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Fish population responses to climate change

Causes and consequences

MATILDA L. ANDERSSON



ACTA
UNIVERSITATIS
UPSALIENSIS
UPPSALA
2021

ISSN 1651-6214
ISBN 978-91-513-1262-0
URN urn:nbn:se:uu:diva-450553

Dissertation presented at Uppsala University to be publicly examined in Friessalen, EBC, Norbyvägen 18, Uppsala, Friday, 1 October 2021 at 13:00 for the degree of Doctor of Philosophy. The examination will be conducted in English. Faculty examiner: Dr. Brian Hayden (Canadian Rivers Institute, Biology Department, University of New Brunswick).

Online defence on Zoom: <https://uu-se.zoom.us/j/8614642061>

Abstract

Andersson, M. L. 2021. Fish population responses to climate change. Causes and consequences. *Digital Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology* 2060. 50 pp. Uppsala: Acta Universitatis Upsaliensis. ISBN 978-91-513-1262-0.

Lake environments are heterogeneous, and animals show a variety of adaptations to deal with this heterogeneity. Fish often show intraspecific variation in diet, metabolism, and behavior, corresponding to their habitat use. Studies on climate change often ignore this heterogeneity and its importance in determining population-level responses to climate change.

This thesis can be broken into two interacting pieces. First, my goal was to assess how water color and temperature changes impact the size, number, and distribution of a common predator, Eurasian perch (*Perca fluviatilis*), in Swedish lakes. Second, I aimed to examine whether metabolism and resource use differed between lake habitats, corresponding with documented patterns of polymorphism and whether diet differences were maintained along a thermal and water color gradient. By combining the information gleaned from these studies, the overarching goal of my thesis is to better understand how climate change will impact fish populations and how intraspecific variance in these responses will impact ecosystem functioning.

I found that warming and browning will likely decrease fish biomass but via different mechanisms. Warming reduces average fish size through its impact on metabolism and energy requirements. Browning decreases fish abundance likely due to its negative effects on resource abundance, increasing mortality, and decreasing reproductive effort. Though warming decreases biomass at the lake level, pelagic perch abundance increases. I found that these pelagic perch have higher metabolic rates and, especially in darker lakes, rely heavily on pelagic resources. As more fish shift into the pelagic habitat, this will increase top-down pressure on pelagic resources and decrease energy transfer from littoral to pelagic habitats altering energy flow within lakes.

Variation in metabolic phenotype across habitats, combined with the positive scaling of metabolic rates with temperature, will likely determine which fish can persist under climate change scenarios. Studies that measure this variation rely heavily on respirometry to measure fish metabolism. I found that current respirometry methods underestimate maximum metabolic rate and suggest an updated method to improve the accuracy of future studies.

Overall, I conclude that habitats should be examined separately to better understand population-level responses to climate change. Perch caught in different habitats have different energy requirements and respond differently to warming and browning. These differences will affect the distribution of top-down pressure and habitat coupling within lake ecosystems, with implications for broader ecosystem functioning in the future.

Keywords: browning, climate change, DOC, intraspecific variation, metabolism, resource use, warming

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ISSN 1651-6214

ISBN 978-91-513-1262-0

URN urn:nbn:se:uu:diva-450553 (<http://urn.kb.se/resolve?urn=urn:nbn:se:uu:diva-450553>)

“The truth is rarely pure and never simple”
- *Oscar Wilde*

For my family

List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

- I. Andersson, M.L., Holmgren, K., Eklöv, P. Habitat specific impacts of warming and browning on ecosystem functioning mediated by a generalist freshwater predator (manuscript)
- II. Andersson, M.L., Scharnweber, K., Holmgren, K., Mehner, K., Eklöv, P. Habitat coupling is modified by dissolved organic carbon but not temperature in lake ecosystems (manuscript)
- III. Andersson, M.L., Scharnweber, K., Eklöv, P. The interaction between metabolic rate, habitat choice, and resource use in a polymorphic freshwater species (submitted)
- IV. Andersson M.L., Sundberg F., Eklöv P. Chasing away accurate results: exhaustive chase protocols underestimate maximum metabolic rate estimates in European perch *Perca fluviatilis*. *J Fish Biol.* 2020;1–7.

Paper IV is published open access (CC BY-NC 4.0)

Additional Papers

In addition to the papers included in this thesis, the author contributed to the following paper:

- I. Scharnweber, K.*, Andersson, M. L.*, Chaguaceda, F., & Eklöv, P. (2021). Intraspecific differences in metabolic rates shape carbon stable isotope trophic discrimination factors of muscle tissue in the common teleost Eurasian perch (*Perca fluviatilis*). *Ecology and Evolution*, 00, 1– 11. <https://doi.org/10.1002/ece3.7809>

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Contents

Introduction	9
Intraspecific variation and resource use	9
Intraspecific variation and niche width	10
Climate change in lake systems	11
Metabolism	12
Impacts of warming on fish	13
Impacts of browning on fish	13
Aims of the Thesis.....	15
Methods	16
Model system.....	16
Study methods	16
Database and lake sampling procedures	17
Resource use	19
Morphology.....	20
Metabolic rates.....	21
Statistical analyses	22
Results and Discussion.....	23
Gradient studies	23
Warming	23
Browning.....	25
Habitat coupling across morphs	27
Metabolism and polymorphism	29
Testing respirometry methods	31
Conclusions and Future Perspectives.....	33
References	35
Popular summary.....	43
Sammanfattning på Svenska	46
Acknowledgements	49

Glossary

Aerobic Scope	The capacity to increase oxygen consumption above baseline requirements. Calculated: MMR-SMR. Abbreviated: AS
Benthic light climate	The amount of light reaching the sediment surface at the average lake depth. Measured as % of incident photosynthetically active radiation.
Browning	An increase in the brown color of lake water caused by increases in terrestrially derived dissolved organic carbon (DOC) comprised mainly of humic matter, and iron.
Habitat coupling	The process of linking spatially distinct energy channels within or between ecosystems.
Littoral habitat	The illuminated nearshore benthic habitat of a lake. Often dominated by macrophytes.
Maximum Metabolic Rate	The maximum aerobic metabolic, measured as the maximum oxygen consumption rate that a fish can achieve. Abbreviated MMR
Pelagic habitat	The open water region of a lake which lies beyond the littoral zone
Morph	A phenotypic variant within a population. Morphs show differences in feeding ecology and habitat use, and in the context of this research, perch have littoral and pelagic morphs.
Standard Metabolic Rate	The minimum aerobic metabolic rate needed for subsistence, measured as the minimum oxygen consumption rate. Abbreviated SMR

Introduction

Natural systems are heterogeneous. They vary over space and time and can be divided into habitats with differing abiotic and biotic conditions. Individuals within a single population can also vary widely. Their distribution within the ecosystem depends on their phenotype, competitive ability, and the abundance and distribution of resources. As the climate changes, an individual's survival in newly modified systems may depend largely on their ability to respond to change. Highly specialized species may be negatively impacted by climate change if they are forced into a habitat where they lack the adaptations to succeed. Generalist species may be more resilient to climate change if they are able to use a variety of prey, flexibly shifting feeding behavior to respond to shifts in prey abundance across space or time. Incorporating this heterogeneity of systems and species into study design can help to reveal the variance in responses that ultimately make up mean species-level responses to climate change.

Intraspecific variation and resource use

Most studies on climate change treat fish populations as a single entity ignoring the potential for intraspecific variation in responses to environmental change and how that may impact broader ecosystem functioning. In lakes, especially comparatively young northern lakes, the existence of "open niches" or underutilized resources can prompt a subset of a population to shift into a previously unexploited environment when interspecific competition is low, or intraspecific competition is high (Robinson & Wilson, 1994; Smith & Skúlason, 1996; Svanbäck et al., 2008). This shift in resource use and spatial distribution is often accompanied by changes in morphology, feeding ecology, and behavior, which are primarily due to phenotypic plasticity, but over time may also include genetic components (Skúlason & Smith, 1995; Smith & Skúlason, 1996; Svanbäck & Eklöv, 2006). As a result of this resource polymorphism, a single population can have multiple distinct morphs with differentiated niches, associated with specific feeding ecology and habitat use (Figure 1) (Skúlason et al., 2019). This pattern is pervasive in fishes but has also been identified in amphibians and birds and is often viewed as a precursor to speciation (Smith & Skúlason, 1996). The most common resource

polymorphism in fish is along the littoral-pelagic axis, in which the littoral morph feeds primarily on benthic macroinvertebrates and the pelagic morph primarily on zooplankton. To optimize feeding in littoral habitats, littoral fish are often deeper bodied, to improve maneuverability in structurally complex habitats and have downturned mouths for feeding on benthic invertebrates (Smith & Skúlason, 1996; Kahilainen et al., 2014). In contrast, pelagic fish have streamlined bodies better suited to constant movement, maximizing feeding efficiency on zooplankton living in the pelagic habitat (Smith & Skúlason, 1996; Skoglund et al., 2015). These morphs may serve different roles within lakes reflecting their differing habitat and prey selection. By examining morphs separately, we can better understand how these groups are affected by climate change and how their roles within lakes will change in the future.

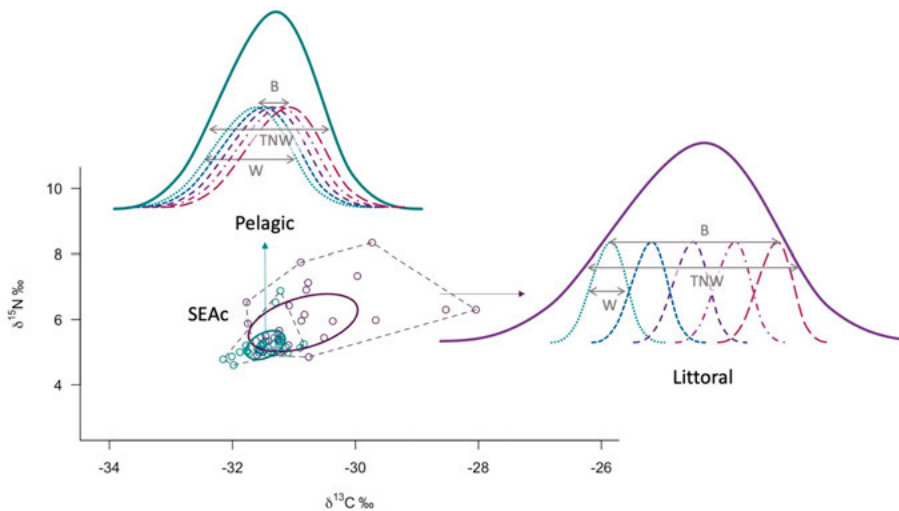


Figure 1. The relationship between group niche width and individual niche width. In this lake the littoral (purple) group is made up of many specialists, with narrow individual niches (W), that vary widely in their resource use (B). The littoral fish have a larger total niche width (TNW) than the pelagic (teal) group which is made up of more generalist individuals (larger W), with more similar diets to each other (smaller B). The isotopic niche width is illustrated using standard ellipse area (SEAc). The figure is based on data from Marklund et al., (2019) and illustrations of variation in individual and total niche width in Bolnick et al. (2010).

Intraspecific variation and niche width

When a subset of a population begins to specialize on previously underutilized resources, as is the case with resource polymorphism, the total niche size of the population expands (Sjödin et al., 2018). A population's niche width is

determined by the size of each individual's niche (narrow niches indicate specialist feeding strategies and wide indicate generalist) and the overlap between the niches of each individual (variation in prey selection) (Bolnick et al., 2003) (Figure 1). Past studies have shown that within different morphs there are individuals with differing levels of specialization, for example Marklund et al. (2019) found a narrower total niche width in pelagic perch, despite wide individual niches, and a broad total niche in littoral perch despite high individual specialization (Figure 1). Examining niche width can reveal intraspecific responses to ecological opportunities or disturbances, and provide information about a predator's role in the wider ecosystem (Layman et al., 2007; Darimont et al., 2009; Karlson et al., 2015). As niche expansion occurs energy fluxes can change in the ecosystem through altered patterns of habitat coupling. Habitat coupling is an ecosystem process in which spatially distinct energy channels are linked within or between ecosystems (Schindler et al., 2003; Baustian et al., 2014). Animal movement is an important component of habitat coupling and the linkages created provide ecosystem stability, counterbalancing heterogeneous or fluctuating energy production (McCann et al., 2005; Rooney et al., 2006). While generalist individuals often move between habitats, specialists may be more selective in their habitat use, meaning that intraspecific variation in resource use has implications for the broader ecosystem (Marklund et al. 2019). Shifts in productivity between habitats can also impact habitat coupling as it impacts resource distribution and the necessity for fish to feed across boundaries (Bartels et al., 2016). By examining niche width, I can better understand the level of specialization within each morph, which in turn also informs coupling behavior.

Climate change in lake systems

As a consequence of climate change, lakes in Northern Europe are warming, and many of them are warming at rates faster than the global average (O'Reilly et al., 2015; Woolway et al., 2019). This persistent warming co-occurs with browning, resulting from increased terrestrially derived dissolved organic carbon (DOC) and iron in surface waters, which stain the water brown (Larsen et al., 2011; Kritzberg et al., 2020). In lakes, increasing water temperatures can have wide-ranging effects, including deoxygenation, decreased net primary production, and changes in phenology (Meerhoff et al., 2012; Tait & Schiel, 2013; Jane et al., 2021). Browning can reduce thermocline depth, decrease nearshore vegetation, and shift energy production towards systems dominated by pelagic phytoplankton and heterotrophic bacteria (Ask et al., 2009; Estlander et al., 2010; Stasko et al., 2012; Vasconcelos et al., 2016). All of these changes in habitat availability and energy production, will likely impact fish indirectly, and will occur in concert with the direct effects of warming

and browning such as increased physiological rates and reduced foraging efficiency (Ran aker et al., 2014; Craig et al., 2015; Little et al., 2020).

