How do warmer and darker waters influence
population dynamics in size-structured fish communities?

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Abstract

Changes associated with an increased water temperature due to global climate change have potentially large consequences for aquatic organisms. However, not only temperature but also the amount of precipitation is increasing. This increased precipitation leads to increased runoff from terrestrial ecosystems into lakes and coastal waters, introducing brown coloured humic substances containing dissolved organic carbon, leading to browner waters. This browning leads to a decrease of light in the water, which may reduce both primary production and visibility. The reduced visibility can, in turn, impact organisms dependent on light for e.g. feeding, mating, and predator evasion.

Warmer and browner waters can influence aquatic ecosystems on several levels of biological organization: individuals, populations and communities. The impacts on fish populations and communities mostly arise from individual-level impacts and interactions. To understand how this works, knowledge of how food-dependent body growth and size-dependent food intake impact fish population and community dynamics is needed. Some of the separate impacts of warming and browning on fish are well studied on multiple organizational levels. It is known that both warming and browning can have considerable influences on both availability and uptake of resources in aquatic systems. This influence can have immediate impact on fish individuals and populations, but also shift competitive ability among individuals of different sizes. As a consequence, there may be changes in growth rates, mean body size, fish productivity and species composition in response to warming and browning. Climate change often results in both warmer and darker lakes. Still, the combination of warmer and darker water bodies on fish individuals, populations, and communities, have not been studied extensively. In combination, the various effects of warming and browning might even be more pronounced than individually. As fish populations and communities are important for both ecosystem function, and recreational and commercial fisheries, it is important to identify the knowledge gaps concerning the combined impact of an increase in temperature and browning. In this essay I identify big gaps in our current knowledge on the combined effects of temperature and browning on interacting fish individuals and populations. The knowledge arising from future studies on combined climate change effects on interacting fish species can, for example, be used to adapt current fisheries management strategies to a future climate characterized by warmer and darker lakes.

Keywords: climate change, temperature increase, browning, dissolved organic carbon, size-structured populations, inter-specific interactions, intra-specific interactions, population dynamics, community dynamics, physiology

Table of contents

List of Figures

6

Abbreviations

CRD	Critical Resource Density
DOC	Dissolved Organic Carbon
MTE	Metabolic Theory of Ecology
ONS	Ontogenetic Niche Shift
PAR	Photosynthetically Active Radiation
TSR	Temperature-Size-Rule
YOY	Young-Of-the-Year

1   Introduction

Over the last decades our climate has been changing, and will continue to do so over the next century IPCC (2014). In temperate areas a large increase in both mean annual temperatures and precipitation is expected (Whitehead et al. 2009). Since surface water temperatures are strongly correlated with air temperature, water temperatures in Scandinavia have also increased over the last decades. In lakes, increasing temperatures can cause higher epilimnion (the upper layer of a lake) temperatures (2-5 °C), a shorter ice cover in the winter and the cold hypolimnion (the deepest layer of a lake) can become deeper and therefore decrease in size (Lehtonen 1996, IPCC 2014). These changes associated with increased temperature due to global climate change have potentially large consequences for aquatic organisms.

Not only temperature, but also the amount of precipitation has increased over the last decades, and will keep increasing (IPCC 2014). An increase in precipitation in the catchment area of lakes often leads to an increase in runoff from terrestrial ecosystems into lakes and coastal waters. This runoff from the catchment area carries with it brown coloured humic substances containing dissolved organic carbon (DOC) (Roulet and Moore 2006). An increase in brown colouring of the water due to these humic substances is called 'browning' (Larsen et al. 2011, Graneli 2012). Because water and the dissolved substances within it absorb sunlight when it passes through the water column, browning leads to an increase in light absorbance of the water, causing a decrease of light in the water column (Bukaveckas and Robbins-Forbes 2000). The decrease of available light due to browning of the water means there is less light (photosynthetic active radiation, PAR) available for primary producers like phytoplankton and macrophytes. As a consequence, there is less plant biomass production in brown lakes, especially in the benthic zones (Ask et al. 2009, Seekell et al. 2015a). Furthermore, the decrease in light leads to a decrease in visibility in the water, which can impact organisms dependent on light for e.g. feeding, mating, and predator evasion (Estlander et al. 2012, Estlander and Nurminen 2014). However, runoff also leads to nutrient enrichment (nitrogen, phosphorus), which instead could lead to an increase in productivity. Heterotrophic bacteria may also benefit from the increased DOC (Tranvik 1988, Jansson et al. 2007), and their increased productivity may lead to more transfer of biomass to higher trophic levels (Jansson et al. 2007). However, this may not increase overall community biomass production, because the energy transfer from bacteria up the trophic food chain is less efficient than that of e.g. phytoplankton (Berglund et al. 2007).

Both a warmer water temperature and browning of the water can influence aquatic ecosystems on several levels of biological organization: individuals, populations and communities. The impacts of climate change on the population and community level mostly arise from individual level impacts and the interactions among individuals. Therefore, in order to understand the impact of e.g. climate change acting through warming and browning, we need to understand how they affect individuals directly as well as how these effects will manifest at higher organizational levels, i.e. within populations and whole communities. On an individual level an increase in temperature is known to often lead to an increase in immature growth rate, earlier maturation, and a decrease in mature body size-at-age in many different organisms (*temperature-size-rule*) (Atkinson 1994, Berrigan and Charnov 1994, Atkinson 1995, Angilletta et al. 2004). On a population level an increase in temperature often leads to a decrease in mean and maximum population body size, and a shift in size-structure with a greater proportion of small individuals (Daufresne et al. 2009, Jeppesen et al. 2012, Baudron et al. 2014, Arranz et al. 2016). In addition, warmer water may lead to a change in fish productivity and population standing stock biomass, depending on the optimal temperature of the species (Rijnsdorp et al. 2009, Cheung et al. 2010, Jeppesen et al. 2010, Brose et al. 2012). A decrease in fish mean body size is often seen also at the community level, either because all or most of the present populations exhibit a decrease in mean body size, or due to the immigration of smaller-bodied species which often prefer warmer waters (Daufresne et al. 2009). Apart from the changes in body size, a decrease in community productivity and standing stock biomass of fish has also been observed (Cheung et al. 2010, Jeppesen et al. 2010). Furthermore, an increase in temperature can lead to mismatches in phenology between e.g. phyto- and zooplankton, leading to a decrease in food availability for higher trophic levels (Stenseth and Mysterud 2002, Nicolle et al. 2012).

An increase in browning and the consequential decrease in plant primary productivity and visibility in the water column can influence fish on all organizational levels. On an individual level a decrease in primary production can lead to a decrease in available resources, which can lead to a decrease in growth rate and a smaller size-at-age (Horppila et al. 2011). The decrease in visibility can further enhance this pattern, since it may be hard for fish relying on vision to find prey (Estlander et al. 2010, Horppila et al. 2011, Estlander et al. 2015). On a population and community level browning may lead to a decrease in mean body size (Horppila et al. 2010) and a decrease in fish productivity and standing stock biomass (Karlsson et al. 2009, Karlsson et al. 2015). Furthermore, browning can lead to a change in species composition,

since species that are less dependent on visibility when foraging may gain a competitive advantage over species that are more dependent on vision for finding prey (Jönsson et al. 2012, Jönsson et al. 2013).

