Habitat Use in Fish Communities

Size- and Environment-dependent Mechanisms Affecting Biotic Interactions and Population Regulation

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Cover: Lake Judarn, Sweden
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Abstract

Through the influence of abiotic factors, the habitat use of organisms affects their metabolism as well as other species- and size-dependent individual-based rates. The habitat-specific performances of individuals interacting in different habitats thereby affect biotic interactions. Habitat use is thus central for the outcomes of biotic interactions that, in turn, regulate populations and communities.

My aim is to investigate how individual processes are influenced by habitat-dependent abiotic factors, affecting biotic interactions to regulate habitat use and population structures in fish communities. I examined patterns of habitat distribution and population structures of perch (*Perca fluviatilis* L.), roach (*Rutilus rutilus* (L.)), and the zooplankton specialist vendace (*Coregonus albula* (L.)) using a database of standardised test fishing data in lakes. To clarify mechanisms, I experimentally studied predation from perch in pond enclosures as well as relative foraging abilities of the two competitors roach and vendace in aquaria with different temperature and light treatments. To test mechanisms in natural situations, I calculated species- and size-dependent net energy intake, incorporating temperature- and light-dependence, including metabolism, using field data from different habitats in lakes with and without vendace. I also developed and applied a stage-structured biomass model, considering a cold water species (vendace) using two habitats differing in temperature. I thereby studied how climate warming which acts differently on different lake habitats affected temperature-dependent individual-based processes, and results on the population level.

Through multi-species studies, I found that a combination of size- and environment-dependent individual processes determining energy gain, rather than predation risk, could explain size- and species-specific habitat use. The single-species study showed that stage-specific intake rates in one habitat, altered by increased temperature, affected intraspecific competition in both habitats, through a mechanism of 'inter-habitat subsidies' which altered population structure through maturation and reproduction rates. My thesis shows how including size- and environment-dependent individual processes, and interactions across habitats, increases our understanding of population and community structure as well as effects of environmental change.

Keywords: size-based interactions, multi-species, environment-dependent process

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Dedication

To my family and friends

Any knowledge that doesn't lead to new questions quickly dies out:
it fails to maintain the temperature required for sustaining life.

Wisława Szymborska
Quote from Nobel lecture, 1996. Translated from Polish by S. Barańczak and C. Cavanagh.

Contents

List of Publications

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

I   Beier, U. (2001). Habitat distribution and size structure in freshwater fish communities: effects of vendace on interactions between perch and roach. *Journal of Fish Biology* 59(6), 1437–1454.

II Beier, U. (2016). Temperature- and light-dependent ratio of energy gain to metabolic costs explains spatial and temporal habitat use of zooplanktivorous fish. *Ecology of Freshwater Fish* In press.

III Beier, U., Huss, M., Svanbäck, R. and Gårdmark, A. (2016). Size-based and environment-dependent biotic interactions and metabolism affect habitat selection of freshwater fish. *For revision to Oikos.*

IV Beier, U., Huss, M., Svanbäck, R. and Gårdmark, A. (2016). A cold-water fish species in a warming climate – interspecific competition affected by individual-based processes and habitat use. *Manuscript.*

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The contribution of U. Beier to the papers included in this thesis was as follows:

I From an idea of U. Beier to study the distribution of common species among different habitats in lakes, the study was designed and planned jointly with L. Persson and M. Appelberg. U. Beier processed selection of data, conducted statistical analyses, and wrote the manuscript.

II Experiments were designed and planned by U. Beier together with L. Persson and M. Appelberg. U. Beier executed behavioural experiments, processed data, conducted statistical analyses, and wrote the manuscript, with support in analyses and conclusions by A. Gårdmark and R. Svanbäck.

III The field study was planned by U. Beier together with L. Persson and M. Appelberg. U. Beier carried out the field sampling and processed the data. Analyses originated from ideas by A. Gårdmark, U. Beier, M. Huss and R. Svanbäck. U. Beier and A. Gårdmark performed calculations of energy intake, and U. Beier conducted statistical analyses. U. Beier wrote the major part of the manuscript.

IV The modelling originated from ideas by A. Gårdmark, U. Beier, M. Huss and R. Svanbäck. U. Beier and A. Gårdmark performed model development. U. Beier did the major part of the modelling analyses and wrote the major part of the manuscript.

Word list
(including abbreviations and acronyms)

benthivorous	animals eating prey (usually zoobenthos*) from the bottom of aquatic environments
ectothermic	organisms which do not generate body heat; i.e.*, their bodies hold the same temperature as the surroundings
e.g.	*exempli gratia* (Latin), equivalent to "for example"
ecosystem	a community of living organisms in connection with the non-living elements of their environment, linked together through energy flows and nutrient cycles
epilimnion	above the thermocline* in summer
eq.	equation
hypolimnion	below the thermocline*
i.e.	*id est* (Latin), equivalent to "that is"
invertebrate	animal lacking internal skeleton, e.g.*, insects or molluscs
littoral-benthic	close to shores and along the bottom
metalimnion	the part of the water column including the thermocline*
NORS	NatiOnellt Register över Sjöprovfisken / NatiOnal Register of Survey test-fishing
omnivore	organism eating from different trophic levels*
pelagic	the parts of an aquatic environment consisting of open volumes of water without physical structure
piscivorous	fish eating
predation	when one animal eats another
prey	an animal eaten by another animal
SLU	Sveriges lantbruksuniversitet / Swedish University of Agricultural Sciences
thermocline	distinct and limited depth interval in a column of fluid (e.g.*, water) in which temperature changes more rapidly with depth than it does in the layers above or below
trophic level	position in a food chain, where primary producers are level one, herbivores are level two, etc.
zoobenthos	invertebrates*, usually larger than zooplankton*, living on the bottom of aquatic environments
zooplankton	in the following text referring to miniature crustacean animals, filtering green algae or smaller animals

* word or abbreviation explained in the list

1 Introduction

1.1 Habitat selection in community organization

The world we live in is not homogenous. The life space of organisms can be divided into several different environments or habitats, and most animals will make choices of which habitats to stay in. Whether organisms switch environment at distinct developmental stages in their lives, or more continuously while looking for food or shelter, decisions of where to stay, and when, will be essential for their survival and future reproduction.

Ecological communities are usually complex in their structure and function (Cornell & Lawton, 1992; Wootton, 1994; Werner & Peacor, 2003; Banašek-Richter *et al.*, 2009). Community studies may be clarified by first specifying different habitats separated by different abiotic factors, such as light, temperature, or physical substrate and structure.

Habitats can also be separated by biotic factors, such as types and amounts of prey and competitors, as well as predator abundance (Southwood, 1977). If there is a flow of individuals between habitats, the ecology of the community will depend not only on abiotic and biotic factors which define the habitats themselves, but also on relative amounts of the different habitats in the ecosystem (Morris, 1988; Oksanen, 1990; Pulliam & Danielson, 1991).

Abundances of populations reflect the outcomes of regulating factors which act on biomasses, population structures, and distribution of individuals between habitats. To better understand how ecological communities function, and thereby foresee possible changes, it is essential to study the underlying mechanisms behind distributions among habitats, and to connect this knowledge to observed patterns in nature.

1.2 Habitat selection in ecological studies

Habitat selection theory is a central theme in ecology and evolutionary biology as it depicts that individuals follow certain rules to maximize fitness when they make choices of which habitat to use. The theory of habitat selection concerns mechanisms for the organisms' specialisations and choices of habitats, as well as the resulting patterns in growth, survival and reproduction (Svärdson, 1949; Fretwell & Lucas, 1969; Holt, 1977; Gilliam & Fraser, 1987; Rosenzweig, 1987; Brown, 1988; Gilliam & Fraser, 1988; Morris, 1988; Bernstein *et al.*, 1991; Pulliam & Danielson, 1991).

No standard definition exists for "habitat selection", although habitats have been described as "infinite patches" where the resource production rate is equal

in magnitude to the consumption rate (Stephens & Krebs, 1986). Individuals may then choose to stay in, or migrate between, habitats on a shorter or longer time scale to maximize their lifetime fitness. Within habitats, individuals will find patches where to forage, i.e., find and ingest food. Certain assumptions in habitat selection theory state that individuals are free to choose between habitats for which they have information regarding quality, i.e., potential energetic gains as well as predation risk, and that there are no costs of switching habitat (Fretwell & Lucas, 1969). Habitat selection theory thus provides a theoretical basis for factors that regulate populations and communities spatially (Morris, 1988), including density dependence in connection to available space (MacArthur, 1958), and source-sink dynamics implying relative quantities of rich and poor habitats (Oksanen, 1990; Pulliam & Danielson, 1991).

According to habitat selection theory, individuals disperse between habitats as a result of the rule of ideal free distribution (Fretwell & Lucas, 1969). Following this rule, all individuals in a population are able to move free of costs between habitats, while having full information of their relative qualities, resulting in equal fitness among individuals. In such a perfect situation, no selection from differences in fitness would occur, except resulting from genetic drift, which is an alternative way in which evolution occurs. Because of variation within habitats as well as between individuals, and because of continuous changes in population densities, we may assume that ideal free distribution might be continuously approached, although never perfectly attained.

Not surprisingly, as it deals with organisms and their environment, habitat selection theory has for decades been a major theme in theoretical ecology as well as within various fields in ecology, e.g., evolutionary and population biology, and behavioural ecology. The habitat selection concept is a theoretical framework specifying mechanisms to explain why organisms are found in different places at different times, implying an active choice (Fretwell & Lucas, 1969; Stephens & Krebs, 1986; Morris, 1988). Habitat use involves more straightforward observations of patterns, i.e., which habitats are used by which organisms, and when. To be able to distinguish between "selection" and "use" is dependent on methods (Craig & Crowder, 2000). As the title describes, my foremost aim with this thesis is to study habitat use, and to explain it in the light of habitat selection theory.

1.3 Abiotic factors set limits to niches

In addition to being differently adapted for consuming different prey, organisms are also adapted to abiotic factors and their variability. These adaptations imply that the use of different habitats will have consequences for fitness. A

combination of morphological, physiological and behavioural adaptations is known as the ecological niche. The fundamental niche of a species is the wider spectrum of abiotic and biotic factors where the species can persist, whereas the realised niche is the actual, reduced spectrum in an ecosystem limited by geographical factors, available habitats and intra- and inter-specific interactions. A part of the niche concept thus includes abiotic factors, e.g., temperature, light, salinity, and oxygen levels on different temporal and spatial scales. Abiotic factors affect individual physiological processes which are fundamental for existence, and as such abiotic factors form the basic structure and function of ecological communities (Dunson & Travis, 1991). Temporal heterogeneity of the environment, to which species can be differently adapted, is another factor affecting communities (Menge & Sutherland, 1976).

Temperature is a geographical and physical factor to which fish species are differently adapted. Being ectothermic organisms, fish depend on the surrounding temperatures for metabolic activity, which allows for mobility and somatic growth. However, the total energy costs increase with temperature, as an increased activity level in higher temperatures also leads to higher energy expenditure. As a consequence, cold water species, for example salmonids, have their physiological optimum temperature range below 20 °C (Rahel *et al.*, 1996).

Besides temperature, visually hunting fish depend on their sight to find food (Guthrie & Muntz, 1993). Species may be differently adapted to different light intensities, which may affect their relative competitive abilities (Bergman, 1988; Diehl, 1988). This is particularly important for fish communities in lakes, where the light regime changes depending on season, time of day, as well as depends on the water depth. Additionally, water colour and turbidity affects the light climate in the water column, which may differently affect behaviours of different fish species (Guthrie & Muntz, 1993; Jönsson *et al.*, 2012; Ranåker *et al.*, 2012a; Ranåker *et al.*, 2012b) as well as their invertebrate prey (Pekcan-Hekim *et al.*, 2013). Increased water colour may affect individual growth and thereby population structure, as exemplified for perch by Horppila *et al.* (2010).

1.4 Biotic interactions

Just by being alive, organisms interact with their environment, and thereby with other organisms within the ecological community. Individuals compete for food or other resources, and consume other organisms, sometimes including conspecifics. Both direct and indirect biotic interactions among individuals, affecting populations, highly influence the structure of communities (Kerfoot & Sih, 1987; Strauss, 1991). A common direct interaction in a food web is the consumption of prey by a consumer population, affecting prey densities, which

will have consequences for other populations. Indirect interactions are by definition secondary effects of a direct interaction (Strauss, 1991). Two populations exploiting the same resource is a common indirect interaction, usually with negative effects for both populations (Abrams, 1987). If two competing populations are different in how efficiently they exploit a resource, this may also act as a complicating factor, i.e., an asymmetry in an effect chain (Persson, 1988). According to Allee's principle (Fretwell & Lucas, 1969) the per capita reproductive rate and survival increases with population size to a maximum and then decreases, as a result of competition and increased predation pressure. As populations become denser and biotic interactions become more intense, the ideal free distribution rule may together with density dependence regulate the strength of biotic interactions by changing the distribution of populations among different habitats (Svärdson, 1949; Werner *et al.*, 1983a).

The reduction of a prey population by a predator may also have indirect positive effects, e.g., on prey or competitors of the prey population (Abrams, 1987). Trophic cascades are essentially chains of indirect interactions, where the effects on subsequent trophic levels in a food chain are often opposite compared to the preceding level (Carpenter *et al.*, 1985; Werner & Peacor, 2003; Terborgh *et al.*, 2010). Another indirect effect of predation is "apparent competition" (Holt, 1977), meaning that when two populations share a common predator, an increase in one of the prey populations causes a decrease in the other. This could be perceived as a result of competition, but is in this case a result of the predator population increasing as a result of the population increase of the first prey population, and thereby causing the predator to exert more predation pressure also on the other prey population.

To attain maximal fitness, organisms should maximize their energy gain while minimizing the mortality risk (Cerri & Fraser, 1983; Gilliam & Fraser, 1987). Animals may choose less profitable habitats to avoid predators, or take the risk of exposing themselves to predators if their energy need is large enough (Rennie *et al.*, 2010; Vijayan *et al.*, 2012). Altered competition and predation intensity may affect habitat use and thereby change the biomass distribution across habitats among populations, or among life stages within populations (Werner *et al.*, 1983a; Gilliam & Fraser, 1987; Brown, 1988). Furthermore, flexible niche occupation may fluctuate with population density, which will be reflected in relative resource availabilities among habitats (Svanbäck & Persson, 2004). Hence, intraspecific density dependence as well as direct and indirect interactions with non-conspecifics may affect the habitat use of species. In turn, habitat use will mediate changes in biotic interactions as well as phenotypic expressions (Werner & Peacor, 2003; Svanbäck *et al.*, 2008).

