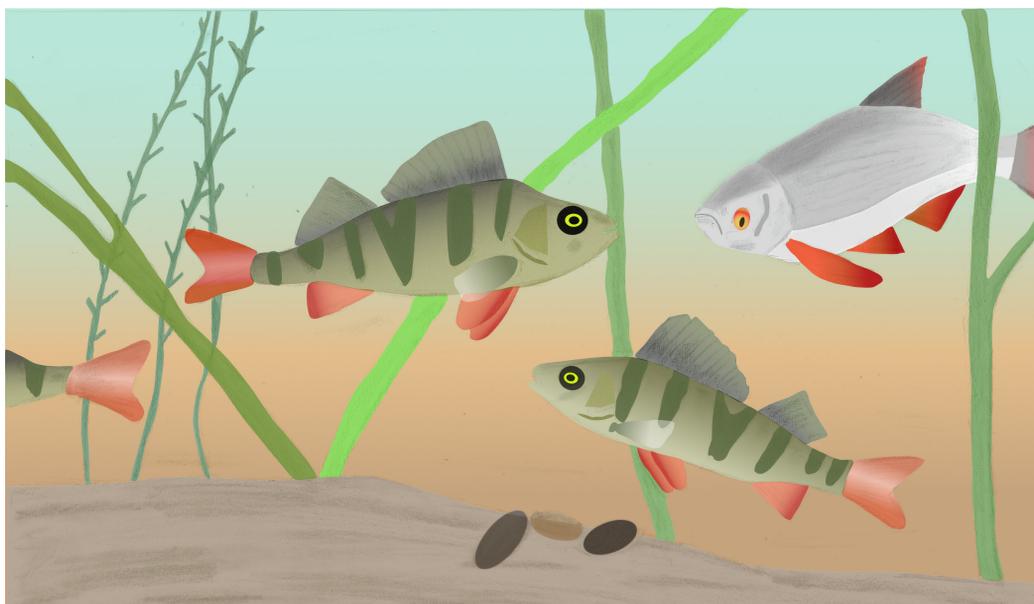




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Warmer and browner waters: fish responses vary with size, sex, and species

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Abstract

Current understanding of fish population responses to climate change is often limited to studies on the effect of temperature, ignoring potential co-occurring changes in other environmental variables. However, next to getting warmer, temperate and boreal aquatic systems are getting browner due to increased concentrations of dissolved organic carbon. Studies also generally predict mean population responses to climate change, thereby ignoring the potential for size, sex, and also species-specific responses.

In this thesis, I aim to study the effects of warmer and browner waters on individual and population level responses in fish, and investigate if these responses vary with size, sex, and between species (Eurasian perch, *Perca fluviatilis* or common roach, *Rutilus rutilus*). To do this I used multiple methods, including space-for-time analyses, a whole-ecosystem warming experiment, and aquaria and mesocosm experiments.

I found that both warming and browning of lakes will likely decrease fish biomass production. Warming may cause a shift in size-structure towards smaller perch individuals and a lower perch population biomass, while browning will likely affect perch biomass production through lower body growth. Body growth responses to warming likely depend on body size, as small but not large individuals in my study were positively affected by high temperatures, and also sex, as males were more negatively affected by warming than females. Responses to browning may vary with body size and between species, as I found browning had a stronger negative effect on body growth of larger individuals in perch, while in roach browning only affected very small individuals.

Overall, my findings suggest that future warming and browning will negatively affect fish individuals and populations, but that responses will vary with size, sex, and species, with potential consequences for ecological interactions and ecosystem functioning. This thesis highlights the importance of considering multiple climate stressors, integrating responses across several levels of biological organization, and acknowledging within- and between species variation, in order to understand and predict fish population responses to further climate change.

Keywords: climate change, warming, browning, lakes, body growth, biomass production, ontogeny, size-specific responses, sex-specific responses, perch, roach

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Varmare och brunare vatten: effekter av klimatförändringar beror på storlek, kön och art

Abstract

Förståelsen om hur fiskpopulationer svarar på klimatförändringar är ofta begränsad till studier om effekten av temperatur, utan att ta hänsyn till förändringar i andra miljövariabler. Utöver att akvatiska miljöer blir varmare blir tempererade och boreala akvatiska miljöer även brunare på grund av ökade koncentrationer av löst organiskt kol. Dessutom är studier generellt fokuserade på förändringar på populationsnivå, och ignorerar därmed att arter eller individer av olika storlek och kön kan svara på olika sätt.

I den här avhandlingen studerar jag effekterna av varmare och brunare vatten på individer och populationer av fisk, och undersöker om dessa effekter varierar med storlek, kön och mellan arter (abborre, *Perca fluviatilis* och mört, *Rutilus rutilus*). Jag använde flera metoder, inklusive plats-för-tid-analyser, ett uppvärmningsexperiment på ekosystemnivå samt akvarie- och mesocosmexperiment.

Jag fann att både uppvärmning och brunifiering av sjöar sannolikt kommer att minska biomassaproduktionen hos fiskar. Uppvärmning kan också orsaka en förändring i storleksstrukturen mot mindre individer av abborre, samt en minskad biomassa av abborrpopulationer. Brunifiering kommer även sannolikt att påverka produktionen av abborrbiomassa genom att minska kroppstillväxten. Effekterna av uppvärmning på kroppstillväxten beror på kroppsstorlek, då små men inte stora individer påverkades positivt av höga temperaturer, och även kön, eftersom hanar påverkades mer negativt av uppvärmningen än honor. Effekterna av brunifiering kan variera med kroppsstorlek samt mellan arter, eftersom jag fann att brunifiering påverkade kroppstillväxten negativt hos stora individer mer för abborre, medan det bara påverkade mycket små individer av mört.

Sammantaget tyder mina resultat på att framtida uppvärmning och brunifiering kommer att påverka fiskindivider och -populationer negativt, men att effekterna kommer att variera med storlek, kön och mellan arter. Denna avhandling belyser vikten av att beakta flera klimatvariabler, integrera effekter på flera nivåer av biologisk organisation samt att ta hänsyn till inom- och mellanartsvariation för att förstå och förutsäga fiskpopulationers svar på ytterligare klimatförändringar.

Nyckelord: klimatförändringar, uppvärmning, brunifiering, sjöar, kroppstillväxt, biomassaproduktion, storlekspecifika effekter, könspecifika effekter, abborre, mört

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If there is magic on this planet, it is contained in water

Loren Eiseley

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List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

- I. 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 (4), 1395-1408.
- II. Van Dorst*, R.M., Nurminen, L., Gårdmark, A., Estlander, S., Huuskonen, H., Kahilainen, K.K., Olin, M., Rask, M., Huss, M. Warming promotes sexual size dimorphism in a freshwater fish. (submitted manuscript)
- III. 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 (5), 947-959.
- IV. Van Dorst*, R.M., Gårdmark, A., Svanbäck, R., Huss, M. Fish body growth responses to browning-induced light limitation vary over ontogeny (manuscript)

Papers I and III are open access publications (CC BY 4.0).

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The contribution of Renee M. van Dorst to the papers included in this thesis was as follows:

- I. Planned and designed the study in collaboration with the co-authors, conducted the data gathering and analyses, primary author of manuscript and handled the review process.
- II. Planned and designed the study in collaboration with the co-authors, conducted the data gathering and analyses, primary author of manuscript.
- III. Planned and designed the study in collaboration with the co-authors, performed the experimental work, conducted the data gathering and analyses, primary author of manuscript and handled the review process.
- IV. Planned and designed the study in collaboration with the co-authors, performed the experimental work, conducted the data analyses, primary author of manuscript.

1. Introduction

Ongoing global climate change is changing environmental conditions in aquatic ecosystems. However, knowledge on how aquatic organisms like fish will respond in for example body growth, average size, and population biomass to these environmental changes, and especially if responses will vary over fish size, sex, and species, is limited. As fish responses will also influence population structure and dynamics, competitive and predator-prey interactions, and therefore the functioning of entire aquatic ecosystems, it is of great importance we gain more knowledge on fish responses to climate change.

1.1 Biological rates

Many fish species exhibit indeterminate body growth and thus continue to grow their whole lives. The amount of energy an individual fish can use for this somatic (body) growth is often assumed to be proportional to the difference between energetic gains (related to feeding rates) and costs (related to resting and active metabolism and in adults also reproductive costs). Biological processes such as body growth, feeding rates, and metabolism differ between individuals (even of the same age, Figure 1), and are both size and sex dependent. This is important to take into account when studying populations, as natural fish populations are made up of individuals of different sizes, ages, and sexes.



Figure 1. Perch individuals from the same age and population can show high variation in body size. Picture by Renee van Dorst

1.1.1 Variation in biological processes with body size

Many biological processes in fish scale with body size. For example, metabolic rate increases with body size (Brown *et al.*, 2004; Glazier, 2005), which is why larger individuals need a higher energy intake to sustain a positive energy balance. Body size also governs feeding rates. The amount of prey of a certain size a fish can eat (maximum feeding rate) increases with predator body size, due to improved mobility, overcoming gape-size constraints (Christensen, 1996; Claessen *et al.*, 2000), increased visual acuity (Miller *et al.*, 1993), and increased digestive capacity (Mittelbach, 1981; Persson, 1987).

