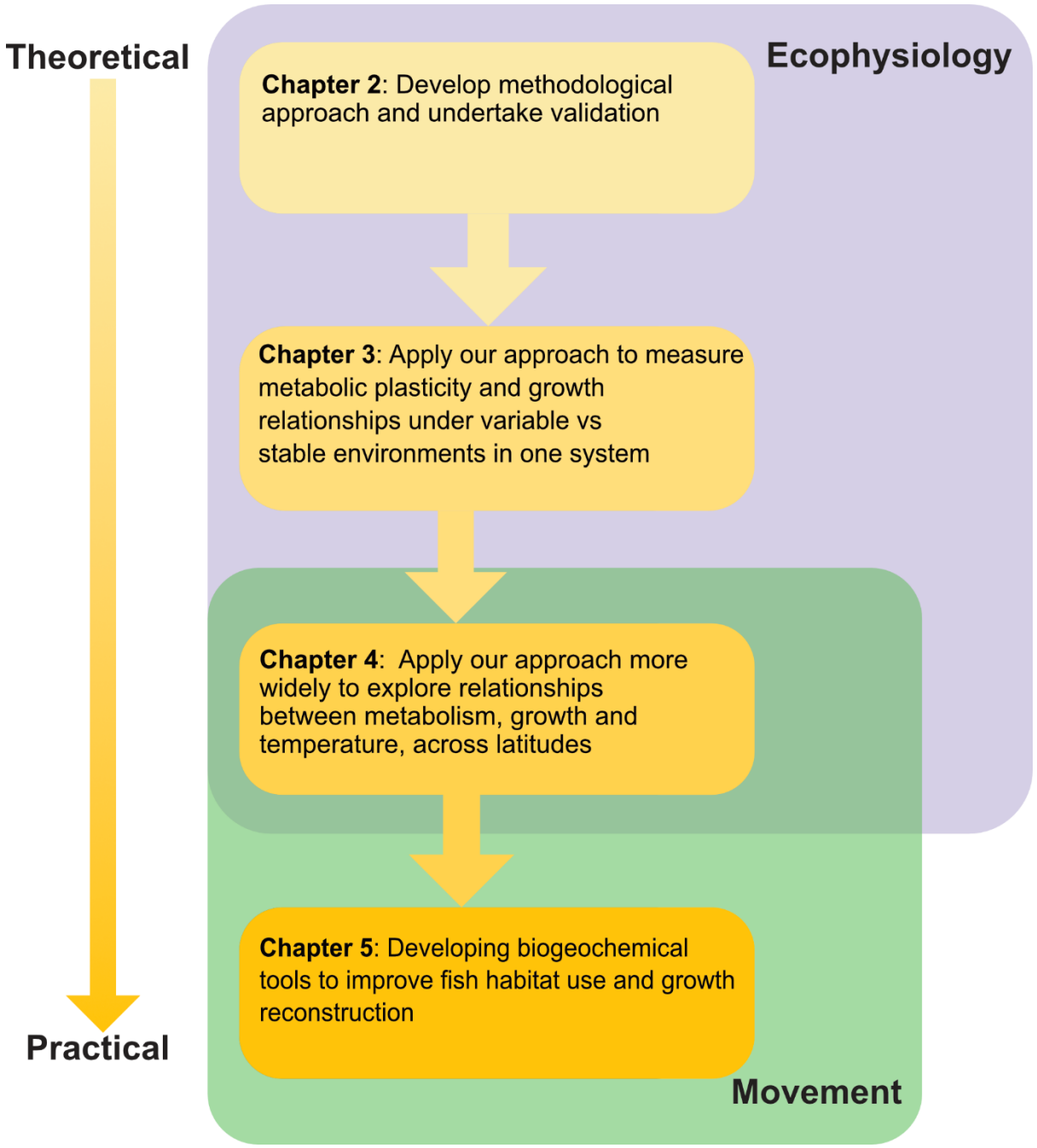



**Figure 6.1** - Conceptual figure showing the thesis structure and among-chapter linkages, and how they contribute to the general field of ecology.

Metabolism underpins the ecology of all life on this planet, and thus provides a mechanistic framework with which to explain and understand life history choices and their drivers across taxa, ranging from individuals to populations and even communities (Brown et al., 2004; Savage et al., 2004). This “metabolic framework” is of particular relevance in the face of climate change, with increasing long-term mean temperatures and greater environmental variability (IPCC, 2023). These higher temperatures will tend to elevate metabolic demand within species-specific thermal windows, reshaping energy budgets and altering allocation trade-offs among growth, reproduction, and survival (Jutfelt et al., 2021). Therefore, it is becoming increasingly pressing to understand how metabolism influences ecology today so that accurate predictions can be made of how organisms will respond tomorrow. Salmonids provide a model species, integrating stressors across both freshwater and marine phases of their life cycle and acting as sentinel species for co-occurring taxa (Clark-Wolf et al., 2024; Stewart, 2005). In addition, their large cultural and economic value makes them particularly worthy of study to understand and predict the influences of climate change on fish communities across the major aquatic biomes (Kochalski et al., 2022; NASCO, 2008).