Thus, both warming and browning alone can affect individuals, populations and whole communities in aquatic systems. However, climate change often leads to the combination of warmer and darker water in lakes, and concurrent changes in other parameters (e.g. nutrients). Still, the impacts of this combination of warmer and darker water bodies on fish individuals, populations, and communities have not been studied extensively. Both warming and browning can have a considerable influence on the resource availability and resource uptake in aquatic systems, which has an immediate influence on the individuals and populations in these systems. However, it is largely unknown how these direct effects on the physiology on individuals scale up to influence populations of interacting individuals and communities of interacting species.

The aim of this essay is to identify the knowledge gaps concerning the combined impact of an increase in temperature and browning on fish individuals, populations and communities. In order to do so I first discuss food-dependent body growth and size-dependent food intake, and their consequences for fish population and community dynamics. Thereafter, I review the impacts of increased water temperatures and browner waters separately on fish individuals, populations, and communities, in the context of food dependent development and size dependent food intake. Finally, I identify knowledge gaps concerning the effects of the combined impacts of warming and browning on fish, and potential implications for future fisheries management.

2   From ontogenetic development to community ecology

2.1   Food-dependent body growth and energy allocation

For an individual to grow it needs energy and nutrients, and therefore food. Next to somatic growth, energy is needed for standard (resting) metabolism, active metabolism (cost of activity) and reproductive costs. Exactly how energy is divided over these factors is often not known and can vary among organisms. Still, there are different models that try to explain this energy allocation. The net assimilation model assumes that energy first goes to reproductive costs, and the remainder is used for somatic growth and metabolism (resting + active) (Kooijman and Metz 1984). The net production model, commonly used for fish, instead claims that energy first is used for metabolism, and the remainder is divided between somatic growth and reproduction (Kooijman and Metz 1984, Persson et al. 1998, Persson and De Roos 2006). However, metabolic costs are not the same for all individuals. Generally, metabolic demand 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, allowing for growth and reproduction.

The energy reserved for somatic growth is not equally allocated to different body parts. And it is also used differently depending on life stage and food conditions (Heino and Kaitala 1999). For example, energy may be converted to mass that can be starved away and converted to energy to sustain metabolic function, like muscles, fat and gonads. In contrast, mass like bones and organs, cannot be starved away (Persson et al. 1998). For fish, maturation usually occurs when a certain body size (Persson et al. 1998) and/or condition (mass to length ratio) is reached (Morgan 2004). Time to reach maturity often increases when food is scarce, as somatic growth, which is needed to reach the desired maturation condition, is food-dependent. Food-limitation may in addition lead to a smaller size-at-maturation (Berrigan and Charnov 1994, Teder et al. 2014). After maturation, adults generally have a slower growth than juveniles due to an increased allocation of energy to the gonads (Persson et al. 1998).
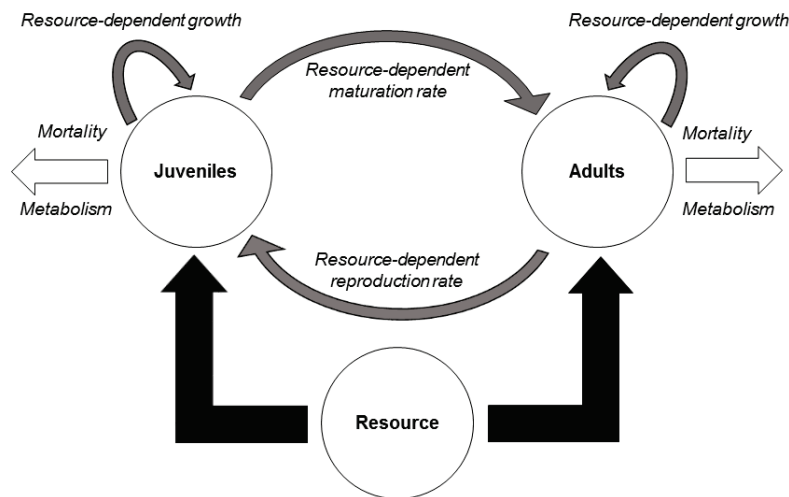
Figure 1. Schematic illustration of the energy paths in a consumer life cycle. Juvenile and adult consumers gain energy from food consumption (black arrows). This energy is first used for metabolism or lost by mortality (open arrow), and the remaining energy is put into somatic growth (juveniles and adults), maturation (juveniles) and reproduction (adults) (open arrows) (adapted from De Roos and Persson, 2013).

2.2   Size dependent food intake and ontogenetic asymmetry

The rate at which predators capture their prey, and therefore the rate at which they gain energy, varies depending on prey density and the prey:predator size ratio. Most models in fish ecology assume that capture rate as a function of prey density follows a Holling type 2 (decelerating) functional response, as this response has been experimentally observed in many fish species (Petersen and DeAngelis 1992, Moustahfid et al. 2010, Murray et al. 2013). The functional response is a function of prey mass encounter (attack rate x resource density), and the capacity to digest the prey (handling time) (Mittelbach 1981, Persson 1987, Byström and García-Berthou 1999, Hjelm and Persson 2001). The rate by which predators attacks prey of a specific size first increases monotonically with predator size, due to an increase in visual acuity, improved mobility, and for gape-limited predators such as fish because they overcome gape constraints (Christensen 1996, Claessen et al. 2000). After an optimum predator size is reached the attack rate often decreases again because the prey item will be too small to see (for visual predators) and because fine scale mobility of predators often decreases at large body sizes (Claessen et al. 2000). This leads to a hump shaped function of attack rate with predator size (Fig. 2a) (Persson et al. 1998). Handling time, on the other

hand, commonly decreases with predator body size, due to e.g. increased digestive capacity (Fig. 2b) (Mittelbach 1981, Persson 1987). Together, the size-dependencies of attack rate, handling time and metabolism determine the minimum prey density needed for individuals of different sizes to meet metabolic demands (commonly referred to as the *critical resource density*, CRD) (Persson et al. 1998). CRD often increases with body size in fish (as shown experimentally for planktivorous fish such as Arctic char (*Salvelinus alpinus*) and roach (*Rutilus rutilus*) (Hjelm and Persson 2001, Byström and Andersson 2005), because of the previously mentioned faster increase in metabolism (Fig. 2c) than in foraging efficiency with body size (Fig. 2d) (Persson et al. 1998). A monotonically increasing CRD with body size means that the smaller individuals are superior competitors relative to larger conspecifics for shared resources (Persson et al. 1998). Given a relationship between CRD and body size, either small or large individuals are more efficient in acquiring and/or using resources to produce new body mass, leading to *ontogenetic asymmetry* (De Roos and Persson 2013, see more below).
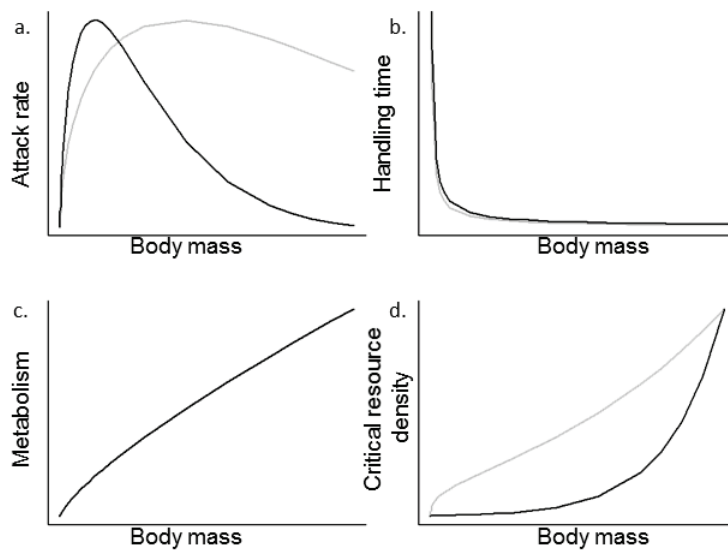
Figure 2. A schematic presentation of a) attack rate, b) handling time, c) metabolism and d) critical resource density (CRD) as a function of body mass for zooplanktivorous perch, *Perca fluviatilis* L (black) and roach (grey). All perch parameters are set according to Claessen et al. (2000), and the roach parameters are set according to van de Wolfshaar et al. (2006), assuming they feed on 1 mm cladocerans.