An increase in energy intake with body size can also be accomplished by shifting to feeding on larger and more energy rich prey. Such ontogenetic diet shifts are common in many animal taxa (Miller & Rudolf, 2011; Mittelbach & Persson, 1998; Werner & Gilliam, 1984). In fish it is, for example, common to switch from feeding on pelagic zooplankton to feeding on zoobenthos, and in some cases later also to fish. If and at what size and/or life stage ontogenetic shifts in diet take place depends on many factors, such as food availability (Mittelbach & Persson, 1998), competition for resources

(Schoener, 1974; Werner & Gilliam, 1984), and predation risk (Mittelbach & Persson, 1998).

Because key biological processes such as metabolism and feeding depend on body size, it is important to take body size into account when assessing external stressors that could impact these processes.

1.1.2 Variation in biological processes with sex

Mean and maximum body size within a species often varies between males and females. This size difference between sexes is called sexual size dimorphism (SSD) and is widespread among animals (Berry & Shine, 1980; Parker, 1992; Teder & Tammaru, 2005). Large female body size has a selective advantage for many species, when fecundity increases with female but not with male body size (Darwin, 1871; Roff, 1984). In many fish species females benefit from a substantial increase in egg numbers with body size (Barneche *et al.*, 2018), while males benefit more from maturing at a smaller size (and younger age) and instead have more reproductive seasons. In addition, males can invest excess energy not spend on body growth on reproductive behaviour (Henderson *et al.*, 2003), or reduce their food intake to decrease predation risk (Rennie *et al.*, 2008). This may lead to female biased SSD, where females are larger than males. Males and females may thus differ in their energy intake and/or energy allocation to body growth or reproductive costs over ontogeny, with SSD as a consequence.

1.2 Climate change in aquatic systems

The earth and the water bodies on it are subject to ongoing climate change. In temperate aquatic ecosystems in the Northern hemisphere this is visible as an increase in water temperature (IPCC, 2014) and browning of lakes and coastal areas (Solomon *et al.*, 2015; Weyhenmeyer *et al.*, 2016).

An increase in global surface temperature between 0.3 and 4.8 °C is expected by 2100, which may be even higher in northern regions (IPCC, 2014). Because water temperatures are strongly correlated to air surface temperatures, lake and coastal water temperatures have increased over the past decades, and continue to do so. Next to an increase in water temperature, warming can also lead to a shorter ice cover, longer growing seasons, and a deeper and therefore smaller hypolimnion (deepest layer of the lake) (Lehtonen, 1996).

Besides an increase in temperature, climate change also has led, and will continue to lead, to an increase in precipitation in temperate areas in the Northern hemisphere (IPCC, 2014). A longer growing season on land also leads to an increased vegetation cover (Larsen *et al.*, 2011). The combination of increased precipitation, a higher vegetation cover, and changes in land use may lead to an increased runoff of organic (humic) substances into streams and eventually lakes and coastal areas. In combination with recovery of acidification of soils and lakes this leads to an elevated level of dissolved organic carbon (DOC) and iron (Fe) in lakes and coastal areas, a process called browning (Graneli, 2012; Kritzberg *et al.*, 2019; Larsen *et al.*, 2011; Solomon *et al.*, 2015). This coloured DOC and iron absorbs light in the water column, and therefore browning leads to an increase in light attenuation (Creed *et al.*, 2018; Larsen *et al.*, 2011; Roulet & Moore, 2006). Next to a reduced light availability, browning can lead to an increase in nutrients (Creed *et al.*, 2018; Findlay, 2003).

1.3 Ecological impacts of climate change

1.3.1 Primary producers and fish resources

Primary production (by phytoplankton/algae) will likely increase with warming (O'Connor, 2009; Yvon-Durocher *et al.*, 2010). However, metabolic rates of (invertebrate) consumers increase with temperature as well (Vasseur & McCann, 2005), and the increase in primary production with warming in many cases does not compensate for the increase of metabolic rates of the consumers. This often leads to an increase in top-down control and a resource limitation of consumer growth with warming (O'Connor, 2009; Yvon-Durocher *et al.*, 2012). Overall consumer biomass (like zooplankton and zoobenthos) will likely not be altered by warming (Vasconcelos *et al.*, 2019; Yvon-Durocher *et al.*, 2011).

Browning can affect primary producers in two main ways. The first one (which I will focus on in this thesis), is through decreasing light availability which limits primary production (Ask *et al.*, 2009; Jones *et al.*, 2012; Solomon *et al.*, 2015), and the second is by increasing concentrations of organic carbon and nutrients, stimulating the microbial food web (Ask *et al.*, 2009; Jones *et al.*, 2012; Solomon *et al.*, 2015). Decreased light availability due to browning can reduce primary production and algal biomass by

limiting photosynthesis (Ask *et al.*, 2009; Jones *et al.*, 2012; Seekell *et al.*, 2015a; Vasconcelos *et al.*, 2016). Browning has been shown to negatively affect benthic primary production (benthic macro algae). Findings of effects of browning on pelagic production (phytoplankton) vary a lot, and range from negative (Jansson *et al.*, 2000), to neutral (Ask *et al.*, 2012) and even positive (chl *a*) (Kelly *et al.*, 2016). These effects of browning on primary producers may in turn affect the biomass (Karlsson *et al.*, 2009; Kelly *et al.*, 2016; Vasconcelos *et al.*, 2019) and composition (Robidoux *et al.*, 2015) of fish resources like zooplankton and zoobenthos through bottom-up processes. As responses of primary producers differ between habitats, effects on pelagic and benthic consumers may also differ. Zoobenthos (benthic invertebrates) biomass and production has been shown to be negatively affected by browning (Estlander *et al.*, 2010; Karlsson *et al.*, 2009; Vasconcelos *et al.*, 2019), while zooplankton biomass and production is less or even positively affected by browning (Kelly *et al.*, 2016; Vasconcelos *et al.*, 2016).

1.3.2 Fish individuals

Both warming and browning may affect fish body growth. Responses may, however, vary with body size and sex, and between species.

Warming

Temperature influences rates of physiological (Brown *et al.*, 2004) and ecological processes (Dell *et al.*, 2011). Body growth in ectotherms, such as fish, is especially affected by temperature (Angilletta *et al.*, 2004) due to the influence of temperature on rates of metabolism (Brown *et al.*, 2004), feeding (Rall *et al.*, 2012), and energy allocation (Kozłowski *et al.*, 2004). Depending on how these different processes change with increasing temperature, warming may have either a positive or negative direct effect on body growth (Brown *et al.*, 2004; Lemoine & Burkepile, 2012). As mentioned before, resource levels likely do not increase with warming. Thus, if metabolic demands increase more than feeding rates can, a decrease in body growth with warming can be expected. How these rates change relatively to each other is also partially dependent on body size. Usually small individuals have a higher optimal growth temperature than larger individuals (Lindmark, 2020; Ohlberger, 2013; Pörtner & Farrell, 2008). This often leads to increased body growth rates of young and small

individuals with warming, while growth rates of older and larger individuals may even decrease if ambient temperatures exceed optimum temperatures (Huss *et al.*, 2019; Imsland *et al.*, 1996; Ohlberger, 2013). As a consequence, warming is predicted to lead to higher growth rates for small or immature individuals, a lower age and size at maturation, and a decrease in maximum body size (i.e. the temperature-size-rule) (Atkinson, 1994). However, such a differential effect of warming over ontogeny has not been shown in many (experimental and observational) studies (but see Baudron *et al.*, 2014) and if such size-specific responses to warming are also sex dependent is unknown.

Warming is generally assumed to affect males and females similarly. However, as mentioned before, males and females likely have different trade-offs between food acquisition and predation risk (Holtby & Healey, 1990) because of sex-specific differences in energy demands and allocation (Malison *et al.*, 1985). It is therefore important to study drivers that may affect an individual's energy budget and patterns of body growth over ontogeny (Vendl *et al.*, 2018). Because in many fish species females have a large benefit of high fecundity when reaching a large body size (Shine, 1989), they perhaps will maintain high growth rates with warming throughout ontogeny. They may achieve this by increasing feeding rates to compensate for increased metabolic costs at high temperatures. However, increased feeding rates also increase predation risks (Rennie *et al.*, 2008). As male fish often do not have a large reproductive gain with a larger body size (Shine, 1989), they perhaps will not increase their feeding rates to compensate for increased metabolic rates at high temperatures. This suggests that body growth of males at high temperatures may not increase, but perhaps even decrease.

Next to potential size- and sex-specific responses to warming, body growth responses may also vary between species. Temperatures at which biological rates are optimized differ between species (Pörtner & Farrell, 2008). In addition, there is large variation in degree of phenotypic plasticity between species for traits that are temperature dependent, which may influence the magnitude of the response to changes in temperature (Crozier & Hutchings, 2014; Ficke *et al.*, 2007).

Browning

Browning can potentially affect fish individuals in many ways, but in this thesis I will focus on two: the effect of browning-induced light limitation on

fish resources and on visual feeding by fish. To understand potential different responses between individuals, it is important to remember that fish species differ in their diets. In addition, some fish species have ontogenetic diet shifts, where fish of different body sizes have diverse food preferences, due to e.g. different energy requirements, gape size, or visual acuity (Miller *et al.*, 1993; Mittelbach & Persson, 1998; Werner & Gilliam, 1984).