My thesis examines the ecophysiology of the European salmonids Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). The first step in Chapter 2 involved validating an *in-situ* form of closed respirometry that allows high throughput measurement of fish metabolism in the field. I then applied this approach to explore how two primary impacts of climate change will influence metabolism in Chapters 3 and 4. Specifically, Chapter 3 demonstrates that exposure of populations to higher temperature variability increases thermal sensitivity of metabolism and fitness traits. Chapter 4 reveals how metabolism underpins thermal impacts on growth, with positive effects of increasing temperature on growth for individuals with high metabolism, but negative effects for those with low metabolism. It also suggests that higher metabolism and temperatures can be associated with reduced survival and earlier seaward migration of salmon smolts. Finally, Chapter 5 aims to improve the management of salmonids by providing a conceptual framework to use emerging chemical tools to track their movements and growth. The major contributions of each chapter to salmonid ecology and ecophysiology are discussed below, and the broader implications of the findings are placed in a broader context. Key knowledge

gaps are identified and priority directions for future research outlined, with particular emphasis on how research can inform efforts to mitigate and adapt to the impacts of anthropogenic climate change. Finally, the principal conclusions of this thesis are synthesised.

## 6.1 Chapter contributions to salmonid ecology and ecophysiology

### 6.1.1 Chapter 2: Low-cost field respirometry for wild fish: validation of a rapid closed-chamber approach

Chapter 2 aimed to validate closed-chamber respirometry as a robust and practical approach for quantifying fish metabolic rates *in situ*, using three freshwater species (*Salmo trutta*, *Phoxinus phoxinus*, and *Gasterosteus aculeatus*). Closed-chamber respirometry has a long history in fish ecophysiology (Humboldt and Provencal, 1809; Rasmussen et al., 2012), yet its contemporary use has declined relative to more complex approaches such as intermittent flow respirometry (Svendsen et al., 2016). This shift reflects the high precision and experimental flexibility of intermittent flow methods, including the capacity to repeatedly measure standard (SMR), routine (RMR), and maximum metabolic rates (MMR)(Norin and Clark, 2016; Svendsen et al., 2016). However, the increasing dominance of laboratory-based intermittent flow systems has also limited the application of portable, rapid approaches that may be better suited to field-based questions, particularly where infrastructure, power supply, or animal transport are constrained.

This chapter demonstrates that estimates of routine metabolic rate obtained in the field ($RMR_F$) via closed-chambers are strongly correlated with laboratory-derived metabolic rates. Repeated field measurements further reveal that coefficients of variation for $RMR_F$ overlap with those obtained from intermittent flow respirometry, indicating that closed-chamber measurements do not exhibit substantially greater variability than laboratory-based approaches. Importantly, individuals with relatively high $RMR_F$ in the field also tended to display elevated $RMR_L$ and SMR under controlled laboratory conditions, suggesting that closed-chamber respirometry captures biologically meaningful inter-individual differences rather than methodological noise. Together, these findings support the use of closed-chamber respirometry as a valid tool for quantifying metabolic performance in natural settings. However, the relative rank orders of the field measurements were not significantly

similar to that of the lab and the repeatability was lower than lab measurements. This suggests that the $RMR_F$ measurement has a lower level of precision than lab-based alternatives unsurprising given all the additional environmental and biological noise inherent in singular field measurements.

The portability and rapid deployment of closed-chamber systems make them particularly well suited to remote or logistically challenging field locations where intermittent flow respirometry is impractical or impossible. In addition, the high throughput achievable with this approach enables the sampling of larger numbers of individuals, which is especially advantageous for population-level comparisons. From an animal welfare perspective, reduced handling time, minimal holding, and the absence of transport to laboratory facilities may also lessen stress relative to laboratory-based protocols (Iversen et al., 1998; Portz et al., 2006). However, these benefits remain context- and species-dependent.

A key advantage of the field-based closed-chamber approach is that it allows metabolic measurements to be made while fish remain within their native environmental conditions, thereby capturing physiological responses under ecologically relevant contexts. While field-deployable intermittent flow systems have been developed, they typically require substantial equipment, power supply, and extended measurement periods, which can limit throughput and spatial replication (Mochnacz et al., 2017). Nevertheless, closed-chamber respirometry conducted in the field inevitably introduces additional sources of variation, including behavioural responses to visual cues, reduced confinement, and environmental heterogeneity (Helfman, 1986; Portz et al., 2006). These factors must be carefully considered during experimental design and interpretation, as they may contribute both noise and biologically meaningful variation.