1.5   Mechanisms for habitat use

1.5.1 It starts with size

Body size regulates individual processes of feeding, growth, metabolism, and reproduction, and is hence fundamental for the ecology of organisms (de Roos & Persson, 2013). Body size is therefore central also in biotic interactions, such as competition and predation. The ability to escape predators and the consumption of prey depend on the relative sizes of predators and prey (Cohen *et al.*, 1993; Byström & Garcia-Berthou, 1999; Ohlberger *et al.*, 2013; ten Brink *et al.*, 2015). Trade-offs involving size-dependent individual processes that regulate energetic profit and the risk of predation mortality will thus govern the distribution of individuals among habitats (Werner *et al.*, 1983b; Fraser & Gilliam, 1987; Gilliam & Fraser, 1987).

Increased body size often makes ontogenetic niche shifts necessary, and this necessity may, in turn, induce complex life cycles (Werner, 1988). Complex life cycles involve abrupt morphological, physiological, and behavioural changes which include ontogenetic niche shifts. Fish are size-structured and can continue to grow throughout their life, and accordingly they may change food sources or habitat several times during their lifetime. Large-bodied fish are generally omnivorous, i.e., predate on more than one trophic level, which implies that individuals can, depending on their relative sizes, be prey, competitors or predators to others (Polis, 1991). Furthermore, if organisms go through ontogenetic niche shifts by changing their diet or habitat choice between different size stages in their life cycle, a changed situation in one life stage may have consequences for the whole population, as well as for the structure and dynamics of other populations (Ebenman & Persson, 1988).

The mortality-to-growth trade-off is related to the life-cycle, and in particular body size. In size-structured populations, distribution among habitats is governed by size-dependent trade-offs between growth and mortality (Werner *et al.*, 1983a). As fish are size-structured and have indeterminate growth, biotic interactions will depend on the ontogenetic niche-shifts that fish go through, i.e., how and when fish change food sources and/or habitat during their life span. These ontogenetic shifts will in turn interact with the size structures and habitat use of populations in the ecosystem, with feedbacks on biotic interactions and other individual-based processes. Therefore, interactions within and among size-structured populations with ontogenetic niche shifts will also have implications for the whole community.

1.5.2 Influence of abiotic factors

Metabolism is a principal force in ecology, linking, e.g., temperature to the ecology of individuals, populations and whole communities (Clarke & Johnston, 1999; Brown *et al.*, 2004). As an example of species-specific metabolic adaptations to different temperatures, salmonid fish have a higher active metabolic rate than, e.g., cyprinid fish at 15 °C, which is approximately the temperature optimum of many salmonid species (Clarke & Johnston, 1999). Several studies have shown that cyprinid fish can instead benefit from temperatures warmer than 15 °C (Persson *et al.*, 1991; Holmgren & Appelberg, 2000; Graham & Harrod, 2009; Jeppesen *et al.*, 2012).

As explained above (see section 1.3), adaptations to abiotic conditions will affect performance, behaviour as well as net energy gain in different habitats (Elliott, 2011; Carmona-Catot *et al.*, 2013). Previous studies have shown that biotic interactions, e.g., the capture abilities of predators are directly affected by abiotic factors, as well as indirectly through altered behaviour or habitat use of their prey (Eklöv & Persson, 1995; Martin *et al.*, 2010; Einfalt *et al.*, 2012). For example, behavioural responses of zooplankton to fish predation may be to migrate vertically during the day (Zaret & Suffern, 1976; Iwasa, 1982), or to mainly use an energetically less profitable habitat as a refuge from predation (Larsson & Lampert, 2012).

Abiotic factors such as light intensity and temperature may affect the magnitude of biotic interactions. This can reverse competitive relationships and enable species co-existence through habitat partitioning (Bergman, 1987; Rodtka & Volpe, 2007; Mehner *et al.*, 2010), or possibly lead to competitive exclusion (Oyugi *et al.*, 2012; Carmona-Catot *et al.*, 2013). An example of two closely related species having fine-tuned physiological adaptations which impede competitive exclusion is vendace (*Coregonus albula*) and the endemic Fontane cisco (*C. fontanae*) in Lake Stechlin (Ohlberger *et al.*, 2008). A study of how warming might affect this species pair when assuming plasticity in habitat use resulted in the prediction that increased temperatures would decrease habitat segregation resulting in increased intra-specific competition (Busch *et al.*, 2012).

In addition to abiotic factors, metabolic costs also depend on body size (Clarke & Johnston, 1999). Metabolic rate may also scale differently with body size and temperature for different fish taxa (Ohlberger *et al.*, 2012). As a consequence, mechanisms regulating habitat use are both species- and size-specific. It has been suggested that energy costs caused by activity, e.g., swimming, might be a major factor for understanding variability in foraging performance and growth rates (Boisclair & Leggett, 1989; Giacomini *et al.*, 2013). In connection to adaptations to different temperatures, average swimming

speeds at different temperatures may differ depending on the morphology, metabolism and functional specialization of the species. The energetic cost of swimming is important to recognize in connection with foraging efficiency, to be able to understand the mechanisms for habitat selection and the competitive abilities of different species. Metabolic traits as well as costs of moving can, together with foraging efficiency, aid in understanding of patterns of migration, and the distribution of species at a larger scale (Lucas *et al.*, 2008).

Habitat use of competing species may be affected by temperature through differences in relative foraging abilities in different habitats (Okun & Mehner, 2005), or metabolic demands under different environmental conditions on different scales (Huey, 1991; Hölker, 2006; Ohlberger *et al.*, 2008; Rosenfeld *et al.*, 2015). Combined effects of temperature on metabolism and foraging efficiency have been exemplified and accompanied by predicted consequences of climate change by, e.g., Finstad *et al.* (2011), and Seth *et al.* (2013). One general prediction is that organisms will respond to warming by a general decrease in body size (Edeline *et al.*, 2013). Depending on, e.g., productivity regulating intraspecific competition, larger quantities of small fish may however result in increased profitability for piscivorous fish, which may result in larger overall size (Ohlberger et al., 2013). To increase the understanding of combined effects of abiotic factors for communities, studies incorporating size-dependence of physiological rates of individuals, which may occupy habitats differing in, e.g., temperature, and thus with consequences for biotic interactions, are needed.

1.6   Species distribution patterns

Niche shifts caused by changes in the abiotic or biotic environment may cause feedbacks, from interactions among individuals to population and community dynamics. Individual-level processes affected by abiotic factors may affect biotic interactions and habitat segregation (Einfalt et al., 2012; Rosenfeld et al., 2015). For example, adaptations to temperature and light often result in that species that in allopatry use similar resources separate their range of habitats when they co-exist (Magnuson et al., 1979; Mehner et al., 2010; Carmona-Catot et al., 2013). Through such feedbacks, habitat shifts will continuously shape communities as well as species distribution patterns, and will also contribute to micro-evolution (Brown, 1990; Svanbäck & Persson, 2004).

A current challenge is to understand and predict effects of climate change for ecosystems. Incorporating effects of abiotic factors and species interactions is essential to foresee changes in species distributions, and guide in amendments for management. Both direct and indirect effects of increased temperature or changes in other climate variables such as precipitation may have positive or

negative effects for fish species, depending on their tolerance and adaptive abilities, with different total effects for communities depending on community composition, region, and latitude (Reist *et al.*, 2006). One general prediction is that habitats favourable for warm-water fish would increase (Magnuson *et al.*, 1990; Graham & Harrod, 2009). However, most studies predicting community changes resulting from climate change do not take species interactions, which are results of individual-level processes, into account. Knowledge about factors regulating biotic interactions and also habitat use are needed to forecast results of environmental change for ecological communities. Also, when predicting species distributions resulting from climate change, the effects of abiotic factors for biotic interactions as well as habitat use need to be accounted for (Hayden *et al.*, 2013; Hayden *et al.*, 2014).

1.6.1 Multi-species studies across habitats are needed

Habitat use depends on abiotic factors influencing biotic interactions both within and among populations. There is at present a knowledge gap concerning studies including biotic interactions involving several species, including individual-based processes affected by the environment, which are manifested into biotic interactions regulating habitat use, and, in turn, have feedbacks for communities.

Recent studies have included effects of abiotic factors when considering both habitat use and biotic interactions, while size-dependence was not included (Ciannelli *et al.*, 2012; Muska *et al.*, 2013; Hayden *et al.*, 2014). Other studies where mechanisms regulating niche use and interspecific interactions were identified did consider size-dependent individual processes (Huss *et al.*, 2013; van Leeuwen *et al.*, 2013), or stage-dependent habitat use within populations (van de Wolfshaar *et al.*, 2011), however, without accounting for abiotic factors. To advance the role of habitat selection in community ecology, multi-species studies on both environment- and size-dependent individual processes, across habitats, are needed. In my thesis I address the above features (multi-species studies including both environment- and size-dependent processes, across habitats and systems).

The studies presented in my thesis includes patterns and mechanisms at the ecological time scale, and not the evolutionary scale. Furthermore, I study habitat use disregarding patchiness within habitats. The thesis is focused on fish communities and deals with mechanisms underlying food web interactions, although excluding cascading effects. The main focus is how abiotic factors are affecting fish habitat use, as well as regulating population and community structure.

1.7 The study system

Using lakes for ecological studies has an advantage because lakes represent semi-closed ecosystems, allowing for the use of several samples in studies of ecosystem functions (Schindler, 1990). Lakes also respond rapidly to environmental change, and lakes as samples may integrate information over geographical and abiotic gradients (Adrian *et al.*, 2009; Moiseenko *et al.*, 2013).

Two distinct spatial zones may be defined in lakes: the littoral-benthic zone and the pelagic zone. The littoral-benthic zone extends from the shallow, near-shore areas, close to the bottom all over the lake. This is heterogeneous in terms of physical structure, as well as numbers and sizes of available prey types. The pelagic zone is constituted by the open water volume further away from the shore, where the water is deeper. The pelagic zone is more homogenous, although food is often aggregated vertically and horizontally. Furthermore, the water temperatures often differ between different depths during summer as a result of thermal stratification. Consequently, for ectothermic organisms such as fishes, the littoral-benthic and pelagic zones of lakes can be further divided into habitats that are distinguished by environmental factors. The cold water in the lower parts of the water column, i.e., the hypolimnion, thus constitutes a different habitat compared to the warm water above the thermocline, i.e., the epilimnion. Studying the distribution of three fish species; roach (*Rutilus rutilus* (L.)), perch (*Perca fluviatilis* L.), and vendace (*Coregonus albula* (L.)) among lake habitats within the littoral-benthic and pelagic zones (Fig. 1) may illustrate how their habitat use is governed by size-dependent trade-offs between growth and mortality.

Roach and perch are often the two numerically dominant fish species in Scandinavian lake systems (Svärdson, 1976; Rask *et al.*, 2000). Roach is an efficient zooplanktivore that may shift to feeding on zoobenthos as they grow in size, but is also able to use algae and detritus as a food source (Hellawell, 1972; Persson, 1983c). Roach uses both the shallow habitat in the littoral zone, but earlier studies have documented that roach perform horizontal migrations out to the upper parts of the pelagic zone zone at night (Bohl, 1979; Gliwicz & Jachner, 1992).

Perch has a life-history including shifts in habitat and diet (Persson, 1983b). Shortly after hatching in the littoral zone, perch fry move to the pelagic zone to feed on zooplankton (Byström *et al.*, 2003), and at a size of 10-30 mm shift back to mainly using the littoral-benthic zone (Treasurer, 1988; Wang & Eckmann, 1994; Byström *et al.*, 2003) where a large variety of food items, including small fish, is available (Horppila *et al.*, 2000; Kahl & Radke, 2006). Being an ontogenetic omnivore, perch go through diet shifts, from zooplankton to zoobenthos, and eventually to fishes (Alm, 1946; Craig, 1974). This implies that

the competitive relationship between small perch and roach may be changed as a result of predation from perch. The asymmetric competitive relationship between perch and roach is a well-studied example of where the ontogenetic omnivory in perch is an important mechanism behind dominance relationships between these two species (Persson, 1983a; Persson, 1988). As roach are more effective predators on zooplankton than perch, the degree of interspecific competition between the two species for this resource will limit the proportion of the perch population reaching the piscivorous stage (Persson, 1986, 1987b; Persson & Greenberg, 1990; Persson & de Roos, 2012). On the other hand, if piscivorous perch are present and are able to reduce populations of smaller planktivorous fishes, the competitive pressure experienced by non-piscivorous perch may be reduced (Persson, 1983a, b; Johansson & Persson, 1986; Svanbäck & Persson, 2004; Persson & de Roos, 2012). If perch individuals will begin to eat fish, usually at intermediate sizes, they will normally grow faster (Le Cren, 1987; Claessen *et al.*, 2000; Persson *et al.*, 2000). Piscivorous perch with fast individual growth will be able to consume more fish prey. This situation may initiate a causal loop, where competing prey fishes are consumed to an extent that individual smaller perch will grow faster as a result of reduced competition. In turn, if perch grow fast they can more easily switch to piscivory, which reinforces the feedback between individual growth and biotic interactions between perch and roach.

