Which underlying mechanisms can explain the habitat distribution of species? In this thesis, observed patterns of habitat use and population structures of three fish species common in lakes have been explored. Results from predation and competition experiments could not fully explain the habitat use of competing species. However, when also incorporating metabolism, the estimated net energy gain of competitors could increase the understanding of observed patterns in nature.

Ulrika Beier received her Bachelor of Science degree, with a major in limnology, at Lund University. She has since 1990 worked within various fields concerning aquatic ecology in lakes and running waters, environmental monitoring and assessment, as well as fisheries related research at the Institute of Freshwater Research, Department of Aquatic Resources, SLU.

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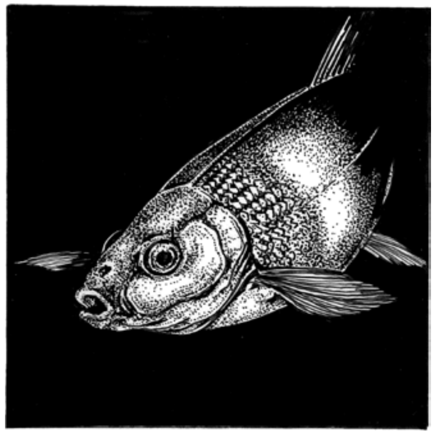
Mechanisms to Explain Spatial Distribution of Perch, Roach, and Vendace

Ulrika Beier



Licentiate Thesis
Swedish University of Agricultural Sciences
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Uppsala

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Mechanisms to Explain Spatial Distribution of Perch, Roach, and Vendace

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Habitat Selection and Indirect Interactions in Fish Communities.

Mechanisms to Explain Spatial Distribution of Perch, Roach, and Vendace

Abstract

To increase the understanding of freshwater lake ecosystems, I have studied the habitat selection of perch (*Perca fluviatilis* L.), roach (*Rutilus rutilus* (L.)), and vendace (*Coregonus albula* (L.)). These fish species use the pelagic and the littoral-benthic habitats in lakes to different extents. Perch and roach are omnivorous, and perch become piscivorous at larger sizes. Vendace is a pelagic species specialized in eating zooplankton. Vendace was expected to affect biotic interactions and habitat use of roach and perch, both directly and indirectly.

I used monitoring data to examine how species distribution patterns, as well as population structures, depended on species composition. In a predation experiment, I studied the relative predation sensitivity as well as evasive behaviours of roach and vendace, with piscivorous perch used as predators. In foraging experiments in aquaria, I studied foraging efficiencies and swimming performances of roach and vendace eating zooplankton in different temperature and light treatments. I then applied metabolic models for roach and vendace, respectively, to compare their net energy gain in different abiotic conditions.

Roach used the pelagic habitat less, and the biomass of roach was lower in lakes with vendace. Results did not support the prediction that perch populations would benefit from the presence of vendace. However, results indicated that a release of competition for small perch may be mediated by vendace, through changed habitat use of roach, increasing the possibilities for predation. Roach and vendace were similar in their sensitivity to predation, indicating that energy gain can explain their habitat use. Foraging efficiencies did not explain the habitat use of roach and vendace in the field. However, the net energy gain in different abiotic conditions, could explain observed patterns of their habitat use in lakes.

This thesis shows how the trade-off between mortality and net energy gain is manifested in habitat use. Including habitat selection in ecological studies may increase our understanding of biotic interactions. Metabolic costs as well as foraging abilities in different abiotic conditions are important for explaining the habitat use of species. Such knowledge can make it possible to forecast how interacting fish species may be affected by environmental change.

Keywords: active metabolic rate, net energy gain, size-dependent interactions, environment, foraging efficiency, competition, predation

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Dedication

To the memory of my grandmothers Saga and Inga

“Tho' much is taken, much abides; and though
We are not now that strength which in old days
Moved earth and heaven; that which we are, we are;
One equal temper of heroic hearts,
Made weak by time and fate, but strong in will
To strive, to seek, to find, and not to yield.”

Alfred Tennyson. Quote from “Ulysses”. *Poems.* London: Edward Moxon, Dover Street. 1842.

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. (2013). Winning the loser's game: implications of temperature and light for habitat selection of roach and vendace (submitted manuscript).

Paper I is reproduced with the permission of the publisher.

The contribution of U. Beier to the papers 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 compiled the manuscript.

II From the ideas of L. Persson, experiments were designed and planned jointly with L. Persson and M. Appelberg. U. Beier executed behavioural experiments, processed data, conducted statistical analyses, and compiled the manuscript.