Rather than viewing closed-chamber respirometry as a replacement for intermittent flow methods, this approach should be considered a complementary component of a broader ecophysiological toolkit. The choice of method should be dictated by the research question, balancing experimental control, and precision against ecological realism, and practicality. In particular, closed-chamber field respirometry is well suited to addressing questions focused on *in situ* environmental effects on metabolic physiology, especially where large sample sizes or comparisons across populations

are required. By validating this approach against established laboratory techniques, this chapter provides a methodological foundation for expanding metabolic measurements beyond the laboratory and into ecologically relevant field settings, which is the approach taken in the subsequent two chapters.

### 6.1.2 Chapter 3: Thermal variability can increase the thermal sensitivity of metabolism, growth, and condition in brown trout (Salmo trutta)

Chapter 3 examines whether prior exposure to thermal variability predisposes organisms to cope more effectively with variable and elevated temperatures by analysing the thermal sensitivity of metabolism and fitness traits in fish from naturally variable versus stable streams. Because metabolic traits underpin a range of ecological processes, this shift in thermal sensitivity may also cascade into ecological performance through altered feeding, activity, or competitive interactions. This approach therefore aims to assess how environmental variability shapes an organism's capacity to respond to future warming.

Fish originating from more thermally variable streams exhibit greater metabolic thermal sensitivity, this was also correlated with increased growth at mid and low temperatures. This pattern suggests that populations experiencing variable conditions over successive generations may develop more plastic metabolic responses, enabling individuals to adjust energetic expenditure more effectively under changing temperatures (Norin and Metcalfe, 2019). We also observed increased thermal sensitivity of condition in variable streams, whereby condition was generally lower in most variable streams but reached the same level as stable streams at the same temperature at which growth declined. This suggests that condition is prioritised over growth in warmer or more stressful environments. This begins to fill a vital knowledge gap as very little is known about how exposure to variability influences fish ecology and this will only become more relevant as climatic variability increases (Wiel and Bintanja, 2021).

Although heightened thermal sensitivity may confer advantages within the range of temperatures under examination, these benefits are likely context dependent. Measurements are restricted to a relatively narrow thermal window; if temperatures rise substantially above this range during extreme events such as heatwaves, and if

elevated thermal sensitivity is maintained, metabolic rates may increase disproportionately relative to consumption as has been observed in sea urchin, starfish, and others (Iles, 2014; Lemoine and Burkepile, 2012). This could reduce aerobic scope and constrain growth, ultimately limiting fitness.

The increased thermal sensitivity of metabolism, growth, and condition could represent adaptive differentiation, i.e. evolution across multiple generations, across streams. However, some gene flow within river networks is also likely to occur due to straying (Källo et al., 2023), which suggests that the response may also be acclimatory, i.e. phenotypic changes within a single generation, or a combination of both processes. If so, increasing thermal variability under climate change could induce greater flexibility, potentially enhancing growth under moderate warming as observed here. Plasticity has more generally been linked to growth particularly in studies looking at starvation (Auer et al., 2015). However, such benefits would be expected only over a narrow temperature increase. As ambient temperatures approach physiological limits, the limits of flexible responses will be reached and fitness will decline (Neubauer and Andersen, 2019). Furthermore where plastic traits may allow a population to avoid the deleterious effects of temperature, this may reduce selection pressure on thermal adaptation potentially reducing the populations fitness in the longer term as demonstrated by Buckley and Kingsolver (2021).

No clear metabolic costs associated with increased plasticity were detected. Empirical evidence for costs of plastic traits remains mixed, with one review finding no evidence in 62% of cases across taxa and another finding a consistent but weak effect across environments (Auld et al., 2010; Buskirk and Steiner, 2009). However, plasticity is generally not retained without selection pressure, suggesting that some cost or constraint on its maintenance exists (Morgan et al., 2022). Since $RMR_F$ was the measure of cost in my study, which integrates multiple energetic demands including movement and behaviour, any additional energetic expenditure associated with regulating metabolic machinery and maintaining plasticity may have been masked. Such costs would be more detectable in SMR, which isolates baseline maintenance costs by removing these additional factors (Chabot et al., 2016b). Finally, this chapter also built on the approach validated in Chapter 2, to show that closed-chambers can be used to successfully detect ecologically relevant

physiological responses in the field. In the next chapter I now sought to apply this approach more widely to understand how metabolism and growth interact across different species and populations, and the influence of temperature upon this.