Perch and roach may use the pelagic habitat to varying degrees (Horppila *et al.*, 2000; Svanbäck *et al.*, 2008). To explore how altered biotic interactions may affect the distribution of roach and perch populations among different habitats, my chosen study system includes vendace, which has a strong preference for the pelagic habitat. Vendace is highly specialized for preying on zooplankton during its entire life cycle (Hamrin, 1983; Hamrin & Persson, 1986). Based on morphology, i.e., a protruding lower jaw and a high number of gill rakers, vendace is expected to be the superior competitor of the three species in the pelagic habitat (Svärdson, 1976). Although viewed as an obligate zooplanktivore, cannibalism has been observed in laboratory conditions and cannot be entirely excluded in vendace (Urpanen *et al.*, 2012). Vendace exploit zooplankton in the low temperatures of the hypolimnion of the pelagic zone (Northcote & Rundberg, 1970; Dembiński, 1971; Hamrin, 1986; Mehner *et al.*, 2007; Mehner *et al.*, 2010) (Paper I). However, based on studies which found coregonids to be comparatively inactive at night in the field (Huusko & Sutela, 1998; Gjelland *et al.*, 2004), vendace can be expected not to be particularly adapted to low light levels. Aside to having a preference for colder water in the hypolimnion (Mehner *et al.*, 2011), vendace have been found to use water depths with light levels compatible with visual foraging as well as reduced predation

risk (Gjelland *et al.*, 2009). The reasons for vendace to prefer deeper, colder water, as well as to perform daily vertical migration between water layers differing in temperature, have been explained by overall bioenergetic gains (Mehner *et al.*, 2007; Mehner *et al.*, 2010). The use of deeper water by vendace has also been explained by specific metabolic rewards in combination with seeking refuge from predation (Mehner, 2012), as well as being driven by density dependence (Mehner, 2015). Vendace have been found to use the warm water of the epilimnion, although to a lesser extent than the hypolimnion (Hamrin, 1986; Lilja *et al.*, 2013). Vendace may also migrate vertically in unstratified conditions (Sydänoja *et al.*, 1995).
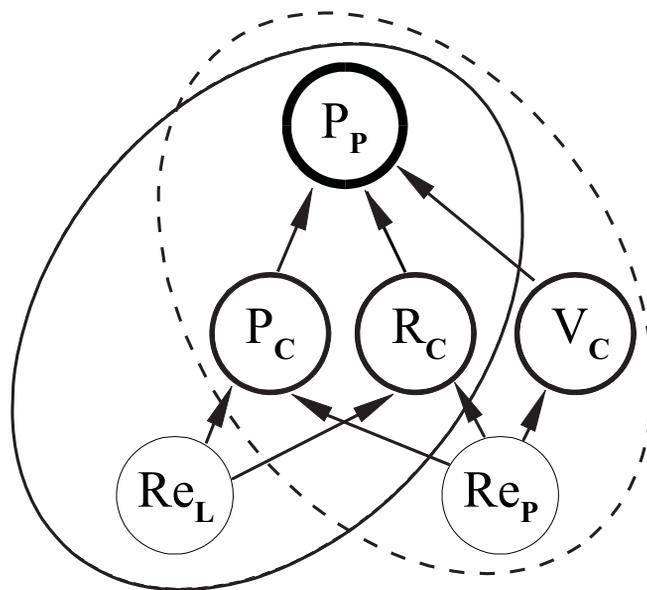
Figure 1. Simplified food web of the three focal fish species and their resources in two lake zones: — Littoral-benthic zone; – – – Pelagic zone. P_P is piscivorous perch, P_C, R_C, and V_C are perch, roach and vendace competing in one or both zones. Re_L and Re_P are the food resources in the littoral-benthic and pelagic zones, respectively.

It has been predicted that vendace may counteract the effect of increased lake productivity, which normally benefits roach before perch (Persson *et al.*, 1991; Persson *et al.*, 1992). Piscivorous perch was found to be favoured in systems with vendace (Appelberg & Degerman, 1991; Persson *et al.*, 1991) which would affect fish prey populations (Persson *et al.*, 1992). Positive effects for piscivorous perch may be explained by effects that vendace might have on roach,

either by reducing the common food resource consisting of zooplankton in the pelagic habitat which roach uses more than perch, which, in turn, may lead to a decrease in total roach biomass resulting in less competition for perch. Another possible explanation for positive effects for piscivorous perch is apparent competition caused by vendace constituting an alternative prey for piscivorous perch, and thereby indirectly increasing predation pressure for roach as a larger proportion of the perch population may become fish eating. Alternatively, it may be an indirect effect of altered habitat use, where increased competition may affect the habitat use of roach. Vendace may force roach to increase its use of the littoral zone as a result of competition, leading to that roach may be subdued to a larger predation risk if there are more piscivorous perch in the littoral zone. This situation would describe apparent competition mediated by altered habitat use, which is one example of where indirect interactions are linked through habitat selection.

2　Objectives

As shown above, studies on quantitative metabolic requirements and other individual-based rates in connection with abiotic factors to explain habitat use with consequences for population and community structures, are lacking to date. Including outcomes of such mechanisms and how they manifest into biotic interactions is essential for predicting the effects of environmental change, and to design appropriate management for fish communities. Still, how size- and environment-dependent interactions among several coexisting species shape their habitat use has not been explicitly studied.

My overall aim with this thesis is to increase the understanding of how individual processes, influenced by habitat-dependent abiotic factors, are linked to biotic interactions and regulate habitat use as well as population structures in fish communities. Specific questions in the manuscripts (marked below by their roman numbers) include:

➢ Does habitat use and community structure of predators, consumers and prey differ depending on whether a specialist is present or not? (I, III)
➢ Which mechanisms can explain the habitat use of different species and size groups? (I, II, III, IV)
  • How may predation affect the habitat distribution? (I, II, III)
  • How does habitat use affect the possibilities for growth? (II, III, IV) (and vice versa)
  • How can the trade-offs regarding energy intake and risks of being eaten be understood in connection to habitat use? (II, III)
➢ Accounting for both habitat use and environment- and size-dependence of individual processes, what consequences can a warmer climate have for the population regulation of a cold-water species? (IV)

3   Materials and methods

I examined patterns of habitat distribution and population structure of perch, roach and vendace in whole-lake studies (Papers I and III). To clarify basic mechanisms for habitat use, I experimentally studied biotic interactions, including effects of abiotic factors for individual processes (Paper II). To test mechanisms for habitat use in natural situations, I calculated species-specific and size-dependent net energy intake including the temperature- and light-dependence of empirically derived rates of physiological processes, using data from field sampling (Paper III). Finally, I developed and applied a stage-structured biomass model, considering a population using two habitats differing in temperature. Thereby I could examine consequences of climate warming on how size- and temperature-dependence of individual processes, which together with habitat use were manifested in mechanisms affecting population structure and regulation (Paper IV).

3.1   Habitat use of perch, roach and vendace

The aim of Paper I was to test hypotheses regarding mechanisms to explain patterns of habitat use and possible effects of vendace on population structures of perch and roach (Appelberg & Degerman, 1991; Persson *et al.*, 1991; Persson *et al.*, 1992; Holmgren & Appelberg, 2000). Positive effects of vendace on perch populations found in a previous study was based on a relatively low number of lakes within a limited geographical area (Persson *et al.*, 1991). In Paper I, I explored data from a larger number of lakes (N=115), to test the generality of earlier findings (Fig. 2). Data were collected from the NORS database containing standardized test fishing data from monitoring programmes (SLU, 2016). The lakes were oligotrophic to mesotrophic, within a range of total phosphorous of 2-33 $\mu g \cdot L^{-1}$.

Fishing occasions where multi-mesh gillnets had been used in both the littoral-benthic and pelagic zones were selected. Lakes were divided into groups having only perch (N=39); perch and roach (N=52); or perch, roach and vendace (N=24). I analysed relative biomasses of the species in the littoral-benthic and pelagic habitats for comparisons between lake groups. For perch, I divided the biomass into non-piscivorous and piscivorous perch. Furthermore, I compared size structures of the three species among lake groups and across habitats. I also examined the depth distribution of roach and vendace in the pelagic zone of lakes with and without vendace. To strengthen the test of effects of vendace for piscivorous perch, I also compared size-dependent individual growth of perch between lakes with perch and roach and with perch, roach, and vendace.

Figure 2. Map of Sweden with locations of lakes used in Paper I (lakes with perch = ×, with perch and roach = •, and with perch, roach and vendace = ○), and in the study of Persson *et al.* (1991) (red circles).

Based on previous studies regarding competitive abilities of roach and perch as well as their population dynamics, I predicted that:

(1) Habitat choice will be a trade-off between foraging gain and risk of predation. Thus, the pelagic habitat will be less used by zooplanktivorous perch and roach in lakes with vendace, as a consequence of resource competition. As a consequence of trade-offs between growth and mortality rates, habitat choice will also be size dependent so that the sizes of roach found in the pelagic zone will be within the range where foraging on zooplankton is profitable, and where the risk of predation in an open habitat is significantly reduced.

(2) The relative biomass of perch in the pelagic habitat will be related to the biomass of zooplanktivores (a positive relation for the biomass of piscivorous perch and a negative relation for non-piscivorous perch).

(3) The proportion of piscivorous perch will be higher in perch-roach-vendace lakes than in perch-roach lakes, because of a higher growth for perch in lakes with vendace as an additional prey.

(4) Roach size distributions will be skewed towards larger sizes in lakes with vendace compared to lakes without vendace. As piscivorous perch are expected to be more abundant in perch-roach-vendace lakes (3, above), a higher mortality for small roach from perch predation will result in higher proportions of larger roach, as larger size confers a refuge from predation by perch.

3.2   Underlying mechanisms for habitat distribution patterns

Using experiments to investigate both sensitivity to predation, relative foraging abilities as well as energetic gain in competing species would help to understand the relative importance of these factors, which could explain habitat distribution patterns in the field. In Paper II, I therefore performed both predation and feeding experiments on roach and vendace to study mechanisms underlying the trade-off in mortality risk to energy gain (Gilliam & Fraser, 1987).

There are several examples of earlier studies of biotic interactions and behaviour in fish using enclosure experiments with semi-natural conditions (Werner *et al.*, 1983a; Werner *et al.*, 1983b; Eklöv & Persson, 1995, 1996). By performing experiments in pond enclosures, it is normally possible to both study natural behaviour of the organisms in focus, as well as quantitatively measure consumption of prey items. In enclosures I used predatory perch to study the relative sensitivities of roach and vendace to predation, as well as their evasive behaviour (Paper II).

The enclosures were lacking vegetation, with mean water depth 1.1 m (Fig. 3; Paper II). I used either roach or vendace as prey, as well as a mixed prey treatment with both species. Behaviour of predators and evasive behaviour of

Figure 3. Photograph showing pond enclosures with the observation tower, used in predation experiments at Drottningholm (Paper II).

prey, as well as swimming speeds for the different species were recorded. After two days, the remaining prey fish were collected and counted to determine the capture success of perch in the different treatments with different fish prey.

The effects of environmental factors for foraging abilities may be studied in controlled environments using laboratory experiments. The efficiency of vendace as a zooplankton consumer compared to, e.g., roach had so far not been quantified, although metabolic requirements had been collected for both species separately (Hölker, 2003, 2006; Ohlberger *et al.*, 2007). To better understand mechanisms for competition-driven patterns underlying habitat use and relative abundances of roach and vendace, I used experiments in constant climate rooms, where I studied foraging under varied temperature and light conditions. The size of fish used matched the predominant size interval of roach found in the pelagic zone in lakes (Paper I). I designed experiments to resemble a standard situation in temperature stratified lakes during summer (Paper II). The temperatures used were 6 °C (hypolimnion), 12 °C (metalimnion), and 18 °C (epilimnion). At 18 °C, corresponding to the epilimnion where roach and vendace may coexist in lakes (Paper I), I used two different light treatments as to resemble normal light

levels in the epilimnion; during daylight (10 lux), and during dusk and dawn (1 lux). In the experiments, I let fish forage in aquaria with different densities of zooplankton, to investigate functional responses and energy gains under varying light and temperature conditions (Fig. 4; Paper II). By taping commentaries for later event recording, I documented prey captures, and using a grid on the aquaria, I also recorded positions to calculate swimming speed. I could thereby estimate species-specific metabolism in different temperatures (Paper II).
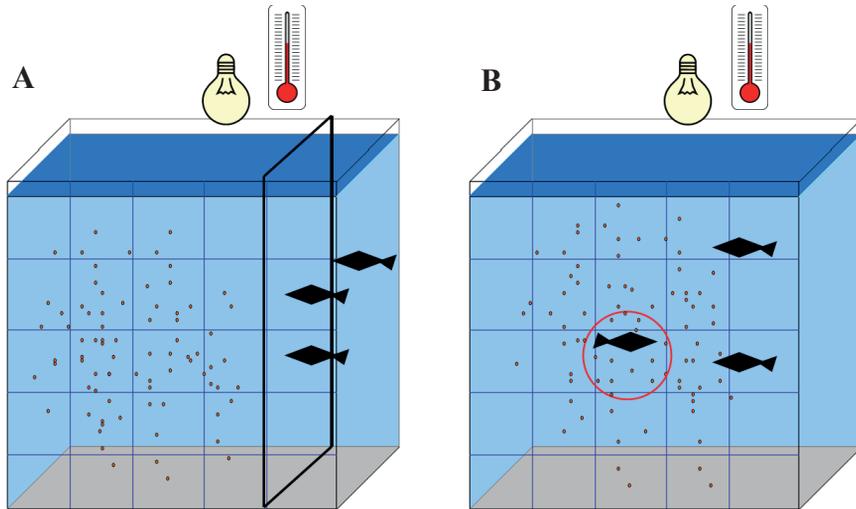
Figure 4. Schematic picture of aquarium experiment (Paper II). A) Before fish were released, and B) when recording the capture rate and swimming speed of one randomly selected individual (of the same species) when eating zooplankton (*Daphnia magna*) during the experiments.

As field data show that vendace rarely use the littoral-benthic zone and are more common in deeper, darker water in the pelagic zone (Hamrin, 1986; Mehner *et al.*, 2007), (Paper I), where they would have a predation refuge from perch, I predicted that:

(1) vendace would be more susceptible than roach to predation from perch. Based on general increased activity with increased temperature for ectotherms, I predicted that:

(2) both roach and vendace increase capture rates as well as swimming speeds with increased temperature.

Based on spatial distribution patterns observed in lakes (Paper I), confirming that vendace was normally found in deeper and thus colder and darker water than roach, I predicted that:

(3) the capture rate of vendace would be less affected by low temperatures and light levels than it would be for roach,

(4) vendace would have higher metabolic costs compared to roach in warmer waters, and

(5) the net energy gain of vendace would be higher than for roach at lower temperatures, while (6) the net energy gain of roach at the highest temperature would be higher than for vendace.

3.3 Consequences of individual processes and biotic interactions

To further clarify underlying mechanisms for the size-specific distribution of individuals among habitats, energy intake and energy costs, and predation risk were calculated using empirically derived rates of temperature- and light-dependent individual processes (Paper III). In the calculations, fish and invertebrate densities of prey and predators were sampled in different lake habitats, and compared with the size-specific biomass distributions of fish. Two of the sampled lakes contained vendace, and two lakes did not, which enabled comparisons regarding size-distributions and habitat use of roach and perch in systems containing or lacking the specialist species vendace.

Sampling was carried out when lakes were thermally stratified using multi-mesh gillnets in the littoral and benthic zones according to standardised methods (Paper III). Samples of invertebrate prey for fish were taken by collecting zooplankton samples in the pelagic zone, in the area at the deepest part of each lake. Three zooplankton samples were collected at each depth representing the epilimnion and hypolimnion, respectively. To account for horizontal variation in the littoral zone, zooplankton samples were collected in three bays of each lake. Zooplankton were classified to genus, counted, and body lengths were measured from subsamples for estimating biomasses. Zoobenthos samples from the littoral zone were collected from the same three bays in each lake using an Ekman grab at depths 1-3 meters within each bay. Zoobenthos individuals were sorted to genus, counted, and lengths were measured to estimate biomasses.