Changes in fish populations are important ecologically because of the structuring role of fish in the broader ecosystem and societally because of their role in global food security (Hammerschlag et al., 2019). As a result of this, many broad-scale studies have examined the impacts of warming on fish populations (Jeppesen et al., 2010; Emmrich et al., 2014). However, due to the more regionally constrained nature of browning, there are few studies on its impact on fish across large gradients (but see Finstad et al. (2014) and Craig et al. (2017)), and even fewer on the possible interactive effects of warming and browning in lakes (but see Hansson et al. (2013); and van Dorst et al. (2019)). Studies that use space-for-time approaches also typically combine littoral and pelagic catch into a single measure (Emmrich et al., 2014; van Dorst et al., 2019). This constrains results to patterns of lake-wide responses to climate change, limiting understanding of how these patterns may translate to altered ecosystem processes not just between lakes but within them.

Metabolism

Metabolic rates reflect an individual's cost of living. They govern growth rates and energy requirements and help decide an individual's competitive ability in a given environment, ultimately shaping a population's response to climate change (Brown et al., 2004). Standard metabolic rate (SMR) is the minimum oxygen consumption rate ($\dot{M}O_2$) needed to sustain life, while maximum metabolic rate (MMR) is the maximum $\dot{M}O_2$ reached by an individual (Chabot et al., 2016). The difference between SMR and MMR is the aerobic scope (AS) which determines an individual's capacity for oxygen-consuming functions such as movement, growth, and reproduction (Eliason et al., 2011; Clark et al., 2013; Auer et al., 2015). The combination of these rates determines an individual's cost of living, and differences in individual and species-specific metabolic phenotypes can decide their fitness and ultimately success in a given environment (Hulbert & Else, 2000; Burton et al., 2011). Metabolic rates scale with body mass and differ between sexes, but even controlling for these and other confounding factors, metabolic rates can still vary up to three-fold between individuals (Burton et al., 2011). Across species, SMR correlates with foraging strategies and habitat use (Seibel & Drazen, 2007), and within a single species, there is evidence of differences in metabolic rates between morphs (Kahilainen et al., 2014; Bergstrom et al., 2019). By examining intra-specific differences in metabolic rates in the context of broader phenotypic divergence, I explore a mechanism that can lead to differing growth rates or biomass between habitats. Any differences may help to explain existing patterns and provide additional information about the potential consequences of warming in lake ecosystems.

Impacts of warming on fish

Ectotherms, such as fish, are particularly vulnerable to the increases in temperature associated with climate change because their physiological processes such as metabolic rate and growth scale with temperature (Clarke & Johnston, 1999; Woodward et al., 2010). Higher temperatures lead to increased SMR and consumption rates. Provided sufficient food availability and that temperatures remain suboptimal, increased water temperature leads to increased juvenile growth rate and increased size-at-age before maturity (Ohlberger, 2013; Auer et al., 2015; Little et al., 2020). After maturity, more resources are allocated to reproduction than growth decreasing size-at-age in adult fish (Atkinson, 1994; Ohlberger, 2013). Together with the competitive advantage of small individuals at high temperatures (Huss et al., 2019; Christensen et al., 2020), these mechanisms result in populations made up of smaller and younger individuals (Daufresne et al., 2009; van Dorst et al., 2019). Examining habitat-specific changes in biomass and abundance along a thermal gradient will improve understanding of how climate change will affect both the fish population and the distribution of top-down pressure within lake ecosystems.

Impacts of browning on fish

As opposed to warming, which changes physiological rates, browning can decrease fish size and abundance by reducing foraging efficiency in visual predators and reducing resource availability (Estlander et al., 2010; Ranåker et al., 2014; Benoit et al., 2016; van Dorst et al., 2020). Brown water has higher light attenuation which decreases the amount of light reaching the sediment surface and decreases macrophyte and benthic algae growth (Estlander et al., 2010). This decrease in benthic algae production frees up sediment-derived nutrients, stimulating phytoplankton growth and increasing pelagic primary production (Vasconcelos et al., 2016). At the same time, the increased DOC, responsible for the brown water color, is utilized by heterotrophic bacterioplankton, resulting in comparatively high heterotrophy in brown lakes (Ask et al., 2012). Fish in lakes with higher DOC use more pelagic resources (Bartels et al., 2016; Hayden et al., 2019), but the lower fish biomass in these browner lakes indicates that this shift in resource use does not compensate for the decreased benthic primary production (Finstad et al., 2014; Karlsson et al., 2015). Mobile generalist predators such as fish can switch habitats frequently, linking disparate habitats. As visual conditions or productivity across habitats change, fish may switch habitats less frequently, decoupling compartments of the broader food web (Bartels et al., 2016; Tunney et al., 2018). By examining the effects of browning by habitat, I can evaluate how it impacts fish size and distribution within the lake. Measuring individual resource use along this same water color gradient provides additional information about the distribution of top-down

pressure within a lake, linkages between habitats, and how they may change with browning.

Aims of the Thesis

The overarching aim of this thesis is to study how fish populations respond to climate change and how these responses differ between habitats. Because metabolism scales with temperature, governing energy requirements, and pace-of-life as the climate warms, I also aim to determine whether intraspecific variation in metabolic rates relate to habitat use and phenotypic differences within populations. By combining this information, this thesis aims to show how climate change will impact broader lake ecosystem functioning through its impact on; fish distribution within lakes, resource use, and energy requirements.

The questions addressed in each chapter are:

What is the impact of climate change (in the form of increased temperature and water color) on the size, abundance, and within-lake distribution of a polymorphic predator fish? (**Paper I**)

How will resource use and niche size of a polymorphic predator fish be impacted by climate change (in the form of increased temperature and water color), and will this alter patterns of habitat coupling? (**Paper II**)

Do metabolic rates differ between littoral and pelagic perch morphs and if so, does this variation relate to morphology or resource use? (**Paper III**)

Is there a reason I'm chasing these fish around in a circle? What is the best method to elicit maximum metabolic rate in perch and what is the magnitude of difference between common methods? (**Paper IV**)

Methods

Model system

European perch (*Perca fluviatilis*, henceforth perch) is the focal species used throughout my research. Perch are a well-studied and widely distributed predator in Europe, inhabiting lakes along a temperature and water color gradient. They are visual predators that undergo ontogenetic niche shifts during their lifetime. Juvenile perch feed on zooplankton and as they grow and reach an intermediate size class they shift diets and begin to niche partition littoral and pelagic resources, feeding on benthic macro invertebrates and zooplankton, respectively (Figure 2) (Svanbäck & Eklöv, 2003). The largest size classes of perch shift diets again becoming primarily piscivorous (Persson, 1988; Eklöv & Diehl, 1994; Hjelm et al., 2000). Niche partitioning by intermediate size classes results in resource polymorphism along the littoral-pelagic axis, similar to other polymorphic fish (Skúlason & Smith, 1995; Svanbäck & Eklöv, 2002). Individuals living in each habitat show differences in resource use and individual specialization, resulting in different niche widths between individuals as well as between morphs (Marklund et al., 2019; Chaguaceda et al., 2020). For the purpose of my research I classify perch caught in the littoral zone as “littoral perch” and perch caught in the pelagic zone as “pelagic perch.” Though perch as a species are generalists and individuals show varying degrees of cross-habitat resource reliance, past studies have shown average differences in morphology and diet between littoral and pelagic catch (Faulks et al., 2015; Scharnweber et al., 2016a)

Study methods

Papers I, II, and III all differentiate between perch caught in littoral and pelagic habitats, emphasizing; a) the heterogeneity in responses to climate change between habitats and b) how collective differences between morphs shape their responses to climate change and potentially impact ecosystem functioning within habitats and the lake as a whole. To evaluate how perch populations will respond to climate change, in **Paper I**, I used catch and environmental data from 49 Swedish lakes to examine trends in perch size and number along temperature and water color gradients (Figure 3). By using latitudinal data, I can see the potential outcome of climate change in complex

systems that include the cumulative effects of gradual warming and browning. In **Paper II**, I caught fish from 17 lakes along thermal and water color gradients similar to **Paper I** (Figure 3). I used stable isotopes composition to examine differences in resource use and niche width that could be contributing to the patterns seen in **Paper I**. Based on differences in resource use I also evaluated how shifts in fish size and water color could alter current patterns of habitat coupling, impacting energy flow within the broader lake food webs. In **Paper III**, I used geometric morphometrics, stable isotope analysis, and respirometry to examine whether individual differences in metabolic rate covaried with other traits that diverge along the littoral-pelagic axis in polymorphic fish. Using morphometrics allowed me to explore whether a specific aspect of morphology (for example, body depth) was related to oxygen consumption. Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope composition reveals long-term resource use, providing information about foraging style and prey availability. **Paper IV** focuses on the methodology used to elicit maximum oxygen consumption, and by using a Latin square with repeated measures design, I was able to minimize the number of individuals needed in the trials and account for individual differences in metabolic rates.

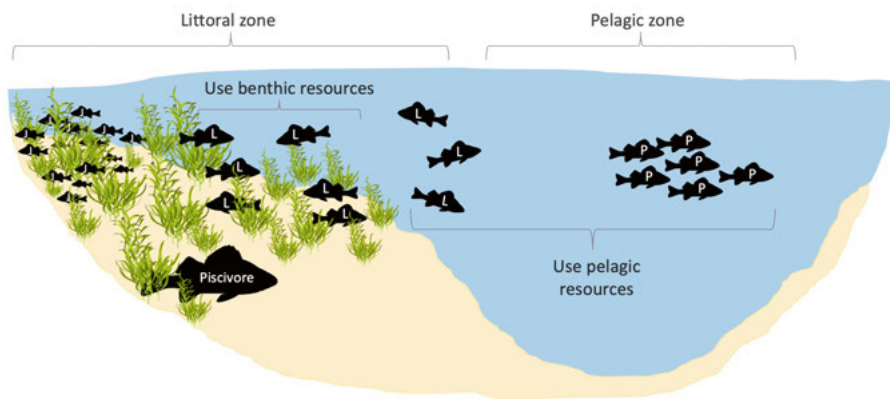


Figure 2. Habitat use and resource partitioning by perch. Juveniles (J) use littoral areas along the shoreline with dense vegetation that offers refuge. At high densities, intermediate-sized perch are polymorphic, separating into littoral (L) and pelagic (P) morphs. Littoral perch are caught in the littoral zone. They can have higher individual specialization in which a subset of littoral individuals use pelagic resources (LP). Pelagic perch (P) have lower individual specialization and feed primarily on pelagic resources.

Database and lake sampling procedures

Papers I and II, use a space for time approach using fish collected from lakes along air temperature and water color gradients (Figure 3). Data for **Paper I** was selected from a dataset with fish catch and environmental data from 424

Swedish lakes (Holmgren et al., 2018). All selected lakes were fished using benthic multi-mesh gillnets (30 x 1.5 m) and pelagic multi-mesh gillnets (27.5 x 3 m) according to European standard (EN 14757: 2015). Perch used in **Paper II** were caught in nets set using the same European standard. In both **Papers I and II**, perch were divided into littoral and pelagic groups depending on their catch location, with any perch caught in benthic nets set at less than 6 m depth classified as littoral and perch caught in pelagic nets between 0-6 m depth (**Paper I**) or 0-8 m depth (**Paper II**) classified as pelagic. All perch caught during sampling for **Paper II** were immediately weighed, measured, and photographed on their left side for geometric morphometric analysis of their body shape, and a dorsal muscle tissue sample was dissected and frozen for later stable isotope analysis.

For **Paper I**, average annual air temperature was calculated as the mean of the average monthly air temperatures from the climate model described by New et al. (2002), interpolating air temperature measurements by SMHI. In **Paper II**, I use average air temperature from the sampling year and four years prior, measured at the weather station closest to the lake. Absorbance at 420 nm (Abs_{420}) was used as a proxy for water color in **Paper I** since it reflects both allochthonous DOC and iron concentrations which impact light climate and are explicitly linked to climate change, while DOC was used in **Paper II** to allow for the inclusion of data from a previous sampling season. For both **Papers I and II**, light reaching the sediment surface at the average lake depth (% incident PAR, and henceforth referred to as the benthic light climate) was calculated using the equation $100\exp(-K_d z)$, where K_d is the vertical light attenuation coefficient, and z is the average lake depth (Vasconcelos et al., 2016). Information about additional variables used in my models can be found in the methods section of each paper.

For **Paper III and IV**, perch were caught in August 2018 via angling in the vegetated nearshore (littoral) and illuminated open water (pelagic) zones of lake Erken (Figure 3). These perch were transported to the Uppsala University aquarium facility and, upon arrival, were anesthetized, weighed, measured, and photographed. Perch were maintained in flow-through aquaria at 18°C with similar sized conspecifics until respirometry trials began. After respirometry trials, all perch were sacrificed, then weighed and measured a second time (**Paper III and IV**), and a dorsal muscle tissue sample was dissected and frozen for later stable isotope analysis from individuals used in **Paper III**.

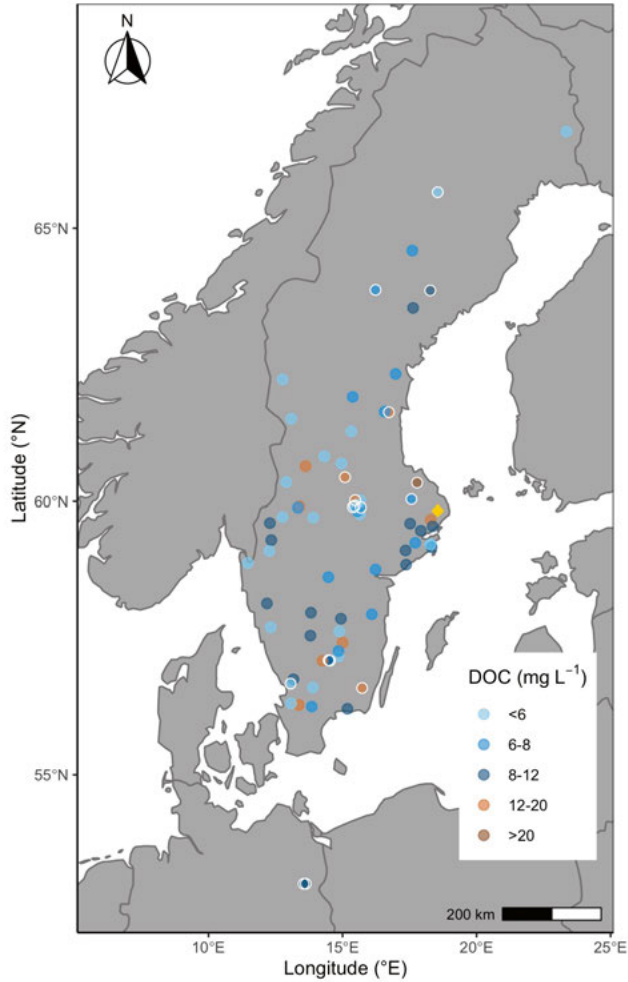


Figure 3. Map of the location of all study lakes. Lakes used in **Paper I** (n = 49) are represented by filled dots. Lakes with white circles were used for **Paper II** (n = 17). Lake Erken is represented by a yellow diamond (**Paper III** and **IV**). Mean annual air temperature ranged from -1.25 to 7.13 °C from northern to southern sites.