### 6.1.3 Chapter 4: Thermal regime shapes metabolic effects on growth, survival, and migration in salmonid fish

Chapter 4 uses a natural latitudinal thermal gradient to examine how temperature influences metabolism and, in turn, growth, survival, and migration in two species of salmonid (*Salmo salar* and *Salmo trutta*). By exploiting geographic variation in thermal regimes as an analogue for future warming, this approach provides insight into how key life-history traits may respond to ongoing climate change.

After accounting for temperature and body size, measurements of $RMR_F$ were remarkably similar across latitudes and displayed difference in thermal sensitivity. This convergence suggests a relatively strong constraint on routine energy expenditure across the geographic ranges of both species, consistent with a uniform optimum rather than pronounced region-specific specialisation. From a climate change perspective, this finding is concerning. High-latitude populations often show reduced acclimation capacity (Seebacher et al., 2015), while low-latitude populations are already approaching upper thermal limits (Borgwardt et al., 2020). Together, these patterns imply that the thermal window within which individuals can maintain a viable energy balance may narrow from both ends of the distribution, potentially outpacing the capacity for physiological or behavioural adjustment, though more work is needed on the rate of adaptation (Crozier et al., 2008; Manhard et al., 2017).

Despite this overall pattern, one river (Deveron) exhibited a significantly different size and temperature-adjusted metabolic rate, indicating that local adaptation or plastic divergence is possible under certain conditions (Somero, 2010). However, the rarity of this response suggests that such divergence is strongly constrained and may only emerge under particularly distinctive environmental pressures or may be due to local environmental changes, such as flooding or rapid temperature change. This altered energy allocation could reflect reduced food availability, lower energetic inputs, or selection to minimise metabolic costs (Auer et al., 2015). Regardless of the underlying mechanism, the existence of alternative energetic strategies may provide a portfolio effect whereby multiple strategies reduce overall risk, within species,

potentially conferring limited resilience to environmental change (Schindler et al., 2010).

Growth responses revealed a clear interaction between metabolism and temperature. Growth increases with increasing temperature for high metabolism but decreases for low metabolism. Laboratory studies in salmonids demonstrate that elevated metabolism can increase dominance and growth, but only when food availability is sufficient (Metcalfe et al., 2016; Reid et al., 2012, 2011). Further studies have then introduced differing thermal regimes and shown that MMR correlates with increased growth under higher temperatures but decreased growth in the colder temperatures (Archer et al., 2021). The present results extend this concept to natural systems, suggesting that higher metabolic phenotypes may be favoured in warm, productive environments, whereas lower metabolic rates may be advantageous in cooler, less productive systems, particularly those with prolonged low productivity winters. Importantly, although fish reduce metabolic rates under food limitation, individual rank order is retained, such that high metabolism individuals remain relatively high even during starvation and may therefore suffer disproportionately (Hvas et al., 2020; O'Connor et al., 2000; Richards, 2010). As a whole this implies that in high productivity food rich environments high metabolic rate may facilitate dominance and thereby increased feeding and growth. But in cooler environments especially with long winters the increased costs of this high rate may outweigh the increased summer feeding opportunities.

In parallel, survival (from parr to downstream smolt migration) declined with increasing temperature. When considered alongside growth patterns, this suggests that future warming may selectively benefit dominant, high-metabolism individuals while reducing overall survival at the population level. Such a mismatch highlights a potential conflict between individual-level performance and population persistence, with important consequences for cohort strength and long-term population viability. Furthermore, these impacts are going to be most pronounced at mid to high latitudes where temperatures are still well below thermal limits.

Finally, higher temperatures were associated with earlier downstream migration of early life stages, consistent with other observations (Frechette et al., 2023). Earlier migration if not seen alongside increases in growth may result in individuals entering

the marine environment at smaller sizes, thereby increasing predation risk or mismatch with prey availability, thereby potentially reducing marine survival (Cushing, 1990; Gregory et al., 2019; Koenings et al., 1993). Taken together, these results suggest that warming will restructure salmonid life histories through tightly coupled effects on metabolism, growth, survival, and migration timing, with outcomes that may differ markedly between individuals and populations.

Viewed together in a climate-warming context, Chapters 3 and 4 show that salmonid responses to rising temperatures are likely to be constrained despite some capacity for short-term buffering. Chapter 3 demonstrates that exposure to thermal variability increases metabolic sensitivity and can enhance growth under moderate warming, indicating capacity for flexibility. However, Chapter 4 shows that routine metabolic rates are constrained across latitudes and that higher temperatures reduce survival and alter migration timing, with benefits accruing mainly to high-metabolism individuals rather than populations. Combined, these results suggest that increasing thermal variability may temporarily mask the impacts of global warming by enhancing performance in some environments, but that fixed energetic constraints and survival costs will ultimately dominate, limiting long-term resilience of salmonid populations as temperatures continue to rise. Shifts in migration phenology and routing can have substantial conservation implications, particularly in regulated river systems where successful passage depends on active management (e.g., modifying abstraction regimes or suspending thermal effluent discharges during migration windows). Accordingly, I now aimed to develop a practical toolkit for managers to reconstruct salmonid lifetime movements and growth, in order to estimate the prevalence of different behavioural and physiological phenotypes within and among populations and identify the key habitats supporting their growth.