The attack rates and handling times which determine the energy intake rates were first adjusted for different temperatures and light conditions in different habitats; the littoral epilimnion, the pelagic epilimnion, and the pelagic hypolimnion. Temperature was adjusted for using the scaling factor (r_a) derived from (Kitchell *et al.*, 1977), including adjustments for size by (Karås & Thoresson, 1992), and further adjusted by Ohlberger *et al.* (2011) (Paper III: Tables 1, 2). As the temperature scaling factor r_a was originally developed for perch, and lacking an equivalent temperature adjustment for roach, r_a was also

applied for roach, supported by both perch and roach having relatively high temperature optima (van Dijk *et al.*, 2002; Fiogbé & Kestemont, 2003). However, as vendace is more adapted to cold temperatures (Rudstam & Magnuson, 1985), and was observed to be relatively efficient in foraging also at low temperatures (Paper II), an alternative adjustment was made for vendace. The calculated attack rates and handling times for vendace at 6 °C were thus multiplied by two conversion factors (Y_T and Z_T), respectively (Paper III: Tables 1, 2). The conversion factors were derived from foraging experiments in different temperatures (Paper II), assuming no size-variation, as this was not accounted for in these experiments.

Light-dependent attack rates and handling times were derived using data from experiments on roach and vendace foraging under two light intensities, 10 lux and 1 lux (Paper II) as well as data from corresponding experiments for perch (Bergman, 1988). Thereby, the derived species-specific scaling factors for light (Y_L and Z_L) were used to convert attack rates and handling times for the applied light intensities (Paper III: Table 2). In lack of size-specific experimental data, the same relationships for light-dependency within each species, irrespective of size, was assumed (Paper III: Table 2).

To calculate potential energy intake rates based on sampled prey abundances, taking the effects of prey size and consumer size on foraging rates into account, sampled zooplankton were divided into two size classes for which empirically derived parameters were applied (Paper III: Table 2). Total potential zoo-plankton prey intake as a function of consumer size, temperature, and light intensity, was calculated for each fish species, assuming that fish could catch zooplankton from both size classes simultaneously, while handling time was limited by the intake of both prey size classes, according to an adjusted Holling type II functional response equation (Holling, 1959) (Paper III: Tables 1, 2). The same scaling for zooplankton prey size and consumer body size was assumed for vendace as those derived from experiments using roach (Hjelm & Persson, 2001).

Furthermore, the littoral-epilimnion also contained zoobenthos as a potential food resource. The potential energy intake rate in the littoral-epilimnion habitat was then calculated as the total potential intake from zooplankton as well as the potential intake from sampled zoobenthos, and using the ratio of benthic foraging habitat volume to zooplankton foraging habitat volume.

The habitat-specific abundances and length distributions of perch were applied to calculate predation risk in the different habitats, by using attack rates of perch on fish prey, estimated from previous experiments (Lundvall *et al.*, 1999; Huss *et al.*, 2010). Attack rates were depending on the relative sizes of predator and prey, and adjustments for temperature of attack rates were made

using the scaling factor r_a (Paper III: Tables 1, 2). All prey fish species were assumed to be similar in their size-dependent vulnerability to predation by perch. First, attack rates for fish victim sizes (5 mm to 170 mm) were calculated for each predator size (40 mm to 380 mm). The attack rates were summed together for each predator size for ranges of victims representing size groups <80, 80-160, and >160 mm. The predator-size-specific sum of attack rates were then multiplied by the relative abundance of perch for that specific predator size, and summed together to a relative population attack rate for each victim size group (<80, 80-160, and >160 mm), respectively, as a measure of size-specific predation risk in each habitat.

My predictions were:

(1) Responses in habitat use of perch and roach to the presence of the specialist, vendace, are species- and size-specific, as they depend on species-specific size-dependent individual rates regulating net energy intake.

(2) The predation pressure will differ between habitats, and following expected effects of vendace on piscivorous perch, also depending on whether vendace is present, thereby explaining size-dependent habitat use.

Furthermore, based on the predictions, the aim was to investigate whether accounting for abiotic habitat conditions in the calculations of individual-based rates could increase the understanding of species- and size-specific habitat use.

3.4 Effects of climate change for population regulation of a cold-water fish species

To study the effect of temperature on the population structure and regulation of a cold-water fish species (vendace), a biomass-based population modelling approach (de Roos *et al.*, 2008) was used (Paper IV). Two life stages (juveniles and adults) were considered, which were distributed in two habitats at fixed proportions. The two habitats represent two temperature environments in the pelagic zone of thermally stratified lakes; the epilimnion (above the thermocline), where the temperature was varied, and the hypolimnion (below the thermocline), where the temperature was constant at 6 °C (Fig. 5).

The population model developed in the study (Paper IV) includes size- and temperature-dependent individual-level processes based on a size-structured consumer-resource model (Persson *et al.*, 1998). Under equilibrium conditions, the model predictions are equal to those of a physiologically structured population model (PSPM), where a continuous size-distribution is used (de Roos *et al.*, 2008).
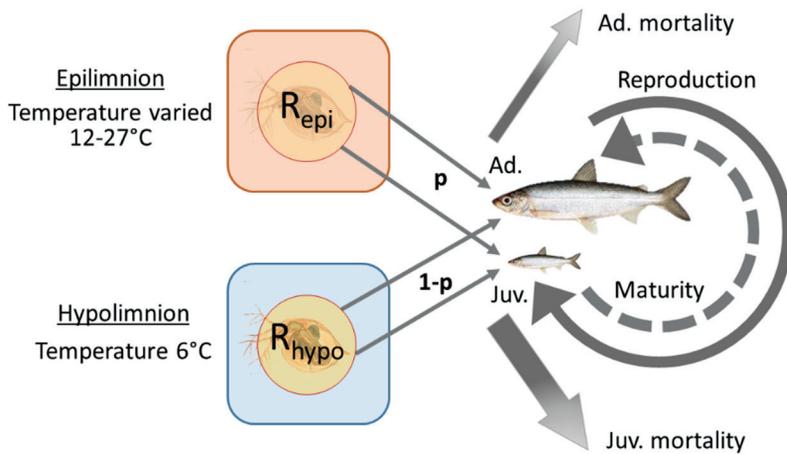
Figure 5. Schematic illustration of the stage-structured biomass-based consumer-resource model including two habitats (Paper IV). The two stages (Ad. = adults and Juv. = juveniles) in the consumer population have metabolic costs as well as energetic gains from exploiting zooplankton resources R_i in the epilimnion and hypolimnion habitats, at proportions p and 1-p, respectively. The temperatures in the epilimnion are varied in the range 12-27 °C while the temperature in the hypolimnion is constant at 6 °C. Consumer intake rates are adjusted for temperature and representative size of each stage, and depend on the resource densities in each habitat, which are, in turn, affected by consumption. Consumption (arrows connecting resources with consumer stages), minus temperature-dependent metabolism by the same proportions for each habitat as for energy intake, minus biomass loss from mortality, regulates net biomass production of consumers. Biomass production is transformed into reproduction for adults (circular arrow), resulting in juvenile biomass, and maturity for juveniles (hatched circular arrow), resulting in adult biomass.

Adjustments for temperature of individual-level processes were made according to Ohlberger *et al.* (2011); Ohlberger *et al.* (2012). Furthermore, the model was calibrated by using parameter values for foraging rates originally derived for roach (Hjelm & Persson, 2001), and adjusted for vendace based on data from foraging experiments (Paper II). As the temperature scaling factor r_a was originally developed for the warm-water species perch (Karås & Thoresson, 1992; Ohlberger *et al.*, 2011), it needed adjustment to account for the relatively high foraging efficiency of vendace in cold temperatures. By fitting data on ratios of measured capture rates obtained from foraging experiments with vendace at temperatures 6, 12, and 18 °C (Paper II) to the calculated intake rates, adjusted to temperature solely by the temperature scaling factor r_a (Paper III: Table 1; Paper IV: Table 2), the temperature-dependent adjustment factor F_V for vendace could be obtained (Paper IV: Appendix). F_V was then multiplied with r_a to obtain size-dependent attack rates and handling times adjusted for temperature, to use in the model (Paper IV: Table 2). The effect of temperature

on size-dependent individual processes was studied to help in interpreting model results (Paper IV: Fig. 1).

From the calculated size- and temperature-dependent energy intake and metabolism (Paper IV: Tables 2, 3), a set of differential equations were used to produce values of net biomass production of resources as well as consumer stages in the two habitats (Paper IV: eqs. 9, 10, 11). The zooplankton dynamics were treated as separate for each habitat, as the densities were assumed to be depending on the intrinsic semi-chemostat dynamics as well as the consumption in each habitat. The changes in biomass of consumers were added together for both habitats as consumers were assumed to alternate between habitats. Using the net energy intake rate for each population stage and time step, the net production of juvenile biomass and the net production of adult biomass (equal to the maturation of juvenile biomass into the adult stage), was derived.

To investigate effects of increased temperature, bifurcation analysis was used, where epilimnion temperature was systematically increased or decreased in small steps within the temperature range 12-27 °C. At every change in temperature, dynamics were integrated over a period of 10 000 time steps, and the means of sampled values from the last 100 time steps were used as end values (Paper IV: Figs. 2, 3, 4). The outcome of consumers and resource biomasses, habitat-specific rates of intake, consumption, as well as maturation and reproduction of the consumers were investigated with bifurcation analysis to study the dynamics of the model system as a function of epilimnion temperature (Paper IV: Table 1, Figs. 2, 3, 4).

To further support interpretations of the model, calculations were made of relative size-, temperature-, and resource-dependent limits for growth, to illustrate the competitive ability of the two population stages (Paper IV: Fig. 1). The critical resource density (CRD) at which the individual biomass production is zero (Byström & Andersson, 2005) was calculated (Paper IV: eq. 12).

Other studies have shown that warmer temperatures result in small-bodied individuals becoming relatively more common (Sheridan & Bickford, 2011; Baudron *et al.*, 2014), with effects for population structure and dynamics (Ohlberger *et al.*, 2011). I predicted that smaller size would be advantageous at higher temperatures also for this cold-water species. Furthermore, taking size-dependent individual-level responses to temperature in different habitats into account, my aim was to reveal how size-dependent performance affected by temperature in combination with habitat use will feed back on population structure and regulation.

4 Results and discussion

4.1 Patterns of species distributions among habitats

The distribution of the three species differed between the pelagic and littoral-benthic habitats, as perch and roach used mainly the littoral-benthic habitat and vendace used mainly the pelagic hypolimnion (Paper I and III). In accordance with predictions, the responses to the presence of vendace, reflected in habitat use, differed between perch and roach, and these differences were also size-dependent. Roach biomass was generally lower in lakes with vendace, and roach used the pelagic habitat to a lesser extent in the presence of vendace (Fig. 6a; Paper I and III). The relative biomass in the pelagic habitat, i.e. the ratio of pelagic biomass to littoral-benthic biomass, was significantly lower for roach in the presence of vendace (Fig. 6b). This supports the prediction that roach are negatively affected by competition from the zooplanktivorous specialist, i.e., vendace, and that the effect is mainly expressed in the pelagic zone. Furthermore, roach mainly used the 0-6 m depth interval in both the pelagic zone and the littoral-benthic zone, and were least common in the pelagic zone below 6 m, irrespective of vendace presence (Paper I and III).

Vendace were found mostly below 6 m in the pelagic zone, which indicates that vendace in contrast to roach exploit the zooplankton food resource in deeper water (Paper I and III). As zooplankton may perform diel horizontal migrations and move into deeper waters to avoid predation (Lampert, 1993; Larsson & Lampert, 2012), the predation pressure on zooplankton may be stronger when vendace is present, as their refuge from predation in deeper water might be lacking with vendace present. In support of this view, vendace has been shown to strongly deplete the zooplankton resource (Helminen & Sarvala, 1997), which suggests a potential strong effect for competing species in the pelagic zone. This was also supported by results from Paper III (see section 4.4.3).

The relative biomass of perch in the pelagic habitat was lower in lakes with only perch present compared to lakes including roach, or both roach and vendace (Paper I: Fig. 3b). This may be explained by combined inter- and intra-specific competition for perch in the littoral-benthic habitat, leading to that perch use the pelagic zone to a greater extent in lakes with competing zooplanktivores (Paper I). It can be expected that interspecific competition from zooplanktivorous species should increase intra-specific competition for non-piscivorous perch in the littoral-benthic zone, by reducing available food resources. This explanation is supported by results from Svanbäck *et al.* (2008), who found that intra-specific competition was important for the habitat use of both perch and roach. However, results from Paper III, where lakes with perch and roach are compared with

perch, roach, and vendace, support predictions that vendace presence should result in a decreased use by perch of the pelagic epilimnion. This was hypothesized as being a result of size-dependent depletion of zooplankton in lakes with vendace (see section 4.4.3).

4.2   Effects of biotic interactions on population structures

Results from Paper I showed that the biomass of piscivorous perch in both the littoral-benthic and the pelagic habitats was positively related to the biomass of roach and vendace, but in contrast to predictions, when controlling for total biomass the relationship was not significant. In contrast, when comparing lakes with vendace with the two lakes without vendace in Paper III, perch biomass was as predicted larger in lakes with vendace present, and the biomass of large perch was higher in the littoral-epilimnion in lakes with vendace. The difference between Paper I and III, regarding support for the prediction that piscivorous perch biomass would be higher in lakes with vendace, may be a result of larger variation resulting from, e.g., productivity and lake morphology in the larger dataset of lakes in Paper I (Holmgren & Appelberg, 2000; Arranz *et al.*, 2016; Mehner *et al.*, 2016). The population dynamics of perch, with year classes varying in strength as a result of competitive bottlenecks and ontogenetic niche shifts, could also add to variability in perch biomass in a larger sample of lakes (Claessen *et al.*, 2000; Persson *et al.*, 2000; Persson *et al.*, 2004).

   A relatively large proportion of piscivorous perch in the population can be expected to result in a greater reduction of biomass of small perch, as piscivorous perch are also cannibalistic. A large proportion of piscivorous perch biomass can be predicted to be sustained by a high maturation rate into the adult stage, as a result of the reduction in juvenile biomass through cannibalism leading to decreased competition in the juvenile stage (de Roos *et al.*, 2013). The results from Paper II support that a relatively large proportion of piscivorous perch in lakes with vendace results in an accumulation of adult biomass, also in agreement with perch biomass peaks predicted to occur at intermediate productivity levels (Persson *et al.*, 1991).