14

In addition to increasing the number of consumed prey as predators grow in size, an increase in energy intake can be accomplished by shifting to feeding on larger and more energy rich prey. Such ontogenetic niche shifts (ONS) in diet are common in many animal taxa (Werner and Gilliam 1984, Mittelbach and Persson 1998, Miller and Rudolf 2011). If there are no alternative resources available in the present habitat, individuals often shift habitat as they grow in size to accomplish a shift in diet. 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/stage ontogenetic shifts in diet take place depends on many factors, such as food availability (Mittelbach and Persson 1998), intra- and interspecific competition (Schoener 1974, Werner and Gilliam 1984) and predation risk (Mittelbach and Persson 1998).

2.3 Population and community-level consequences of ontogenetic asymmetry

2.3.1 Bottlenecks and cohort cycles

Ontogenetic asymmetry may cause an energetic bottleneck between life stages caused by intraspecific competition (De Roos et al. 2007, Persson and De Roos 2013). If juveniles are competitively superior over adults, the maturation rate will be higher than the reproduction rate. In this case, adults will constitute most of the biomass in the population and experience high competition, leading to a low reproduction rate. Consequently, in this situation, in which juveniles have a higher mass-specific rate of biomass production, referred to as *reproduction regulation*, the bottleneck will be in the adult stage. In contrast, when adults are competitively superior and have a higher energetic efficiency, referred to as *maturation regulation*, the reproduction rate will be higher than the maturation rate. In this case, juveniles will constitute most of the biomass and the bottleneck will be in the juvenile stage (De Roos et al. 2007, De Roos and Persson 2013, Persson and De Roos 2013). Note also that competitive juvenile bottlenecks because of interspecific competition are common in nature (Persson and Greenberg 1990, Byström et al. 1998).

In addition to its effects on biomass distribution among life stages, the relationship between the CRD and body size influences population dynamics (Persson et al. 1998). When CRD increases with body size, populations can exhibit cycles in cohort abundance as large newborn cohorts will outcompete older (larger) individuals. In the extreme case this results in cycles of single cohorts with high abundance being outcompeted after maturation (i.e. single-

cohort cycles) (Persson and De Roos 2006). Consequently, in such systems cycles will have the same length as the organisms generation time. Conversely, if CRD would decrease with body size, older individuals outcompeting most of the newborns would drive the cycles. For planktivorous fish it is most often found that CRD increases with body size, which results in cycles driven by young-of-the-year (YOY) cohorts (Persson et al. 1998, Persson and De Roos 2006). Actually, most cyclic populations, of many different species, seem to exhibit cycles that scale to the generation time of the organism, rather than predator-prey cycles, which have longer cycle periods (Murdoch et al. 2002).

2.3.2   Biomass overcompensation and the emergent Allee effect

Ontogenetic asymmetry in prey population can also have consequences for predators. A common assumption in ecological models is that mortality (e.g. by predation) leads to a lower prey population biomass. However, given ontogenetic asymmetry in energetics, mortality can lead to an increase in standing stock biomass (in one stage, or the whole population), referred to as biomass overcompensation (De Roos et al. 2007, Schröder et al. 2014) or the Hydra effect (Abrams and Matsuda 2005, Abrams 2009). This biomass overcompensation can be stage specific (e.g. only occur for juveniles or adults) or occur on a population level and can occur regardless of whether mortality affects a specific life stage or the whole population (Persson and De Roos 2013). If mortality increases from low levels in a *maturation regulated* population, juvenile biomass will decrease, directly through predation and indirectly through a decreased reproduction due to initial adult mortality. This will release the juvenile bottleneck, because competition decreases and more energy will be available (per individual) for growth and maturation, which will lead to an increase in adult biomass. If mortality increases in a *reproduction regulated* population, the previously dominating adult biomass will decrease. This will release the adult bottleneck and individual adult fitness will increase, leading to an increase in reproduction rate and therefore juvenile biomass. However, as mortality rate increases to high enough levels, both juvenile and adult biomass will decrease (De Roos et al. 2007, Schröder et al. 2009, Persson and De Roos 2013).

As predators often prefer prey of certain body sizes to maximize energy intake (see 2.2), but are constraint e.g. due to gape size constraints, they are often limited to impose mortality on certain size classes, in fish often being juveniles (Mittelbach and Persson 1998, Nilsson and Brönmark 2000). When

predators induce a high juvenile mortality in a *reproduction regulated* system, which is originally dominated by adults, competition among adults will decrease, due to decreased number of juveniles maturing. This means more energy available for reproduction which will lead to an increase in juvenile prey, which will benefit predators selectively feeding on juveniles. Thus, predators can by their own consumption increase the density of their preferred prey, a mechanism referred to as an *emergent Allee effect* (De Roos et al. 2003, De Roos and Persson 2013). The presence of an emergent Allee effect also implies that high predator densities may be needed to maintain a stable state of high abundance of suitable sized prey (Gårdmark et al. 2015) and also that predators may not be able to re-invade systems from low densities due to lack of prey of suitable sizes (De Roos et al. 2003).

2.3.3 Emergent facilitation

Many systems have multiple predator species feeding on the same pool of prey species. Two predators may, for example, feed on different life stages of a prey species, e.g. when there is a predator specialized on juvenile prey and another predator specialized on adults (De Roos et al. 2008). Given a scenario with a high amount of juvenile prey with a limited food source (i.e. a juvenile bottleneck and maturation regulation) and low adult biomass, an adult-specialized predator cannot invade. However, when a juvenile-specialized predator invades and induces a competitive release in the juvenile prey stage, maturation rate and adult biomass increase. This creates a perfect situation for the adult-specialized predator, which now has enough food to establish its population. This is referred to as *emergent facilitation*, meaning that one predator species creates an environment that facilitates the invasion of a second predator (De Roos et al. 2008, Huss et al. 2012). This mechanism was demonstrated in an experiment with zooplankton (Huss and Nilsson 2011).