Resource use

I used stable isotope analysis to measure the time-integrated resource use of perch in my study systems to estimate energy utilization from benthic compared to pelagic pathways (**Papers II** and **III**). I collected zooplankton, mussels (when available), and invertebrates as pelagic and littoral baselines, respectively. I used these baselines in two-source mixing models to calculate the % pelagic resource reliance using the equation:

$$\% \text{pelagic} = (\delta^{13}\text{C}_{\text{consumer}} - \delta^{13}\text{C}_{\text{littoral resources}}) / (\delta^{13}\text{C}_{\text{pelagic resources}} - \delta^{13}\text{C}_{\text{littoral resources}})$$

Assessments of habitat coupling were based on cross habitat resource use, meaning that littoral fish preying primarily on littoral resources couple habitats less than littoral fishing relying heavily on pelagic resources. I used the SIBER package (Stable Isotope Bayesian Ellipses version 2.1.5, Jackson et al. 2011) in R to determine the niche breadth of littoral and pelagic morphs in each lake based on the carbon and nitrogen isotope composition of each fish. Standard ellipses area corrected for small sample size (SEA_c) was calculated to allow for accurate comparisons between littoral and pelagic groups, which are often numerically biased in favor of littoral morphs.

Morphology

I used geometric morphometrics to explore shape differences between littoral and pelagic perch as individuals (**Paper III**) and collectively (**Paper II and III**). Perch were photographed on their left side, and I used TPS-dig2 to digitize 16 landmarks on each fish which were then analyzed using MorphoJ (Figure 4). Briefly, I extracted the shape information by running a Procrustes fit and then regressed the Procrustes coordinates on centroid size to correct for body size. The residuals of this regression were used in a discriminant function analysis (DFA) (Figure 4) and principal component analysis (PCA). A DFA (**Paper II and III**) is used to describe morphological differences between two pre-determined groups (fish caught in the littoral and pelagic habitats in my case) and uses Mahalanobis distance as a measure of that difference. A PCA describes differences between individuals instead of groups, making it a more appropriate measure to use in regression analyses (**Paper III**). I used PC2 and PC3, which described differences in body depth, mouth direction, and tail length, which are morphological features hypothesized to correspond with drag, habitat, and resource use.

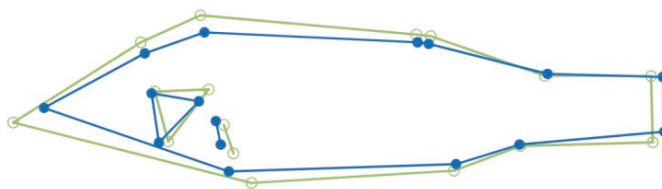


Figure 4. A visualization (with 4x magnification) of the morphological differences between littoral (green - open dot) and pelagic (blue - filled dot) perch from lake Erken, based on a discriminate function analysis (DFA) (**Paper III**). The wireframes also show locations of the 16 landmarks used in all morphological analyses (**Paper II and III**).

Metabolic rates

In order to estimate Standard Metabolic Rate (SMR), Maximum Metabolic Rate (MMR), and Aerobic Scope (AS) for **Papers III** and **IV**, I measured oxygen consumption rate ($\dot{V}O_2$) using intermittent-flow respirometry based on the protocols described by Clark et al. (2013) and Svendsen et al. (2016). In **Paper III**, fish were chased in a circular arena for 3-minutes in order to elicit MMR before placing them in the respirometry chamber. In **Paper IV**, I tested this method against a 3-minute chase with 1-minute air exposure and a control treatment where fish were not chased. Fish remained in the respirometry chamber (Figure 5) in a dark room overnight (during which time they are presumed to be resting) to estimate an accurate SMR. I calculated MMR as the single highest measurement of $\dot{V}O_2$ during each trial and SMR as the average of the lowest 10% of measurements (**Paper III** and **IV**).

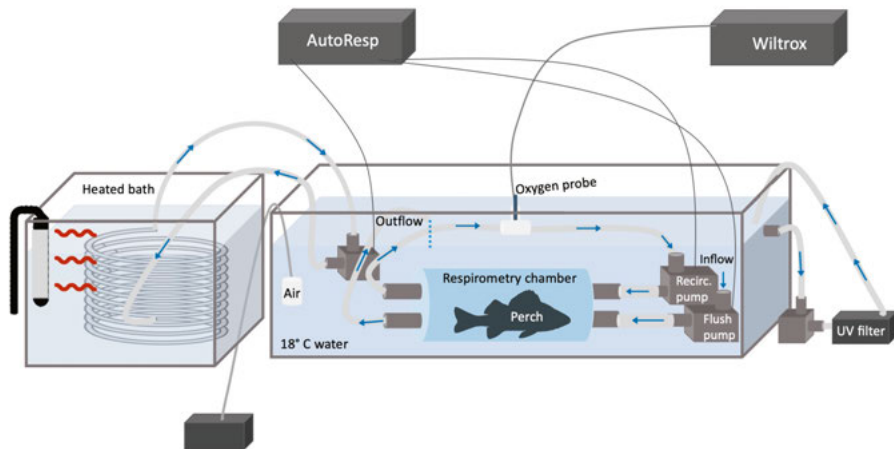


Figure 5. This figure illustrates the critical system components and direction of water flow through an intermittent-flow respirometer. During trials, a fish is placed in the respirometry chamber, which has constantly circulating water flowing through the chamber and past the oxygen probe. During the measurement phase, the system is closed, and the oxygen concentration decreases. When the decreasing oxygen concentration hits approximately 80%, a flush phase begins, during which well-oxygenated water from the surrounding tank is flushed through the system via the flush pump and out the outflow, renewing water in the chamber with clean well-aerated water. Water within the larger tank is constantly pumped through the UV filter to decrease bacterial growth (which increases background respiration), and AutoResp software monitors water temperature, turning on a pump that warms water in an external heating bath, maintaining the system at 18° C. (**Paper III** and **IV**).

Statistical analyses

Below is a summary of the statistical analyses used in this thesis but detailed descriptions can be found within each paper. I used multiple linear regressions in **Paper I** to examine the effects of temperature and water color (Abs_{420}) on fish size and abundance in each habitat while controlling for confounding variables including lake area and total phosphorous concentrations, which are also known to correlate with fish biomass. I also used a multiple linear regression in **Paper III** to examine the relationship between morphology and metabolic rates but used a two-way ANOVA on a reduced dataset that was limited to sex and a measure of habitat and/or resource use. In **Paper II** and **IV**, I used linear mixed-effects models in order to account for the random effects of lake and habitat (habitat was nested within lake) (**Paper II**) and fish individual (**Paper IV**). All analyses were performed in R (R Core Team, 2019).

Results and Discussion

In **Papers I** and **II**, I found differences in the impact of water color and temperature on size and abundance (**Paper I**) and niche size and habitat coupling (**Paper II**) of littoral and pelagic perch. In **Paper III**, I reveal metabolic differences between these groups. These results demonstrate that the response of fish populations to climate change is likely to be heterogeneous across habitats. Climate change induced shifts towards higher pelagic habitat and resource use, accompanied by higher metabolic rates in pelagic perch, will increase top-down pressure in the pelagic compartment of food webs, with potential implications for habitat stability. In dividing perch catch by habitat, I built intraspecific variation into my studies and can evaluate how climate change may ultimately impact ecosystems through its impacts on different perch morphs.

Gradient studies

Warming

I found that along a latitudinal gradient, as temperature increases, average perch length within the lake as a whole and the average weight of littoral perch both decrease (**Paper I**) (Figure 6). These findings are in line with the temperature-size-rule, which predicts higher growth rates but reduced body size in ectotherms as temperatures increase. The increase in metabolic rate associated with higher temperatures (Fry, 1971; Gillooly et al., 2001) is likely responsible for decreasing perch mean size along a latitudinal gradient. Smaller fish also have a competitive advantage at higher temperatures. Since metabolic rate increases faster than foraging rate with body size, the optimum growth temperature decreases with size, decreasing growth rates in large fish and leading to populations dominated by younger and smaller sized fish (Persson L., 1987; Ohlberger et al., 2011; van Dorst et al., 2019; Lindmark et al., 2021). In size-structured populations, these shifts in size distribution can impact broader community dynamics.

Unlike the littoral perch and contrary to expectations, the average weight of pelagic perch, was not impacted by temperature (Figure 6). Perch abundance in the pelagic habitat increased with temperature, increasing the proportion of the perch population found in the pelagic zone (**Paper I**) (Figure 6).

Intermediate-sized perch partition resources (Svanbäck & Eklöv, 2003). When intraspecific competition is high, this leads to resource polymorphism and the development of a pelagic morph, which lives and feeds in the pelagic zone (Svanbäck et al., 2008) (Figure 2). The increase in the number of pelagic perch that I observe could be triggered by increasing competition. Increasing temperatures cause average perch size to decrease and metabolism to increase. The shift to smaller and more uniformly sized individuals may increase competition within intermediate size classes, resulting more perch using the pelagic habitat (Svanbäck et al., 2008). Higher metabolic rates may further increase competition if energy requirements increase without a comparable increase in prey abundance, reinforcing this pattern. This increase in pelagic perch abundance was correlated with air, not water temperature (at 3 m depth), and combined with the fact that water temperatures in all lakes at the time of sampling were below both optimal growing temperatures and the lethal limit for perch, indicate that this pattern was likely not caused by perch seeking thermal refuge (Karås & Thoresson, 1992; Mélard et al., 1996; Huss et al., 2019).

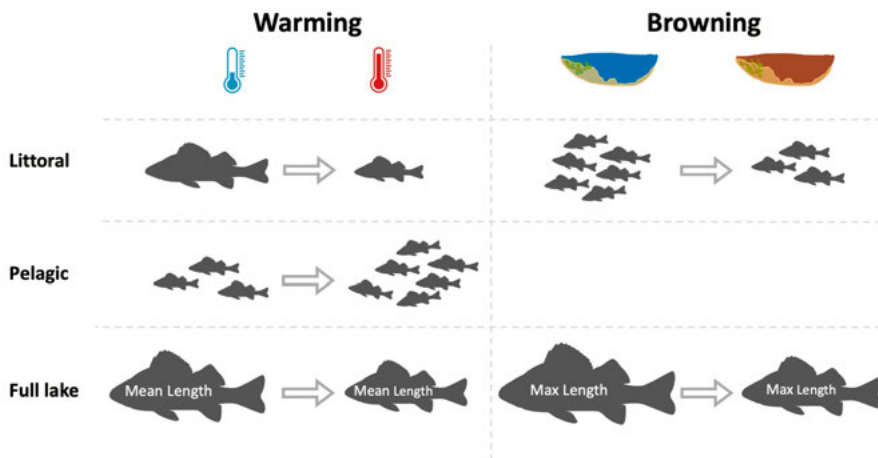


Figure 6. There are habitat-specific responses to warming and browning in perch. Along a latitudinal gradient, I found that in warmer lakes, perch in the littoral habitat and the lake as a whole were smaller than in cold lakes. The size of pelagic fish was not impacted by water temperature or color, but the number of perch caught in the pelagic habitat increased with air temperature. Browner lakes had fewer perch in the littoral habitat, and within the lake as a whole, they reached a smaller maximum size. (Paper I)

Decreased average size also positively correlated with littoral niche width (**Paper II**). Resource polymorphism due to competition forces some perch into the pelagic zone completely, but there can also be resource partitioning within the littoral group, leading to individual specialization (Svanbäck et al., 2015). In some lakes, this includes a subset of perch that are caught in the littoral

zone but feed on pelagic resources (Figure 2) (Marklund et al., 2019; Chaguaceda et al., 2020). Large perch undergo a second ontogenetic niche shift and becoming mostly piscivorous (Persson, 1988; Eklöv & Diehl, 1994; Hjelm et al., 2000). Because of these differences in diet between size classes, large perch will compete less with intermediate-sized perch for resources. This reduced competition may explain why littoral niche width was related to average perch size, suggesting that increased competition within size classes is causing these patterns (Svanbäck & Bolnick, 2007). Pelagic niche width was not impacted by fish size, likely because the morph is made up of generalists with similar diets, so even as numbers increase, niche width remains unchanged (Quevedo et al., 2009; Marklund et al., 2019) (**Paper II**). As lakes warm, there will be increased top-down pressure in the pelagic habitat caused by a higher proportion of perch living in the pelagic (**Paper I**) and higher standard metabolic rates in these perch (**Paper III**) (Figure 9a), as well as higher pelagic resource use by small individuals which are more prevalent in warm lakes (**Paper II**).

Browning

I analyzed two aspects of browning; increases in water color (Ab_{s420} in **Paper I** and DOC in **Paper II**) and decreases in the benthic light climate (**Paper I** and **II**). The variable ‘water color’ should correspond more closely with the effects of adding terrestrially derived DOC into lake ecosystems, which includes decreasing primary production due to shading, but also increases in the growth of heterotrophic bacteria (Ask et al., 2009). Water color interacts with lake depth to determine the proportion of light penetrating the water column and reaching the sediment surface (benthic light climate). This measure should more closely correspond to the extent of benthic algae production and macrophyte cover in the littoral zone since both require benthic light to grow (Estlander et al., 2010; Vasconcelos et al., 2016).