   Persson *et al.* (1991) predicted that the higher proportion of piscivorous perch biomass observed in lakes with vendace could be explained by indirect biotic interactions favouring perch. The suggested indirect effects of changed habitat utilization by foremost roach (see section 1.7), resulting in increased competition for small perch, are supported by the observed patterns of individual growth in perch (Paper I). In the smallest size class (<60 mm), individual growth rate of perch was lower in lakes with vendace, thereby indicating a higher competitive pressure for small perch. However, in the 150–180 and 180-210 mm size classes,
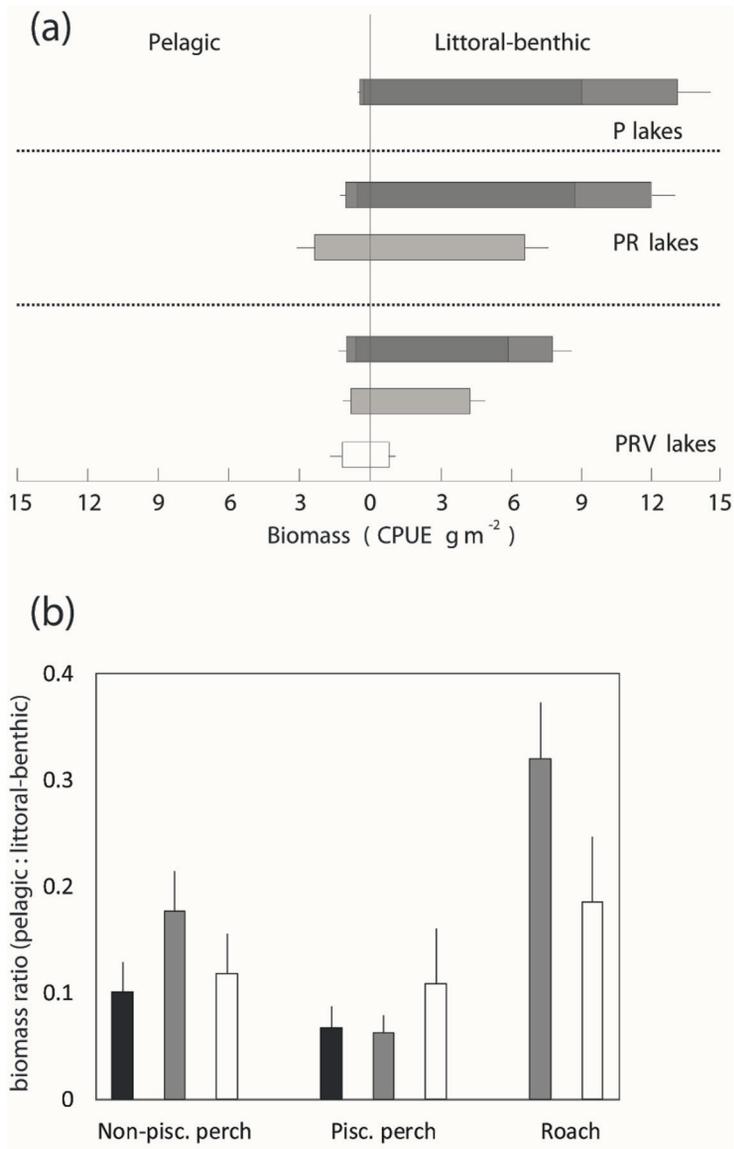
Figure 6. (a) Biomasses ± 1 S.E. in the littoral-benthic and pelagic habitats of three groups of lakes (Paper I). P, perch; PR, perch and roach; PRV, perch, roach and vendace. Top bar in each lake group = perch biomass; middle bar = roach and lowest bar = vendace. For perch, darker shading indicates the piscivorous proportion of the biomass. (b) Mean ratios ± 1 S.E. of the total biomass of non-piscivorous perch, piscivorous perch and roach in the pelagic to that in the littoral-benthic habitat. Black bars represent lakes with perch, grey staples lakes with perch and roach, and white staples represent lakes with perch, roach and vendace.

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where perch switch to eating fish, individual growth rate of perch in lakes with vendace was higher compared to in lakes with only perch and roach (Paper I). This supports the prediction that the energetic gain for piscivorous perch was higher in lakes with vendace. The switch from lower individual growth rate for small perch to comparatively higher growth rates for intermediate and large perch in lakes with vendace thus supports the prediction of released competition from intra-guild predation (Claessen *et al.*, 2000; Persson & de Roos, 2012). However, as individual growth rates of the smallest size class of perch was lower in lakes with vendace, this indicates that the competitive pressure for small zooplanktivorous perch was still higher in lakes with vendace, and that released competition, as supported by increased growth rate, instead appeared at intermediate sizes (150-180 mm), where the main food resource of perch is zoobenthos (Persson, 1987b; Horppila *et al.*, 2000). The higher growth rate for medium-sized perch in lakes with vendace may be explained by an earlier switch to piscivory, although this has not been confirmed. The lower biomass of roach in lakes with vendace may also facilitate for medium-sized perch in the benthivorous stage, as perch are competitively superior feeding on benthic invertebrates compared to roach (Persson, 1987a; Hjelm *et al.*, 2003).

There may be increased predation possibilities for perch in lakes with vendace, either by access to vendace as an alternative prey species, or generally increased access to prey fish. A general increased access to prey fish could be explained by small perch and roach experiencing a higher competitive pressure in lakes with vendace, in accordance with previous studies where higher risk taking behaviour in hungry prey organisms was found (Jakobsen *et al.*, 1988). Another possible explanation for reduced intra-specific competition, leading to faster individual growth for intermediate sized perch in lakes with vendace, is apparent competition through predation by northern pike (*Esox lucius* L.). To clarify, if pike has an advantage through vendace being present in the system as an additional available prey, or by vendace causing changed habitat use or behaviours of roach and perch, the pike population may increase, and the consumption of perch and roach by pike would also increase.

Comparing size distributions of roach in the pelagic zone, where roach in the size range 120-150 mm were relatively more common in vendace lakes (Paper I), supports that the predation pressure in the littoral-benthic habitat was higher in lakes with vendace, causing this size range of roach to use the pelagic habitat more. Pike is a common fish predator in lakes, and was documented from test-fishing data in 66% of the lakes (Paper I), but pike is not representatively sampled and can be missed when sampling with gillnets because of its stationary behaviour. The potential role of pike in apparent competition was previously discussed by Persson and de Roos (2012), who however interpreted their results

as apparent competition by pike predation being absent on the short term, in systems with perch and introduced roach.

In contrast to Persson *et al.* (1991), I found that size structures of perch were not significantly different in lakes containing roach and vendace compared to lakes without vendace (Fig. 6a; Paper I). One alternative explanation for this pattern is that the predicted positive effects for piscivorous perch in systems with vendace (Persson *et al.*, 1991), leading to a higher proportion of piscivorous perch individuals in the population, could be counteracted by apparent competition caused by increased predation from pike in systems with vendace.

According to my predictions, size distributions of roach were skewed toward larger sizes in lakes with vendace (Fig. 7b; Paper I). Roach in the size range 60-90 mm were less common, while 180-210 mm roach were more common, in the littoral-benthic habitat in lakes with vendace. If piscivorous perch are more abundant in lakes with vendace, as supported by Paper III, a larger body size would confer a refuge from predation from perch, and also from pike. As there were more roach in the size range 180-210 mm, i.e., a size refuge from predation from perch in lakes with vendace (Fig. 7b; Paper I; Paper III: Fig. 5), the lack of support regarding perch population structure from Paper I may require alternative explanations. Such explanations may be related to, e.g., high growth rate of piscivorous perch, or apparent competition through pike, as given above.

To investigate the relative importance of pike predation for population structures of perch and roach would require detailed studies regarding pike densities and diet in different lake systems, using other data than those assembled for Paper I and III. Mechanisms underlying the population structures of perch and roach in response to competition and predation from both perch and pike, might instead be elucidated by analyzing time series data of single lakes.

4.3   Mechanisms to explain habitat use

4.3.1 Effects of predation

In the study of fish community structures in 115 lakes, I found differences among habitats regarding size distributions of roach and vendace (Fig. 7b, c; Paper I). Roach in the size range 90-120 mm were significantly over-represented in the pelagic zone compared to the littoral-benthic zone (Figure 7b). This indicates that the pelagic habitat for roach in the size range 90-120 mm is profitable, when balancing energy gain and predation risk. On the other hand, the open pelagic habitat can be assumed to be less safe from predation for smaller roach. It can be hypothesized that the trade-off in predation risk to energy gain changes markedly with size for roach, which in this case is reflected in that small roach were using the open pelagic habitat less.

Indeed, roach in the size range 60-90 mm were relatively less common in the littoral-benthic habitat of lakes with vendace compared to in lakes without, indicating a possible higher predation pressure in those lakes (Fig. 7b). The mechanisms underlying different size distributions of roach and vendace in different habitats can be suggested to be results of size-dependent performances affecting their energetic gains, as well as behavioural differences which may differently affect their sensitivities to predation. Roach may be more adapted to a habitat with vegetation, while the opposite may hold for vendace (Paper II).

Small vendace in the size range 60-120 mm were under-represented in the littoral-benthic habitat (Fig. 7c). This can be explained by vendace being expected to utilize the hypolimnion of the pelagic zone more than the warm littoral epilimnion because they are adapted to colder temperatures, in accordance with previous studies (Northcote & Rundberg, 1970; Dembiński, 1971; Hamrin, 1986; Mehner et al., 2007). Explanations for this may also be sought in behavioural adaptations to avoid predation. The results in Paper III were in accordance with this pattern, as vendace were relatively more scarce in the littoral-epilimnion and benthic-hypolimnion (Paper III: Fig. 2c), supporting the prediction that a habitat closer to the shore and bottom may be less suitable for vendace, while an open habitat away from the shore may instead be less suitable for roach.

In the predation experiment (Paper II), roach and vendace showed different evasive behaviours when being pursued by perch. Both species normally schooled together. However, roach dispersed and jumped above the surface upon attack from perch, while vendace schooled more tightly, i.e., to a tight ball, and moved downwards. These are examples of evasive behaviours that may have evolved in connection with the species' principal habitat use; roach which is predominantly found in more shallow habitats in or near to vegetation, and vendace in a deep water column of the pelagic zone.

In contrast to the prediction that vendace would be more sensitive than roach to predation by perch, there was no significant difference in the consumption of roach or vendace by perch when comparing treatments with only roach, only vendace, or a mixture (Fig. 8; Paper II). One explanation may be that neither species had access to a potential species-specific predation refuge. The enclosures lacked vegetation, i.e., a potential refuge for roach, and were possibly not deep enough for the evasive strategy of vendace to be efficient. The lack of corroboration may also indicate that the differences in habitat use between roach and vendace could instead be explained by other mechanisms than predation, e.g., relative abilities of energy intake, and metabolism, in the trade-off between mortality and energy gain for the two species.
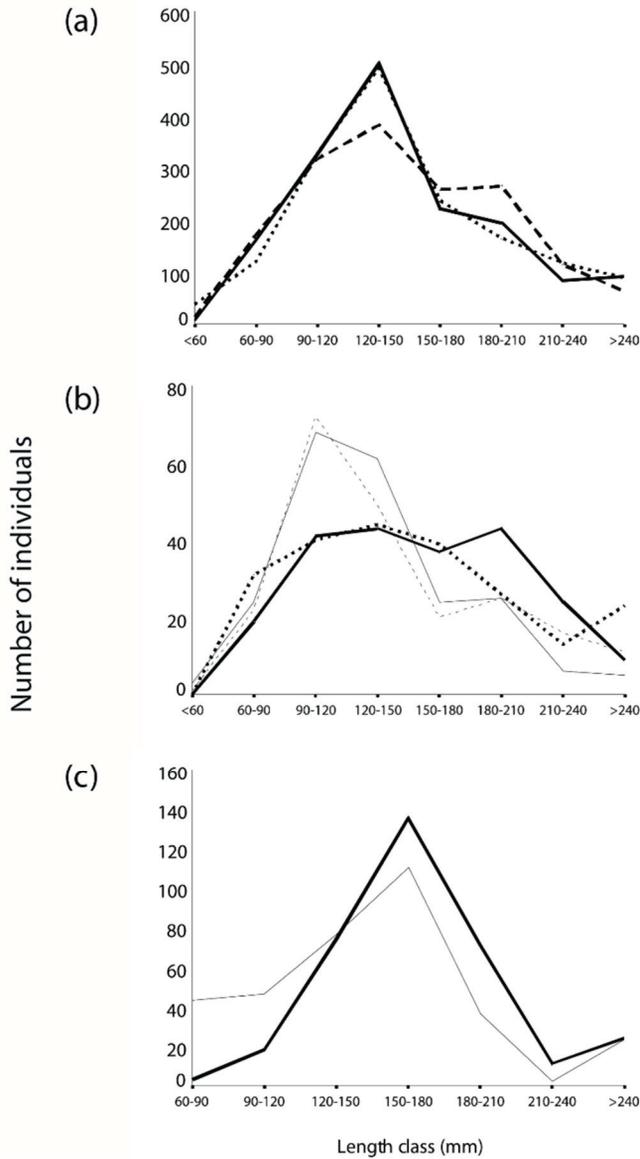
Figure 7. Number of individuals in 30 mm length classes (Paper I), of (a) perch from the littoral-benthic habitat (72 lengths randomly selected from each of 22 lakes); (b) roach from the littoral-benthic and pelagic habitats, respectively, in nine lakes with vendace and nine lakes without vendace (24 lengths randomly selected from each habitat in each lake); (c) vendace from the littoral-benthic and pelagic habitat (24 lengths randomly selected from 14 lakes). Dashed lines = lakes with only perch, dotted lined = lakes with perch and roach, solid lines = lakes with perch, roach and vendace. Lines in bold represent the littoral-benthic zone, thinner lines represent the pelagic zone.
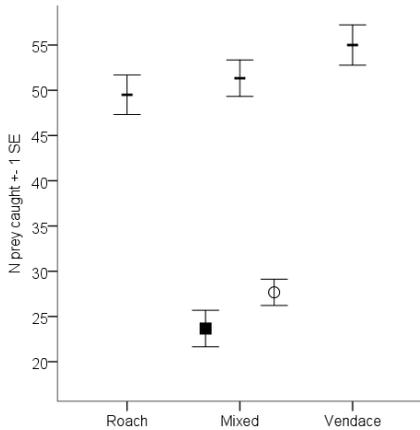
Figure 8. Captured prey (mean N ± 1 SE) in pond enclosure experiments (Paper II) with perch used as predators and roach (black squares) and vendace (white circles) used as prey (six replicates of each treatment). Horizontal bold bars represent total number of prey caught in each treatment.