### 6.1.4 Chapter 5: A framework for using tissue chemistry and biochronologies to reconstruct fish habitat use and growth

Chapter 5 develops and applies a structured framework that integrates tissue chemical tracers and biochronological information to reconstruct habitat use, migration, and growth in brown trout from a river system near Trondheim, Norway. The primary contribution of this chapter lies less in the novelty of these particular chemical tracers, but in explicitly linking their selection, statistical treatment, and

ecological inference within a clear decision-making framework. This approach was designed to improve the reliability and accessibility of life-history reconstruction, particularly in systems without previous information, where chemical gradients are subtle, and/or where the potential for using more traditional tagging approaches is limited. In addition, the chapter aimed to advance understanding of how individual life histories change across and within freshwater and marine habitats, and how this variation may influence performance and resilience.

Application of this framework suggested relatively strong juvenile trout site fidelity within the freshwater network, and a higher contribution of the larger, more productive upstream lake for juvenile rearing to the adult trout population. This pattern is consistent with previous observations in brown trout and other salmonids, (Jonsson and Jonsson, 2021; Källo et al., 2023). Here, however, the results were gleaned from retrospective reconstruction rather than direct tagging, highlighting the utility of archival tissues for resolving early-life habitat use. Although chemical differentiation among lakes was modest, particularly when individual tracers were considered in isolation, the multi-tracer approach was nevertheless able to resolve natal origins with moderate accuracy. Importantly, this level of resolution proved sufficient to detect ecologically meaningful differences in habitat contribution rates, while also making explicit the uncertainty associated with classification between chemically similar habitats.

Reconstruction of migration histories further demonstrated pronounced life-history diversity within the population, consistent with expectations for adult brown trout (Ferguson et al., 2019; Jonsson, 1989). Most individuals undertook at least one marine migration, often repeatedly, while a smaller proportion remained resident or exhibited ambiguous or mixed strategies. The otolith core chemistry suggested that some individuals switched between resident and anadromous phenotypes across generations supports previous work suggesting that migration in brown trout is best understood as a conditional strategy rather than a fixed trait (Ferguson et al., 2019). Such plasticity has historically been interpreted as a buffer against environmental variability and an asset to invasion across freshwater and marine domains (Jensen et al., 2008; Kovach et al., 2019; Valiente et al., 2010). However, results in Chapter 3 indicate that the benefits of this flexibility are strongly context dependent and may be diminished under environmental change.

Adult growth did not differ strongly between anadromous and resident trout, contrary to the expectation that anadromy confers consistently higher growth rates. Several non-mutually exclusive mechanisms may explain this pattern. High productivity within this particular freshwater system may have allowed residents to achieve growth rates comparable to those of sea-migrating trout, thereby reducing the relative advantage of marine foraging (Ulsund, 2013; Winnem, 2010). Alternatively, potential marine growth benefits in these coastal habitats may have been constrained by anthropogenic pressures, particularly sea lice associated with the high numbers of salmon farms in Norway, which can reduce feeding success, growth, and marine residence duration in sea trout (Thorstad et al., 2015). Finally, individual variation combined with limited sample sizes - especially for resident adults – reduced our statistical power to detect subtle differences.

Methodologically, Chapter 5 highlights both the strengths and limitations of using archival tissues to reconstruct complex life histories. Eye lenses and otoliths provided complementary information on habitat use and growth, but also imposed constraints related to temporal resolution, detection limits, and uncertainty associated with threshold-based classifications (Sturrock et al., 2012; Vignon, 2015; Walther and Limburg, 2012). The framework makes these limitations explicit, embedding uncertainty directly into the process allowing differentiation of within and between individual variation (Walther, 2019). This moves the approach beyond case-specific inference and offers a transferable structure for researchers and managers seeking to apply the breadth of chemical tracer techniques across systems with varying levels of chemical difference and data availability (Grønkjær, 2016).

When considered alongside Chapters 3 and 4, Chapter 5 adds a further spatial and ontogenetic dimension to the thesis. While earlier chapters focus on how temperature and metabolic constraints shape growth, survival, and migration across thermal gradients, Chapter 5 demonstrates how individual behaviours and phenotypes co-occur within a heterogeneous habitat mosaic and attempts to provide managers with new practical tools. Together, these chapters suggest that success and resilience to environmental change depends not only on physiological plasticity or metabolic capacity, but also on access to different habitat options at key stages of the life cycle. As climate change and other anthropogenic pressures increasingly increase variation in thermal regimes while constraining habitat connectivity and

structure, integrative frameworks that link physiology, behaviour, and habitat use will be essential for predicting population-level responses and informing effective management plans.