In a scenario where the prey shows ontogenetic shifts in diet there may, at a certain ratio of available resources for adult and juvenile prey, be a mutual facilitation between the juvenile- and adult-specialized predators. The latter implies that neither can survive without the other (De Roos and Persson 2013). It may also be that there is a generalist predator that feeds on the whole prey population and thereby facilitates a juvenile-specialized predator that only feeds on part of the prey population (De Roos and Persson 2013). Emergent facilitation, as well as emergent Allee effects, are consequences of biomass overcompensation and are therefore only possible in prey populations with ontogenetic asymmetry, which is true for most (if not all) populations (De Roos and Persson 2013).

2.3.4 Implications of ontogenetic niche shifts

One common predator-prey interaction in size structured predator-prey systems, is intra-guild predation (Polis et al. 1989). In populations with ontogenetic niche shifts, it is common that adult predators feed on the prey species while the juvenile predators compete with this prey for a shared resource. In fish populations, competition from prey fish for shared invertebrate resources can limit predator recruitment, leading to a juvenile competitive bottleneck for the predator (Byström et al. 1998). When predator abundance is high, they control the prey population (i.e. keep it at a low density), and therefore cultivate a better environment with less competition for their young, of which more will grow to become adults. This leads to a stable state with high predator abundance (*cultivation*) (Walters and Kitchell 2001, Gårdmark et al. 2015). It has been suggested that one condition for cultivation is that there should be a discrete dietary switch of the predator between the shared invertebrate resource and piscivory (van Leeuwen et al. 2013), such that the top-down control from the predator on the prey fish is strong enough to release juveniles from interspecific competition. On the other hand, when the predator is at low abundance the predator is not able to control the prey abundance resulting in high interspecific competition between juvenile predators and the prey fish. The latter results in that the predator population biomass stays low (*depensation*) (Walters and Kitchell 2001, Gårdmark et al. 2015).

ONS can thus have significant impacts on the population and community level by affecting both intra- and interspecific interactions, and are therefore important to take into account when studying ecological systems (Miller and Rudolf 2011, Rudolf and Rasmussen 2013). As some individuals of a population switch diet and/or habitat, also intraspecific competition may decrease as fewer individuals utilize the same limiting resource, all else equal leading to increased individual growth and fitness (Schellekens et al. 2010). ONS can also lead to resource partitioning between species, when for example one species switches to a piscivorous diet, while the other keeps a benthivorous diet throughout its life. This can decrease interspecific competition (Schoener 1974). The latter may in many cases actually be key for coexistence of species sharing the same limiting resources, otherwise expected to lead to competitive exclusion (Schellekens et al. 2010).

3 Fish community responses to warmer waters: scaling up from individual-level processes

An increase in temperature may influence all organizational levels of an eco-system; individuals, populations and communities. These three levels of or-ganization and how temperature influences them are strongly interrelated. The impacts of climate change on the population and community level mostly arise from individual level impacts and the interactions among individuals. Therefore, in order to understand the impact of warming and browning, we need to look at the effects on individuals directly as well as how these effects will manifest themselves at higher organizational levels.

3.1 Individuals

In ectothermic organisms the rate of biological processes depends on temper-ature (Yvon-Durocher et al. 2010). Therefore, the preferred temperature range of ectothermic organisms is largely determined by biological rates such as metabolism and food intake (i.e. attack rate and handling time). According to the metabolic theory of ecology (MTE) (Brown et al. 2004), the metabolic rate increases exponentially with temperature until it reaches an optimum, after which it shows a sharp decrease - like all other biochemical reaction rates (Ohlberger 2013). With an increase in metabolic rate with temperature, animals need an equal increase in food intake to cover metabolic costs (Brown et al. 2004, Lemoine and Burkepile 2012). For the latter, the attack rate should increase and/or handling time decrease with temperature, which indeed has been shown to be the case (Rall et al. 2012). However, attack rate often has a hump-shaped relationship with temperature (Johnston and Mathias 1994, Englund et al. 2011, Rall et al. 2012, Lefébure et al. 2014). In contrast, handling time often decreases with temperature until an optimum after which it increases (Englund et al. 2011, Rall et al. 2012). Still, food intake often does not increase as fast as metabolism with increasing temper-ature (Rall et al. 2010, Ohlberger et al. 2011, Rall et al. 2012). Food intake may not keep up with metabolism when temperature increases, which has been shown, for example, for a sea urchin species where an increase in tem-perature eventually led to a strong decrease in net energy intake (Lemoine and Burkepile 2012). In contrast, Lefébure et al. (2014) showed that three-

spined sticklebacks (*Gasterosteus aculeatus*) had such a sharp increase in attack rate with an increase in temperature that food intake could easily keep up with the increase in metabolic costs. Consequently, for sticklebacks CRD even decreased with temperature.

Because food intake cannot keep up with an increased metabolism indefinitely there will often be a temperature threshold above which the energy surplus available for growth decreases. This will lead to a hump shaped growth curve with temperature (Lemoine and Burkepile 2012). Thus, the growth response following a temperature increase depends on the current temperature, the optimum temperature of the individual, and the extent of temperature increase. When the new temperature is above the optimum performance temperature of the individual, growth rate will decrease and individuals will remain small (Ohlberger 2013). However, even with a new temperature below the optimal temperature, ectotherms often show a phenotypic response by having a faster pre-mature growth rate, earlier maturity at smaller size, a smaller (mature) size-at-stage, shorter lifespans and less energy used for reproduction than organisms in colder environments, a pattern referred to as *the temperature size rule* (TSR) (Atkinson 1994, Berrigan and Charnov 1994, Atkinson 1995, Jeppesen et al. 2010). However, there are also cases where a higher water temperature led to an increase in maximum body size (O'Gorman et al. 2012). It is still unclear what the exact mechanism(s) behind the TSR is, although many have tried to find out (e.g.Berrigan and Charnov 1994, Angilletta and Dunham 2003). The TSR might just be a consequence of the adaptive advantage of a smaller body size at higher temperatures, due to the higher optimum temperature for metabolism and food intake of small compared to large individuals (Kozłowski et al. 2004, Ohlberger 2013). The higher demand for oxygen (due to an increased metabolic rate) with size and temperature, and the decrease of dissolved oxygen present in warmer waters could also be an underlying factor explaining the temperature size rule in aquatic organisms (Pörtner and Knust 2007, Baudron et al. 2014, Hoefnagel and Verberk 2015).
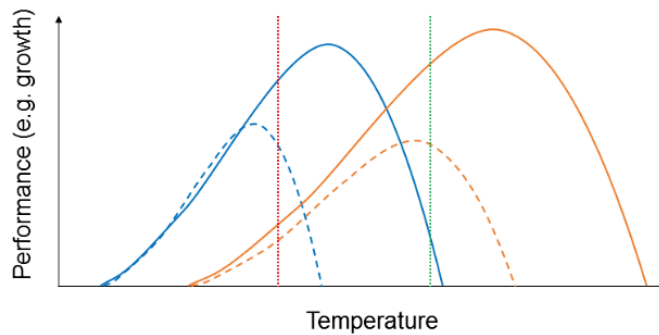
Figure 3. Performance as a function of temperature for adults (dashed) and juveniles (solid) of species 1 (blue) and species 2 (orange), or for two individuals of the same species experiencing either high (solid) or low (dashed) food availability.