Along a water color gradient, I found that the abundance and subsequently total biomass of littoral perch decreased as water color increased and this co-occurred with a decrease in the lake-wide maximum perch size (**Paper I**) (Figure 6). I also saw a decrease in littoral perch biomass as benthic light decreased, likely due reduced littoral habitat size (Seekell et al., 2018) (**Paper I**). Unlike in the littoral habitat there was no decrease in perch abundance or biomass in the pelagic as water color increased or benthic light decreased (Figure 6), but I did find that in lakes with low benthic light, a larger proportion of perch were caught in the pelagic zone (**Paper I**). There was also an increase in pelagic resource use in low benthic light lakes, especially by littoral perch (**Paper II**) (Figure 7a). Multiple mechanisms can contribute to the decrease in littoral perch abundance. Prey availability decreases with browning as shading reduces both benthic primary production and well-oxygenated habitat (Karlsson et al., 2009; Kelly et al., 2014; Craig et al., 2015; Vasconcelos et

al., 2019). Lower macrophyte growth in low light lakes (Estlander et al., 2010; Choudhury et al., 2019), may directly affect perch abundance by decreasing the structural complexity that serves as a refuge for juveniles (Eklöv, 1997) and allows perch to outcompete competitors such as roach (Persson, 1993).

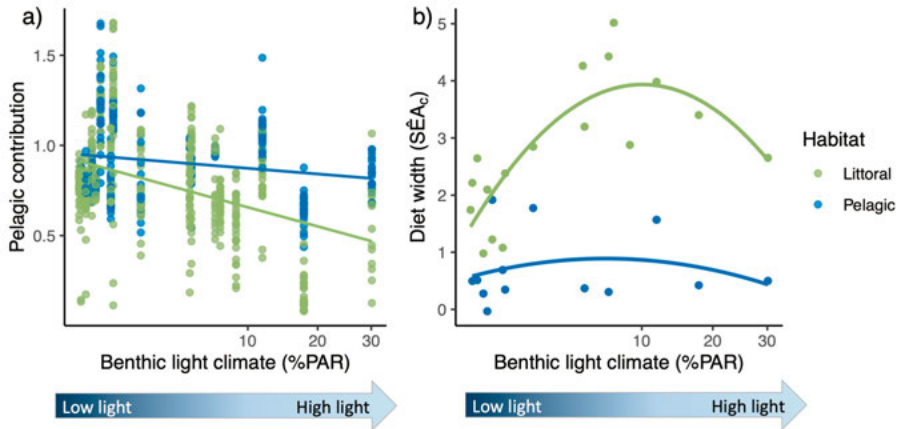


Figure 7. Panel a) shows the negative relationship between benthic light climate and pelagic resource use (pelagic contribution) and the interaction between light and habitat. points represent the partial effects from a linear mixed model, and each point represents an individual fish. Panel b) shows the relationship between benthic light climate and isotopic niche width (diet width), controlling for the effect of average fish length. Each point represents the isotopic niche width of the littoral (green) or pelagic (blue) morph from each lake. Lines show the unimodal relationship between benthic light climate and diet width, which is significant for the littoral morph. (**Paper II**)

Lower benthic resource availability may also be the cause of reduced niche widths found in low-light lakes (Figure 7b) (**Paper I**). As the benthic light climate improves, the size and complexity of the littoral habitat should increase and with it invertebrate density (Rennie & Jackson, 2005). Abundant benthic invertebrates and zooplankton in mid-light lakes, should enable individual specialization, likely driving the observed increase in littoral niche width (Layman et al., 2007) (Figure 7b). In extremely clear and shallow lakes, pelagic primary production may decrease due to high nutrient capture by benthic algae and the harmful effects of UV radiation (Williamson et al., 1996; Karlsson et al., 2009; Stasko et al., 2012; Finstad et al., 2014; Seekell et al., 2014). This may explain the observed contraction of niche width with high benthic light, leading to the overall unimodal relationship between niche width and benthic light climate in my lakes (Figure 7b) (**Paper II**).

In browner lakes, there is a higher percent of pelagic resources in both littoral and pelagic perch diets (Figure 8) (**Paper II**). As water color increases and benthic primary production decreases, more nutrients may be available for pelagic primary production, shifting the energy source within lakes (Vasconcelos et al., 2016, 2019). However, darker water decreases the

catchability of whatever resources are present (Bartels et al., 2012; Scharnweber et al., 2016b; van Dorst et al., 2020). Brown lakes also have high bacterial production fueled by high DOC (Ask et al., 2009), but these heterotrophic food webs have lower transfer efficiency than the autotrophic food webs in clear lakes (Cole et al., 2006; Berglund et al., 2007). In my shallow systems, increases in pelagic primary production, and potentially bacterial production, in the pelagic zone appear to supplement the food webs and appear in both littoral and pelagic perch diets, as indicated by carbon isotope composition (**Paper II**). However, it is not enough to make up for the loss of benthic production, and lake-wide biomass decreases with decreases in the benthic light climate, as well as increases in water color (**Paper I**).

Increased DOC and decreased benthic light climate may decrease fish abundance in the short term due to decreased resources and refuges (Leech et al., 2021), but it may take multiple generations for the full impact of lake browning on fish abundance to be realized. Lower resource abundance can decrease lifetime growth and maximum size (Craig et al., 2017), as a consequence of fish preferentially allocating resources to reproduction over somatic growth in resource-poor environments (Lester et al., 2004; Barneche et al., 2018). Since fecundity is size-dependent, scaling hyper-allometrically with size, the decrease in maximum size along a water color gradient (**Paper I**) can severely decrease yearly reproductive effort (Barneche et al., 2018). With a maximum size of approximately 50 g, the largest fish in one of my darkest lakes (Brunnsjön) will produce approximately 296 eggs per spawning event, while the largest fish (~ 500 g) in one of the clearest lakes (Västra Skälsjön) will produce around 4,483 eggs. This relationship shows that it is not just increased mortality due to low or poor-quality resources that reduce fish abundance, but the long-term effects of resource limitation on lifetime growth as well.

Habitat coupling across morphs

Habitat coupling is the process of moving energy between discrete habitats within a larger ecosystem providing links within food webs and impacting habitat stability (McCann et al., 2005; Guzzo et al., 2017). Coupling can occur across different spatial scales. In lakes, gravity and diel vertical migration can couple pelagic and profundal habitats, but this happens on a much smaller spatial scale than the littoral-pelagic coupling that results from the movement of generalist predators throughout lakes in response to the heterogeneous distribution of prey (Schindler & Scheuerell, 2002; Baustian et al., 2014). In **Paper I**, I show that as lakes get browner and decreasing amounts of light reach the sediment surface, there is a shift towards a higher proportion of the population being made up by pelagic perch. When DOC concentrations increase, both littoral and pelagic perch use more pelagic resources, though on average

pelagic perch use more pelagic resources than their littoral counterparts (Figure 8). This shift in habitat and resource use has implications for habitat coupling. Higher pelagic resource use will reduce habitat coupling by pelagic fish in browner lakes, as they increasingly live and feed in the same habitat (Figure 8b) (**Paper II**). With a larger proportion of fish living in the pelagic zone in warm lakes (**Paper I**), a larger proportion of the population will show low coupling behavior. Littoral fish also increase their pelagic resource use along a DOC gradient (Figure 8a). This shift will increase habitat coupling as fish feed on pelagic resources but move back into the littoral zone, shifting energy in the form of waste products or as they become prey for larger fish. Smaller littoral niche widths in low-light lakes indicate that coupling may be more equally distributed among littoral individuals compared to in high light lakes, where there is higher individual specialization and few littoral perch feed in the pelagic zone (**Paper II**) (Bolnick et al., 2007). The effects of DOC on coupling discussed above, will be further magnified by the negative effect of temperature on fish size (**Paper I**) since pelagic resource use is higher in smaller individuals (Figure 8). By separating populations into littoral and pelagic morphs, I can better understand how a population-wide shift towards higher pelagic resource use, will impact broader ecosystem dynamics.

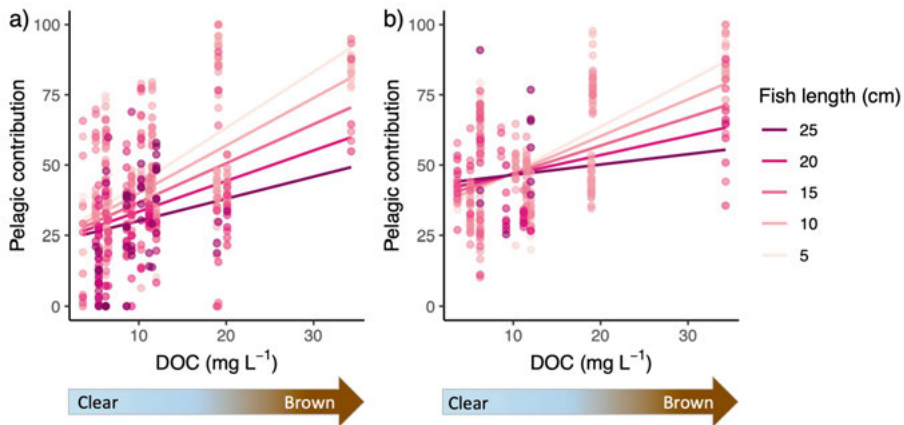


Figure 8. An interaction plot showing the combined effects of DOC and fish size on the pelagic carbon contribution to fish diets (pelagic contribution) in a) littoral and b) pelagic perch. Each point represents an individual fish, and point colors correspond to fish length. Lines show the significant interaction between fish length and DOC and how the relationship between DOC and pelagic contribution differs depending on the size of the fish in the lake. (**Paper II**)

Metabolism and polymorphism

Polymorphism in fish is associated with the divergence of several morphological traits and differentiated resource use (Skúlason & Smith, 1995), resulting in high intraspecific variation in these traits within a single population. Much like morphology and resource use, there is high intraspecific variation in metabolic rates. Even when controlling for known covariates such as size and sex, there can be up to 3-fold variation among individuals (Burton et al., 2011). **Paper III** was designed to test whether morphological differences such as body depth (which should increase hydrodynamic drag) and resource use (which should alter foraging strategies and resource quality) impact perch metabolic rates and account for some of the intraspecific variation between individuals. Using littoral and pelagic perch from lake Erken, which historically show high divergence in morphology and resource use between morphs (Bartels et al., 2012; Scharnweber et al., 2016a), I was able to show that while SMR (and as a result AS) does diverge along a littoral-pelagic axis (Figure 9a), there was no correlation between individual measures of metabolism and morphology, or metabolism and resource use (Figure 9c) (**Paper III**). This study suggests that metabolic rates should be considered part of the larger suite of traits that diverge between morphs, but further studies are needed to identify the drivers of this divergence.

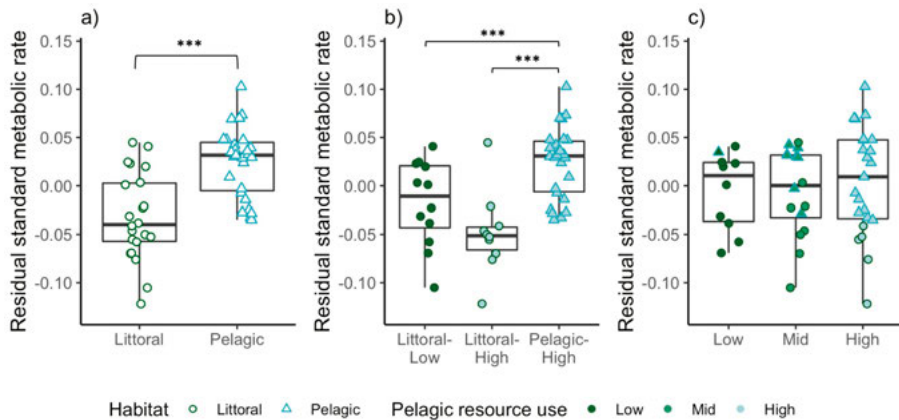


Figure 9. Residual standard metabolic rate (mg O₂ h⁻¹) across a) habitat b) habitat + resource use, and c) resource use groups in perch. Asterisks indicate significant differences (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) based on pairwise comparisons controlling for sex. Boxplots depict median, 25th, and 75th percentile, and whiskers extend to the maximum and minimum values. Outliers ($> 1.5 \times$ interquartile range) are represented by dots. (**Paper III**)

Metabolic rates are fundamentally responsible for a food web's response to climate change, with individual-level changes radiating up through the system (Woodward et al., 2010). The differences in SMR between littoral and pelagic

perch have implications for lake-level responses to climate change, but the drivers of this divergence need to be identified to fully understand the consequences of these differences. Potential explanations to be explored in the future are: 1) differences in SMR are plastic and change in response to physical differences between habitats 2) there is natural variation in SMR within the population, and high SMR individuals selectively utilize the pelagic habitat 3) assortative mating results in the inheritance of genes related to SMR in pelagic individuals.

Vegetation density and temperature profiles are key physical characteristics that differ between littoral and pelagic habitats and that will change as lakes get warmer and browner (Vasconcelos et al., 2016). Interspecific comparisons show that mobile, visual predators inhabiting structurally simple habitats benefit from high metabolic rates (Webb, 1984; Seibel & Drazen, 2007; Rosenfeld et al., 2015; Auer et al., 2020). If decreases in habitat complexity that accompany browning force littoral perch to increase activity levels, there may be less differentiation in SMR between morphs, either as a result of a plastic response to the open water environment or a competitive advantage of more active individuals with higher SMRs. Warming will increase surface water temperatures and strengthen thermoclines in stratified lakes, while browning decreases the depth of the thermocline resulting in warmer surface waters but cooler deep waters (Creed et al., 2018; Pilla et al., 2020). If my observed differences in SMR are caused by metabolic cold adaptation (Song et al., 2019; Pilakouta et al., 2020), the difference in metabolic rate between morphs may increase as littoral habitats warm and pelagic fish continue to have access to cool waters under the thermocline. If metabolic differences between habitats are shaped by fish selecting the habitat in which their metabolic rate is most advantageous (e.g., high metabolic rate fish in the pelagic), persistence of this pattern will likely depend on whether increases in water temperature shift the competitive advantage between metabolic phenotypes as energy requirements increase. If differences are genetically fixed, fish may be less able to respond plastically to environmental change. Pelagic fish will be more vulnerable to climate change if their consumption rate or the density of pelagic resources do not scale with temperature induced increases in SMR (Lindmark et al., 2017, 2021). Exploring these drivers of SMR differentiation across habitats may prove crucial in exploring habitat and population-level responses to climate change. Beyond the potential interaction with climate change, these differences in metabolic phenotype across habitats may be valuable for future studies exploring drivers of intraspecific differences in metabolic rates and maintenance of these patterns in spatially constrained systems.