Decreases in resources with browning (Karlsson *et al.*, 2009; Vasconcelos *et al.*, 2019) can potentially lead to decreased food intake and therefore decreased body growth of fish. However, resources may be differently affected by browning (Kelly *et al.*, 2016; Vasconcelos *et al.*, 2016, 2019). As fish of different sizes and species might have different diets, they may be affected differently by browning-induced resource limitation. For example, fish feeding on benthic resources may be more affected by browning than fish feeding on zooplankton (as benthos is likely more affected by browning than zooplankton).

Another way browning can affect fish body growth is by affecting visibility in the water. Many fish are visual foragers, meaning they need to see their prey to be able to catch it. With a decrease in light in the water column, visual feeding by fish is likely to be impaired, which could lead to decreased fish body growth rates. Impaired feeding has been shown for fish feeding on benthic invertebrates and on other fish (Jönsson *et al.*, 2013; Ranåker *et al.*, 2012). However, for fish feeding on zooplankton findings vary between fish species (Jönsson *et al.*, 2012; Weidel *et al.*, 2017), and feeding is not negatively affected by browning for all fish species. As fish of different sizes and species may feed on different prey items, they may also be differently affected by altered light conditions.

The browning-induced decrease in potential resources and the potential decrease in feeding rates are together expected to limit fish body growth in brown waters. However, growth responses to browning likely depend on preferred prey type, and therefore on fish individual body size and fish species identity.

1.3.3 Fish populations

The potential size-, sex-, and species-specific effects of warming and browning on fish body growth will likely influence population level attributes such as size- and age-distributions, population biomass, and ultimately fish biomass production (Figure 2). Higher temperatures have

been shown to lead to a smaller average fish body size (Arranz *et al.*, 2016; Baudron *et al.*, 2014; Daufresne *et al.*, 2009; Jeppesen *et al.*, 2012) and an increase in the proportion of small and young individuals in fish populations (Arranz *et al.*, 2016; Daufresne *et al.*, 2009; Jeppesen *et al.*, 2012; Ohlberger, 2013). These changes in population size-structure can affect intra- and inter-specific interactions and population dynamics (Brose *et al.*, 2012; Lindmark *et al.*, 2018; Ohlberger *et al.*, 2011). In addition, the potential sex-specific body growth responses to warming may affect the degree of SSD in populations. On the other hand, browner water has been shown to lead to lower mean length-at-age (Estlander *et al.*, 2010; Horppila *et al.*, 2010), lower fish population biomass (Finstad *et al.*, 2014), and lower fish biomass production (Karlsson *et al.*, 2015; Karlsson *et al.*, 2009). However, it is still unknown if observations from natural systems over relatively small spatial scales (Karlsson *et al.*, 2015; Karlsson *et al.*, 2009; O'Gorman *et al.*, 2016) or theoretical predictions (Lindmark *et al.*, 2018; Ohlberger *et al.*, 2011) hold for how the combination of warming and browning affects population level responses in natural lakes and across large spatial gradients.

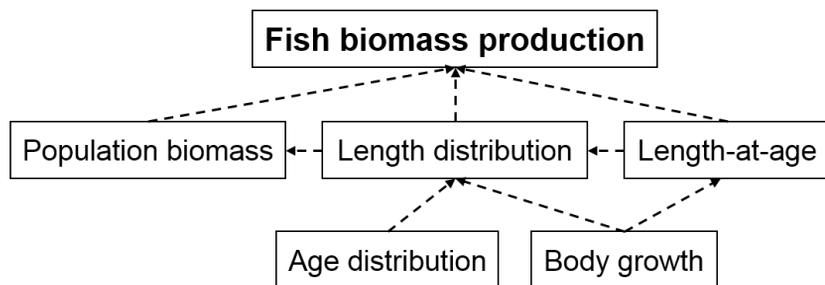


Figure 2. Fish biomass production and underlying individual- and population-level responses. Body growth underlies changes in length-at-age, and together with population age-distribution (mean age and skewness), also changes population length distributions (mean length and skewness), fish biomass, and eventually fish biomass production. The effects of warming and browning on fish biomass production may thus depend underlying responses of individuals and populations. Reproduced from **Paper I** (van Dorst *et al.*, 2019).

2. Aims of the thesis

In this thesis I aimed to assess the impacts of warming and browning on individual fish and populations, and unravel some of the underlying mechanisms. In addition, I aimed to assess if the particular effects of warming and browning depend on an individual's body size, age, sex, or species identity.

To reach these aims, I addressed the following core questions:

- How does warming affect fish responses (in body growth, population biomass, size- and age-structure, and biomass production), and do these responses vary with body size and/or sex? (**Paper I and II**)
- How does browning affect fish responses (in body growth, population biomass, size- and age-structure, and biomass production), and do these responses vary with body size and/or between species? (**Paper I, III and IV**)
- Are there any interactive effects of warming and browning on these fish responses? (**Paper I**)

3. Material and methods

3.1 Study species

My research was based on two fish species, Eurasian or European perch (perch from here on, *Perca fluviatilis*) (**Paper I, II, III**) and (common) roach (roach from here on, *Rutilus rutilus*) (**Paper III and IV**). Both are common and widespread freshwater fish in Europe, and two of the most common fish species in many Scandinavian ponds and lakes and along the Swedish Baltic Sea coast.

Perch has an optimum growing temperature between 23 and 25 °C (Mélard *et al.*, 1996), but this may be higher for small individuals (Huss *et al.*, 2019). It usually reaches a length of 25 cm, but can reach lengths up to 60 cm (Kottelat & Freyhof, 2007). Perch exhibit strong sexual size dimorphism, where females are usually larger than males (but the degree of this depends on environmental conditions, see **Paper III**). During its lifetime perch undergo strong ontogenetic shifts in diet; feeding mainly on zooplankton when very young, switching to a diet with more benthic invertebrates when they grow larger, and from about 12 cm often they include fish in their diet (Amundsen *et al.*, 2003; Hjelm *et al.*, 2000; Mittelbach & Persson, 1998). Percids are visual predators, and need good light conditions to find resources (Helfman, 1979).

Roach has an optimum temperature between 20 and 27 °C (van Dijk *et al.*, 2002). It usually reaches a length of 25 cm, but can grow up to 50 cm (Muus & Dahlstrøm, 1971). Roach do not have strong ontogenetic shifts in diet; their diet consists of zooplankton, algae, and benthic invertebrates (Horppila, 1994; Persson, 1983). Roach are very efficient zooplankton feeders over their lifetime, even in low light conditions (Bohl, 1979; Estlander *et al.*, 2012).

3.2 Study methods

My research consisted of four main components, which differed in study systems and methodology. Each paper included one or a combination of these components. The first component is based on observational lake data (**Paper I, II and III**), the second one consists of data from a whole-ecosystem warming experiment (**Paper II**), the third one consists of aquaria experiments (**Paper III and IV**), and the final component consists of mesocosm experiments (**Paper III and IV**). All data handling and statistical analyses in this thesis were done with R 3.4.2 – 3.6.3 (R Core Team, 2017).

3.2.1 Observational lake data (Paper I, II, and III)

In **Paper I, II, and III** I aimed to study the effects of warming and browning through space-for-time analyses by using observational data from lakes over a large temperature and/or water colour gradient (Figure 3). In **Paper I** I assessed the effects of temperature and water colour on perch biomass production, and the individual and population level responses leading to this response in biomass production (see Figure 2). In **Paper II** I assessed if there are sex-specific growth responses to temperature, and if potential sex-specific variations in body growth with temperature affect sexual size dimorphism (SSD) in perch. In **Paper III** I assessed if water colour affects length-at-age of perch and roach, and if effects of water colour vary with age. To do this I used fish data and environmental data from lakes in Sweden and Finland.

Lake fish data

I extracted data for **Paper I, II, and III** on fish biomass (catch per unit effort), abundance, size, age, and/or back-calculated length-at-age from the National register of survey test-fishing (NORS, 2016). Data in this database was collected with benthic and pelagic gillnets. Dependent on the study I selected data from certain species and time frames, which (in combination with available environmental data), gave me a specific selection of lakes for each of the papers. For **Paper II** I used data from Finnish lakes in addition to data from Swedish lakes, which came from a number of sources (Estlander *et al.*, 2017).

For **Paper I** I selected biomass, abundance, size, age, and backcalculated length-at-age data of perch and biomass data for each species in the whole

fish community from the years 2006-2015. This resulted in data from 52 lakes in Sweden (Figure 3A and B).

For **Paper II** I used both the NORS database, as well as data from Finnish lakes provided by my Finnish co-authors. I selected back-calculated length-at-age data of perch from the years 1995-2015, and presence/absence data of all fish species. This resulted in a total of 100 lakes, 65 from Sweden and 35 from Finland (Figure 3C).

For **Paper III** I selected length-at-age data of perch and roach from the years 2006-2015, resulting in data from 49 lakes. 43 of these lakes contained perch, while 40 contained roach (Figure 3D).

Environmental data

For the Swedish lakes I extracted environmental data from the Miljödata MVM database (<https://miljodata.slu.se/mvm/Default.aspx>). Data was extracted for similar periods as the fish data (**Paper I and III**), or for the period before fish data was collected (**Paper II**). Summer or growing season water temperature and absorbance of filtered water at 420 nm (which is a measurement of intensity of brown water colour, and here noted as the Napierian coefficient (a_{420} , in m^{-1})) were the most important environmental variables (for distribution of lakes, see Figure 3). However, I also extracted the covariates total phosphorus, total nitrogen, pH, and turbidity. Data on lake morphology (mean or max depth, area, and location) was extracted from the NORS database (NORS, 2016).