Each species has their own preferred range of temperatures at which their biological rates are optimized (Fig. 3). Such species-specific adaptations combined with spatial variation in water temperatures influence geographical distributions of aquatic species and community composition. (Pörtner and Farrell 2008). Still, some species (or populations) have a high phenotypic plasticity for traits that are temperature dependent, and are therefore able to cope with a wide range of temperatures. Other species may have a low phenotypic plasticity for these traits and may therefore be more strongly influenced by even a small increase in temperature (Ficke et al. 2007, Crozier and Hutchings 2014, Merilä and Hendry 2014). Over time there may also be an evolutionary response to rising temperatures as genetic adaptations arise (Crozier and Hutchings 2014).
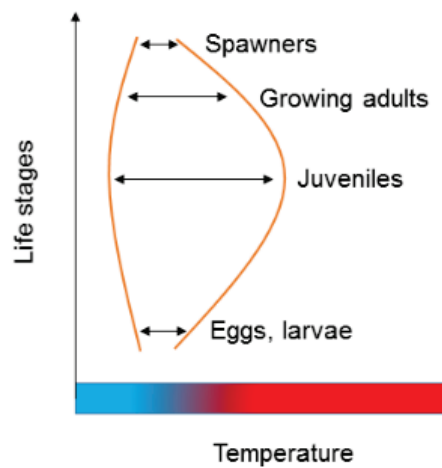
Figure 4. A hypothetical example of how preferred temperature ranges may change through ontogeny. The length of the arrows indicates the width of the thermal range which the different life stages prefer (figure adapted from Pörtner and Forrel 2008).

The width of preferred temperature ranges and the optimum temperature does not only differ between species, in many cases it also differs between life stages and as a function of body size within species. Eggs and reproducing adults often have a rather narrow preferred temperature range, while juveniles are able to handle a wider range of (higher) temperatures (Pörtner and Farrell 2008) (Fig. 4). However, preferred temperatures do not just depend on life stage, but also on actual fish size, as optimal temperature seems to decrease with body size within species. Metabolic rate and other vital rates change both with body size and with temperature, but there may also be an interaction between body size and temperature. Ohlberger et al. (2011) developed a theoretical model to study the change in energy gain with body size and temperature in fish and found that energy gain increases faster with temperature for small bodied individuals than for large ones. This means (all else equal) that high temperatures should favour small individuals over large ones. However, this relationship between body size and temperature may not always exist and can also differ between species (Ohlberger et al. 2012). An increase in temperature (from red to green line in Fig. 3) might therefore have very different effects on different life stages, e.g. juveniles might still be below their optimal temperature and experience an increased growth rate, while larger adult individuals are above their optimal temperature and experience a decreased growth rate (Ohlberger 2013)(Fig. 3).

22

The preferred temperature range and optimal temperature are strongly dependent on food availability. If food is a limiting factor the preferred temperature range may narrow and the optimal temperature decreases (Fig. 4) (Ohlberger 2013), which was shown in an experiment with brown trout (*Salmo trutta*) (Elliott and Hurley 2000). An increase in juvenile growth rate, as predicted by the TSR, can only be achieved if the food intake can keep up with the increased metabolism (Gillooly et al. 2001). Therefore, in a high competition environment with resource limitation, an increase in temperature can lead to a decrease in growth rate for all life stages. On the other hand, if predation pressure (including cannibalism) increases at high temperatures, competition may weaken, leading to an increase in prey growth rate. Thus, if the increase in temperature is accompanied by an increase or decrease in growth rate is partly dependent on how the strength of intra- and interspecific interactions and competitive intensity vary with temperature (Ohlberger 2013).

3.2 Populations

3.2.1 Body size distributions, standing stock biomass and production

Population body size distributions may change with temperature due to the impacts of temperature on individuals' vital rates. A common observation is that when temperature increases the mean body size in the population decreases, even when food is not a limiting factor (Daufresne et al. 2009, Jeppesen et al. 2012, Baudron et al. 2014, Arranz et al. 2016). There are multiple (non-exclusive) explanations for a decrease in population mean body size, which stem from changes at the level of individuals. The first is the TSR, which implies that after a high initial growth rate, individual size-at-age and maximum size decrease when temperature increases (Atkinson 1994, Daufresne et al. 2009). Another explanation is that there is an asymmetry between life stages in thermal optima and competition for shared resources, which in fish often leads to a higher proportion of competitively superior young and small fish in the population (i.e. a structural shift) at high temperatures (Daufresne et al. 2009, Jeppesen et al. 2010, Ohlberger 2013, Arranz et al. 2016). However, this pattern is species-dependent and in some species also the opposite pattern has been observed; Belk and Houston (2002) found that for many North American freshwater fish species mean population body size actually increased with increasing temperature.

Because body growth is food-dependent, temperature effects on population size distributions should be strongly density dependent. At high popula-

tion density and a limited food supply there is strong competition for resources, which can lead to a decrease in individual growth rates and maximum body size (Crozier et al. 2010, Ohlberger 2013). Accordingly, for Chinook salmon (*Oncorhynchus tshawytscha*), Crozier et al. (2010) observed a decrease in the growth rate of young individuals with temperature when population density was high, but an increased growth rate with temperature at low density. As stated above (chapter 2.2), next to the dependence of body growth on food intake, food intake itself is size-dependent due to changes in attack rate and handling time with body size. Therefore, a smaller mean body size and a change in the size structure of the predator population may change the size and/or species of prey that is consumed with increasing temperatures (Elliott and Hurley 2000, Persson and De Roos 2006, Englund et al. 2011). It could also influence the timing of ontogenetic niche shifts, which may have to happen at a smaller size to keep up with the increased energy demands at high temperatures (Pörtner et al. 2010).

In addition to a change in body size distributions, an increase in water temperature could lead to a change in both biomass production and standing stock population biomass. As shown above, population responses to an increase in temperature depend, among other things, on the preferred temperature range of the population, the amount of temperature increase and food availability (Vasseur and McCann 2005, Ohlberger et al. 2011). Cold- and cool-water adapted fish species with low phenotypic plasticity are more likely to be negatively affected by an increase in water temperature, than warm-water-adapted fish species. If the new temperature is above their optimum temperature and food is limited, their production and therefore population biomass may decrease, unless they can migrate to more suitable areas. Warm-water adapted fish species may instead benefit from an increase in temperature, if the new temperature is still below their optimum temperature and food is not limited, leading to an increase in production and population biomass (Rijnsdorp et al. 2009, Cheung et al. 2010, Jeppesen et al. 2010, Brose et al. 2012). Accordingly, an increase in production and standing stock biomass has been observed for some marine fish species at their northern distribution limits, while a decrease was observed at the southern distribution limit (Rijnsdorp et al. 2009).

Given that physiological thermal responses are life-stage- and size-dependent, biomass responses to higher temperatures are likely to differ among life stages and sizes (Daufresne et al. 2009, Jeppesen et al. 2010, Ohlberger 2013). In addition to these direct physiological responses to temperature, there can be stage-specific indirect biomass responses to temperature. Differ-

ent sizes/stages may feed on different food resources (ONS) and/or be exposed to different predators, which may respond differently to an increased temperature. This may lead to size/stage-specific shifts in competition and/or predation pressures (Yang and Rudolf 2010), which could lead to differential temperature biomass responses, depending on life stage and body size. Thus, there may be shifts in body size distributions among life stages due to differences in both direct and indirect temperature impacts. However, this is likely to be very species- and situation specific and has as far as I know not been studied extensively.