Testing respirometry methods

Metabolic rates are key physiological traits for understanding fish performance in the context of climate change, and it is, therefore, crucial that an appropriate respirometry technique is used to characterize them (Pörtner & Farrell, 2008; Norin & Clark, 2016). Accurately characterizing maximum metabolic rate (MMR) requires fish to reach their peak oxygen consumption rate ($\dot{M}O_2$), while measures of standard metabolic rate (SMR) require fish to be in a quiescent state. The difference between these two measures is the aerobic scope (AS). Static respirometry is a popular method for measuring oxygen consumption rate in fish that do not naturally swim for prolonged periods and is less cost-prohibitive than other methods (Norin & Clark, 2016; Killen et al., 2017). In order to prompt the exhaustive swimming behavior that is expected to maximize $\dot{M}O_2$, the majority of static respirometry studies use a chase protocol, in which the focal fish is chased until exhaustion and then placed directly into an intermittent-flow respirometer (Clark et al., 2013; Rummer et al., 2016; Killen et al., 2017).

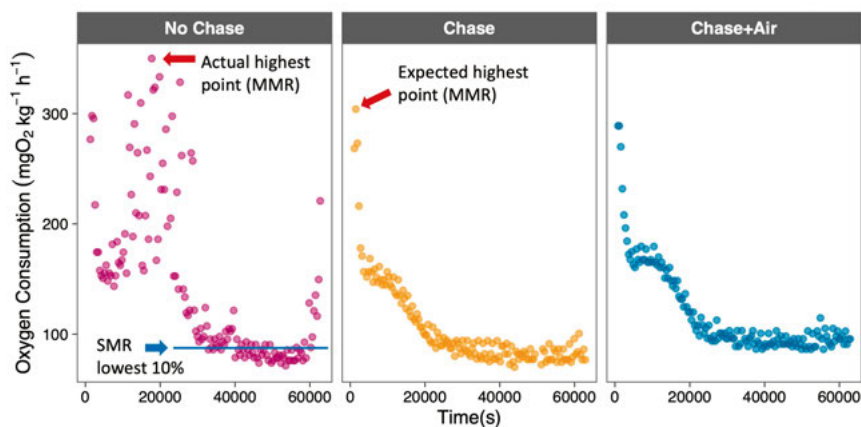


Figure 10. An example of the differences in maximum metabolic rate (MMR) calculated using chase protocols compared to a no-chase control. Each panel shows oxygen consumption rates ($\dot{M}O_2$) from a single fish over time, where the single highest point is MMR, and the lowest 10% of points are averaged to calculate the standard metabolic rate (SMR). Only $\dot{M}O_2$ measures with an $R^2 > 0.95$ are displayed. (**Paper IV**)

Contrary to expectations, I found that methods using a 3-minute chase protocol to elicit maximum $\dot{M}O_2$ underestimated MMR by an average of 16% compared to a no-chase control (**Paper IV**). Chase protocols also resulted in underestimates of AS, but not SMR (**Paper IV**). The first three measurement cycles immediately following a chase are expected to capture the highest $\dot{M}O_2$ which is used as an estimate of MMR (Baktoft et al., 2016; Jensen et al., 2017), but I found that many individuals reached maximum $\dot{M}O_2$ during spontaneous periods of activity hours into the trial period (Figure 10). I also found that $\dot{M}O_2$

during these spontaneous periods was higher in non-chased fish than the $\dot{M}O_2$ following exercise in chased fish (Figure 10). The resulting underestimates of MMR have implications for studies examining differences in metabolic performance across species if there are species-specific responses to chase protocols or when species with different swimming modes require different respirometry set-ups (Seibel & Drazen, 2007; Killen et al., 2016; Rummer et al., 2016). Underestimates could also impact studies examining metabolic performance in responses to climate change scenarios, which are likely to continue to be a substantial portion of the literature in the future as global temperatures continue to increase (Dillon et al., 2010; Clark et al., 2013; Sandblom et al., 2016; Christensen et al., 2020). Respirometry trials for **Paper III** were conducted before **Paper IV** and therefore use a 3-minute chase protocol. While this means that MMR estimates in **Paper III** are likely underestimates, I found no effect of chase protocol on SMR, and the underestimates should therefore not impact my conclusions.

A potential limitation of my methods study is that all of the trials were performed at 18°C. Studies on the impacts of climate change on metabolic rates often perform tests at multiple temperatures to examine the impacts of acute or chronic warming (Sandblom et al., 2016; Sandersfeld et al., 2016; Auer et al., 2018). Respirometry at lower temperatures may require an external stimulus to stress fishes instead of relying on the spontaneous activity during the trial period, which occurred at my moderate study temperatures. To account for this, I suggest that future experiments use an overnight measurement period followed by a stressful stimulus near the end of the trial and that the MMR should be the global maximum $\dot{M}O_2$ measured during the entire study period. Though in **Paper IV** I suggest using a chase as this stimulus, more recent studies have shown that a retrofitted respirometry chamber with a soft brush that can be turned (Zhang et al., 2020) or a short period of tapping on the respirometry chambers (Christensen et al., 2020) are better alternatives. This updated method should ensure that all fish undergo a stressful period, inducing MMR across study temperatures, while still including an extended measurement period to capture both SMR and any MMRs caused by spontaneous activity. My study offers an updated method for estimating MMR using intermittent flow respirometry that should improve studies on the intersection of climate change and metabolism and highlights the importance of testing that methods have their intended effect.

Conclusions and Future Perspectives

The major findings of my thesis are:

- The effects of climate change (warming and browning) on body size, number, and resource use of fish varies across habitats (**Paper I, II**).
- Shifts in body size alter habitat use, resource use, and metabolic rates and increased temperatures will likely change ecosystem functioning through its effects on body size. (**Paper I, II, and III**).
- Increased browning will likely change ecosystem functioning through its effects on primary production. Shifts in primary production, favoring the pelagic habitat, alter prey density and distribution, necessitating higher pelagic resource use by all fish. Lower total primary production in brown lakes may reduce maximum body size and fecundity, decreasing total fish abundance (**Paper I, II**).
- In addition to morphology and diet, average SMR differs between littoral and pelagic morphs and should be part of the larger suite of traits examined in studies on polymorphic species (**Paper III**).
- Though using an exhaustive chase to induce MMR is common in intermittent flow respirometry, it underestimates the true MMR compared to placing fish directly in the respirometry chamber (**Paper IV**).

This thesis highlights the importance of intraspecific variation in driving species' responses to climate change. Fish habitat use and morph prevalence appear to reflect changes in resource availability and population size structure. By including this variability instead of focusing on mean population responses, future research can better evaluate how changes at the predator level will radiate through ecosystems.

While **Papers I and II** answer questions regarding how the response to climate change can vary within a population, **Paper III** raises as many questions as it answers and will hopefully prove a jumping-off point for additional research.

Future studies can examine whether differences in SMR between littoral and pelagic morphs are widespread and whether these differences are maintained across lake conditions. To evaluate whether differences in SMR are maintained along an abiotic gradient (productivity, thermal, or water color) and how metabolic differences interact with *in situ* conditions to determine

growth, future studies could incorporate direct measurements of oxygen consumption rate and calculations of growth rates and size-at-age in each habitat. Swedish lakes are also the perfect system to examine whether morph specific metabolic phenotypes are consistent across species because of the frequency of polymorphic species in Swedish lakes.

Since the metabolic divergence in our system occurs across habitats with no distinct barriers to dispersal, perch may also be a good model system for exploring the drivers of the intraspecific difference in metabolism. Future studies can examine whether there is a genetic basis for this variation or whether, like morphology, metabolic rates can respond plastically to habitat use. Existing differences in SMR and the drivers causing this variation have broad implications for morph persistence and habitat stability since the interaction between metabolism and temperature determines resource requirements and top-down pressure in the system. This should make the drivers and consequences of morph-specific metabolic rates an important field of study.

References

- Ask, J., Karlsson, J., Persson, L., Ask, P., Bystrom, P. & Jansson, M. (2009) Terrestrial Organic Matter and Light Penetration: Effects on Bacterial and Primary Production in Lakes. *Limnology and Oceanography* **54**, 2034–2040.
- Ask, J., Karlsson, J. & Jansson, M. (2012) Net Ecosystem Production in Clear-Water and Brown-Water Lakes. *Global Biogeochemical Cycles* **26**, 1–7.
- Atkinson, D. (1994) Temperature and Organism Size—A Biological Law for Ectotherms? In *Advances in Ecological Research* pp. 1–58.
- Auer, S. K., Salin, K., Rudolf, A. M., Anderson, G. J. & Metcalfe, N. B. (2015) The Optimal Combination of Standard Metabolic Rate and Aerobic Scope for Somatic Growth Depends on Food Availability. *Functional Ecology* **29**, 479–486.
- Auer, S. K., Salin, K., Anderson, G. J. & Metcalfe, N. B. (2018) Individuals Exhibit Consistent Differences in Their Metabolic Rates across Changing Thermal Conditions. *Comparative Biochemistry and Physiology -Part A: Molecular and Integrative Physiology* **217**, 1–6.
- Auer, S. K., Solowey, J. R., Rajesh, S. & Rezende, E. L. (2020) Energetic Mechanisms for Coping with Changes in Resource Availability. *Biology Letters* **16**, 20200580.
- Baktoft, H., Jacobsen, L., Skov, C., Koed, A., Jepsen, N., Berg, S., Boel, M., Aarestrup, K. & Svendsen, J. C. (2016) Phenotypic Variation in Metabolism and Morphology Correlating with Animal Swimming Activity in the Wild: Relevance for the OCLTT (Oxygen- and Capacity-Limitation of Thermal Tolerance), Allocation and Performance Models. *Conservation Physiology* **4**.
- Barneche, D. R., Ross Robertson, D., White, C. R. & Marshall, D. J. (2018) Fish Reproductive-Energy Output Increases Disproportionately with Body Size. *Science* **360**, 642–645.
- Bartels, P., Hirsch, P. E., Svanbäck, R. & Eklöv, P. (2012) Water Transparency Drives Intra-Population Divergence in Eurasian Perch (*Perca fluviatilis*). *PLoS ONE* **7**.
- Bartels, P., Hirsch, P. E., Svanbäck, R. & Eklöv, P. (2016) Dissolved Organic Carbon Reduces Habitat Coupling by Top Predators in Lake Ecosystems. *Ecosystems* **19**, 955–967.
- Baustian, M. M., Hansen, G. J. a., de Kluijver, A., Robinson, K., Henry, E. N., Knoll, L. B., Rose, K. C. & Carey, C. C. (2014) Linking the Bottom to the Top in Aquatic Ecosystems: Mechanisms and Stressors of Benthic-Pelagic Coupling. *Eco-DAS X Symposium Proceedings* 25–47.
- Benoît, P. O., Beisner, B. E. & Solomon, C. T. (2016) Growth Rate and Abundance of Common Fishes Is Negatively Related to Dissolved Organic Carbon Concentration in Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **73**, 1230–1236.

- Berglund, J., Müren, U., Båmstedt, U. & Andersson, A. (2007) Efficiency of a Phytoplankton-Based and a Bacterial-Based Food Web in a Pelagic Marine System. *Limnology and Oceanography* **52**, 121–131.
- Bergstrom, C. A., Alba, J. M., Pacheco, J., Fritz, T. & Tamone, S. L. (2019) Polymorphism and Multiple Correlated Characters: Do Flatfish Asymmetry Morphs Also Differ in Swimming Performance and Metabolic Rate? *Ecology and Evolution* **9**, 4772–4782.
- Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D. & Forister, M. L. (2003) The Ecology of Individuals: Incidence and Implications of Individual Specialization. *The American Naturalist* **161**, 1–28.
- Bolnick, D. I., Svanback, R., Araujo, M. S. & Persson, L. (2007) Comparative Support for the Niche Variation Hypothesis That More Generalized Populations Also Are More Heterogeneous. *Proceedings of the National Academy of Sciences* **104**, 10075–10079.
- Bolnick, D. I., Ingram, T., Stutz, W. E., Snowberg, L. K., Lau, O. L. & Pauli, J. S. (2010) Ecological Release from Interspecific Competition Leads to Decoupled Changes in Population and Individual Niche Width. *Proceedings of the Royal Society B: Biological Sciences* **277**, 1789–1797.
- Brown, J. H., Gillooly, J., Allen, A., Savage, V. M. & West, G. (2004) Toward a Metabolic Theory of Ecology. *Ecology* **85**, 1771–1789.
- Burton, T., Killen, S. S., Armstrong, J. D. & Metcalfe, N. B. (2011) What Causes Intraspecific Variation in Resting Metabolic Rate and What Are Its Ecological Consequences? *Proceedings of the Royal Society B: Biological Sciences* **278**, 3465–3473.
- Chabot, D., Steffensen, J. F. & Farrell, A. P. (2016) The Determination of Standard Metabolic Rate in Fishes. *Journal of Fish Biology* **88**, 81–121.
- Chaguaceda, F., Eklöv, P. & Scharnweber, K. (2020) Regulation of Fatty Acid Composition Related to Ontogenetic Changes and Niche Differentiation of a Common Aquatic Consumer. *Oecologia* **193**, 325–336.
- Choudhury, M. I., Urrutia-Cordero, P., Zhang, H., Ekvall, M. K., Medeiros, L. R. & Hansson, L. A. (2019) Charophytes Collapse beyond a Critical Warming and Brownification Threshold in Shallow Lake Systems. *Science of the Total Environment* **661**, 148–154.
- Christensen, E. A. F., Svendsen, M. B. S. & Steffensen, J. F. (2020) The Combined Effect of Body Size and Temperature on Oxygen Consumption Rates and the Size-Dependency of Preferred Temperature in European Perch *Perca fluviatilis*. *Journal of Fish Biology* **97**, 794–803.
- Clark, T. D., Sandblom, E. & Jutfelt, F. (2013) Aerobic Scope Measurements of Fishes in an Era of Climate Change: Respirometry, Relevance and Recommendations. *Journal of Experimental Biology* **216**, 2771–2782.
- Clarke, A. & Johnston, N. M. (1999) Scaling of Metabolic Rate with Body Mass and Temperature in Teleost Fish. *Journal of Animal Ecology* **68**, 893–905.
- Cole, J. J., Carpenter, S. R., Pace, M. L., Van De Bogert, M. C., Kitchell, J. L. & Hodgson, J. R. (2006) Differential Support of Lake Food Webs by Three Types of Terrestrial Organic Carbon. *Ecology Letters* **9**, 558–568.
- Craig, N., Jones, S. E., Weidel, B. C. & Solomon, C. T. (2015) Habitat, Not Resource Availability, Limits Consumer Production in Lake Ecosystems. *Limnology and Oceanography* **60**, 2079–2089.
- Craig, N., Jones, S. E., Weidel, B. C. & Solomon, C. T. (2017) Life History Constraints Explain Negative Relationship between Fish Productivity and Dissolved Organic Carbon in Lakes. *Ecology and Evolution* **7**, 6201–6209.