Word list including abbreviations

epilimnion	above the thermocline* in summer
ectothermic	organisms which do not generate body heat; i.e., their bodies hold the same temperature as the surroundings
foraging	searching for food and eating
habitat	spatially defined life-space, characterized by physical or chemical factors, for example temperature or substrate
hypolimnion	below the thermocline*
littoral-benthic	the parts of a lake close to shores and along the lake bottom
metalimnion	thermocline*
omnivore	organism eating from different trophic levels*
pelagic	the parts of a lake consisting of open volumes of water without physical structure
piscivorous	fish eating
predation	when one animal eats another
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 – primary producers are level one, herbivores are level two, etc.
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 ecological studies

Ecological communities are normally complex by nature. Community studies may be simplified by specifying different habitats within the spatial borders of the community. Habitats have been described as ‘infinite patches’, where the renewal of resources is in the same magnitude as the rate of gain of foragers (Stephens & Krebs, 1986). The theory of habitat selection concerns mechanisms for the organisms’ specialisation and choice of habitat, and resulting patterns in growth, survival and reproduction (Svärdson, 1949; Fretwell & Lucas 1970; Holt, 1984; Gilliam & Fraser, 1987, 1988; Rosenzweig, 1987; Bernstein *et al.*, 1988; Brown, 1988; Morris, 1988; Pulliam & Danielson, 1991).

One habitat may be separated from other habitats 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 one or several populations 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).

In addition to being differently adapted for consuming different prey, organisms are also differently adapted to abiotic factors and their variability. These adaptions will often imply that different species are more or less inclined to choose certain habitats. A framework of morphological, physiological and behavioural adaptions 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 and intra- and inter-specific interactions.

1.2 Biotic interactions influence habitat selection

The strength and magnitude of biotic interactions may change the distribution of populations among different habitats (Svärdson, 1949; Werner *et al.*, 1983b; Gilliam & Fraser, 1987; Rosenzweig, 1987; Brown, 1988; Morris, 1988). A reason for this is density-dependent habitat selection, as individuals will move from a more crowded habitat to another less crowded, if it is more profitable per individual (Fretwell & Lucas 1970). Natural selection will favour individuals that maximize fitness when choosing between habitats. Individuals will therefore try to maximize energy gain and minimize predation risk (Cerri & Fraser, 1983; Gilliam & Fraser, 1987).

The capacities to forage as well as to escape predators are size dependent, making the interactions between predators and prey depend on their relative sizes (Persson, 1988; Polis, 1988). Thus, in size-structured populations, such as characterize fish species, distribution among habitats is governed by size-dependent trade-offs between growth and mortality (Werner *et al.*, 1983a; Werner & Gilliam, 1984; Fraser & Gilliam, 1987; Gilliam & Fraser, 1987). As fish continue to grow throughout their life, biotic interactions in fish communities will then depend on the ontogenetic niche-shifts that fish go through, i.e., how and when fish change food sources and/or habitat, from the origin throughout development, during their life span. These ontogenetic shifts will interact with the size structures of populations in the ecosystem. The cost of foraging can also be influenced by the physiological status of organisms (Taylor, 1984; Godin & Smith, 1988). This has been exemplified by Godin and Smith (1988), and Jakobsen *et al.* (1988), who found that risk-taking behaviour increased with hunger or energy deficit.

Larger sizes of many fish species are omnivorous (predators 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 during different size stages in their life cycle, a changed situation in one life stage may have consequences for the population itself, as well as for the structure and dynamics of other populations (Ebenman & Persson, 1988). Therefore, interactions within and among size-structured populations with ontogenetic niche shifts will affect the whole fish community.

Biotic interactions affecting community structure can be both direct and indirect (Kerfoot & Sih, 1987; Strauss 1991). Direct interactions in a food web are the consumption of prey by a predator. Indirect interactions on the other hand are the effects one species have on the interactions between a second and a third species (Miller & Kerfoot, 1987; Strauss 1991). Competition based on two species exploiting a resource can be seen as an indirect interaction with negative effects for both species (Abrams, 1987; Levitan, 1987). Furthermore, a predator which reduces the population of one prey species may have indirect positive effects on a) the species competing with the prey species (Abrams, 1987), or b) the species which themselves are subject to predation from the prey species (Vanni, 1987). A chain of indirect interactions is also known as a trophic cascade (Carpenter *et al,*. 1985). A negative indirect effect of predation is “apparent competition” (Holt, 1977), meaning that when two species share a common predator, an increase in one of the prey species causes a decrease in the other, as the predator population may benefit from the increase in the first species and thereby indirectly exerting more predation pressure also on the other species.