3.2.2 Impacts of a temperature increase on population dynamics

Expected changes in mean population body size, size structure shifts and changes in abundance with increasing temperature will affect intraspecific interactions and population dynamics, and vice versa (Jeppesen et al. 2010, Brose et al. 2012, Ohlberger 2013). For example, Ohlberger et al. (2011), studied the effect of temperature on intraspecific competition and resource density of a fish population using a size-structured population model. Their model predicts a decrease in resource density with temperature, due to an increase in individual energy requirements and hence feeding, and therefore, an increase in intraspecific competition between consumers. Above a critical temperature the population dynamics therefore shifted from a stable equilibrium to generation cycles driven by intraspecific competition. The latter resulted in an increase in the ratio of young/small to old/large individuals (Ohlberger et al. 2011). As cycle length is generally related to generation time (Murdoch et al. 2002), which should decrease with temperature (due to earlier maturation) (Atkinson 1994), it can be hypothesized that cycle lengths should decrease with an increasing temperature. However, there are to my knowledge no empirical examples of this and there are also few examples of other impacts of temperature on fish population dynamics.

3.3   Communities

3.3.1 Body size distributions

Shifts in community body size distributions and mean body size in response to increased temperature may, in addition to the intraspecific factors discussed above (e.g. TSR, size-structure-shift), be caused by shifts in species composition (Perry et al. 2005, Daufresne et al. 2009). Shifts in body size distributions accompanying shifts in species composition can arise because

smaller species that are competitively superior at warm temperatures migrate to these warming areas, while larger species which are not able to cope with the increased temperature migrate away (Emmrich et al. 2014). Shifts in community size-structure and mean body size can be caused by either a body size shift in the populations already present or a shift in community composition, or a combination of the two (Daufresne et al. 2009, Cheung et al. 2013, Ohlberger 2013, Emmrich et al. 2014). Furthermore, changes in body size and biomass of a species can strongly influence the body size and productivity of other species it interacts with (e.g. its prey, predator or competitor), in turn, changing community body size distributions.

3.3.2 Bottom-up vs. top-down in a warming climate

When the population structure or abundance of one trophic compartment changes due to an increase in temperature, it can lead to cascading effects among trophic levels, i.e. indirect warming effects (Brose et al. 2012). When either the top consumer population or basal resource populations are affected by climate change there can be a change in top-down relative to bottom-up control. (Estes et al. 2011, Jonsson and Setzer 2015). Several studies have suggested that top-down control increases relative to bottom-up control with temperature (Kratina et al. 2012, Shurin et al. 2012). This has been explained by increased food intake with temperature, especially at the highest trophic level (Shurin et al. 2012). For example, in two freshwater mesocosm experiments with three-spined sticklebacks their influence on the lower trophic levels increased with temperature (Kratina et al. 2012, Shurin et al. 2012). In contrast, bottom-up control decreased due to a decrease in phytoplankton biomass (irrespective of nutrient level), and a change in phytoplankton community composition with an increase in temperature, without associated changes in consumer biomass like you would expect with bottom-up control (Kratina et al. 2012, Shurin et al. 2012). Also, as an increase in temperature can shift species distributions and community composition, there is potential for new top-predator species to enter the system, in turn, shifting top-down control and inducing a trophic cascade. An example of the latter arose when pike invaded a subarctic lake and caused a collapse of the Arctic char population, a decrease in the nine-spined stickleback (*Pungitius pungitius*) population, and an increase in zoobenthos and zooplankton biomass (Byström et al. 2007).

3.3.3 Phenology and match-mismatch

Due to climate change the phenology (periodic biological events that are climate dependent) of many populations changes, which can lead to mismatches in interspecific interactions and therefore decoupling of trophic levels (Durant et al. 2005, Yang and Rudolf 2010). In aquatic systems, the increase in temperature influences timing of many biological processes, like plankton blooms and egg hatching, which start earlier in the spring time, especially in northern regions (Stenseth and Mysterud 2002, Winder and Schindler 2004). An example of a mismatch was seen by Jonsson and Setzer (2015), where great Arctic charr (*Salvelinus umbla*) eggs hatched earlier due to a sharp increase of the water temperature in winter, while the timing of the zooplankton bloom did not change as much. Consequently, the Arctic charr eggs hatched during a time with low resource levels. This mismatch in resource levels and hatching, among other factors, led to a decline in the Arctic charr abundance (Jonsson and Setzer 2015). Also other studies have shown that fish larvae are very sensitive to mismatches with their zooplankton prey (e.g. Brander 2010).

4 Fish community responses to browner waters: scaling up from individual-level processes

Browning of waters, due to the input of coloured terrestrial organic (humic) material (dissolved organic carbon, DOC), leads to an increased light attenuation. This has two major consequences, 1) a decreased light availability for primary producers and 2) a decreased visibility for the consumers in the water (Wetzel 2001, Ask et al. 2009, Karlsson et al. 2009, Seekell et al. 2015a, 2015b). However, up to a certain level browning may have a positive influence on primary production, since it is a major source of nutrients (Finstad et al. 2014). However, after a threshold is reached the increase in light attenuation negatively influences primary production of phytoplankton, benthic microalgae and macrophytes and decreases visibility (Ask et al. 2009, Finstad et al. 2014, Seekell et al. 2015a, Seekell et al. 2015b). This threshold level of browning is very much dependent on abiotic factors such as lake morphometry, especially the size of the littoral area and mean depth (Finstad et al. 2014). Within lakes, the benthic habitat seems to be more affected by browning than the pelagic habitat (Bartels et al. 2016). Since primary production through bottom up processes determines how much energy is available for higher trophic levels, browning may also affect food availability for fish (Karlsson et al. 2009, Karlsson et al. 2015). Furthermore, the decrease in macrophytes with browning also leads to decreased complexity in littoral habitats, which may impact certain fish species (and light stages) more than others (e.g. perch, Estlander et al. 2010).

4.1 Individuals

The decreased visibility in the water due to browning could impede fish foraging ability, as many fish rely on vision to find prey (Jönsson et al. 2011, Ranåker et al. 2012). However, the lower visibility can have very different impacts on feeding abilities of different sexes, sizes and species (Estlander et al. 2010, Horppila et al. 2011, Estlander et al. 2015). While some fish species or size classes might rely heavily on visual predation, others rely more on the movements of the prey in the water or on chemical cues (Estlander et al. 2010). Foraging efficiency in brown waters has also been shown to vary with prey-type (Jönsson et al. 2012). For example, Estlander et al. (2010, 2012) showed that perch is inferior to roach at feeding on zooplankton in humic

lakes, because perch is more affected by low visibility while foraging for zo-oplankton. Therefore, roach may gain a competitive advantage over perch when feeding on the same prey type in dark waters. They also found that perch switched to a benthic diet (benthic feeding may be less dependent on visibility) at a smaller size in humic lakes (Estlander et al. 2010, Estlander et al. 2012). For piscivorous ambush predators like Northern pike (*Esox Lucius*), prey encounter rate depends very much on visibility and was shown to be much lower in highly humic (i.e. brown) waters compared to slightly humic waters (Jönsson et al. 2013). Another study found that the reaction distance of pike to larval roach decreased in brown water, while reaction distance to zooplankton was less affected. The latter was explained by the fact that the visibility in the brown water was still further than the reaction distance to zooplankton prey (Jönsson et al. 2012). Overall, it appears that benthic feed-ing may be least affected by decreased visibility and piscivorous feeding most negatively affected. A decrease in reaction distance can lead to a decrease in encounter rate (and thus lower food intake) if not counteracted by an increase in attack rate and/or swimming activity (Jönsson et al. 2012). Because preda-tion risk generally decreases with water colour individuals might become more active in brown water, leading to an increase in prey encounter, which may decrease the negative effects of a lower visibility on predator foraging rates (Horppila et al. 2011). However, in highly brown water it has also been shown that some prey see the predator later than the predator sees the prey, which instead can lead to increased predation rates (Ranåker et al. 2012, Jöns-son et al. 2013).