## 6.2 Future Directions

This thesis spans multiple disciplinary perspectives, integrating ecophysiology, fish ecology, and chemical tracers to examine how fish respond to environmental change and how this can be measured or tracked. In doing so, it highlights several important gaps in our current understanding of how climate change influences fish ecology across spatial, temporal, and organisational scales. Addressing these gaps is increasingly urgent as climate change accelerates and interacts with other anthropogenic pressures to reshape both freshwater and marine ecosystems.

Beyond empirical knowledge gaps, this work also exposes more fundamental limitations in how climate-change impacts on fish are studied. In particular, there remains a tendency to address physiological, behavioural, and habitat-mediated responses in isolation from each other and the real world, despite growing evidence that resilience to environmental change emerges from their interactions (Miller et al., 2010; Rustad, 2008). If researchers are to improve anticipation of biological responses to inform effective management, greater emphasis must be placed on integrative approaches that explicitly link mechanisms, life-history processes, and environmental context. The following sections outline key directions where such advances are most needed, building directly on the findings of this thesis.

### 6.2.1 Incorporating Climatic Variability and Extremes into Future Research

Much attention has been paid to the effects of increases in mean ambient temperature on organisms and ecosystems. However, as outlined in Chapter 3, comparatively little emphasis has been placed on the ecological consequences of thermal extremes and increasing climatic variability (Benedetti-Cecchi, 2003; Jentsch et al., 2007; Thompson et al., 2013). Though this is beginning to change, this imbalance still persists despite strong evidence that climate change is expected to increase the frequency and intensity of droughts, extreme rainfall events, and heatwaves (so-called ‘whiplash weather’ or hydroclimate volatility (Swain et al., 2025)). Such variability and extremes in both environment but also the knock on effects on timing and phenology may be more biologically damaging than gradual

mean warming alone (Coumou and Rahmstorf, 2012; Easterling et al., 2000; Vasseur et al., 2014).

While the IPCC estimates a 1.5 - 4.4°C increase in mean ambient air temperature over the coming century, many studies predict that such moderate warming may result in neutral or even positive effects on fitness for some mid- or high-latitude fish species (Deutsch et al., 2008). However, fish thermal performance typically increases only up to a species-specific optimum, beyond which it declines rapidly (Angilletta, 2006). Short-term thermal extremes and increased variability are therefore far more likely to push organisms beyond physiological limits than changes in mean temperature, as heatwaves can elevate experienced temperatures well above those predicted by mean warming scenarios. Under these conditions, even brief excursions beyond thermal optima may lead to rapid declines in performance, increased mortality, or local extinction. Consistent with this, models that explicitly incorporate temperature variability often predict that mid-latitude species frequently assumed to be relatively buffered under mean-based projections may in fact be among the most vulnerable (Vasseur et al., 2014).

Future research should therefore place greater emphasis on quantifying how climatic variability and extreme events influence fitness, population persistence, and range expansion or contraction. For example, using mesocosms and field studies in highly variable regions or habitats though this is often not done due to the difficulties inherent in reliably sampling highly variable regions. In particular, incorporating maximum predicted heatwave temperatures and their frequency into models of species presence and absence will be essential for improving predictions of ecological responses to climate change. Attention should also be paid to how increasing variability interacts with gradual warming to shape biological responses, rather than treating these processes in isolation, as will be discussed below.

### 6.2.2 The Capacity for Plasticity and Adaptation

Organisms can exhibit substantial capacity for phenotypic plasticity and evolutionary adaptation in response to environmental change (Harvey et al., 2014; Reusch, 2014). However, these processes are rarely incorporated explicitly into climate-based models of future species distributions and ecological responses (Huey et al., 2012; Urban et al., 2024). This omission reflects, in part, limited understanding of

both the magnitude of plastic and adaptive capacity across taxa, and the timescales over which such responses can occur relative to the pace of ongoing climate change (Huey et al., 2012).

This thesis has sought, in part, to explore how environmental variability and prior exposure to thermal extremes may influence the capacity for plastic responses. However, much work remains to be done to understand how organisms modify behaviour, physiology, and ultimately fitness in response to increasingly variable and extreme environmental conditions. This knowledge gap is particularly consequential given that conservation and management resources are finite, making it essential to identify species and populations with limited capacity to buffer or adapt to rapid environmental change in order to prioritise effective intervention.