- Creed, I. F., Bergström, A.-K., Trick, C. G., Grimm, N. B., Hessen, D. O., Karlsson, J., Kidd, K. A., Kritzberg, E., McKnight, D. M., Freeman, E. C., et al. (2018) Global Change-Driven Effects on Dissolved Organic Matter Composition: Implications for Food Webs of Northern Lakes. *Global Change Biology* **24**, 3692–3714.
- Darimont, C. T., Paquet, P. C. & Reimchen, T. E. (2009) Landscape Heterogeneity and Marine Subsidy Generate Extensive Intrapopulation Niche Diversity in a Large Terrestrial Vertebrate. *Journal of Animal Ecology* **78**, 126–133.
- Daufresne, M., Lengfellner, K. & Sommer, U. (2009) Global Warming Benefits the Small in Aquatic Ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 12788–12793.
- Dillon, M. E., Wang, G. & Huey, R. B. (2010) Global Metabolic Impacts of Recent Climate Warming. *Nature* **467**, 704–706.
- van Dorst, R. M., Gårdmark, A., Svanbäck, R., Beier, U., Weyhenmeyer, G. A. & Huss, M. (2019) Warmer and Browner Waters Decrease Fish Biomass Production. *Global Change Biology* **25**, 1395–1408.
- van Dorst, R. M., Gårdmark, A., Svanbäck, R. & Huss, M. (2020) Does Browning-induced Light Limitation Reduce Fish Body Growth through Shifts in Prey Composition or Reduced Foraging Rates? *Freshwater Biology* **65**, 947–959.
- Eklöv, P. (1997) Effects of Habitat Complexity and Prey Abundance on the Spatial and Temporal Distributions of Perch (*Perca Fluviatilis*) and Pike (*Esox Lucius*). *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 1520–1531.
- Eklöv, P. & Diehl, S. (1994) Piscivore Efficiency and Refuging Prey: The Importance of Predator Search Mode. *Oecologia* **98**, 344–353.
- Eliason, E. J., Clark, T. D., Hague, M. J., Hanson, L. M., Gallagher, Z. S., Jeffries, K. M., Gale, M. K., Patterson, D. A., Hinch, S. G. & Farrell, A. P. (2011) Differences in Thermal Tolerance among Sockeye Salmon Populations. *Science* **332**, 109–112.
- Emmrich, M., Pédrón, S., Brucet, S., Winfield, I. J., Jeppesen, E., Volta, P., Argillier, C., Lauridsen, T. L., Holmgren, K., Hesthagen, T., et al. (2014) Geographical Patterns in the Body-Size Structure of European Lake Fish Assemblages along Abiotic and Biotic Gradients. *Journal of Biogeography* **41**, 2221–2233.
- Estlander, S., Nurminen, L., Olin, M., Vinni, M., Immonen, S., Rask, M., Ruuhijärvi, J., Horppila, J. & Lehtonen, H. (2010) Diet Shifts and Food Selection of Perch *Perca Fluviatilis* and Roach *Rutilus Rutilus* in Humic Lakes of Varying Water Colour. *Journal of Fish Biology* **77**, 241–256.
- Faulks, L., Svanbäck, R., Eklöv, P. & Östman, Ö. (2015) Genetic and Morphological Divergence along the Littoral – Pelagic Axis in Two Common and Sympatric Fishes: Perch, *Perca Fluviatilis* (Percidae) and Roach, *Rutilus Rutilus* (Cyprinidae). *Biological Journal of the Linnean Society* **114**, 929–940.
- Finstad, A. G., Helland, I. P., Ugedal, O., Hesthagen, T. & Hessen, D. O. (2014) Unimodal Response of Fish Yield to Dissolved Organic Carbon. *Ecology Letters* **17**, 36–43.
- Fry, F. E. J. (1971) The Effect of Environmental Factors on the Physiology of Fish. In *Fish Physiology* pp. 1–98 Academic Press, Inc.
- Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M. & Charnov, E. L. (2001) Effects of Size and Temperature on Metabolic Rate. *Science* **293**, 2248 LP – 2251.
- Guzzo, M. M., Blanchfield, P. J. & Rennie, M. D. (2017) Behavioral Responses to Annual Temperature Variation Alter the Dominant Energy Pathway, Growth, and Condition of a Cold-Water Predator. *Proceedings of the National Academy of Sciences of the United States of America* **114**, 9912–9917.

- Hammerschlag, N., Schmitz, O. J., Flecker, A. S., Lafferty, K. D., Sih, A., Atwood, T. B., Gallagher, A. J., Irschick, D. J., Skubel, R. & Cooke, S. J. (2019) Ecosystem Function and Services of Aquatic Predators in the Anthropocene. *Trends in Ecology & Evolution* **34**, 369–383.
- Hansson, L.-A., Nicolle, A., Granéli, W., Hallgren, P., Kritzberg, E., Persson, A., Björk, J., Nilsson, P. A. & Brönmark, C. (2013) Food-Chain Length Alters Community Responses to Global Change in Aquatic Systems. *Nature Climate Change* **2**, 1–6.
- Hayden, B., Harrod, C., Thomas, S. M., Eloranta, A. P., Myllykangas, J. P., Siwertsson, A., Præbel, K., Knudsen, R., Amundsen, P. A. & Kahilainen, K. K. (2019) From Clear Lakes to Murky Waters – Tracing the Functional Response of High-Latitude Lake Communities to Concurrent ‘Greening’ and ‘Browning’. *Ecology Letters* **22**, 807–816.
- Hjelm, J., Persson, L. & Christensen, B. (2000) Growth, Morphological Variation and Ontogenetic Niche Shifts in Perch (*Perca fluviatilis*) in Relation to Resource Availability. *Oecologia* **122**, 190–199.
- Holmgren, K., Kinnerback, A., Svensson, J., Sandlund, O. T., Hesthagen, T., Saksgård, R., Sandoy, S. & Poikane, S. (2018) *Intercalibration of the National Classification of Ecological Status for Northern Lakes: Biological Quality Element: Fish Fauna, ERU 29335 EN*. Luxembourg.
- Hulbert, A. J. & Else, P. L. (2000) Mechanisms Underlying the Cost of Living in Animals. *Annual Review of Physiology* **62**, 207–235.
- Huss, M., Lindmark, M., Jacobson, P., van Dorst, R. M. & Gårdmark, A. (2019) Experimental Evidence of Gradual Size-Dependent Shifts in Body Size and Growth of Fish in Response to Warming. *Global Change Biology* **25**, 2285–2295.
- Jackson, A. L., Inger, R., Parnell, A. C. & Bearhop, S. (2011) Comparing Isotopic Niche Widths among and within Communities: SIBER - Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology* **80**, 595–602.
- Jane, S. F., Hansen, G. J. A., Kraemer, B. M., Leavitt, P. R., Mincer, J. L., North, R. L., Pilla, R. M., Stetler, J. T., Williamson, C. E., Woolway, R. I., et al. (2021) Widespread Deoxygenation of Temperate Lakes. *Nature* **594**, 66–70.
- Jensen, D. L., Overgaard, J., Wang, T., Gesser, H. & Malte, H. (2017) Temperature Effects on Aerobic Scope and Cardiac Performance of European Perch (*Perca fluviatilis*). *Journal of Thermal Biology* **68**, 162–169.
- Jeppesen, E., Meerhoff, M., Holmgren, K., González-Bergonzoni, I., Teixeira-de Mello, F., Declerck, S. A. J., De Meester, L., Søndergaard, M., Lauridsen, T. L., Bjerring, R., et al. (2010) Impacts of Climate Warming on Lake Fish Community Structure and Potential Effects on Ecosystem Function. *Hydrobiologia* **646**, 73–90.
- Kahilainen, K. K., Patterson, W. P., Sonninen, E., Harrod, C. & Kiljunen, M. (2014) Adaptive Radiation along a Thermal Gradient: Preliminary Results of Habitat Use and Respiration Rate Divergence among Whitefish Morphs. *PLoS ONE* **9**.
- Karås, P. & Thoresson, G. (1992) An Application of a Bioenergetics Model to Eurasian Perch. *Journal of Fish Biology* **41**, 217–230.
- Karlson, A. M. L., Gorokhova, E. & Elmgren, R. (2015) Do Deposit-Feeders Compete? Isotopic Niche Analysis of an Invasion in a Species-Poor System. *Scientific Reports* **5**, 1–8.
- Karlsson, J., Byström, P., Ask, J., Persson, L. & Jansson, M. (2009) Light Limitation of Nutrient-Poor Lake Ecosystems. *Nature* **460**, 506–509.

- Karlsson, J., Bergström, A.-K., Byström, P., Gudas, C., Rodríguez, P. & Hein, C. (2015) Terrestrial Organic Matter Input Suppresses Biomass Production in Lake Ecosystems. *Ecology* **96**, 2870–2876.
- Kelly, P. T., Solomon, C. T., Weidel, B. C. & Jones, S. E. (2014) Terrestrial Carbon Is a Resource, but Not a Subsidy, for Lake Zooplankton. *Ecology* **95**, 1236–1242.
- Killen, S. S., Glazier, D. S., Rezende, E. L., Clark, T. D., Atkinson, D., Willener, A. S. T. & Halsey, L. G. (2016) Ecological Influences and Morphological Correlates of Resting and Maximal Metabolic Rates across Teleost Fish Species. *The American Naturalist* **187**, 592–606.
- Killen, S. S., Norin, T. & Halsey, L. G. (2017) Do Method and Species Lifestyle Affect Measures of Maximum Metabolic Rate in Fishes? *Journal of Fish Biology* **90**, 1037–1046.
- Kritzbeg, E. S., Hasselquist, E. M., Škerlep, M., Löfgren, S., Olsson, O., Stadmark, J., Valinia, S., Hansson, L.-A. & Laudon, H. (2020) Browning of Freshwaters: Consequences to Ecosystem Services, Underlying Drivers, and Potential Mitigation Measures. *Ambio* **49**, 375–390.
- Larsen, S., Andersen, T. & Hessen, D. O. (2011) Climate Change Predicted to Cause Severe Increase of Organic Carbon in Lakes. *Global Change Biology* **17**, 1186–1192.
- Layman, C. A., Quattrochi, J. P., Peyer, C. M. & Allgeier, J. E. (2007) Niche Width Collapse in a Resilient Top Predator Following Ecosystem Fragmentation. *Ecology Letters* **10**, 937–944.
- Leech, D. M., Clift, T. L., Littlefield, J. L., Ravagli, N. R. & Spain, J. E. (2021) Indirect versus Direct Effects of Freshwater Browning on Larval Fish Foraging. *Canadian Journal of Fisheries and Aquatic Sciences*.
- Lester, N. P., Shuter, B. J. & Abrams, P. A. (2004) Interpreting the von Bertalanffy Model of Somatic Growth in Fishes: The Cost of Reproduction. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **271**, 1625–1631.
- Lindmark, M., Huss, M., Ohlberger, J. & Gårdmark, A. (2017) Temperature-Dependent Body Size Effects Determine Population Responses to Climate Warming. *Ecology Letters* 181–189.
- Lindmark, M., Ohlberger, J. & Gårdmark, A. (2021) Preprint: Optimum Growth Temperature Declines with Body Size within Fish Species. <https://doi.org/10.1101/2021.01.21.427580> **46**.
- Little, A. G., Loughland, I. & Seebacher, F. (2020) What Do Warming Waters Mean for Fish Physiology and Fisheries? *Journal of Fish Biology* 328–340.
- Marklund, M. H. K., Svanbäck, R., Faulks, L., Breed, M. F., Scharnweber, K., Zha, Y. & Eklöv, P. (2019) Asymmetrical Habitat Coupling of an Aquatic Predator—The Importance of Individual Specialization. *Ecology and Evolution* **9**, 3405–3415.
- McCann, K. S., Rasmussen, J. B. & Umbanhowar, J. (2005) The Dynamics of Spatially Coupled Food Webs. *Ecology Letters* **8**, 513–523.
- Meerhoff, M., Teixeira-de Mello, F., Kruk, C., Alonso, C., González-Bergonzoni, I., Pacheco, J. P., Lacerot, G., Arim, M., Beklioglu, M., Brucet, S., et al. (2012) *Environmental Warming in Shallow Lakes. A Review of Potential Changes in Community Structure as Evidenced from Space-for-Time Substitution Approaches*. Vol. 46.
- Mélard, C., Kestemont, P. & Grignard, J. C. (1996) Intensive Culture of Juvenile and Adult Eurasian Perch (*P. fluviatilis*): Effect of Major Biotic and Abiotic Factors on Growth. *Journal of Applied Ichthyology* **12**, 175–180.