A complicating factor in an effect chain may be if the direct or indirect interactions are asymmetric, i.e. when two competing species are different in how efficient they are at exploiting a resource (Persson, 1988). Because energy gain and mortality determine the net profitability of a habitat, altered competition and predation situations may affect habitat selection and thereby change the distribution of species, or size groups within species, between habitats (Werner *et al,*. 1983a; Gilliam & Fraser, 1987; Brown, 1988). Thus, direct and indirect interactions may be mediated by altered habitat use, and may also affect the habitat use of species.

1.3 Abiotic factors define niches

Abiotic factors are the base of existence for species, forming the structure and function of ecological communities (Dunson & Travis, 1991). Temperature, light and oxygen levels at different depths are important factors for fish. Temporal heterogeneity of the environment 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 are depending on the surrounding temperatures for metabolic activity, which allows for mobility and somatic growth. However, the total energy cost increases with temperature, as an increased activity level in higher temperatures also leads to higher energy expenditure.

Besides temperature, visually hunting fish are highly depending on their sense of vision 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 depends on time of season, time of day, as well as the water depth. Additionally, water colour and turbidity affects the light climate in the water column (Ranåker *et al.*, 2012), which may differently affect behaviours of different fish species (Guthrie & Muntz, 1993; Ranåker, 2012).

1.4 Metabolism is affected by abiotic factors

Metabolism is a principal force in ecology, linking e.g. temperature to the ecology of populations and whole communities (Brown *et al.*, 2004). As an example of different metabolic adaptions to different temperatures, salmonid fish have a higher active metabolic rate than cyprinid fish at 15°C, which is approximately the temperature optimum of many salmonid species (Johnston & Dunn, 1987; 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).

It has been suggested that energy costs caused by activity, e.g. swimming, might be one of the most important factors for understanding among-population variability in fish growth rates (Boisclair & Leggett, 1989). In connection to adaptions to different temperatures, average swimming speeds at different temperatures can differ depending on the morphology, metabolism and functional specialization of the species. As swimming activity infers an energetic cost, it 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 also help to understand the distribution of species at a larger scale.

Metabolic costs often also depend on body size (Clarke & Johnston, 1999). Moreover, how metabolic costs change with temperature and body size differ between species (Ohlberger *et al.*, 2012). As a consequence, mechanisms for habitat selection may vary between species, and between differently sized individuals.

1.5 The study system

There is an advantage in using lakes in ecological studies, as each lake constitutes a sample of a semi-closed ecosystem, thus enabling the use of many samples when studying ecosystem functions (Schindler, 1990). In Scandinavia there is a further advantage in the availability to a great number of lakes, however individually unique. In lakes, two distinct habitats may be defined: the littoral-benthic zone and the pelagic zone. The littoral-benthic zone extends from shallow, near-shore areas, next to the bottom all over the lake. This is a heterogeneous habitat 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 away from the shore, where the water is deeper. This is more homogenous, although available food is often aggregated vertically and horizontally. Studying the distribution of roach (*Rutilus rutilus* (L.)), perch (*Perca fluviatilis* L.), and vendace (*Coregonus albula* (L.)) in these two habitats can then illustrate how habitat selection may be governed by size-dependent trade-offs between growth and mortality (Fig. 1).

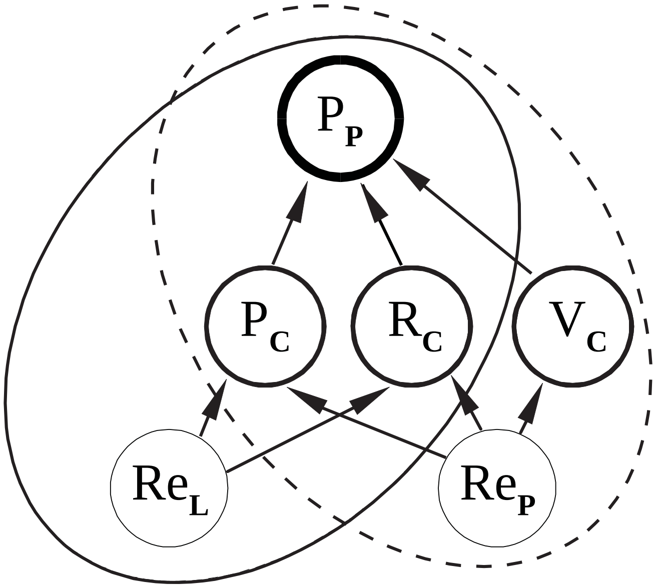


Figure 1. Simplified food-web of the three focal fish species and their resources in two habitats. P_P is piscivorous perch, P_C, R_C, and V_C are perch, roach and vendace competing in one or both habitats. Re_L and Re_P are the food resources in the littoral-benthic and pelagic, respectively. —, Littoral-benthichabitat; – – –, pelagic habitat.