Generally, a decrease in food availability and/or foraging ability may lead to a decrease in growth rate, a later maturity at smaller size and smaller size-at-age (Berrigan and Charnov 1994). Therefore, such a response could be ex-pected with browning of waters. However, because different species are dif-ferently sensitive to dark waters, this may lead to different effects on growth and maturity depending on the species. For the visually hunting perch, brown-ing leads to slower growth rates (Horppila et al. 2010) and smaller size-at-age (Estlander et al. 2010). Also three-spined stickleback showed a decrease in overwintering condition and increase in mortality in humic waters com-pared to clear waters (Hedstrom et al. 2016). However, for roach, which is less of a visual feeder, there seems to be no difference in growth rates between brown and clear lakes (Estlander et al. 2010). In addition to differences be-tween species, the effect of browning may also vary within species depending on body size. This is because large individuals may be more vulnerable to food scarcity than small individuals, due to a higher CRD needed to sustain metabolism (see chapter 2.2) (Persson et al. 1998). However, there are, to my

knowledge, no studies on size-specific responses to browning within a species (that feed on the same prey item). Another factor that could lead to a size-specific response to browning is a difference in sensitivity to browning between planktivorous and piscivorous fish, given that small individuals often feed on zooplankton and larger fish within the same population more often are piscivores.

The number of studies done on the effect of browning on higher trophic levels, like fish, is limited. However, there are many studies on the effects on fish of a decreased visibility due to turbidity (Utne-Palm 2002, De Robertis et al. 2003, Radke and Gaupisch 2005). Browning is, however, not the same as turbidity, and can have very different effects on foraging ability (Jönsson et al. 2012, Ranåker et al. 2012, Jönsson et al. 2013).

4.2 Populations

The decrease in individual growth and smaller size-at-age with browning may lead to a decrease in population mean body size (Horppila et al. 2010), and/or a decreased fish production and population biomass (Karlsson et al. 2009, Karlsson et al. 2015). These effects of browning of fish populations are most likely highly species-specific since individuals of different species have different tolerances to reduced light and food availability (see above). Eloranta et al. (2016) showed that brown trout biomass in Norwegian lakes decreased with an increase in browning. Finstad et al. (2014) noted the same response for lakes with a high DOC content, whereas lakes with an intermediate DOC level had higher brown trout biomasses. This is probably a consequence of the positive effect of DOC, below a certain threshold level, on primary production (Seekell et al. 2015a, Seekell et al. 2015b). Furthermore, Horpilla et al. (2010) studied six lakes in Finland with different humic contents, and noted that the most humic lake with the lowest visibility had the lowest perch mean body size, but the highest perch biomass production and standing stock biomass. These contrasting responses to browning indicates there are many other, both biotic and abiotic, factors that play a role in the effect of browning on fish populations.

As said before, when resource density decreases due to browning, large individuals may be more negatively affected than small individuals (Persson and De Roos 2006). This may also cause a shift to populations consisting of a higher proportion of small individuals, since being large can be a disadvantage. However, browning may not only have an effect on population body

size distribution, but also on population dynamics. Increased competitive superiority of juveniles could lead to cohort cycles, where a cohort of juveniles outcompetes adults for resources, until they mature themselves and are outcompeted by a new juvenile cohort (Persson and De Roos 2006).

In summary, there is clearly a knowledge gap concerning the effects of increasingly brown waters on fish populations, both with respect to mean body size, biomass production, standing stock biomass and population dynamics and -regulation. More specifically, we lack knowledge on the effects this increased browning may have on different species and size distributions within a species.

4.3   Communities

4.3.1   Body size distributions, standing stock biomass and production

Since browning of waters generally leads to a decrease in primary production, an overall decrease in the production and standing stock biomass of fish may be expected in very brown lakes (Karlsson et al. 2009, Finstad et al. 2014, Karlsson et al. 2015). This decrease in biomass may either be due to a decrease in mean body size and/or a decrease in the number of individuals, as a consequence of a reduced primary productivity. However, even though we expect an overall decrease in fish biomass/production at the community level, this may not be true for all species. As mentioned earlier, some species may be superior to others in foraging under decreased visibility and/or may feed on resources which are more or less affected by browning. Furthermore, foraging on certain resources may be more or less dependent on visibility (Estlander et al. 2010, Horppila et al. 2011, Estlander et al. 2015). Therefore, interspecific interactions, such as competition and predation, may change, indirectly leading to a shift in species composition and distribution of biomass over fish species. While there may be a decrease in piscivorous species, an increase the biomass of planktivorous species might be expected, since planktivorous feeding is the least negatively affected by browning. Benthivorous fish species will probably be negatively affected, since their resource will be strongly affected by browning, even though their foraging efficiency may not be. These prey-specific responses to browning may lead to species changing their prey use (Estlander et al. 2010, Estlander et al. 2012) and even specializing on certain prey types. On the other hand, with lower overall food availability a more opportunistic feeding strategy may be advantageous. Also, how populations respond to an increase in browning can also vary depending on fish species composition (Eloranta et al. 2016), due to species interactions. In

a Norwegian study, browning affected brown trout negatively when it competed for resources with other species, while it did not when it was the only fish species present (Eloranta et al. 2016).

4.3.2 Benthic-pelagic coupling

There are many fish species that utilize both the pelagic and benthic zones of lakes, which leads to a coupling of pelagic and benthic food webs (Polis et al. 1997). Because the benthic habitat and its production of resources seem to be more affected by browning than the pelagic habitat (Ask et al. 2009, Craig et al. 2015), many fish may switch to feeding in the pelagic zone and the pelagic-benthic coupling through fish predation may weaken (Bartels et al. 2016). As a consequence, there may be a shift from dominance of fish biomass in the benthic to the pelagic habitat. However, foraging on benthic prey may be less affected by a decrease in light than foraging on pelagic prey. Nonetheless, the evidence so far is that the effects of browning on fish communities is mainly due to bottom-up effects rather than from the direct effect of browning on foraging efficiency (Bartels et al. 2016).

5 Interacting climate stressors: Warming and Browning

When studying the impacts of climate stressors on individuals, populations and communities, it is common to look at only one climate stressor and thereby ignore potential interactions among them. As shown above, many studies have been conducted on the impacts of temperature on fish (chapter 3), and some studies have looked at the impacts of browning on fish (chapter 4). However, in reality these, and many other climate-related factors (Rosenzweig et al. 2007), impact organisms simultaneously. Unfortunately, how these climate stressors interact in affecting fish populations and communities is not well-known. In this chapter I discuss what is known on the combined effect of warming and browning and identify essential knowledge gaps.