The calculated predation pressure (Paper III: Fig. 5) in different habitats, based on size structures of perch occurring in different habitats, showed a habitat-dependent effect when comparing lakes with and without vendace. In the littoral-benthic habitat, the predation risk for the smallest size class of fish (< 8 cm) was similar among lakes with and without vendace, while the predation risk was lower in the pelagic-epilimnion in lakes with vendace, as intermediate-sized and large perch were almost absent from this habitat with vendace present. Relatively higher individual growth rates of large perch (Papers I and III), in spite of their relatively higher biomass found in lakes with vendace (Paper III), indicates better access to fish prey for piscivorous perch in lakes with vendace (see section 4.2). For intermediate sized and large prey fish the predation risk from perch was found to be negligible in all habitats. Larger fish could be potential victims to other predators such as pike which is normally foraging closer to the shore. However, pike was not included in these studies, although it was documented from all four lakes studied in Paper III.

4.3.2 Temperature and light affecting competitive abilities

Ectothermic species are differently adapted to forage efficiently in different temperatures, and also have different adaptations to different light levels, i.e., they have different fundamental niches. Therefore, it is important to include temperature and light when studying interactions between roach and vendace in the pelagic habitat. To investigate their competitive abilities, I estimated species-

and size-specific metabolism as well as net energy gain, using data collected from experiments in aquaria with different temperature and light treatments (Paper II).

As predicted, capture rate increased with temperature in both roach and vendace (Paper II), supporting that foraging efficiencies generally increase with temperature within the applied temperature range. The capture rate of vendace was higher than for roach at all temperature and light treatments. In contrast to predictions, roach capture rate was lower than for vendace also at 18 °C. The comparatively higher foraging rates of vendace at lower temperatures may partly explain why the two species are spatially separated, so that vendace mainly use the deeper, and roach use the shallow water. However, the foraging efficiency on its own does not explain why roach are found in the pelagic zone, and neither why vendace is relatively less common in warmer water.

Because light affects the foraging success of many species, it could be predicted that light as an additional factor could explain the habitat distribution of roach and vendace. However, the prediction that the capture rate of vendace would be relatively less affected by low light levels than for roach, based on that vendace are normally found in deeper water, was not supported. On the contrary, vendace capture rate was higher at 10 lux compared to 1 lux, while the capture rate of roach did not differ significantly with light treatment. Furthermore, vendace are not primarily found in shallow water with more light, although their foraging ability was greater in the higher light level. Thus, different light levels could not further explain the distribution of vendace.

I predicted that both species would increase their swimming speed with temperature (Paper II), as that can be expected in ectotherms. This was supported by the results. Also according to predictions, the swimming speed of vendace was higher than for roach in all temperature and light treatments when fish were foraging. The estimated active metabolic rate for vendace was lower than for roach only at 6 °C (Fig. 9a). However, the swimming performance when not foraging, measured at 18 °C without prey, was similar between species. These results support predictions that active metabolic rate, including the energy expenditure from swimming when foraging, is an important factor to determine relative competitive abilities (Giacomini *et al.*, 2013).

4.3.3 Net energy gain and the trade-off for mortality

From the foraging experiment (Paper II), I found that the energy gain ratio of roach was equal to that of vendace in one treatment, i.e., the lowest light level at the highest temperature (Fig. 9b). This may explain why roach migrate out to the pelagic zone at night to eat zooplankton (Bohl, 1979; Okun & Mehner, 2005), as roach were similar in efficiency even to the highly efficient zooplanktivore

vendace in warmer water and lower light conditions. Furthermore, the relatively
high metabolic costs in colder temperatures for roach in combination with low
foraging efficiencies, manifested in the ratio of energy gain to energy loss (Fig.
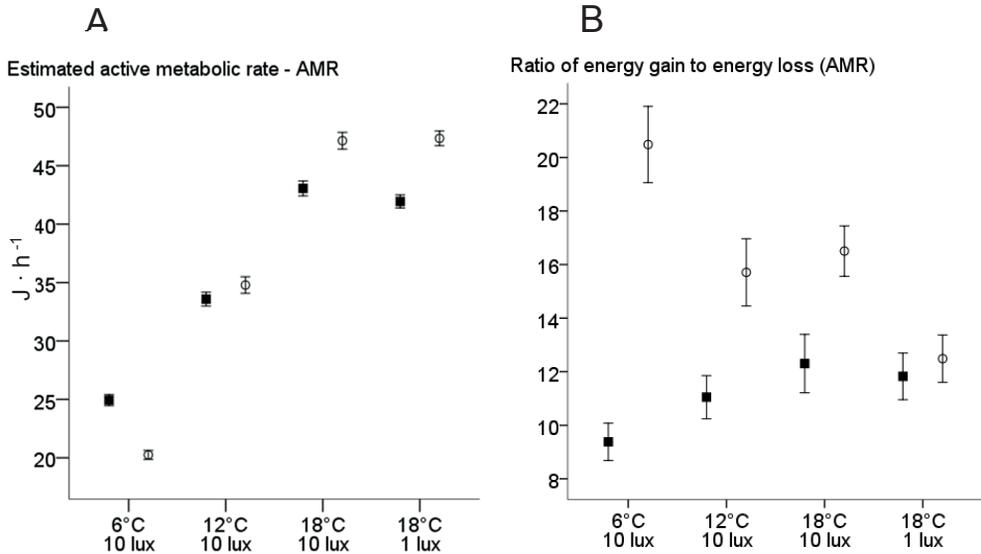9), may explain why roach avoid the deeper, colder water.

Figure 9. A) Estimated active metabolic rate (AMR, Joules · h^{-1}) and B) ratio of energy intake from
capture rate (prey · s^{-1} converted to Joules · h^{-1}) to estimated active metabolic rate (mean ± 1 SE)
for roach (black squares) and vendace (white circles) in different temperature and light treatments
when foraging on *Daphnia magna* (Paper II). Active metabolic rates were estimated according to
Hölker and Breckling (2002) for roach and Ohlberger *et al.* (2007) for vendace. Swimming speed
and capture rate for each replicate were applied together with mean lengths and weights of roach
and vendace, respectively.

The opposite pattern regarding energy gain ratio was observed for vendace
(Paper II). Results from Paper II show that the habitat distribution of vendace
and roach could mainly be explained by how their energy gain ratios are affected
by temperature and light. However, focusing on individual processes in
connection to abiotic factors in an experimental study does not take into account
the variation of prey composition and abundance among habitats in lakes.

By applying metabolic models for capture rate and metabolism together with
sampled densities of zooplankton and zoobenthos prey in different habitats
(Paper III), the size-specific potential net energy intake of the studied species
could be compared for lakes with and without vendace. For small perch, the
calculated net energy intake was highest in the epilimnion, but there were no
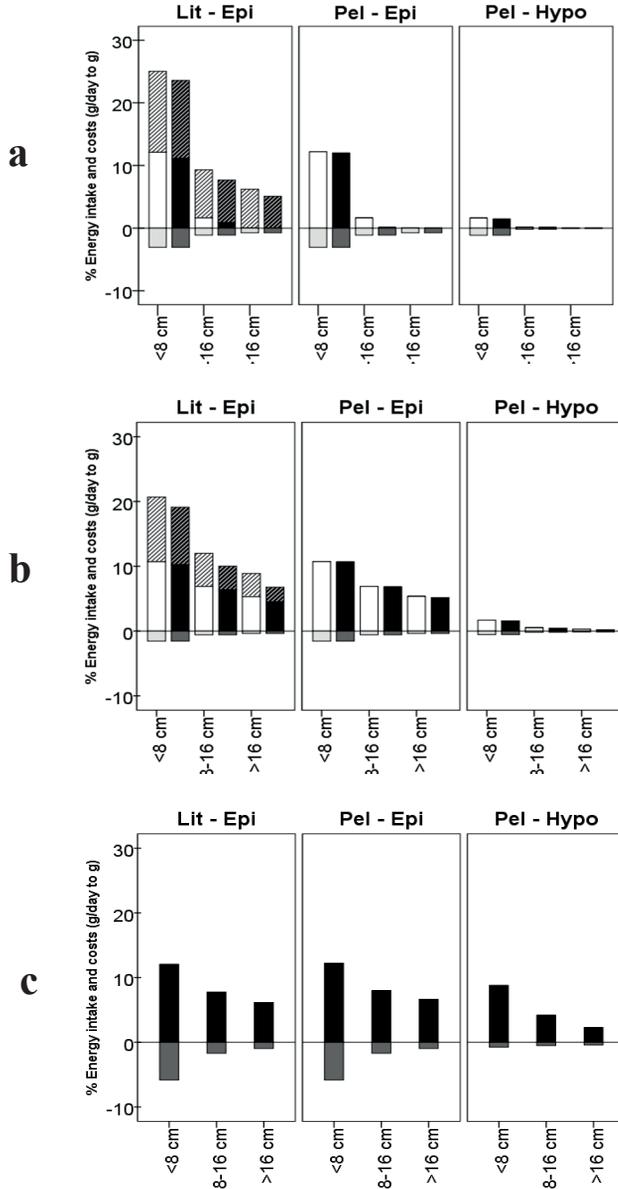differences between the littoral-epilimnion and the pelagic-epilimnion, neither

Figure 10. Mean % size-specific potential energy intake (SPI) to body weight (positive values); from zooplankton (solid staples) and zoobenthos (hatched staples), and size-specific energy costs to body weight (negative values), for a) perch, b) roach, and c) vendace, in three different size classes (Paper III). Habitats represented are the littoral-epilimnion (Lit-Epi), the pelagic-epilimnion (Pel-Epi), and the pelagic-hypolimnion (Pel-Hypo). Size-, temperature- and light dependent energy intake were estimated from food abundances found in lakes without vendace (light staples to the left, N=2), and lakes with vendace (darker staples to the right, N=2).

when comparing lakes with or without vendace. For medium and large-sized perch, however, the net energy intake in lakes with vendace was negative in the pelagic-epilimnion, which may explain why perch in this size range abandon this habitat with vendace present. As the total biomass of zooplankton in the pelagic-epilimnion did not differ significantly when comparing lakes with and without vendace, the poorer energetic reward for perch in the medium size range could be attributed to that larger zooplankton were lacking in the pelagic-epilimnion in lakes with vendace (Paper III: Fig. 3b). As foraging abilities on zooplankton depends on relative sizes of consumer and prey, and these relationships differ between perch and roach, the lack of large zooplankton did not have the same negative effect for roach as it did for medium-sized perch. Neither the total biomass of zooplankton nor the biomass of small zooplankton differed in the littoral-epilimnion or the pelagic-epilimnion when comparing lakes with and without vendace (Paper III: Table 3). However, the taxonomic and size-dependent composition of zooplankton differed, as small-bodied *Bosmina* sp. were comparatively more abundant in all habitats, and large zooplankton were lacking in the pelagic-epilimnion in lakes with vendace (Paper III: Fig. 3). Furthermore, the biomass of zooplankton in the pelagic-hypolimnion was lower in lakes with vendace, which together with the composition of sizes and taxa indicated a higher predation pressure on zooplankton in lakes with vendace.

Also in the littoral-epilimnion, the size-dependent net energy intake for perch in the medium size range was low in lakes without vendace, and negative in lakes with vendace (Paper III: Fig. A1). In comparison with perch, medium- and large-sized roach had a positive and higher energy intake in the littoral-epilimnion. The potential energy intake from zoobenthos in the littoral-epilimnion shows that zoobenthos prey is comparatively more important for perch than for roach (Fig. 10). This can be explained by the relatively higher foraging efficiency of perch on zoobenthos, while roach instead have a higher foraging efficiency on zooplankton (Paper III: Table 2). Furthermore, the low calculated energy intake for perch, based on zoobenthos and zooplankton food resources, points to that perch would need another food source to grow and persist, i.e., fish prey. As densities of fish in the smallest size-class could not be quantified, for reasons of sampling methods, this source of prey could not be included in the calculations of potential energy intake for perch.

One of the mechanisms which has been described as fundamental for habitat selection is the rule that individuals should minimize the ratio of mortality risk (μ) to growth (g), i.e., their μ/g ratio (Gilliam & Fraser, 1987). This rule has been tested theoretically as well as experimentally (Gilliam & Fraser, 1988; Werner & Anholt, 1993; Dahlgren & Eggleston, 2000). In Paper II and III, I compared net energy intake and predation risk separately in relation to the size-dependent habitat use of the studied species. Combining these mechanisms would enable testing of the "minimize-μ/g-ratio-rule" using data from different habitats in lakes, i.e., on a larger scale in natural systems. Therefore, to further attempt to clarify mechanisms regulating habitat use in my thesis, I calculated this ratio using the estimated predation pressure based on perch size structures to the estimated size-dependent individual net energy gain for individuals of roach and vendace in different habitats (Paper III). Results for the two lakes with and the two lakes without vendace are shown in Fig. 11. As the calculated net energy intake did not include fish prey of perch (Fig. 10), and the net energy intake based on zooplankton and zoobenthos indicated that perch also needed fish to grow (Paper III: Fig. A1), perch was omitted from the calculations.