For **Paper II** I also extracted data from the Finnish Environment Institute open data web service (https://www.syke.fi/en-US/Open_information), on maximum depth, area, water colour, total phosphorus, and total nitrogen. I extracted growing season air temperature used in **Paper II** from the Swedish Meteorological and Hydrological Institute (SMHI, <https://www.smhi.se/data/meteorologi/ladda-ner-meteorologiska-observationer#param=airtemperatureInstant,stations=all>) for the Swedish lakes, and from the Finnish Meteorological Institute (FMI, <https://ilmatieteentaitos.fi/havaintojen-lataus#!/>) for the Finnish lakes in this study.

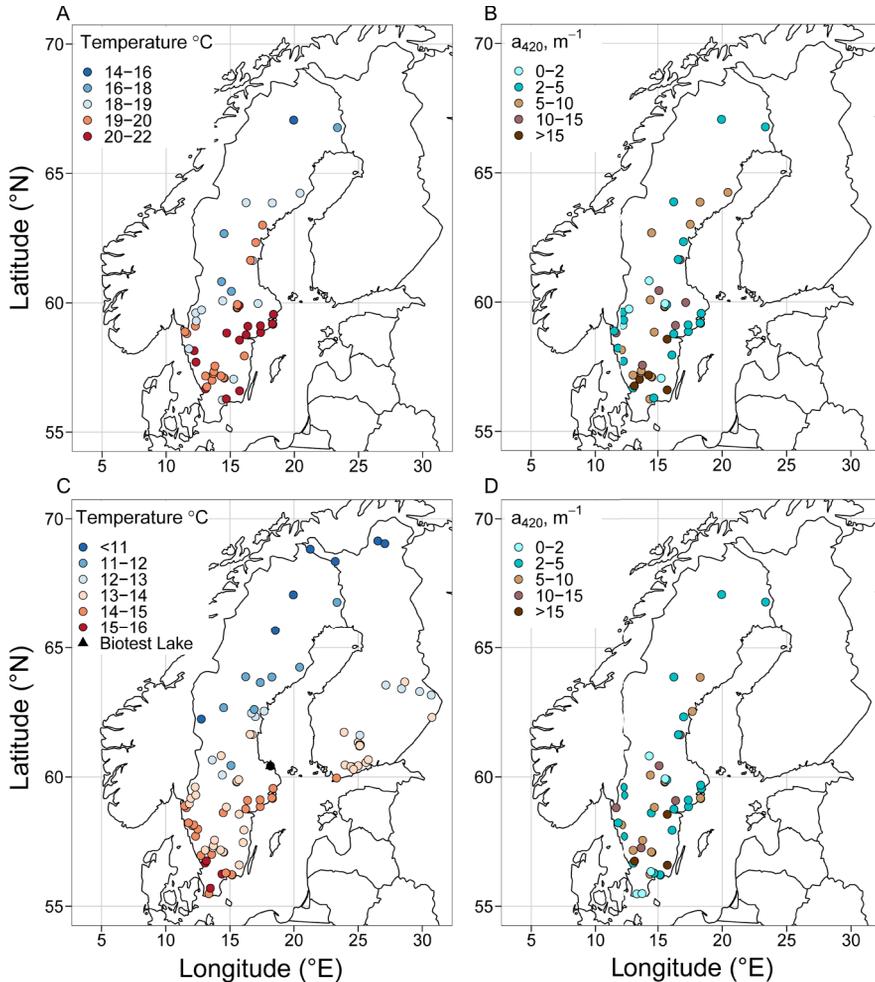


Figure 3. Maps of positions of all lakes used in the three studies using observational lake data and the location of the whole-ecosystem warming experiment, the Biotest Lake (C). Map A (July-August water temperature) and B (water colour as absorbance at 420 nm) are the lakes for **Paper I**, map C (growing season air temperature) are the lakes and the whole-ecosystem warming experiment used for **Paper II**, and D (water colour as absorbance at 420 nm) are the lakes used for **Paper III**. Map A and B are reproduced from **Paper I** (van Dorst *et al.*, 2019).

Data analyses

I measured a number of different individual and population responses from the lake fish data. I calculated catch per unit effort in biomass or abundance, as the biomass or number of fish per square meter of net per night (**Paper I**).

I also calculated mean and skewness of total perch length from total length at catch of all individuals in a lake (**Paper I**), and mean and skewness of perch age from age-at-catch of all individuals in a lake (**Paper I**). I calculated length-at-age at catch (**Paper I and III**), or from back-calculated length-at-age data (L), excluding the final growth season (**Paper II**). From L per sex (f, m) I calculated the sexual dimorphism index (*SDI*, **Paper II**) at age, as the ratio of how much larger females are than males, using

$$SDI = (meanL_f/meanL_m) - 1 \quad (1)$$

Furthermore, I calculated length-specific growth rates for each individual as

$$G_{L,t-1} = (L_t - L_{t-1})/L_{t-1} \quad (2)$$

where $G_{L,t-1}$ is the annual length-specific growth at the length (L) the fish had at age $t - 1$ (**Paper I and II**). From this I estimated a general length-specific growth rate function for each lake, by fitting the individual length-specific growth values $G_{L,t-1}$ as an exponential function of body length (in the previous year) across all individuals in that lake using

$$G_{L,t-1,lake} = \alpha_{lake} * e^{\beta_{lake} * L_{t-1}} \quad (3)$$

with a lake- (and in **Paper II** sex) specific scalar (α_{lake}) and exponent (β_{lake}). Applying this equation, I calculated length-specific growth rates for specific lengths, sexes, and lakes (**Paper I and II**).

Finally I measured fish biomass production as biomass production of perch for each lake, measured as gram biomass production per year and net area, and I derived this from the estimated size-specific annual weight increments of the fish caught in each lake (**Paper I**).

3.2.2 Whole-ecosystem warming experiment (Paper II)

In **Paper II** I used data from a whole-ecosystem warming experiment to study if warming affects body growth of males and females differently over ontogeny, and if this alters SSD in perch. I used fish data collected from the Biotest Lake (Figure 3D). In this long term experiment, heated cooling water from a nuclear power plant is collected in an artificial brackish lake, which is therefore 5-10 °C degrees warmer than the surrounding area (Huss *et al.*, 2019). For this study is used 10 years of data of backcalculated growth and length-at-age of perch before the onset of warming, and 10 years of data after the onset of warming.

I calculated length-at-age and growth increments from back-calculated length-at-age data (L), excluding the final growth season. I calculated SDI as in equation 1 for the period before and after warming, and length-specific growth per individual as in equation 2.

3.2.3 Mesocosm experiments (Paper III and IV)

In this thesis I use data from 2 different mesocosm experiments to assess the effects of browning on fish body growth in pelagic food webs. I conducted the experiments on the grounds of the Freshwater institute in Drottningholm (SLU Aqua) during August-September 2017 and 2018 (**Paper III and IV**)

In the first mesocosm experiment (**Paper III**) I studied if browning-induced light limitation affects body growth of perch and roach, and if this is due to the effect of browning on fish resources, or due to the effect of browning on visual feeding by the fish. In order to do this I used 18 mesocosms filled with 7000 L of filtered water from the adjacent lake Mälaren (Figure 4A), with 3 different browning treatments for each fish species. Brown treatments were created by adding Sera Blackwater Aquatan water conditioner (blackwater from now on). The first treatment was a clear control treatment. The second was a treatment where mesocosms were browned at the start of the experiment (19 days before fish addition), to test for both effects of browning on the prey community as well as visual feeding by perch and roach, and how this affects fish body growth. The third one was a treatment where mesocosms were browned when fish were added to the experiment (day 19), to test for the effect of browning on the visual feeding by perch and roach and how this affects fish body growth. On five occasions I sampled for chlorophyll a, zooplankton, photosynthetically active radiation, and water temperature. On the final day (day 32) I removed the fish from the mesocosms with a seine net, euthanized them in a benzocaine solution, blotted them dry, and measured and weighed them to the nearest mm and 0.1 gram. I determined body growth by subtracting the mean start weight from the end weight of each fish. I calculated mean growth rates for each mesocosm, and treatment means were calculated from these.



Figure 4. Experimental setup of A) the mesocosm experiments in Drottningholm (**Paper III and IV**), and B) preparing the pond to hatch fish and keep them over summer. Photo A by Renee van Dorst, photo B by Ola Renman.

In the second mesocosm experiment (Paper IV) I studied if roach body-growth responses to browning-induced light limitation differ over ontogeny due to body size. I also tested if these responses are robust to variation in roach density. In order to do this I set up a mesocosm experiment with a browning and a density treatment, and looked at body growth of two size-classes (small young-of-the-year (YOY) and larger 1-year olds). The experiment was conducted in 16 outdoor tanks (Figure 4A) filled with 7000 L of filtered water from the adjacent lake Mälaren. At the start of the experiment I inoculated all mesocosms with similar amounts of zooplankton from nearby ponds and added blackwater to half of the mesocosms. Creating a clear treatment and a brown treatment. After 10 days fish were added to the experiment, either with a low density, consisting of ten YOY and four 1-year olds, or with a high density, consisting of 25 YOY and ten 1-year olds. On five occasions I sampled for chlorophyll a, zooplankton, photosynthetically active radiation, and water temperature. On the final day (day 30) I removed the fish from the mesocosms with a seine net, euthanized them in a benzocaine solution, blotted them dry, and measured and weighed them to the nearest mm and 0.1 gram. I calculated weight-specific growth rates of each individual fish using

$$G_{W,start} = ((W_{end} - W_{start}) / W_{start}) \quad (4)$$

where $G_{W,start}$ is the weight-specific growth rate (%) during the experiment based on the mean weight (W) the fish (of each size class) had at the start of the experiment. I calculated mean weight-specific growth rates per size class for each mesocosm, and treatment means were calculated from these.