- New, M., Lister, D., Hulme, M. & Makin, I. (2002) A High-Resolution Data Set of Surface Climate over Global Land Areas. *Climate Research* **21**, 1–25.
- Norin, T. & Clark, T. D. (2016) Measurement and Relevance of Maximum Metabolic Rate in Fishes. *Journal of Fish Biology* **88**, 122–151.
- O'Reilly, C. M., Sharma, S., Gray, D. K., Hampton, S. E., Read, J. S., Rowley, R. J., Schneider, P., Lenters, J. D., McIntyre, P. B., Kraemer, B. M., et al. (2015) Rapid and Highly Variable Warming of Lake Surface Waters around the Globe. *Geophysical Research Letters* **42**.
- Ohlberger, J. (2013) Climate Warming and Ectotherm Body Size - from Individual Physiology to Community Ecology. *Functional Ecology* **27**, 991–1001.
- Ohlberger, J., Edeline, E., Vøllestad, L. A., Stenseth, N. C. & Claessen, D. (2011) Temperature-Driven Regime Shifts in the Dynamics of Size-Structured Populations. *The American naturalist* **177**, 211–233.
- Persson L. (1987) The Effects of Resource Availability and Distribution on Size Class Interactions in Perch, *Perca fluviatilis*. *Oikos* **48**, 148–160.
- Persson, L. (1988) Asymmetries in Competitive and Predatory Interactions in Fish Populations. In *Size-structured populations*. (Ebenman, D., Persson, D., eds), pp. 203–218 Berlin: Springer.
- Persson, L. (1993) Predator-Mediated Competition in Prey Refuges: The Importance of Habitat Dependent Prey Resources. *Oikos* **68**, 12–22.
- Pilakouta, N., Killen, S. S., Kristjánsson, B. K., Skúlason, S., Lindström, J., Metcalfe, N. B. & Parsons, K. J. (2020) Multigenerational Exposure to Elevated Temperatures Leads to a Reduction in Standard Metabolic Rate in the Wild. *Functional Ecology* **34**, 1205–1214.
- Pilla, R. M., Williamson, C. E., Adamovich, B. V., Adrian, R., Anneville, O., Chandra, S., Colom-Montero, W., Devlin, S. P., Dix, M. A., Dokulil, M. T., et al. (2020) Deeper Waters Are Changing Less Consistently than Surface Waters in a Global Analysis of 102 Lakes. *Scientific Reports* **10**, 1–15.
- Pörtner, H. & Farrell, A. P. (2008) Physiology and Climate Change. *Science* **322**, 690–692.
- Quevedo, M., Svanbäck, R. & Eklöv, P. (2009) Intrapopulation Niche Partitioning in a Generalist Predator Limits Food Web Connectivity. *Ecology* **90**, 2263–2274.
- R Core Team. (2019) R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing 2019.
- Ranåker, L., Persson, J., Jönsson, M., Nilsson, P. A. & Brönmark, C. (2014) Piscivore-Prey Fish Interactions: Mechanisms behind Diurnal Patterns in Prey Selectivity in Brown and Clear Water. *PLoS ONE* **9**, 1–8.
- Rennie, M. D. & Jackson, L. J. (2005) The Influence of Habitat Complexity on Littoral Invertebrate Distributions: Patterns Differ in Shallow Prairie Lakes with and without Fish. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 2088–2099.
- Robinson, B. W. & Wilson, D. S. (1994) Character Release and Displacement in Fishes: A Neglected Literature. *The American Naturalist* **144**, 596–627.
- Rooney, N., McCann, K., Gellner, G. & Moore, J. C. (2006) Structural Asymmetry and the Stability of Diverse Food Webs. *Nature* **442**, 265–269.
- Rosenfeld, J., Van Leeuwen, T., Richards, J. & Allen, D. (2015) Relationship between Growth and Standard Metabolic Rate: Measurement Artefacts and Implications for Habitat Use and Life-History Adaptation in Salmonids. *Journal of Animal Ecology* **84**, 4–20.
- Rummer, J. L., Binning, S. A., Roche, D. G. & Johansen, J. L. (2016) Methods Matter: Considering Locomotory Mode and Respirometry Technique When Estimating Metabolic Rates of Fishes. *Conservation Physiology* **4**, 1–13.

- Sandblom, E., Clark, T. D., Gräns, A., Ekström, A., Brijs, J., Sundström, L. F., Odelström, A., Adill, A., Aho, T. & Jutfelt, F. (2016) Physiological Constraints to Climate Warming in Fish Follow Principles of Plastic Floors and Concrete Ceilings. *Nature Communications* **7**, 1–8.
- Sandersfeld, T., Mark, F. C. & Knust, R. (2016) Temperature-Dependent Metabolism in Antarctic Fish: Do Habitat Temperature Conditions Affect Thermal Tolerance Ranges? *Polar Biology* **40**, 1–9.
- Scharnweber, K., Strandberg, U., Marklund, M. H. K. & Eklöv, P. (2016a) Combining Resource Use Assessment Techniques Reveals Trade - Offs in Trophic Specialization of Polymorphic Perch. *Ecosphere* **7**, 1–20.
- Scharnweber, K., Strandberg, U., Karlsson, K. & Eklöv, P. (2016b) Decrease of Population Divergence in Eurasian Perch (*Perca fluviatilis*) in Browning Waters: Role of Fatty Acids and Foraging Efficiency. *PLOS ONE* **11**, e0162470.
- Schindler, D. E. & Scheuerell, M. D. (2002) Habitat Coupling in Lake Ecosystems. *Oikos* **98**, 177–189.
- Schindler, D. E., Scheuerell, M. D., Moore, J. W., Gende, S. M., Francis, T. B. & Palen, W. J. (2003) Pacific Salmon and the Ecology of Coastal Ecosystems. *Frontiers in Ecology and the Environment* **1**, 31.
- Seekell, D. A., Lapierre, J.-F., Pace, M. L., Gudas, C., Sobek, S. & Tranvik, L. (2014) Regional-Scale Variation of Dissolved Organic Carbon Concentrations in Swedish Lakes. *Limnology and Oceanography* **59**, 1612–1620.
- Seekell, D. A., Byström, P. & Karlsson, J. (2018) Lake Morphometry Moderates the Relationship between Water Color and Fish Biomass in Small Boreal Lakes. *Limnology and Oceanography* **63**, 2171–2178.
- Seibel, B. A. & Drazen, J. C. (2007) The Rate of Metabolism in Marine Animals: Environmental Constraints, Ecological Demands and Energetic Opportunities. *Philosophical Transactions of the Royal Society B: Biological Sciences* **362**, 2061–2078.
- Sjödin, H., Ripa, J. & Lundberg, P. (2018) Principles of Niche Expansion. *Proceedings of the Royal Society B: Biological Sciences* **285**.
- Skoglund, S., Siwertsson, A., Amundsen, P. A. & Knudsen, R. (2015) Morphological Divergence between Three Arctic Charr Morphs - the Significance of the Deep-Water Environment. *Ecology and Evolution* **5**, 3114–3129.
- Skúlason, S. & Smith, T. B. (1995) Resource Polymorphisms in Vertebrates. *Trends in Ecology & Evolution* **10**, 366–370.
- Skúlason, S., Parsons, K. J., Svanbäck, R., Räsänen, K., Ferguson, M. M., Adams, C. E., Amundsen, P. A., Bartels, P., Bean, C. W., Boughman, J. W., et al. (2019) A Way Forward with Eco Evo Devo: An Extended Theory of Resource Polymorphism with Postglacial Fishes as Model Systems. *Biological Reviews* **94**, 1786–1808.
- Smith, T. B. & Skúlason, S. (1996) Evolutionary Significance of Resource Polymorphisms in Fishes, Amphibians, and Birds. *Annual Review of Ecology and Systematics* **27**, 111–133.
- Song, J., Brill, R. W. & McDowell, J. R. (2019) Plasticity in Standard and Maximum Aerobic Metabolic Rates in Two Populations of an Estuarine Dependent Teleost, Spotted Seatrout (*Cynoscion nebulosus*). *Biology* **8**, 46.
- Stasko, A. D., Gunn, J. M. & Johnston, T. A. (2012) Role of Ambient Light in Structuring North-Temperate Fish Communities: Potential Effects of Increasing Dissolved Organic Carbon Concentration with a Changing Climate. *Environmental Reviews* **20**, 173–190.

- Svanbäck, R. & Eklöv, P. (2002) Effects of Habitat and Food Resources on Morphology and Ontogenetic Growth Trajectories in Perch. *Oecologia* **131**, 61–70.
- Svanbäck, R. & Eklöv, P. (2003) Morphology Dependent Foraging Efficiency in Perch: A Trade-off for Ecological Specialization? *Oikos* **102**, 273–284.
- Svanbäck, R. & Eklöv, P. (2006) Genetic Variation and Phenotypic Plasticity: Causes of Morphological and Dietary Variation in Eurasian Perch. *Evolutionary Ecology Research* **8**, 37–49.
- Svanbäck, R. & Bolnick, D. I. (2007) Intraspecific Competition Drives Increased Resource Use Diversity within a Natural Population. *Proceedings of the Royal Society B: Biological Sciences* **274**, 839–844.
- Svanbäck, R., Eklöv, P., Fransson, R. & Holmgren, K. (2008) Intraspecific Competition Drives Multiple Species Resource Polymorphism in Fish Communities. *Oikos* **117**, 114–124.
- Svanbäck, R., Quevedo, M., Olsson, J. & Eklöv, P. (2015) Individuals in Food Webs: The Relationships between Trophic Position, Omnivory and among-Individual Diet Variation. *Oecologia* **178**, 103–114.
- Svendsen, M. B. S., Bushnell, P. G. & Steffensen, J. F. (2016) Design and Setup of Intermittent-Flow Respirometry System for Aquatic Organisms. *Journal of Fish Biology* **88**, 26–50.
- Tait, L. W. & Schiel, D. R. (2013) Impacts of Temperature on Primary Productivity and Respiration in Naturally Structured Macroalgal Assemblages. *PLoS ONE* **8**, 1–10.
- Tunney, T. D., McCann, K. S., Jarvis, L., Lester, N. P. & Shuter, B. J. (2018) Blinded by the Light? Nearshore Energy Pathway Coupling and Relative Predator Biomass Increase with Reduced Water Transparency across Lakes. *Oecologia* **186**, 1031–1041.
- Vasconcelos, F. R., Diehl, S., Rodriguez, P., Hedström, P., Karlsson, J. & Byström, P. (2016) Asymmetrical Competition between Aquatic Primary Producers in a Warmer and Browner World. *Ecology* **97**, 2580–2592.
- Vasconcelos, F. R., Diehl, S., Rodríguez, P., Hedström, P., Karlsson, J. & Byström, P. (2019) Bottom-up and Top-down Effects of Browning and Warming on Shallow Lake Food Webs. *Global Change Biology* **25**, 504–521.
- Webb, P. W. (1984) Form and Function in Fish Swimming. *Scientific American* **251**, 72–82.
- Williamson, C. E., Stemberger, R. S., Morris, D. P., Frost, T. M. & Paulsen, S. G. (1996) Ultraviolet Radiation in North American Lakes: Attenuation Estimates from DOC Measurements and Implications for Plankton Communities. *Limnology and Oceanography* **41**, 1024–1034.
- Woodward, G., Perkins, D. M. & Brown, L. E. (2010) Climate Change and Freshwater Ecosystems: Impacts across Multiple Levels of Organization. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 2093–2106.
- Woolway, R. I., Weyhenmeyer, G. A., Schmid, M., Dokulil, M. T., de Eyto, E., Maberly, S. C., May, L. & Merchant, C. J. (2019) Substantial Increase in Minimum Lake Surface Temperatures under Climate Change. *Climatic Change* **155**, 81–94.
- Zhang, Y., Gilbert, M. J. H. & Farrell, A. P. (2020) Measuring Maximum Oxygen Uptake with an Incremental Swimming Test and by Chasing Rainbow Trout to Exhaustion inside a Respirometry Chamber Yields the Same Results. *Journal of Fish Biology* **97**, 28–38.

Popular summary

Lake environments are highly variable, and the animals living within them are adapted to take advantage of this variation. Individual fish of the same species vary in body shape, diet, metabolism, and behavior, and these traits will change over the course of their lifetime. Variation in traits often correspond with the major division within lakes, between littoral (well-lit shallow) and pelagic (off-shore deeper open-water) habitats. These habitats differ in energy source (algae growing on the sediment vs. in the open water), physical structure (dense vegetation vs. open water), and types of prey (macroinvertebrates vs. zooplankton).

European perch (my study species) preferentially live along the shoreline. They are better competitors in these vegetated areas than other common fish species and the structure also serves as protection from large predators. When the perch population grows and competition for resources increases, some individuals move off-shore and feed mostly on zooplankton, resulting in two groups of perch - littoral and pelagic. Many studies don't differentiate between fish caught in both habitats losing valuable information. I examine them separately to better understand how fish in each habitat will be impacted by climate change and how this will translate to changes in ecosystem function. In my studies I classify fish based on catch location, referring to fish caught in the shallow littoral zone as 'littoral perch', and fish caught in the deeper pelagic zone as 'pelagic perch'.

In the northern hemisphere, climate change is making lakes warmer and browner. My goal was to examine how these changes in water color and temperature impact the size, number, and diet of perch living in littoral compared to pelagic habitats. Brown lakes are the result of high dissolved organic carbon (DOC) concentrations in the water. DOC increases when changes in temperature or precipitation increase the amount of water running through the soil. Carbon is leached from the soil and flows into lakes, turning them tea-colored. Light penetration is reduced in browner lakes, decreasing plant and algae growth in the littoral habitat and thus reducing the food and shelter available to littoral fish. In browner lakes the open water habitat can become more productive as the nutrients previously used by algae along the shoreline become available for pelagic phytoplankton growth.