The μ/g ratios for the smallest (<8 cm) as well as the intermediate (8-16 cm) size classes of roach were lowest in the pelagic-epilimnion, and there was no difference depending on the presence of vendace. For vendace, the μ/g ratios for
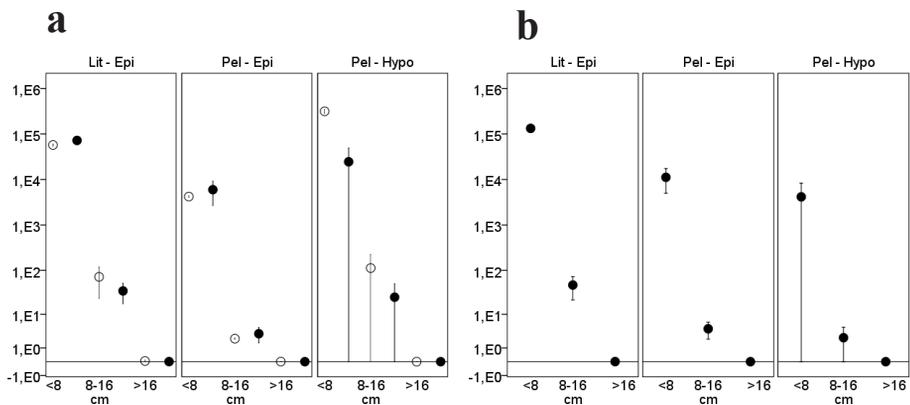

Figure 11. Mean ratios (log-scale) of predation pressure to net energy intake ± S.E., for individuals of a) roach, and b) vendace, in three size classes. Three habitats are represented: the littoral epilimnion (Lit-Epi), the pelagic epilimnion (Pel-Epi), and the pelagic hypolimnion (Pel-Hypo). Estimates were based on food abundances found in lakes without vendace (white circles, N=2), and lakes with vendace (black circles, N=2). Energy costs were estimated according to Ohlberger (2012). See Paper III for details regarding calculated predation pressure and net energy intake.

the smallest and the intermediate size classes were similar in the pelagic-epilimnion and the pelagic-hypolimnion, and ratios were lower in these habitats compared to in the littoral-epilimnion. Based on piscivory from perch from size distributions in different habitats, predation risk was zero, thus the μ/g-ratio was zero for the largest size class (>16 cm).

In comparison with size-dependent net energy intake for roach, which did not differ between the littoral-epilimnion and the pelagic-epilimnion (Paper III: Fig. A1), the lower calculated μ/g ratio in the pelagic-epilimnion indicates that this habitat should indeed be preferred, irrespective of vendace being present or not (Fig. 11). Thus, in contrast to predictions, the observed habitat distributions of roach did not support the μ/g-rule, as roach used the pelagic-epilimnion less in lakes with vendace (Papers I and III). However, in support of the μ/g-rule the μ/g-ratios for vendace were lower in the pelagic-epilimnion and the pelagic-hypolimnion, where they were similar for the small and medium size classes, which could add to explaining why vendace avoid the littoral-epilimnion.

In conclusion, the μ/g ratio could partially explain the habitat use for vendace, but not for roach. To more realistically test the μ/g-rule in natural systems, total predation pressure needs to be considered, i.e., also including other fish predators (see section 4.2). Although the presented studies (Papers I, II, and III) consider predation from perch, which is a numerically dominating species in the studied lakes (Fig. 6; Paper I; Paper III: Fig. 2), predation from pike in the littoral-epilimnion is not considered because of lack of data. Furthermore, as the μ/g-rule can be assumed to formally refer to life-time reproduction, considerations when testing this rule need to be taken regarding life-stage, as well as the temporal and spatial scales (de Roos *et al.*, 1991), concerning food availability of consumers, and predation risk for fish prey in different habitats.

4.4   Effects of warming for population structure and regulation

Warmer temperatures and increased population densities have been found to cause size structures of, e.g., perch and roach to be skewed towards smaller sizes (Arranz *et al.*, 2016). Studying population structure and regulation by modelling long-term effects of changed productivity (van de Wolfshaar *et al.*, 2011) or temperature (van de Wolfshaar *et al.*, 2008; Ohlberger *et al.*, 2011) has yet been done only for single species. By applying dynamic modelling and using two habitats having different temperatures (Paper IV), a population generally adapted for colder water (vendace) was found to be affected by an increased temperature in its secondary, warm habitat (epilimnion), resulting in changes in population structure and total biomass. Size-specific individual vital rates could reveal specific mechanisms for temperature-dependent population regulation.

Juveniles have one advantage over adults, as juvenile individuals need less energy in absolute terms for metabolism. This relative advantage also increases with temperature, as the absolute costs for metabolism follow a steeper slope for adults than for juveniles (Paper IV: Fig. 1). The critical resource density (CRD) required for positive growth (Byström & Andersson, 2005; Byström *et al.*, 2006) is therefore relatively higher for adults up to approximately 20 °C (Fig. 12). In an intermediate temperature range, CRD is (slightly) lower for adult individuals compared to juveniles, resulting in less resources required for a positive net biomass production. However, this competitive superiority for adults in the intermediate temperature range is reversed at higher temperatures. In response to increased temperatures in the secondary (warm) habitat, population structure and total biomass was affected, resulting in a shift in relative biomasses between juveniles and adults. This shift implied that the juvenile biomass became dominating over adult biomass in the highest temperature range.

Maturation is occurring at a higher rate than reproduction within the entire temperature range. This causes an accumulation of adult biomass with low net biomass production, i.e., low reproduction rate. Population growth is hence mainly controlled by reproduction with adult biomass dominating up to 26.5 °C. As temperature rises above 24 °C, there is a marked drop in both maturation and reproduction. The decrease in reproduction rate is proportionally greater compared to maturation, causing the turning point at 24 °C regarding relative juvenile and adult biomasses. A mechanism underlying this shift can be found in temperature- and size-dependent rates on the individual level; rates that thus differ both between juveniles and adults and between habitats as functions of prey density, consumer size, and temperature.

The shift at 24 °C emerges from changed stage-specific intake rates in the epilimnion. As a result of lower consumer biomass, and thereby less prey consumption, leading to higher prey densities, intake rate can increase for juveniles in the epilimnion above 24 °C (Paper IV: Figs. 3a, 4). Through onto-genetic asymmetry, i.e., a stronger negative effect of high temperature on size-specific intake rate for adults (Paper IV: Fig. 1), the intake rate of adults in the epilimnion decreases at 24 °C, which prevents adults to profit from increasing prey densities in the epilimnion (Paper IV: Figs. 3a, 4). The decreasing intake rate of adults in the hypolimnion (at 24 °C epilimnion temperature) can be explained by an increased biomass of juveniles which are supported by their energy gain from the epilimnion (Fig. 13). As a result of increased juvenile biomass, the exploitation by juveniles also increases in the hypolimnion, resulting in a lower prey density (Paper IV: Fig. 4). Because of their smaller size, juveniles can profit more from increasing prey densities in the epilimnion above 24 °C, as the negative effect of increased temperature on their intake rate is less

severe than for adults. Hence, juveniles are able to exploit the resources in the hypolimnion habitat at a close to constant rate, despite the decreasing prey density in the hypolimnion above 24 °C epilimnion temperature. By "inter-habitat subsidies", juveniles are supported by their relatively high net energy gain from the epilimnion; in addition, the decrease adult biomass results in decreased competition from adults.
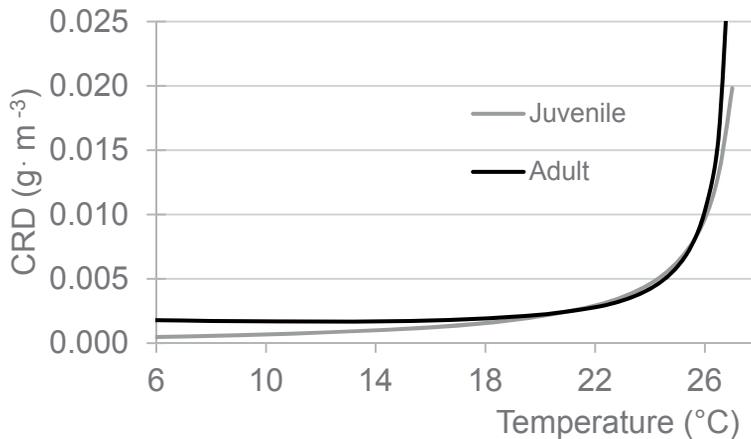

Figure 12. Critical resource density (CRD) of 1 mm *Daphnia* over temperature for juvenile and adult individuals, respectively (Paper IV). CRD was obtained from size-dependent and temperature-adjusted attack rates and handling times for a cold-water species (vendace). Representative weights are 4.7 for juveniles and 45.7 g for adults. (0.015 g · m^{-3} is equivalent to 0.5 *Daphnia* · L^{-1}.)

Ontogenetic asymmetry in energetics, i.e., differences in metabolism and foraging over growth and development (Persson & de Roos, 2013), govern population dynamics (de Roos & Persson, 2013). Such asymmetry can also occur due to, e.g., changes in relative productivity of food resources specific for different developmental stages (Reichstein *et al.*, 2015). In Paper IV, mere temperature-dependent effects on individual performance in different habitats are shown to shift the balance in this asymmetry, even resource productivities are identical in both habitats. Inter-habitat subsidies can be expected to be an essential, although so far overlooked mechanism, governing population dynamics. Changes in the structure and regulation of a population with inter-habitat subsidies will also affect co-existing populations sharing one or more habitats, and thereby also for community dynamics. Therefore, it is essential to take habitat use and temperature-regulated rates on the individual level into account, to foresee effects for communities now and in future climates.
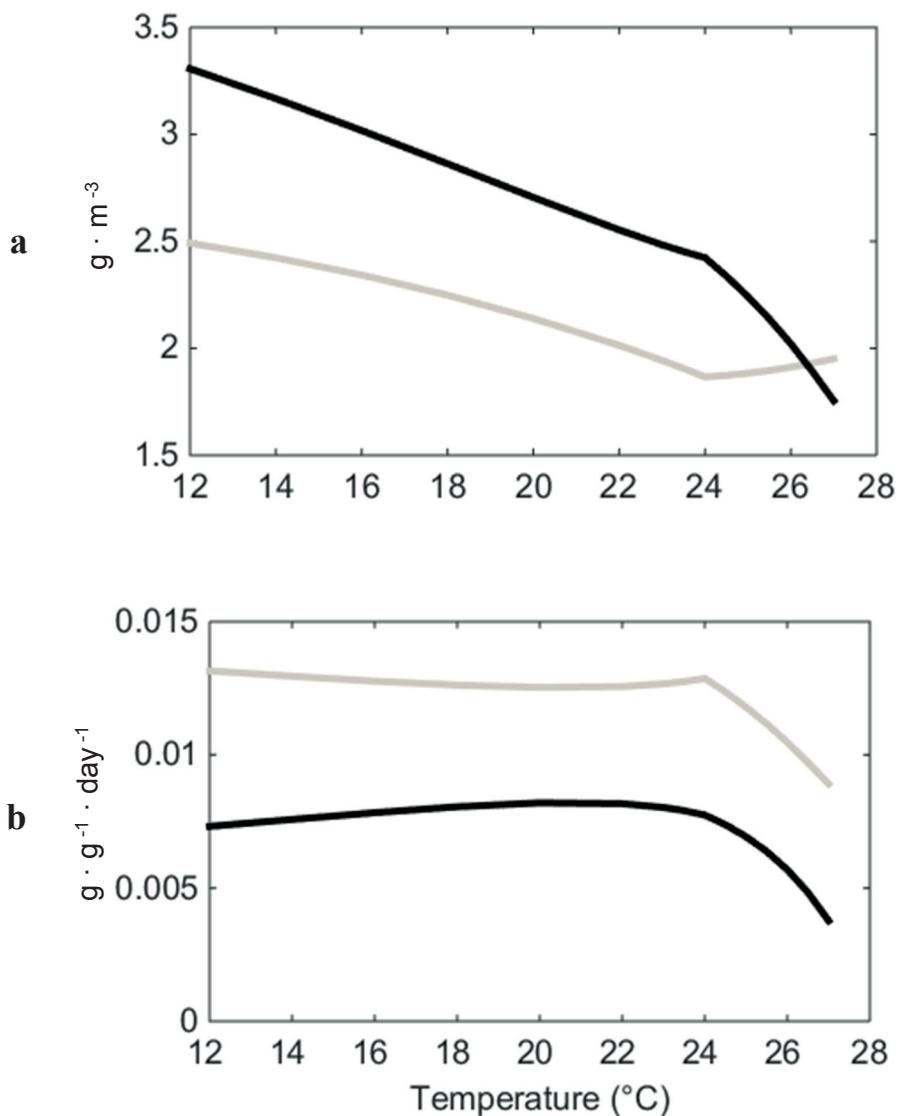
Figure 13. Results from bifurcation analysis of a stage-structured model applied to a cold-water species (vendace) using two habitats (Paper IV). a) Equilibrium biomasses for adults (black) and juvenlies (grey), and b) rates of maturation and reproduction, over the temperature in the epilimnion, when the epilimnion was used in the proportion p=0.2. The temperature in the hypolimnion is 6 °C. ("Equilibrium average" values were used for plotting, based on the mean of the last 100 values for each time series of 10 000 time steps.)

5   Conclusions and future perspectives

My thesis demonstrates how habitat use can be understood in terms of mechanisms on the individual, population and community levels. The thesis has a broad scope in that it includes three species, of which the complex interactions between two of them are particularly well-studied. Broadening the scope, I have investigated how these interactions interplay and link between different habitats. Furthermore, adding to the complexity of the studied system, I have herein included the effects of the third species, which is specialized for one of the habitats. By including field monitoring data from a wide selection of lakes, as well as experiments where factors may be regulated, and applying calculations of physiological individual rates both on sampled field data and in a theoretical model, I was able to explore underlying mechanisms for the further understanding of observed patterns in nature.
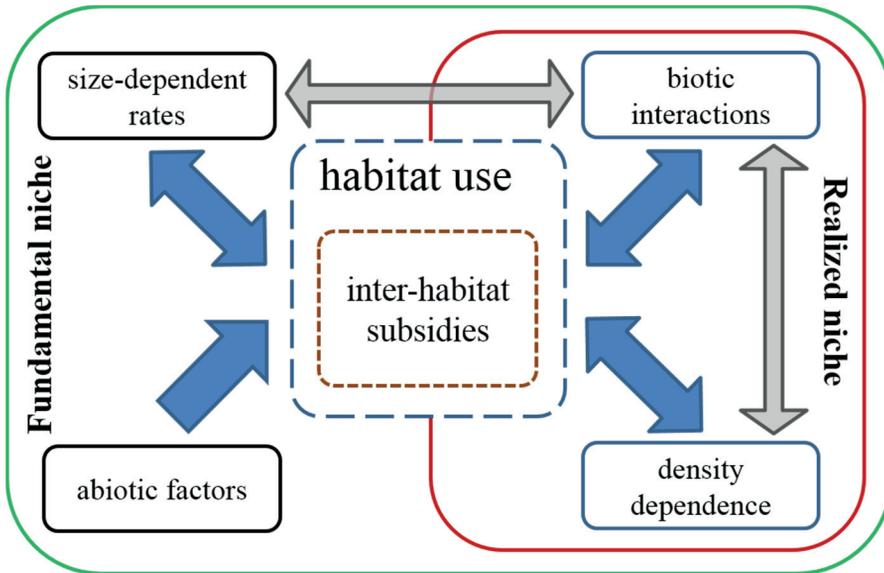
Figure 14. Conceptual figure of ecological components linking habitat use and inter-habitat subsidies to a) individual size-dependent rates (metabolism, energy intake) to b) abiotic factors, c) density dependence, and d) other biotic interactions (predation, interspecific competition). Abiotic factors as well as individual limitations concerning size and metabolism set the borders for the fundamental niche of organisms. Adding density dependence effects and other biotic interactions sets the borders for the realized niche.