3.2.4 Aquaria experiments (Paper III and IV)

I conducted two types of aquaria experiments at the Freshwater institute in Drottningholm (SLU Aqua) to test the effects of browning on two different responses. The first experiment was a capture rate experiment (**Paper III**) and the second a prey selectivity experiment (**Paper IV**).

In the capture rate experiment (**Paper III**) I assessed the effect of water colour/light conditions on capture rates on *Daphnia longispina* (0.7 ± 0.1 mm, mean \pm SD) of perch and roach in aquaria filled with 15 L of filtered lake water (Figure 4A). Perch and roach were of similar size as used in the mesocosm experiment of **Paper III**. I conducted the experiment at three different water colour/light conditions: clear, intermediate and dark brown water. Different levels of browning were simulated by adding blackwater to aquaria. I measured perch and roach capture rate as the visually observed number of *D. longispina* eaten in 1 minute after inoculating each aquarium with 60 *D. longispina*. Each treatment had 3-5 replicates.

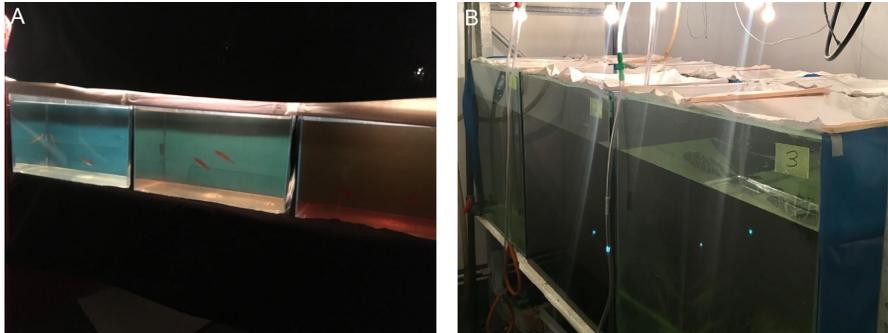


Figure 5. Experimental setup of A) the capture rate experiment (**Paper I**) and B) the prey selectivity experiment (**Paper II**). Photos by Renee van Dorst.

In the prey selectivity experiment (Paper IV, Figure 4B), I assessed if roach of two different sizes (cohorts) selected prey differently, and if this differed in brown compared to clear water. I used roach from two different cohorts: small YOY and larger 1-year olds (same size as mesocosm experiment Paper IV above). The prey selectivity experiment was carried out in larger aquaria (Figure 5B), filled with 156 litre of filtered lake water. I conducted the experiment at two different water colours: clear and brown. I added either 10 YOY or two 1-year olds to each aquarium, after which I added a known mixture of zooplankton to each aquarium. The fish ate for three hours, after which I sampled the zooplankton community left in each

aquarium with a zooplankton net. Each treatment had 3 replicates. I determined zooplankton genus (cladocerans) and groups (copepods) of both the introduced as the sampled zooplankton community. To determine if there was selection for or against a certain prey group I compared the proportion of each prey group after feeding from each treatment to the proportion that was added to the experiment. If proportions after feeding were higher than before fish addition I regarded this as selection against this prey group, if proportions after feeding were lower than before fish addition I regarded this as selection for this prey group, and if proportions after and before feeding did not differ from each other I regarded this as neutral selection for this prey group.

3.2.5 Ethical considerations

The mesocosm and aquaria experiments (**Paper III and IV**) in this study were conducted in accordance with national guidelines for animal care and the procedures employed were reviewed and approved by the regional ethical review board in Uppsala, Sweden (Dnr 5.8.18-03449/2017). At the end of each experiment, fish were removed from the aquaria and euthanized in a benzocaine solution.

4. Results and discussion

In this thesis, I show that the climate change stressors; warming (**Paper I and II**) and browning (**Paper I, III, and IV**), can affect fish individuals and populations, and that these observed responses arise through different mechanisms. I also show that fish responses to warming and browning depend on fish size (**Paper I, II, III, and IV**), sex (**Paper II**), and species identity (**Paper III**). Below I will examine each finding in more detail.

4.1 Fish responses to warming (Paper I and II)

I found that high temperatures overall have a negative effect on mean population size, size-structure, and population biomass and production (**Paper I**), but that effects of temperature and warming on body growth and length-at-age depend both on body size (**Paper I and II**) and sex (**Paper II**).

In **Paper I** I show that high water temperature during summer negatively affects fish (perch) biomass production over a gradient of 52 lakes. I found that this lower fish biomass production in warm compared to cold lakes most likely results from population level responses to warming. In warmer lakes there were smaller population biomasses, a lower mean length and age, and a higher proportion of small and young individuals in the populations (see Figure 2 and 6) than in colder lakes. Because of a low population biomass there is less biomass available for growth and therefore biomass production. This lower fish biomass in warm lakes is, in turn, likely a consequence of the observed shift in size-structure towards a higher proportion of small-bodied individuals and a lower mean body size, which is in line with findings of previous studies (Daufresne *et al.*, 2009; Jeppesen *et al.*, 2010). One explanation for the observed shift towards smaller/younger fish in warm waters is likely that high temperature induces elevated mortality of larger

and older individuals (Sandström *et al.*, 1995). In addition, high temperatures may lead to earlier maturation at a smaller size (Atkinson, 1994; Sandström *et al.*, 1995), which reduces size at older ages due to slower body growth after maturation (Charnov *et al.*, 2001), potentially shifting the size structure. Given that especially small females have a much lower reproductive output than larger ones (Berkeley *et al.*, 2004; Dubois *et al.*, 1996), the shift I observed towards smaller fish in populations in the warm study lakes could lead to a lower population fecundity (however, perhaps females are not as negatively affected by warming, see next section **Paper II**).

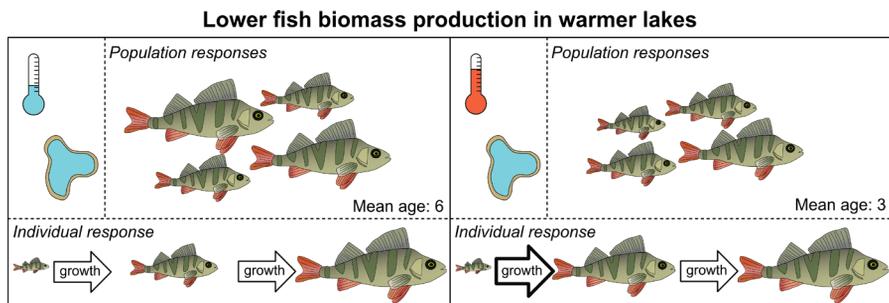


Figure 6. Fish (perch) biomass production is lower in warmer lakes. With warming alone, population biomass decreases and there is a shift toward smaller and younger individuals. Young but not old individuals exhibit higher growth rates. Adapted from **Paper I** (van Dorst *et al.*, 2019).

Although I found no negative effects of high temperatures on fish body growth, I did find that the effects varied with body size (**Paper I**). Body growth and length-at-age of small fish was higher in warm lakes than in cold lakes, while body growth and length-at-age of larger and older fish did not seem to be affected by warm water temperatures. The finding that temperature affected body growth of small but not large fish is likely because metabolic and feeding rates generally increase with both temperature and body size (Brown *et al.*, 2004; Rall *et al.*, 2012), but usually not at the same rate (Lindmark *et al.*, 2018). Due to this small individuals generally have a higher optimum growth temperature than large individuals (Imsland *et al.*, 1996; Ohlberger, 2013; Ohlberger *et al.*, 2011). Thus, with the same increase in temperature, small but not large individuals could exhibit increased growth rates (Daufresne *et al.*, 2009; Ohlberger, 2013), similar to what I found in my study.

Thus, in **Paper I** I show that warming of lakes will likely lead to a lower fish (perch) biomass production (Figure 6), and that this is due to a shift in size-structure and a lower fish population biomass in warm waters. I also show that body growth responses to warming vary with temperature.

As I found size-specific effects of warming in **Paper I**, and perch shows strong sexual size dimorphism (SSD), where females are larger than males, I wanted to see if there were also sex-specific effects of warming. In **Paper II** I show that male and female fish (perch) may indeed respond differently to global warming. In the whole-ecosystem warming experiment (the Biotest Lake) I found that females had a higher growth rate and length at age over their lifetime in the warm compared to the cold period. In contrast, males only had a slightly faster growth rate in the warm period at a young age, after which their growth rates became similar and even lower in the warm compared to the cold period. The difference in length-at-age between the sexes thus became larger over age in the warm period, and was substantially larger than in the cold period. Therefore the sexual size dimorphism index (SDI) increased with age, and was higher in the warm than in the cold period. For example, at age 5 females are expected to be 8% larger than males in the cold period, while after warming females are expected to be 20% larger than males at this age.