Existing research demonstrates that plasticity in key traits, such as metabolic rate, can allow organisms to downregulate energy demand during heatwaves or periods of resource limitation (Affinito et al., 2024; Cavieres and Sabat, 2008; Seebacher et al., 2015), alongside demonstrating that genetic adaptation may also occur under sustained climatic pressure (Hoffmann and Sgrò, 2011; Pilakouta et al., 2020). Nevertheless, these responses are rarely quantified in a way that allows them to be incorporated into predictive models across species and systems. Furthermore the interaction between plasticity, epigenetics, and genetic adaptation must be better understood, especially in the context of phenotypic plasticity which can lead to behaviour that limits exposure to a stressor e.g. behavioural thermoregulation as while beneficial in the short term may stop longer term adaptation (Buckley and Kingsolver, 2021). This is of particular interest in salmonids whose whole genome duplication may increase capacity for plasticity or differential adaptive responses making them a model animal to study in this respect (Lien et al., 2016). Substantial effort is therefore needed to parameterise plastic and adaptive responses more realistically in concert with the rate of adaption, particularly for ecologically important or vulnerable taxa, if models are to reliably inform conservation and management. This is something that I was unable to do and indeed is rarely done, this is in part due to the difficulties in disentangling noise when making measurements in the field. However increased measurement and understanding of animal physiology under natural conditions is increasingly important as will be outlined below.

### 6.2.3 Novel Technologies

While there has been extensive research into the physiological responses of fish to warming, the majority of this work has been conducted under controlled laboratory conditions (Treberg et al., 2016). This body of research has provided a mechanistic foundation for understanding thermal responses, but by design, laboratory studies exclude many of the environmental complexities experienced by organisms in the wild. As a result, translating laboratory-derived relationships into accurate predictions of ecological responses to warming remains a fundamental challenge. Improving understanding of physiological responses under natural conditions therefore represents a critical next step, and this thesis contributes to a growing body of work aimed at bridging this gap.

Recent methodological advances offer promising opportunities to quantify physiological processes *in situ*. New approaches are being developed to apply intermittent-flow respirometry under field conditions, enabling high-resolution measurements of metabolic rate in ecologically realistic settings (Mochnacz et al., 2017). In parallel, field metabolic rates can now be estimated using otolith carbonate chemistry, although current applications are largely restricted to marine systems (Chung et al., 2021; Trueman et al., 2023). This approach nonetheless provides a powerful means of retrospectively quantifying physiological responses to environmental stressors across extended time periods. Additional techniques are also emerging, such as the use of protein synthesis rates as proxies for instantaneous metabolic activity (Lamarre et al., 2015), activity-based proxies including accelerometery and heart rate monitoring (Metcalfe et al., 2016), and other approaches include isotopic tracers assessing metabolic turnover, and bioenergetic models (Chipps and Wahl, 2008; Tomlinson et al., 2013). Each of these approaches has strengths and weaknesses. Further development, validation, and uptake of these methods will be essential for advancing understanding of fish physiology in the wild. By enabling direct measurement of physiological responses under realistic environmental conditions, such tools will improve the capacity to link mechanistic processes with ecological outcomes and ultimately enhance predictions of how fish populations will respond to ongoing and future warming.

Other new technologies are opening up novel avenues of research, novel tags can record ventilation rate, and movement allowing direct estimation of metabolic rates

and links to behaviour (Kolarevic et al., 2021). Combined with other sensors and used in the field could allow continuous measurement of metabolism, temperature, and behaviour. This would facilitate direct energetic inference in the field something that has been impossible at any fine scale until now.

Additional breakthroughs in *in vivo* imaging of metabolic pathways is allowing direct imaging of these pathways and has already been applied to fish (Chandris et al., 2022; Li et al., 2022). This may facilitate greater understanding of individual chemical pathways, and how they contribute to the whole rather than having to rely on proxies of overall metabolic activity via oxygen uptake. Furthermore the rise of 3D printing is now allowing specialised respirometry equipment to be printed (Hejlesen et al., 2024). This will make respirometry more accessible but also allow respirometers to be easily made specifically for different fish and experimental setups allowing greater specialisation. However, technology in data analysis and synthesis is also making great strides forward.

Over the past two decades, the accessibility of advanced statistical approaches has increased dramatically, driven by open-source software, improved training, and rapidly expanding computational power (Acemoglu and Restrepo, 2018; R Core Team, 2024; Thompson et al., 2022). More recently, the emergence of artificial intelligence and automated analytical workflows has further lowered technical barriers, enabling increasingly complex analyses to be applied across ecological and physiological datasets. Together, these developments have facilitated the widespread adoption of Bayesian approaches, hierarchical modelling, clustering techniques, and machine learning methods across ecological research (Brooks, 2003; Greener et al., 2022). This may be particularly useful in modelling metabolic responses to the natural environment which can be noisy and fail to meet the requirements of frequentist models, an issue I encountered during this thesis.