My research showed that in clear lakes where abundant sunlight reaches the bottom, littoral and pelagic perch live and feed primarily in their respective

habitats, but both incorporate littoral prey into their diets. As lakes become browner, fish from both habitats begin to feed more in the open water. There is a decrease in the total amount of perch caught in brown lakes. This is because of a decrease in the number of perch living along the shoreline, likely caused by food limitation. Less food also means that the largest individuals in brown lakes are much smaller than the largest individuals in clear lakes. Small fish have disproportionally fewer offspring, and this may also contribute to the smaller number of perch caught in brown lakes. These multifaceted changes in populations will impact ecosystem functioning by altering the top-down pressure and energy flow within lakes.

Increases in water temperature can change many aspects of the lake ecosystem, but the focus of this research is the effect of temperature on fish themselves. Fish are ectotherms, meaning that as temperatures increase, their metabolic rate increases. Metabolic rate determines how much food individuals need to survive, as well as how fast they can grow given unlimited food. At high temperatures, juvenile fish grow quickly. But they mature earlier and at a smaller size than fish raised at low temperatures. Adults use the majority of their energy to reproduce, so the size at which they reach maturity determines the average size of individuals in the population. This difference in growth means that fish in cold lakes are larger on average than fish in warm lakes. Small fish can also outcompete large fish at high temperatures because they need less food to survive. This combination of factors is projected to lead to populations made up of smaller and younger fish in warm lakes. I found that littoral perch followed this pattern and were smaller in lakes with higher temperatures. Pelagic perch however, showed no change in average size and unexpectedly, the number of them increased. A likely cause of this pattern is increased competition. As fish become smaller on average, more will compete for prey of the same size, and part of the population then moves offshore to feed in the open water instead where competition is lower. The shift in distribution of perch between habitats increases the top-down pressure on zooplankton which is a major part of the pelagic perch diet and changes the flow of energy within lakes.

Metabolism is a central part of many climate change studies because it determines fish growth and increases with temperature. It also varies widely between individuals, even when fish are of the same size and tested at the same temperature. I chose to examine whether there are differences in metabolic rates between littoral and pelagic perch since it may shape their response to climate change. I tested for differences between the groups and tested whether differences were related to diet or body shape. I found that pelagic perch have higher metabolic rates than littoral perch. When there is enough prey, pelagic perch can grow faster than littoral perch, but at high temperatures they may be less competitive, if their energy needs surpass the amount of food available. I didn't find an effect of body shape or diet on metabolism, meaning that future studies should examine what is causing the differences I observed.

Since metabolism is so fundamental to studies on how climate change will impact fish, I also tested how well the most common method for measuring metabolic rates works. I found that the current practice of chasing fish in a circle for 3-minutes and then placing them in a respirometer is accurately estimating the minimum metabolic rate, but that it underestimates the maximum. A better option is to put fish directly into the respirometer, and leave them there for up to 24 hours. They often spontaneously reach maximum oxygen consumption during this time, or researchers can induce a stress response and consequently maximum oxygen consumption, by lightly tapping on the respirometry chambers. The overnight period also allows for fish to reach a calm and inactive state for measurements of minimal oxygen consumption.

The conclusion of my thesis is that, in order to see what is happening to populations, habitats should be examined separately. Perch caught in different lake habitats have different energy requirements and show different responses to warming and browning. These differences will affect where, what, and how much fish eat, impacting their prey and how the greater ecosystem functions. While ecologists will be interested in the scientific implications of altered ecosystem functioning, my results are also important for conservation efforts that aim to maintain biodiversity and protect lakes for recreational use and commercial fisheries.

Sammanfattning på Svenska

Det finns en stor miljövariation i sjöar som ger stora möjligheter till djurs anpassningsmöjligheter. Individer av samma art varierar i kroppsform, val av föda, ämnesomsättning och beteende vilket är egenskaper som förändras under deras livstid. En viktig indelning av sjöars livsmiljöer är den som kallas *strandnära vegetation* och *öppet vatten*. Dessa livsmiljöer skiljer sig åt beträffande energikällor (alger som växer på sedimentet eller i öppet vatten), struktur (tät vegetation eller öppet vatten) och typer av byten som fiskar lever av (stora evertebrater eller djurplankton).

I min forskning använder jag abborre som modellart för att förstå klimatförändringars effekter på fiskpopulationer. Den lever företrädesvis i strandnära vegetation. Arten är bättre än andra fiskar på att konkurrera i den livsmiljön och vegetationen där fungerar som skydd mot stora rovdjur. När abborrbeståndet växer och konkurrensen ökar, rör sig vissa individer ut till öppet vatten och livnär sig då i huvudsak på djurplankton. Det resulterar i två grupper – den litorala (strandnära) och den pelagiska (öppet vatten) abborren. I min forskning bestämmer jag vilken grupp varje fisk hör till baserad på där de fångades.

Många studier kombinerar fisk från olika livsmiljöer, men genom att undersöka fisk från varje livsmiljö var för sig, kan jag bättre förstå hur hela sjöekosystemet påverkas av klimatförändringar.

Klimatförändringarna på norra halvklotet gör sjöar brunare och varmare.

Målet med mina studier är att undersöka hur förändringar av vattnets färg och temperatur påverkar storlek, antal och föda för abborrar som lever i de litorala respektive pelagiska livsmiljöerna. Brunare vatten är resultatet av att löst organiskt kol följer med den ökade mängden nederbörd som sipprar genom jorden. Organiskt kol som vittrar från löv och växtdelar faller ut i sjöar och gör dem tefärgade. Eftersom det är svårare för ljuset att tränga igenom brunt vatten, minskar tillväxten av alger och växter i strandnära livsmiljöer, och därmed minskar mängden mat och skydd för fiskar som lever där. I brunare vatten tas mindre näring upp av bottenlevande alger. Denna näring blir då mera tillgänglig för pelagiska växtplankton. Livsmiljön i öppet vatten kan därmed producera mer växtplankton när näringen där ökar. Min forskning visar att i sjöar med klarare vatten äter de fiskar som fångas i den strandnära vegetationen varierande föda, som exempelvis djurplankton och bottendjur. Fisk som fångas i öppet vatten äter i huvudsak djurplankton. När sjöar blir

brunare börjar både litoral och pelagisk abborre att förlita sig mer på pelagisk föda. Man ser också att de abborrar som fångas vid stranden blir mindre, möjligen på grund av matbrist. I bruna sjöar försvinner andelen riktigt stora fiskar, och eftersom små fiskar har färre avkomor i förhållande till storlek, kan detta vara en förklaring till färre abborrar i bruna sjöar. De många olika förändringar hos fiskpopulationer som jag har observerat kommer att påverka ekosystemets funktion genom att förändra rovfiskars effekter på andra arter och energiflöden inom ekosystemet.

Ökning av vattentemperaturen kan påverka ekosystemet på många olika sätt, och fokus för min forskning är effekten på fisk. Fisk är ektotermer, vilket betyder att när temperaturen stiger ökar även deras kroppstemperatur och därmed deras ämnesomsättning. Förutsatt att de har tillräckligt med mat växer ungfisk snabbare vid höga temperaturer. De blir också könsmogna tidigare, och eftersom den största mängden energi hos könsmogna fiskar används för reproduktion, är vuxna fiskar i varma sjöar i genomsnitt mindre än vuxna fiskar i kalla sjöar.

Små fiskar kan också konkurrera ut stora fiskar vid höga temperaturer eftersom stora fiskar behöver mer energi för att växa. Sammantaget beräknas detta leda till populationer av mindre och yngre fisk när sjötemperaturen stiger. Jag fann att litorala abborrar minskade i storlek när temperaturen ökade, medan pelagiska abborrar inte förändrades. Antalet pelagiska abborrar ökade dock. En trolig orsak är att fiskar av samma storlek konkurrerar med varandra om byten av samma storlek. När det blir brist på mat i strandnära livsmiljö tvingas några av dem att byta livsmiljö till öppet vattnet.

Ämnesomsättningen avgör hur mycket mat en fisk behöver för att överleva och hur snabbt den kommer att växa, och eftersom den ökar med temperaturen är den en central del i många studier av klimatförändringar. Ämnesomsättningen varierar kraftigt mellan individer, även för de som är lika stora och är testade vid samma temperatur. Eftersom litoral och pelagisk abborre skiljer sig åt i val av livsmiljö, kroppsform och mat, valde jag också att undersöka om någon av dessa faktorer påverkar ämnesomsättningen. Jag fann att pelagisk abborre har högre ämnesomsättning än litoral abborre. Det betyder att, när det finns tillräckligt med byte kan den växa snabbare än litoral abborre, men vid höga temperaturer kan den vara mindre konkurrenskraftig. Jag hittade ingen effekt som berodde på kroppsform eller matval, vilket betyder att skillnaderna har andra orsaker.

Eftersom ämnesomsättningen är grundläggande för studier om hur klimatförändringar kommer att påverka fisk, testade jag också hur väl den vanligaste metoden för att mäta ämnesomsättning fungerar. Ett centralt mått är den maximala ämnesomsättningshastigheten där den nuvarande praxisen för detta mått är att i tre minuter jaga runt en fisk i en behållare och sedan att placera den i en respirometer som mäter syreåtgång. Metoden visade sig fungera bra för att mäta lägsta nivån på ämnesomsättning, men visade också att den underskattar maxvärdet. Ett bättre alternativ visade sig vara att placera fisken direkt i

respirometern och mäta syreatgången under 24 timmar. På det sättet når fiskarna ofta spontant maximal syreförbrukning. En alternativ metod hade varit att framkalla en stressrespons genom att knacka lätt på respirometern.

Den slutsats som kan dras av min avhandling är att det är viktigt att undersöka fiskar från olika livsmiljöer för att kunna dra slutsatser om klimatförändringars effekter på hela sjöekosystem. Abborrar som fångas i olika sjömiljöer har olika behov av energi och uppvisar olika reaktioner på uppvärmning och brunare av vatten. Dessa skillnader kommer att påverka var, vad och hur mycket fisken äter, vilket i sin tur påverkar deras byten och hela ekosystemets funktion. Medan ekologer är intresserade av den vetenskapliga innebörden av förändringar i ekosystemfunktion så är mina resultat också viktiga för bevarandebiologiska aspekter, för att bibehålla biodiversitet och bevara sjöar för rekreation och kommersiellt fiske.

Acknowledgements

There are so many people I want to thank and who helped me reach the point where I'm writing an acknowledgements section for my PhD thesis.

First and foremost are my supervisors, Peter and Kristin. Thank you for supporting me through all of the ups and downs over the past 5 years, I don't think that any of us could have predicted everything that happened. I am so grateful for all of the interesting discussions, encouragement, and willingness to give edits when I send you an e-mail saying "here is my introduction, I hate it, please help."

Thank you to Kasparas, Leonie, and Robin for your hard work in the lab and field. And to Holger, if it weren't for you I would have been "angling at dawn" in the middle of the lake with an earthworm on a hook and would have caught 3 perch not 300. Thank you also to Fredrik for letting me recruit you for my pet project and turning it into a great study. My research is stronger because of your collaboration.

Thank you also to all of the seniors at Limno for creating a fun and welcoming work environment and for always asking interesting questions at seminars forcing me to think about my research in different ways. Thank you especially to Eva for always answering my questions when I barged into your office and to Dolly for absolutely everything. Thank you to Göran, David and Elisabeth for all of your patience. I hope my analyses make you proud (or at the very least don't make you cringe).

Thank you to my fellow PhD students. For the discussions about research and the discussions about absolutely everything other than research. Thank you especially to Marloes for the adventures, Annika for sharing your mushroom spot (ultimate act of Swedish friendship), Anna N. for being a calm and collected PhD role model, Xavi for the extensive discussions about food, Fabian for the good-natured arguments, Karolina for your enthusiasm, Lorena for all the pandemic lunches, Theresa for planning everything and always having time to chat, and Fernando for the help on all things fish related. Thank you also to my officemates, Ana A., Katrin, Alina, and Elizabeth for your friendship and not kicking me and my very messy desk out of the office. Thank you also to all the bachelors students, masters students, post docs, field assistants and everyone else who passed through Limno in the past 5 years.

Thank you to Albin and Stella (who get their own section) for the amazing cover design for my book. My thesis title may say ‘Fish’ but the cover art will make sure everyone knows that this thesis is all perch, all the time.

Thank you to everyone from Lund; Anders, Christer, Kaj, and Jerker for getting me started on this journey and Emma for being my role model as a teacher, I hope my students learned half as much from me as I learned from you. Thank you to Martin and Mariana for being my first friends in Sweden and for all the amazing trips we have taken, I hope they continue in the future.

Thank you to my community in Uppsala. To Malin and Lisen for being great roommates. To Cissi, Madde, and Tove, for the dinners, and hikes, and pandemic walks and making Uppsala my home. To MESAICOS and HULK, especially Frank, Vijith, Justine, and Chris, for being such an amazing group of people and being a source of endorphins even in the depths of Swedish winter. To my counterpart at SLU, Renee thank you for your friendship and party invites and letting me bounce warming and browning ideas off of you. To Max and Philip, I would travel across the world to hang out at a conference with you anytime (even though we only live an hour apart in real life). Thank you to Katie, for the baked goods and outings and for convincing Luca that you two should adopt me. And to Zala, Jorge, Theo, Matt and Moa, I wouldn’t have made it through this really difficult year without you.

Lastly, thank you to my family, Per, Andie, Hanna, Sven, Stella, and all of the Anderssons and Forssells who have been my relentless cheerleaders for the past five years, and to my mom for taking me to the tidepools enough that they are my scientist origin story. Special shout out to Hanna for telling me I am now an expert in my field every time I talk to her, you almost have me convinced. Thank you to my high school and college friends, you are all brilliant and supportive and inspiring, I made it this far by just by trying to keep up with all of you. A special thank you to Chelsea for the recipes and political commentary and constant communication that makes me feel loved wherever I am in the world. Thank you to my friends from Tahoe who always make me feel missed by asking when I am moving home and to Kat for trying to convince me to stay. And finally, thank you to Nate for convincing me a PhD was a good idea and to Bray for the advice to look back periodically at how far I’ve come.

Acta Universitatis Upsaliensis

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