In **Paper II** I found a similar pattern over a large temperature gradient including 100 lakes in Sweden and Finland. At young age and size, growth rates of both males and females increased with temperature. However, at larger age and size, growth rates of both males and females decreased over temperature, but growth rates of males decreased faster. Length-at-age therefore differed more between sexes in warm compared to cold lakes, especially at older ages. This led to an increase in SDI with temperature, from age 2 and up. For example with a 4 °C temperature increase (from 10-14 °C mean growing season air temperature), I expect a 3.5 times increase in SDI. At 10 °C females are expected to be 3.7% larger than males, while at 14 °C they are expected to be 13% larger.

These varied responses of males and females to warming and temperature have not directly been shown before, although other studies have shown that other environmental variables related to temperature can influence SSD (Estlander *et al.*, 2017; Garel *et al.*, 2006; Horne *et al.*, 2019; Hoye *et al.*, 2009). The varied responses of males and females to warming and temperature likely arise from differences in the trade-off between the

benefits of being large for fecundity (which is mostly beneficial for females, (Barneche *et al.*, 2018; Craig, 1987)) and the disadvantage of becoming/being large in terms of increasing energy intake and its associated predation risks (Rennie *et al.*, 2008). For females being large and therefore having high fecundity likely outweighs the disadvantages, while for males it does not. Thus, in **Paper II** I show that warming of lakes may lead to sex-specific body growth and length-at-age responses, and consequentially to an increase in SSD. Because large female fish are of high importance for population productivity (Hixon *et al.*, 2014), sustained high body growth and body size of females in (future) warm environments may dampen negative population responses to warming. Overall, our results in **Paper II** imply that it is insufficient to use mean population responses to produce accurate predictions on fish body growth and size, and therefore biomass production and ecological interactions, in a future warmer climate, and therefore variation between sexes over ontogeny has to be taken into account.

Thus, **Paper I and II** show that warming and high temperatures overall negatively affect fish populations, but that the effects of warming and high temperatures on an individual level (body growth) depend on the size and the sex of the individual. As body size in fish governs ecological interactions (Woodward *et al.*, 2005), a warming-induced change in population size structure and an increase in SSD may also contribute to changes in competitive and predator-prey interactions.

4.2 Fish responses to browning (Paper I, III, and IV)

I found that brown water colour overall has a negative effect on population biomass production (**Paper I**), but that effects of water colour on body growth and length-at-age depend both on body size (**Paper I, III, and IV**) and species identity (**Paper III**).

In **Paper I** I show that brown water colour negatively affects fish (perch) biomass production over a water colour gradient of 52 lakes. I found that this observed lower fish biomass production in brown compared to clear lakes is mainly explained by body growth and length-at-age responses (Figure 2 and 7). Fish in brown lakes grew slower and had smaller length-at-age than fish in clear lakes, which can directly explain the decrease in fish population biomass production. This decreased body growth, however, did not affect the population size-structure or biomass. The negative relationship I found

between water colour and body growth across the large geographical gradient supports and generalizes the findings of smaller-scale lake studies (Estlander *et al.*, 2010; Horppila *et al.*, 2010). The lower body growth rates in brown waters can likely be explained by the negative effect of brown waters on (benthic) resource production (Ask *et al.*, 2009; Karlsson *et al.*, 2009; Seekell *et al.*, 2015a; Vasconcelos *et al.*, 2019) and visual feeding by fish (Jönsson *et al.*, 2011; Ranåker *et al.*, 2012). In contrast to temperature, browner water colour did not have a significant negative effect on fish population biomass. This is in contradiction to some previous studies that found negative relationships between fish population biomass and light condition (Karlsson *et al.*, 2009) or DOC (Karlsson *et al.*, 2015). A space-for-time study by Finstad *et al.* (2014), however, found a positive effect of higher DOC concentrations on fish population biomass at very low DOC levels (after a certain DOC level fish population biomass decreased), and also a lake manipulation experiment by Koizumi *et al.* (2018) found no negative effects of increased DOC levels on fish biomass (density). These findings are likely due to a positive effect of increased DOC and associated higher nutrient levels with DOC (See also Kelly *et al.*, 2016; Seekell *et al.*, 2015b; Zwart *et al.*, 2016). However, direct comparisons to these particular studies are difficult, as they had different measures of water colour, different (smaller) geographic ranges and/or different fish species in their studies.

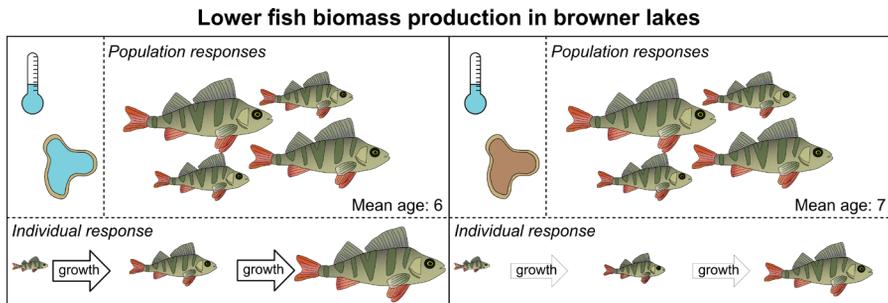


Figure 7. Fish (perch) biomass production is lower in browner lakes. As lakes get browner mean age increases slightly, but there is no shift in population biomass or mean length. Body growth of both small and large individuals is reduced. Adapted from **Paper I** (van Dorst *et al.*, 2019).

Even though perch body growth of all sizes and ages was negatively affected by browning in this study, there was some variation in responses over size (**Paper I**). Small perch (age 1) seemed to be the least negatively affected by brown water colour, while the negative slope between body growth and temperature was steeper for larger perch (age 5). These results are likely a consequence of the strong ontogenetic shifts in diet that perch displays (from zooplankton, to zoobenthos to eventually fish (Hjelm et al., 2000; Mittelbach & Persson, 1998)), and the varying effects browning has on these resources (Estlander et al., 2010; Karlsson et al., 2009) and the feeding on these resources (Jönsson et al., 2012) (e.g. zooplankton may be much less affected than zoobenthos).

Thus, in **Paper I** I show that browning of lakes will likely lead to a lower fish (perch) biomass production (Figure 7), and that this is due to decreases in body growth of especially larger perch. As large perch normally may have a strong structuring effect on their (fish) prey, browning could have severe impacts on the food web.

In **Paper I** I found negative effects of browning even in small perch. In **Paper III** I wanted to see if these results were also true for even smaller perch feeding only on zooplankton and for another common fish species, roach. Furthermore, I wanted to find out the extent to which browning-induced light limitation can affect fish indirectly via changes in the prey community or directly by worsened conditions for visual feeding. In the mesocosm experiment I showed that body growth of perch, but not roach, was negatively affected by browning, and that this was likely due to browning induced changes in the zooplankton prey community composition, possibly in combination with reduced foraging rates. There were likely some reductions in foraging rates, but these were on their own not enough to lead to the lower perch body growth, which was confirmed by the capture rate experiment (limited evidence for reduction in perch and at all for roach, capture rates on *Daphnia longispina*). The results of the lake gradient study in **Paper III** corroborate the results I found in the mesocosm experiment, as I found negative effects on perch, but not roach, body growth. As young roach can sustain positive growth rates on lower zooplankton levels than perch of the same size (Byström & García-Berthou, 1999), roach may have been less affected than perch by any change in preferred zooplankton availability and community composition caused by browning. In addition, the lack of a negative response in capture rate of roach (but not perch)

confirms the findings of other studies that effects of browning on capture rates of zooplankton can be species-specific (Jönsson *et al.*, 2012; Weidel *et al.*, 2017), and my study shows that this might contribute to species-specific growth responses to browning. Thus, in **Paper III** I show once again that browning of waters may lead to decreased fish body growth, which could decrease fish population biomass production (**Paper I**) and suggest that this effect of browning will depend on the fish species present. These browning-induced species-specific reductions in body growth and also biomass production will likely affect competitive- and predator-prey interactions, and community composition in browner lakes.

As I found negative effects of browning on perch but not roach body growth in **Paper III**, but also found in **Paper I** that responses to browning may differ over ontogeny in perch, I tested if responses to browning varied over ontogeny in roach, a species without strong ontogenetic shifts in diet (**Paper IV**). In **Paper IV** I indeed also found size-specific responses to browning, as body growth of YOY but not 1-year old roach was negatively affected by browning. I show that this size-specific difference in body growth is likely a consequence of browning-induced alterations in zooplankton prey community composition and overall differences in prey selectivity between YOY and 1-year olds. Our finding of ontogenetic differences in roach body growth responses to browning differs from my results in **Paper III** and results of a previous study (Estlander *et al.*, 2010), which report no effect of browning on body growth of roach. However, neither of these studies included roach this small. This strengthens our claim that only small YOY roach are affected by browning. The opposite pattern found for perch, with browning reducing growth of large fish more than of small fish (**Paper I and III**) could be a result of the greater shift in diet over ontogeny in perch than in roach (perch shifts from zooplankton to benthic invertebrates to fish, whereas roach does not show such distinct shifts). This shows that body growth responses to browning can vary depending on both species identity and diet over ontogeny. Overall, in **Paper IV** I show that body growth responses to browning can differ over roach ontogeny (i.e. even in a species without strong ontogenetic shifts diet (and habitat)), and that this is due to an effect of browning on zooplankton community composition and an overall difference in prey selectivity between YOY and one-year old individuals.

Overall **Paper I, III, and IV** show that browning and brown water colour negatively affect fish populations of certain species, and that effects of browning and brown water colour on an individual level (body growth) depend on the size and species identity of the individual. These results show that is important to take ontogeny and species identity into account when assessing effects of browning on fish growth and also fish population biomass production, as this may influence competitive and predator-prey interactions, population size and age structure, and thus entire lake ecosystems.