As these trends continue, the availability of more powerful and accessible analytical tools is likely to expand further. Such tools are particularly well suited to addressing the multifaceted challenges posed by climate change, where responses are often nonlinear, context dependent, and structured across multiple spatial and temporal scales. Bayesian frameworks provide a robust means of propagating uncertainty, integrating disparate data sources, and linking process-based understanding with

empirical data (Needham et al., 2007). While machine learning and clustering approaches can help identify emergent patterns in complex datasets that may be difficult to resolve using traditional methods alone (Tarca et al., 2007).

Beyond analytical capability, there is a growing need to translate methodological advances into tools that are practical, transparent, and usable beyond academic research. Developing structured frameworks that guide model selection, data requirements, and interpretation will be essential to ensure that increasingly sophisticated methods can be implemented effectively by managers and practitioners with limited time or technical capacity. Chapter 5 of this thesis has aimed in part to address this need, but more work is needed especially in other areas that relate closely to climate change such as ecophysiology.

In this context, AI and large language models in particular may provide a powerful partner, by synthesising complex and varied methods and providing non-specialists with step-by-step guidelines on the best approach to use, how, and why. While the technology is not at this stage yet, given the speed of improvement it is likely soon and should be embraced (Tang et al., 2020). More broadly, the adaptation of existing scientific tools to applied management contexts regardless of whether they rely on AI represents a critical opportunity to improve evidence-based decision-making for the species and ecosystems under management. Effort should be made to bridge the persistent gap between scientific insight and effective conservation and management action, something that will be touched on in the final section.

### 6.2.4 Science Translation: Moving from Problems to Solutions

A substantial body of research has been devoted to understanding and predicting the effects of climate change across taxa and geographic regions, much of it driven by curiosity-led scientific enquiry. This work has been invaluable in diagnosing the scale, scope, and urgency of climate-driven change, and in building the evidence base that underpins calls for action (Alizadeh, 2022; Behera et al., 2022; Hammer et al., 2001). However, despite this expanding knowledge, a growing disconnect remains between scientific insight and its translation into effective policy, management, and on-the-ground intervention (Colombo et al., 2023).

This gap is evident both at societal and institutional levels, where political inertia and delays in implementation frequently outpace the rate at which new evidence is

generated, and within conservation practice itself, where substantial lags often occur between research publication and management uptake (Colombo et al., 2023; Hulme, 2014). Furthermore research does not always focus on and answer the questions that conservationists and habitat managers need or want answered (Esler et al., 2010; Linklater, 2003). As climate change continues to intensify, these delays increasingly limit the capacity of science to inform timely responses.

Future research should move beyond problem characterisation alone and place greater emphasis on developing, testing, and implementing solutions at ecologically and managerially relevant spatial and temporal scales. This must be done in partnership with conservationists and habitat managers. This underscores the need to better integrate discovery-led research with the development of practical tools, decision-support frameworks, and adaptive management strategies. By explicitly linking mechanistic understanding, predictive modelling, and implementation, climate change research can more effectively inform mitigation, adaptation, and resilience-building efforts, narrowing the gap between knowledge generation and meaningful action. While this is already being done to some degree with millions of trees planted around some Scottish rivers, implantation of Ranunculus habitat in southern chalk streams, and the removal of impassable dams, much more remains to be done to secure the future of European salmonids (Marsh et al., 2020).

## 6.3 Conclusion

The results presented in this thesis provide both methodological advances and new insight into how temperature and climate change may influence salmonid physiology and ecology. Salmonids serve as a model system and many of the tools and concepts developed here are broadly applicable across aquatic taxa, particularly for understanding organismal responses to environmental warming. Central to this thesis is the validation and application of closed-chamber respirometry as a robust approach for measuring metabolic performance under ecologically realistic conditions. Using this framework, the thesis demonstrates that exposure to environmental variability may confer physiological advantages under global warming, and that sustained increases in temperature are likely to reduce survival while interacting with metabolism to mediate growth. Together, these findings highlight the importance of considering both mean thermal conditions and thermal variability when predicting biological responses to climate change.

Beyond its empirical contributions, this work identifies several urgent gaps in the current literature and outlines research directions that have only recently become available. A key priority is to better integrate sources of uncertainty, particularly increasing climatic variability, field measurements, and variation in population plasticity and adaptive capacity, into experimental design and predictive models. Addressing these complexities will be essential for improving forecasts of species persistence under future climate scenarios. Finally, this thesis argues that future research must move beyond description to directly address applied challenges and find solutions. Advances in technology, analytical methods, and data integration offer unprecedented opportunities to link physiology, ecology, and management. Effectively leveraging these tools will be critical for translating mechanistic and academic understanding into meaningful prediction, mitigation, and recovery strategies in the face of accelerating climate change.

The challenges are clear, the tools are available, and the responsibility now lies with us to move towards and ensure success.

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