5.1 Individuals

As reviewed above (chapter 3.1), temperature has a positive effect on metabolic rate, but food consumption might not be able to keep up with that increase (Rall et al. 2010, Ohlberger et al. 2011, Rall et al. 2012). When lakes also receive more high humic content, leading to worsened light conditions, primary production will decrease (Karlsson et al. 2009, Karlsson et al. 2015). Furthermore, resources will be harder to find for visual predators (Jönsson et al. 2011, Ranåker et al. 2012) and feeding rates decrease (Estlander et al. 2015). In one of the few studies on the combined effect of temperature and water colour, Estlander et al. (2015) showed that while the feeding rate of perch increased with temperature, in brown water it never reached the level of feeding it did in clear and warm water. The combination of a higher need for food due to an increased metabolism with increasing temperature, but a lower capability of finding food and lower food availability, could potentially lead to a strong decrease in growth rate and size-at-age. However, Hansson et al. (2012) found a positive effect on roach individual body size of temperature, browning and their combination, in mesocosm experiments. An explanation for this could be that the DOC levels in this experiment were low enough to have a positive effect on phytoplankton growth (Finstad et al. 2014), which could potentially lead to an increase in productivity. Furthermore, planktivorous feeding by roach is known to be only slightly affected by a decrease in visibility (Estlander et al. 2010). Since both the impact of temperature and the impact of browning are very species- and size-specific,

this probably also applies to their combined impact. However, this is yet to be resolved. Because large individuals generally have a higher critical resource density than small individuals, they will possibly respond stronger to a decrease in resources due to a combination of browning and increased temperatures. This may lead to a larger decrease in growth of large compared to small individuals.

5.2   Populations

Even less is known about the population-level consequences of the combination of an increased temperature and browning. Temperature alone may lead to a decrease in mean population body size, a shift in population size-structure and a decrease in production and population biomass (dependent on e.g. initial temperature and species) (Daufresne et al. 2009). Browning by itself may at high enough levels also lead to a decrease in mean body size (Horppila et al. 2010) and a decrease in production and population biomass (dependent on lake morphometry and species) (Karlsson et al. 2009, Karlsson et al. 2015). In combination, an increase in temperature and browning will possibly reinforce each other and there may be a strong decrease in population mean body size, biomass and productivity. However, in a brackish water mesocosm experiment (Lefébure et al. 2013), there was instead an increased production of three-spined sticklebacks (growth) with increasing temperature and browning due to an increased bacterial production and the consequential increase in zooplankton production (Lefébure et al. 2013). Since both temperature and browning separately affect different species in different ways, species-specific responses to the combination of warming and browning are likely, but so far unstudied.

Different sizes/stages are likely to react differently to changes in temperature and water colour. This results from different life stages (at least in some species) having different optimal and critical temperatures for metabolism and foraging (Ohlberger 2013), and differences in their foraging modes (notably the importance of vision for feeding) (Estlander et al. 2010, Jönsson et al. 2012). Therefore, the combined effects of increasing temperature and browning will most likely differ between different size/stage groups. This may, in turn, lead to shifts in population size structure, depending on species and stage. Most likely adults are more negatively affected by warming and browning, which could lead to adult bottlenecks, with a high competition among adults, and a higher maturation than reproduction rate (see chapter 2.3.1). Furthermore, juvenile competitive superiority in warmer and browner

waters could lead to or reinforce cohort cycles where strong juvenile cohorts outcompete older cohorts for resources (see chapter 2.3.1).

5.3   Communities

The combined effect of an increase in water temperature and browning on fish communities is still mostly unknown. With an increase in temperature mean body size of fish communities may decrease, due to a decrease in individual body size for most species or because of a shift to smaller-bodied species (Daufresne et al. 2009). Browning may decrease the production of basal resources and therefore also total community productivity and biomass (Karlsson et al. 2009, Finstad et al. 2014, Karlsson et al. 2015), and there might be a shift in abundance/biomass to species that are better at coping with brown water than others. On the other hand, some researchers have documented an increase in resource production with browning at low levels of browning (Finstad et al. 2014, Karlsson et al. 2015). Therefore, a combined increase in temperature and browning may either lead to a decrease in mean community body size and productivity/biomass, or the negative effects of temperature and the positive effects of browning may cancel each other out. Furthermore, individuals of different fish species likely react differently to a combined change in water temperature and colour. This may lead to a shift in abundance of the species present or even a shift in species composition. Thus, fish community responses to the combination of warming and browning may range from changes in community mean body size, changes in species composition and shifts in productivity that may cause shifts in interspecific interactions, benthic-pelagic coupling, and bottom-up or top-down control. Still, few have studied the combined effects of an increase in temperature and browning on fish communities. Therefore, the combined effects of an increasing temperature and browning are a big knowledge gap, as well as other interacting climate stressors (e.g. eutrophication, acidification) not examined in this essay.

6 Warming and browning: implications for fisheries

Today most inland fisheries in Northern Europe are recreational fisheries rather than commercial fisheries, since catches are often not big enough to make it economically worthwhile. However, these fisheries (both angling and gill-netting) are still important for local communities (Arlinghaus et al. 2002, Arlinghaus et al. 2017). For example, in Sweden, Finland and Norway between 23 and 32% of the population is engaged in recreational fisheries (Arlinghaus et al. 2015). These recreational fisheries are substantial enough that they can influence population and community structure, abundance, and species composition. Because fishermen (commercial and recreational fisheries) prefer large fish, there is often a strong selection against large individuals with fishing. This results in a community dominated by smaller individuals and smaller fish species (Welcomme 1991, Arlinghaus et al. 2002), which, in turn, can influence population dynamics (Lewin et al. 2007, Huss et al. 2014). Furthermore, large piscivorous species in many regions are more valuable for recreational fishers than smaller planktivorous species, and this selective fishing of large piscivorous species can have a large impact on species composition (Rasmussen and Geertz-Hansen 2001, Arlinghaus et al. 2002, Näslund et al. 2010) and therefore interspecific interactions. Also, the biomass of many fish populations has been shown to decline due to recreational fisheries (Post et al. 2002, Lewin et al. 2007).

The consequences of an increase in temperature and/or browning on individuals, populations and communities can strongly impact fisheries. A decrease in fish mean body size and/or a size structure shift to smaller individuals can be negative for fishers, that often prefer large over small fish. Furthermore, a decrease in productivity and standing stock biomass will decrease their catches (Brander 2010). Changes in species distribution, especially extinction of important commercial fish species populations, like the cold-water adapted salmon and trout, may also have large consequences for fisheries (Lehtonen 1996, Schindler 2001). However, new fishing opportunities may arise due to the arrival of new species better adapted to warmer waters (Sumaila et al. 2011).

Thus, both a changing climate and fisheries may lead to changes in community size structure and species composition, with consequences for population and community dynamics. Combined they may even enhance each other and together have a devastating effect on fish communities. But more

precisely how different factors interact still needs to be investigated. Therefore, it is important to get a better understanding of the changes in population and community size structure, species composition and abundance following both an increase in temperature and browning, and fishing pressure. With this knowledge it will be possible to adapt current management strategies (with respect to e.g. pressure and size-selectivity) to a future climate characterized by warmer and darker lakes.

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