4.3 Combined warming and browning (Paper I)

Due to climate change, lakes are likely to get both warmer and browner (Larsen *et al.*, 2011; Roulet & Moore, 2006; Weyhenmeyer *et al.*, 2016), however, it was largely unclear if there are interactive effects of these two climate stressors on fish responses (but see Hansson *et al.*, 2012; and Vasconcelos *et al.*, 2019).

In **Paper I** I found no evidence for interactive effects of temperature and water colour on perch body growth, population biomass, size- and age-structure, or biomass productivity over a gradient including 52 lakes. However, I showed that both high temperatures and brown water colour affected perch biomass production negatively, but through different pathways (Figure 2 and 8). Thus, even though I found no interactive effects of warming and browning, if the two occur in the same lake, this will likely lead to a highly decreased growth of larger individuals, lower population biomass, a lower mean size and age, and more young individuals, which together will lead to a very low fish biomass production (Figure 8).

Considering that climate change is leading to both warmer and browner lakes in temperate and boreal areas (Larsen *et al.*, 2011; Roulet & Moore, 2006; Weyhenmeyer *et al.*, 2016), the results of this thesis suggest a potential widespread decline in lake fish biomass production in the future, given that perch is the dominant fish species in many European lakes (Craig, 1987; Lehtonen *et al.*, 2008; Tammi *et al.*, 2003). This may not only have implications for ecosystem functioning, but also for (sports) fisheries in these lakes. Accordingly, only assessing impacts of warming, ignoring simultaneous impacts of browning (or vice versa), would underestimate the impact of overall climate change on fish populations. Thus, in **Paper I** I show

that in order to predict climate change effects on fish biomass production or its variation across lake environments we simultaneously need to consider multiple climate stressors.

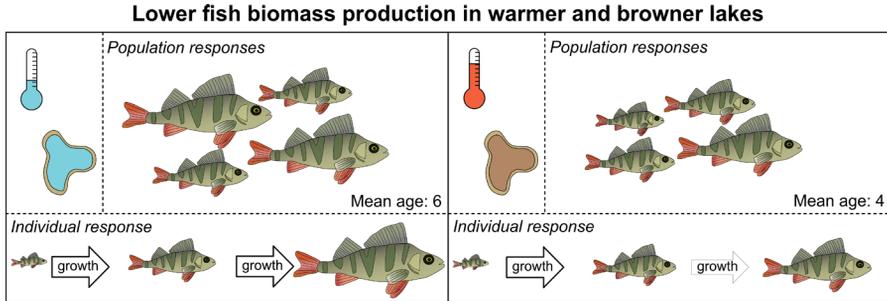


Figure 8. Fish (perch) biomass production in warmer and browner lakes. As lakes get both browner and warmer (from top left to bottom right), there is a strong decrease in fish biomass production due to reduced population biomass, a shift towards smaller and younger individuals and slower body growth. Adapted from **Paper I** (van Dorst et al., 2019).

5. Concluding remarks and outlook

In this thesis, I have assessed the impact of the climate change stressors; warming and browning, on fish individuals and populations, and I have unravelled some of the mechanisms leading to the observed responses to these stressors. I have also assessed if the impacts of warming and browning vary depending on body size, sex, and between species. In order to do this I used a combination of methods, including a space-for-time approach, a whole-ecosystem warming experiment, aquaria-, and mesocosm experiments, and studied the responses with a focus on two common fish species: European perch (*Perca fluviatilis*) and common roach (*Rutilus rutilus*).

My findings show that both warming and browning of lakes will affect fish individuals and populations in a number of ways, and that body growth responses indeed depend on fish body size, sex, and species. I show that warming and higher temperatures increase body growth of small individuals (perch), and that the effect of temperature on body growth may depend on their sex (at least in species with female biased sexual size dimorphism). I also found that browning and dark water colours can negatively affect fish body growth, and that responses vary between species and with body size. Thus, to assess impacts of warming and browning on fish body growth, size, sex, and species identity have to be taken into account. On a population level, I show that warming may lead to a shift in size- and age distribution, towards smaller and younger individuals, a decrease in mean size and age in fish populations, and a decrease in population biomass, and that these responses together lead to a decrease in perch biomass production. I found no evidence for negative effects of browning on body size or population biomass, but because of the decrease in body growth I did find that fish (perch) biomass production will likely decrease when lakes get browner. As lakes in the

future will get both warmer and browner (IPCC, 2014; Solomon *et al.*, 2015; Weyhenmeyer *et al.*, 2016), I also studied if there might be any interactive effects of warming and browning but found no evidence for this. However, my studies predict strong negative effects of warming and browning on fish biomass production.

The results in this thesis come from “space-for-time” analyses and experimental studies (from aquaria to ecosystem scales). The next step should be to study fish populations and prey communities over time in natural environments that are getting warmer and/or browner, for which long term data sets are needed. In addition, more large scale experiments including both temperature and water colour should be conducted, and responses over a larger range of body sizes and of more species should be studied.

In summary, the novel findings presented here suggest there may be substantial changes in fish body growth and size-and age structure, and decreases in population biomass and production in a future warmer and browner climate. As body size for many taxa governs key processes such as fecundity and ecological interactions, size- and sex-specific changes in body growth and size are likely to affect predator-prey and competitive interactions and population productivity. Furthermore, variation between species in response to browning may affect interspecific interactions and thus community composition. In addition, decreases in population biomass and production may have implications ranging from altered ecosystem function to reduced food production. Overall, this thesis stresses the importance of *(i)* considering multiple climate stressors, *(ii)* integrating responses across several levels of biological organization, and *(iii)* acknowledging within- and between species variation, in order to predict fish population responses to further climate change.

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Popular science summary

Many aquatic ecosystems in Northern Europe are getting both warmer and browner due to climate change. This affects the organisms living in lakes and coastal areas. In this thesis I show that warming and “browning” will likely lead to lakes with smaller, younger and slower growing fish, which will lead to less biomass and reduced production of new fish biomass. I also show that effects of warming and browning on fish will depend on their body size, sex, and species. These impacts of warming and browning on fish populations will likely affect interactions with competitors, prey, and predators, and will therefore likely affect entire lake ecosystems. Furthermore, it also may affect (sports) fisheries as there will be fewer and smaller fish to catch!

Climate change in temperate regions causes warming of aquatic systems like lakes. It also leads to more rainfall and vegetation cover on land, which will increase the inflow of organic material into these lakes. Increased concentrations of this organic material will make these lakes appear browner, and decrease the light available in these lakes. Both warming and browning may affect fish living in lakes through a number of pathways. Warming can affect biological rates like metabolism and feeding rates, which determine body growth of fish. Light limitation due to browning may affect visual feeding of fish as well as abundance and composition of the prey they feed on. Fish of different size, sex, and species may potentially be affected differently by warming and browning as e.g. their biological rates may respond differently to increases in temperature, or because they rely more or less on vision to find prey. However, to this day, most studies focus on the average responses of specific fish populations to climate change. This overlooks the fact that populations consist of individuals, which may vary in

their responses to warming due to different body size and sex, and these effects may, in turn, vary between species.

In this thesis I studied the effects of warmer and browner waters on fish individuals and populations, and investigated if these responses vary with fish size, sex, and between species. In order to do this I used a range of methods, including space-for-time analyses, a whole-ecosystem warming experiment, aquaria experiments, and mesocosm experiments. In these studies, I used two fish species: European perch (*Perca fluviatilis*) and common roach (*Rutilus rutilus*), which are two of the most common species in European lakes, and especially perch is a beloved species for both sports and commercial fisheries.

My findings show that both warming and browning of lakes will likely lead to a decrease in fish biomass production. Warming will likely do this by causing a shift in the size-structure of the fish population, towards smaller and younger individuals, and causing a lower fish population biomass. Browning on the other hand will, according to my findings likely affect fish biomass production because it leads to a lower fish body growth. I also found that responses to warming indeed depend on fish body size, as body growth of small individuals was positively affected, while large individuals were not or even negatively affected by warm temperatures. How a fish will respond to warming can also depend on its sex, as I found that body growth of males was more negatively affected by warming than of females. Responses to browning depend on body size and also on species identity. I found that perch body growth was always negatively affected by browning, but effects were stronger for larger fish, while roach only seems to be negatively affected by browning when they are very small.

Overall, my findings in this thesis suggest that climate change, and the warming and browning of aquatic ecosystems that follows, will negatively affect fish individuals and populations, but that responses will vary with size, sex, and species. As fish play important roles in aquatic ecosystems, these impacts of warming and browning will likely affect entire lake ecosystems. This thesis therefore contributes to a broader understanding of how aquatic systems will respond to future climate change and highlights the importance of considering multiple climate stressors, studying responses of both individuals and populations, and acknowledging within- and between species variation, in order to understand and predict fish population responses to further climate change.

Populärvetenskaplig sammanfattning

Många akvatiska ekosystem i Nordeuropa blir både varmare och brunare på grund av klimatförändringar, vilket påverkar organismerna som lever i sjöar och kustområden. I denna avhandling visar jag att uppvärmning och "brunifiering" sannolikt kommer att leda till sjöar med mindre, yngre och långsamväxande fisk, vilket leder till mindre biomassa och en minskad produktion av fiskbiomassa. Jag visar också att effekterna av uppvärmning och brunifiering beror på fiskens kroppsstorlek, kön och vilken art de tillhör. Dessa effekter av uppvärmning och brunifiering på fiskbestånd kommer sannolikt att påverka samspelet med konkurrenter, byten och rovdjur, och kommer därför sannolikt att påverka hela sjöns ekosystem. Detta kan också påverka fisket eftersom det blir färre och mindre fiskar att fånga!