Apart from increasing the knowledge of interactions among freshwater fish species in temperate lakes, this thesis increases the knowledge concerning general mechanisms for observed patterns of habitat distribution. Focusing ecological studies around habitat selection will add to the complexity of food web ecology. However, because habitats are different in abiotic factors as well as food web characteristics, this thesis shows that including the concept of habitat selection may also increase our understanding of biotic interactions.

To further understand the effects of biotic interactions including habitat use, a modelling approach including more than one competing species having different physiological adaptations to, e.g., temperature, is motivated. Furthermore, allowing for flexible habitat use in a model system could further illustrate the relative importance of mechanisms that regulate habitat use and community structure. To realistically study factors regulating population dynamics, a fully size-structured approach, including seasonal effects and allowing for population cycles, could increase the understanding of habitat use of a cold water species such as vendace.

The abiotic factors and individual features such as size, and metabolism, which in turn is affected by size, constitute the basis for the fundamental niche of organisms (Fig. 14). Within their fundamental niche, organisms will use the most profitable habitat, either spatially or temporally. The habitat use is secondarily affected by density-dependence concerning available food or other resources, as well as trade-offs governed by biotic interactions. However, biotic interactions and density-dependence also depend on habitat use, which may vary according to individual, size-specific trade-offs of mortality to growth.

The maximization of energy intake will include metabolism, where especially for ectothermic organisms, different habitats may provide entirely different possibilities or limitations. Thus, the inclusion of metabolic traits in connection with habitat use, behaviour and biotic interactions serves the general purpose to incorporate metabolism of organisms into ecological studies. Knowledge of how changes in abiotic factors may affect species differently can be used in scenario studies, to forecast changes in fish communities on a larger geographical scale. Increasing our understanding of how the function of food webs within different habitats may change may help us in designing management and planning our use of natural resources, to avoid the risk of losing sensitive species.

6   Summary

Mechanisms to explain habitat use and how they manifest into biotic interactions are essential for predicting the effects of environmental change. My aim with this thesis is to increase the understanding of how individual processes, influenced by habitat-dependent abiotic factors, are linked to biotic interactions and regulate habitat use as well as population structures in fish communities.

First, I have investigated patterns and tested hypotheses concerning biotic interactions for habitat distribution of the three fish species in Paper I, using data from a comparatively large number of lakes. The presence of a specialist competitor (vendace) affected the other competitor (roach) to diminish its use of the pelagic habitat in, also resulting in a lower biomass of the latter competitor. This is an expected effect of inter-specific competition. Concerning the competing as well as predatory species (perch), the patterns were less clear, and partly contradictory to predictions. However, support was found for that an increased competitive pressure for perch could be released by increased possibilities for predation, including cannibalism. Results presented in this thesis show that this release of competition may be mediated by the presence of a specialized species (vendace). Vendace may increase the possibilities for predation for perch, both directly as an alternative prey for perch, and indirectly through changed interactions between roach and perch, partly mediated by changed habitat use. The observed patterns may be explained in terms of adding complexity to biotic interactions in the food web, by also involving changes in habitat use induced by the presence of a specialized species.

Second, as field data indicated that small individuals of one competing species (roach) could be more sensitive to predation than the other competing species (vendace), I conducted both a predation experiment and a foraging experiment. I could thereby study two basic mechanisms in biotic interactions, i.e., energy intake for growth as well as predation mortality (by perch) in connection to the observed habitat use of the two species competing in the pelagic zone. However, although roach and vendace showed different evasive behaviours in the experiments, I found no clear differences in sensitivity to predation by perch in an open water habitat. The lack of corroboration for predictions regarding different sensitivities to predation by perch indicated that the use of the pelagic habitat would be mostly governed by the possibilities of energy intake. In the feeding experiments with roach and vendace I quantified relative competitive abilities of competing species (roach and vendace), and how their performance changed in different light and temperature conditions. By using foraging efficiency alone, it was not possible to fully understand the habitat use of the species in the field. The prediction of habitat use being

governed by a trade-off between predation mortality to energetic gains could in essence not be addressed, as these two mechanisms were not studied simultaneously in the experiments. However, by applying species-specific metabolic models, using swimming speed to estimate temperature-dependent metabolic costs, the energy gain ratio in different temperature and light conditions was found to be a mechanism which could partly explain observed patterns of habitat distribution of the competing species in the field in terms of their performance.

Third, to further explain the size-specific distribution of individuals among habitats by both separating mechanisms as well as studying their combined effects in Paper III, I calculated energy intake and energy costs, and predation risk, as snapshots of natural situations. By using data from a field study with sampled biomasses of the studied fish species and their prey in different lake habitats, I calculated energy intake and costs using temperature- and light-dependent individual rates derived from previous experiments, including the experiments in Paper II. The rates were adapted for each species as well as for different size groups, allowing for comparisons of species-, size- and habitat-specific responses to vendace presence. In the search of explanations for habitat use of the studied species, results showed that a combination of size-dependent and environment-dependent individual processes determining energy gain, rather than predation risk, could explain their size-specific habitat use. Furthermore, the study pointed to that knowledge of size- and environment-dependent individual processes, and interactions across habitats, are needed to understand community organization and effects of environmental change.

Fourth, addressing the prevailing issue of climate warming in Paper IV, I applied temperature effects on individual rates in a stage-structured model including habitat use, and could thereby study consequences of warming on the population level. Although predictions of a warming climate for population structure and regulation of cold-water species have been lacking, such species can be expected to be particularly sensitive to warming. As energy intake and metabolism differs with body size, and many fishes experience different temperature environments during the growth season, I used a model where the population (vendace) were using two habitats with different temperatures. Using results of experiments in Paper II, I could develop adjustments for the model regarding temperature adjustment of energy intake rates. By taking size-dependent individual-level responses to temperature into account, and using a non-static modelling approach, vital rates were found to affect individual performance of different life stages, with consequences for maturation and reproduction rates on the population level. Although the upper water layer of thermally stratified lakes was the minor habitat being used by the modelled

species, increased temperatures in this habitat caused a decrease in total biomass. At higher temperatures, the biomass dominance was shifted towards the juvenile stage through changes in population regulation. A mechanism defined as "inter-habitat subsidies" was found to be crucial for intraspecific competition and population regulation. This mechanism emphasizes the importance of also considering habitat use in population and community studies, as individual rates are habitat-dependent, but will have consequences on the population level if populations are distributed between habitats.

The thesis shows that habitat use is a central link in lake ecosystems and food webs. General mechanisms for observed patterns of habitat distribution of ectothermic organisms can be found in species- and size-specific physiological rates which are transmitted into biotic interactions and population regulation. Such knowledge is necessary to predict changes in fish communities resulting from different environmental situations, at present and in the future.

7 Sammanfattning

Mekanismer som förklarar organismers habitatanvändning, det vill säga var de befinner sig, är viktiga för att kunna förstå samspelet mellan arter och förutsäga effekter av förändringar i miljön.

Jag har undersökt mönster i naturen för hur fiskar fördelar sig mellan olika habitat, eller delområden i ekosystemet. I den första studien, då jag använde provfisken från 115 sjöar, testade jag hypoteser för hur tre fiskarter skulle fördela sig i sjöarna beroende på om en av arterna, en födospecialist, fanns där eller inte. De undersökta fiskarterna var abborre och mört som båda har studerats mycket samt siklöja, som är specialiserad på att äta djurplankton mitt ute i den fria vattenmassan (pelagialzonen). När siklöja fanns i sjön fanns det mindre mört i pelagialzonen, där mörten konkurrerar med siklöja, men också mindre mört totalt i hela sjön. Det kan man förvänta sig som en direkt effekt av siklöjans konkurrensfördel när det gäller att äta djurplankton. Abborre är en art som också konkurrerar med mört och siklöja om djurplankton, men abborre kan i stället börja äta mindre fiskar, både mört, siklöja och abborre, då de blir tillräckligt stora. Effekter på abborre av att även siklöja fanns i sjön var inte lika tydliga som för mört när det gäller hur abborrar fördelade sig i sjön. Men resultaten stödde det som förväntades – att större abborrar lättare kunde få tag på fiskar att äta så att de kunde växa snabbt i sjöar med siklöja. Detta skulle kunna förklaras genom att abborre har ytterligare en bytesart om det finns siklöja, utöver mört och abborre. Det kan också förklaras indirekt genom förändrade konkurrens-förhållanden mellan mört och abborre. Att konkurrensförhållanden ändras visar sig genom att mört och abborre ändrar sin habitatanvändning, då särskilt mört använder pelagialzonen mindre om siklöja finns i sjön. De mönster man kan se kan alltså förklaras genom komplicerade samband i födoväven, kopplat till att arter anpassar sin habitatanvändning om det finns en specialistart i systemet.

Resultat från mina undersökningar av provfiskade sjöar antydde att små mörtar kunde vara lättare byten för abborre än siklöja, genom skillnad i storlekar på mört i sjöar med och utan siklöja, samt att mörtar kunde vara sämre konkurrenter än siklöja, eftersom de undvek pelagialzonen då siklöja fanns där. För att studera detta närmare gjorde jag både experiment i damminhägnader, där abborrar fick äta mörtar och siklöjor, och experiment i akvarier där mörtar och siklöjor fick äta djurplankton i olika temperaturer och ljusförhållanden. Experimenten skulle likna situationer ute i den fria vattenmassan (pelagialzonen) på sommaren, när sjöar är temperaturskiktade och vattnet är varmare i det översta vattenskiktet. Dessutom kan ljuset i sjöar variera både beroende på djup och tid på dygnet. Jag kunde då undersöka två grundläggande mekanismer som kan förklara fiskars habitatanvändning: energiintag för att växa så bra som

möjligt respektive risken att bli uppäten. Varken risken att bli uppäten eller möjligheterna att effektivast möjligt få i sig föda kunde förklara habitatanvändningen hos mört och siklöja. Däremot kunde kvoten mellan energiintag och energikostnader (metabolism, eller ämnesomsättning) i olika temperaturer och ljus förklara exempelvis varför mörten finns mitt ute i sjön, i det varma vattnet nära ytan, då det är mörkt. Likaså kunde den kvoten förklara varför siklöja gärna håller sig i det djupare, kalla vattnet, där de har lägre energikostnader men ändå kan äta djurplankton effektivt.

I en tredje studie använde jag data från provfisken, insamlade med standardmetoder, från sjöar med eller utan siklöja för att testa dessa mekanismer på "ögonblicksbilder" i naturliga system. Genom att ta hänsyn till fiskart och storlek räknade jag ut både potentiellt energiintag och energikostnader för de tre arterna, i strandzonen med varmt vatten, samt den fria vattenmassan med varmt ytligt vatten, respektive kallt, djupare vatten. Energiintaget och energikostnaderna baserade jag på hur mycket föda av olika slag som fanns i habitaten och på födointagshastigheter som beror av temperatur och ljus, samt på fiskart och storlek. Dessa födointagshastigheter och metabolism var uppmätta i mina egna och andras experiment. Jag räknade även ut risken att bli uppäten för fiskar av olika storlek, beroende på mängder och storlekar av abborre som fanns där. De uträknade potentiella energivinsterna och riskerna att bli uppätna kunde jag sedan jämföra med fördelningen av arter och storlekar i habitaten beroende på om specialisten siklöja fanns i sjön. Resultaten visade, med vissa undantag, att skillnader i potentiella nettoenergivinster, snarare än risk att bli uppäten, kunde förklara var arter och storlekar befann sig i sjön. Studien pekade på att kunskap om individbaserade processer, såsom metabolism och temperatur- och ljusberoende födointagshastigheter, i kombination med samspelet mellan arter i flera habitat, behövs för att förstå hur fisksamhällen ser ut och kan påverkas av förändringar i miljön.

I den fjärde studien fokuserade jag på effekter av klimatuppvärmning. Jag använde effekter av temperatur på individbaserade processer med en kallvattensart (siklöja) i åtanke, i en teoretisk modell där siklöjepopulationen var uppdelad i två stadier, större könsmogna (adulter) och mindre icke könsmogna (juveniler). Både energiintagshastighet och metabolism varierar med kroppsstorlek och temperatur och jag lät adulter och juveniler använda två habitat med olika temperatur. Systemet skulle motsvara temperaturskiktade sjöar där siklöja tillbringade 20% av tiden i det varma vattnet över språngskiktet och resterande 80% i det djupare, kalla vattnet. Med klimatförändring kan temperaturen i ytvattnet förväntas öka och jag undersökte effekterna hos siklöjepopulationen av en stigande temperatur i det habitatet. I det kalla habitatet var temperaturen densamma (6 °C) oavsett uppvärmning. Trots att populationen

alltså använde det varma habitatet betydligt mindre än det kalla minskade den totala fiskbiomassan ändå med ökande temperatur. Generellt fanns det mer adult biomassa, beroende på att populationen reglerades mest av reproduktion, det vill säga att föryngringen var begränsad. Det innebar att den adulta biomassan fylldes på av juveniler som könsmognade snabbare än vad de adulta kunde föröka sig. Men vid riktigt höga temperaturer (över 24 °C) blev det ett skifte i relativa biomassor, så att det i stället blev relativt mer juvenil biomassa. Förklaringen till detta var att juveniler klarar sig förhållandevis bättre än adulter i höga temperaturer, och att det då också blev svårare för adulter att konkurrera i det kalla habitatet eftersom den juvenila biomassan ökade. En mekanism definierad som "mellanhabitats-subventionering" visade sig vara central för konkurrensen mellan juveniler och adulter och därmed för hur populationen begränsades av könsmognad respektive reproduktion.

Denna avhandling visar att habitatanvändning är en central länk i ekosystem och födovävar. Bakom observerade mönster för hur växelvarma djur fördelar sig mellan habitat finns generella mekanismer. Mekanismerna består bland annat av art- och storleksspecifika fysiologiska hastigheter som styr födointag och metabolism. Dessa hastigheter överförs till mellanartsinteraktioner, det vill säga hur arter samspelar, och i sin tur till hur populationer regleras. Kunskap behövs om mekanismerna och detta samspel i olika habitat för att förutsäga hur fisksamhällen förändras beroende på miljötillstånd, nu och i framtiden.

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