Klimatförändringar i tempererade regioner orsakar uppvärmning av akvatiska system, såsom sjöar. Det leder också till ökad nederbörd och vegetationstäckning på land, vilket kommer att öka inflödet av organiskt material till sjöar och vattendrag. Ökade koncentrationer av löst organiskt material göra att dessa sjöar förefaller brunare och minskar det tillgängliga ljuset i sjöarna. Både uppvärmning och brunifiering kan påverka fiskar som lever i sjöar på olika sätt. Uppvärmning kan påverka biologiska processer som metabolism och födointagshastighet; två processer som är viktiga för kroppstillväxten av fisk. Ljusbegränsning på grund av brunifiering kan påverka fiskens förmåga att se och hitta föda, men även också tillgången på föda och artsammansättningen av födosamhällen. Fisk av olika storlek, kön och arter kan potentiellt påverkas olika av uppvärmning och brunifiering, till exempel genom att vara olika beroende av synen för att hitta föda. Hittills har de flesta studier fokuserat på genomsnittliga effekter av klimatförändringar på fiskpopulationer. Ett ensidigt fokus på effekter på populationer förbiser det faktum att populationer består av individer, som

kan variera i deras svar på klimatförändringar på grund av kroppsstorlek och kön, och dessa effekter kan i sin tur variera mellan arter.

I den här avhandlingen studerade jag effekterna av varmare och brunare vatten på fiskar, både på individ och populationsnivå, och undersökte om dessa effekter varierade med fiskstorlek, kön och mellan arter. För att göra detta använde jag olika metoder, inklusive plats-för-tid-analyser, ett uppvärmningsexperiment på ekosystemnivå samt akvarie- och mesocosm-experiment. I dessa studier använde jag två fiskarter: abborre (*Perca fluviatilis*) och mört (*Rutilus rutilus*). Dessa är två av de vanligast förekommande arterna i europeiska sjöar, och särskilt abborre är en uppskattad art för både fritidsfiske och kommersiellt fiske.

Mina resultat visar att både uppvärmning och brunifiering av sjöar sannolikt kommer att leda till en minskning av fiskars biomassaproduktion och även en lägre fiskbiomassa. Detta sker genom att uppvärmning leder till en förändrad storleksstruktur i populationen då den till större del består av mindre och yngre individer i varma vatten. Brunifiering å andra sidan kommer sannolikt att påverka fiskens biomassaproduktion genom att minska kroppstillväxten. Jag fann också att effekten av uppvärmning beror på fiskens kroppsstorlek, eftersom små individer påverkades positivt, medan stora individer inte påverkades, eller påverkades negativt av varma temperaturer. Hur en fisk kommer att påverkas av uppvärmning kan också bero på dess kön, eftersom jag fann att hanar påverkades mer negativt av uppvärmningen än honor. Effekten av brunifiering beror också på kroppsstorlek och varierar mellan arter. Jag fann att kroppstillväxten hos abborre alltid påverkades negativt av brunifiering, och effekterna var starkare för större fiskar. Mört å andra sidan påverkas negativt av brunifiering endast när de är mycket små.

Sammantaget tyder mina resultat i den här avhandlingen på att klimatförändringar kommer att påverka fiskpopulationer och individer negativt, men att effekterna kommer att variera med storlek, kön och mellan arter. Eftersom fiskar spelar viktiga roller i akvatiska ekosystem kommer dessa effekter av uppvärmning och brunifiering sannolikt att påverka hela sjöekosystem. Denna avhandling bidrar till en bredare förståelse om hur akvatiska system kommer att påverkas av framtida klimatförändringar och belyser vikten av att inkorporera flera klimataspekter, studera både individer och populationer, samt ta hänsyn till variation inom och mellan arter för att förstå och förutsäga fiskpopulationers svar på ytterligare klimatförändringar.

Populairwetenschappelijke samenvatting

Door klimaat-verandering worden veel aquatische ecosystemen in Noord-Europa zowel warmer als bruiner. Dit tast de organismen aan die in meren en kustgebieden leven. In dit proefschrift laat ik zien dat opwarming en “verbruining” waarschijnlijk zal leiden tot meren met kleinere, jongere en langzamer groeiende vissen, wat leidt tot een lagere vispopulatie-biomassa en -productie. Ik laat ook zien dat de gevolgen van opwarming en verbruining voor vissen afhangen van hun lichaamsgrootte, geslacht en soort. De invloeden van opwarming en verbruining op vispopulaties zullen waarschijnlijk de interacties met concurrenten, prooien en roofdieren beïnvloeden en daarom het hele ecosysteem. Daarnaast kan het ook invloed hebben op de (sport)visserij omdat er minder en kleinere vissen zullen worden gevangen.

Klimaatverandering in gematigde streken leidt tot warmere meren en kustgebieden. Ook zorgt het voor meer regen en vegetatiegroei op het land, waardoor de instroom van organisch materiaal naar deze wateren toeneemt. Door verhoogde concentraties van dit organische materiaal worden deze meren bruiner en neemt de hoeveelheid licht onder water af. Zowel opwarming als verbruining kan vissen via een aantal wegen beïnvloeden. Opwarming kan biologische processen beïnvloeden, zoals metabolisme en voedselinname, die de lichaamsgroei van vissen bepalen. Lichtbeperking als gevolg van verbruining kan het vinden van voedsel door visie beïnvloeden, evenals de hoeveelheid en samenstelling van hun prooi. Vissen van verschillende grootte, geslacht en soorten kunnen mogelijk anders reageren op opwarming en verbruining. Bijvoorbeeld doordat hun biologische processen anders reageren op temperatuurstijgingen, of omdat ze meer of minder op hun zicht vertrouwen bij het vinden van voedsel. Tot op de dag van vandaag richten de meeste onderzoeken zich echter op de invloed van klimaatverandering op de gemiddelde vispopulatie. Hierbij wordt genegeerd dat

populaties uit individuen bestaan, voor wie de gevolgen van opwarming en verbruining kunnen verschillen door hun lichaamsgrootte, geslacht of soort.

In dit proefschrift heb ik de gevolgen van opwarming en verbruining van meren op individuele vissen en vispopulaties bestudeerd. Daarnaast heb ik onderzocht of deze gevolgen variëren met de grootte, het geslacht en tussen vissoorten. Hiervoor gebruikte ik verschillende methoden, waaronder “space-for-time” analyses, een opwarmingsexperiment van een heel ecosysteem, aquaria- en mesocosme-experimenten. In deze studies gebruikte ik twee vissoorten: Europese baars (*Perca fluviatilis*) en voorn (*Rutilus rutilus*), twee van de meest voorkomende soorten in Europese meren. Vooral baars is een geliefde vis voor sport- en commerciële visserij.

Mijn bevindingen tonen aan dat zowel opwarming als verbruining van meren waarschijnlijk zal leiden tot een afname van de visbiomassa productie. Opwarming zal hier waarschijnlijk toe leiden doordat populaties kleinere en jongere vissen en een lagere populatiebiomassa krijgen. Verbruining daarentegen zal waarschijnlijk de productie van visbiomassa beïnvloeden omdat het leidt tot een lagere lichaamsgroei. Ik laat ook zien dat gevolgen van opwarming inderdaad afhangen van lichaamsgrootte. Groei van kleine vissen werd positief beïnvloed, terwijl grote vissen niet of zelfs negatief werden beïnvloed door warme temperaturen. Ook verschillen gevolgen van opwarming per geslacht. Lichaamsgroei van mannetjes werd negatiever beïnvloed door opwarming dan van vrouwtjes. Gevolgen van verbruining zijn afhankelijk van lichaamsgrootte en vissoort. Ik ontdekte dat lichaamsgroei van baars altijd negatief werd beïnvloed door verbruining, maar dat de gevolgen sterker waren voor grotere baarzen, terwijl alleen erg kleine voorn negatief werden beïnvloed door verbruining.

Mijn bevindingen suggereren dat opwarming en verbruining van aquatische systemen een negatieve invloed zal hebben op vispopulaties, maar dat de gevolgen zullen variëren met de visgrootte, het geslacht en tussen vissoorten. Aangezien vissen een belangrijke rol spelen in aquatische ecosystemen, zullen deze effecten van klimaatverandering het hele ecosysteem beïnvloeden. Dit proefschrift draagt daarom bij aan een breder begrip van hoe aquatische systemen zullen reageren op klimaatverandering en benadrukt het belang van het overwegen van meerdere klimaatstressoren, het bestuderen van gevolgen op zowel individueel als populatieniveau en het erkennen van variatie binnen en tussen soorten, om zo de gevolgen voor vispopulaties van verdere klimaatverandering te begrijpen en voorspellen.

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Climate change is influencing many aquatic ecosystems, affecting the organisms living in them. This thesis shows that both future warming and browning of waters may negatively influence fish individuals and populations, but that responses will vary with size, sex, and between species. In order to understand and predict fish responses to climate change it is important to consider multiple climate stressors, integrate responses across several levels of biological organization, and acknowledge within- and between species variation.

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