Roach and perch are widespread, and often the two numerically dominant fish species in Scandinavian lake systems. Roach is an efficient zooplanktivore potentially shifting to larger invertebrates, but is also able to use algae and detritus as a food source (Hellawell, 1972; Persson, 1983a). Roach are mainly found in littoral-benthic areas, but earlier studies have documented that roach perform horizontal migrations out to the pelagic zone at night (Bohl, 1980; Gliwicz & Jachner 1992). Perch has a life-history including shifts in diet and habitat (Persson, 1983b). As it grows, perch will shift from feeding on zooplankton to macroinvertebrate prey, and eventually to fishes (Alm, 1946; Craig, 1974; Nyberg, 1979). 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). The habitat use of intermediate-sized and large perch is density-dependent and variable, but in general, perch are mainly found in or close to the littoral-benthic zone of lakes where a large variety of food items, including small fish, is available for this omnivorous species (Horppila *et al.*, 2000; Kahl & Radke, 2006).

The competitive relationship between small perch and roach can eventually be replaced by predation from perch, as perch will change food source and eventually begin to eat fish at a certain size; i.e., perch is an example of a an ontogenetic omnivore (Persson *et al.,* 2000). The asymmetric competitive relationship between roach and perch is a well-studied example of where the ontogenetic omnivory in perch is an important mechanism behind dominance relationships between these two species (Persson, 1983c; 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, 1987; Persson & De Roos, 2012; Persson & Greenberg, 1990; Persson *et al.*, 1992). 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 1983c, 1986b; Persson and De Roos 2012; Johansson & Persson, 1986; Svanbäck & Persson, 2004). If perch individuals will begin to eat fish at intermediate sizes, they will normally grow faster (Claessen *et al.*, 2000; Le Cren, 1992; Persson *et al.*, 2000). Piscivorous perch with fast individual growth will 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, and they can in turn more easily switch to piscivory, reinforcing the feedback between individual growth and biotic interactions between perch and roach.

To explore how altered biotic interactions may affect the distribution of roach and perch populations among different habitats, the study system will include 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; 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; Hamrin, 1986). Vendace may also exploit a temperature refuge in the pelagic zone and forage at low temperatures and at low light levels in the hypolimnion (Northcote & Rundberg, 1970; Dembinski, 1971; Hamrin & Persson, 1986; Persson *et al*., 1991; Mehner *et al*., 2007).

There are indications that vendace may counteract the effect of increased lake productivity, which normally favours roach before perch (Persson *et al.*, 1991; 1992). Piscivorous perch might be favoured in systems with vendace, which would have consequences for all their fish prey populations (Appelberg *et al.*, 1990; Persson *et al.*, 1991; 1992). This can be explained by effects which vendace might have on roach, by reducing the common food resource consisting of zooplankton in the pelagic habitat, and/or through apparent competition. Apparent competition may here be 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, or additionally, it may be an indirect effect of altered habitat use; increased competition may affect the habitat use of roach, forcing roach to increase its use of the littoral zone where there may be more piscivorous perch, leading to that roach may be subdued to a larger predation risk. This situation would describe apparent competition mediated by altered habitat use, which is one example of where indirect interactions are linked with habitat selection.

1.6 Species distribution patterns

The conclusions in earlier studies on the positive effects of vendace on perch, and thereby on the habitat distribution of perch, vendace and roach, were based on a relatively low number of lakes, which were situated in a limited geographical area (Appelberg *et al.*, 1991; Persson *et al.*, 1991, Figure 2). In Paper I, I therefore explore data from a larger number of lakes (N=115) within a widespread geographical area in Sweden (Figure 2). The aim of Paper I was to allow for detailed testing of hypotheses on mechanisms explaining patterns found in earlier studies of species distributions and population structures (Appelberg *et al*., 1991; Persson *et al*., 1991), concerning the habitat use and possible indirect effects of vendace on perch and roach (see Materials and methods). I used fish sampling data from both littoral and pelagic habitats in lakes to test the generality of earlier findings. Data were collected from the NORS database containing standardized test fishing data from national and regional monitoring programmes (Kinnerbäck, 2013). Fishing occasions where multi-mesh gillnets had been used in both the littoral-benthic and pelagic habitats were selected.

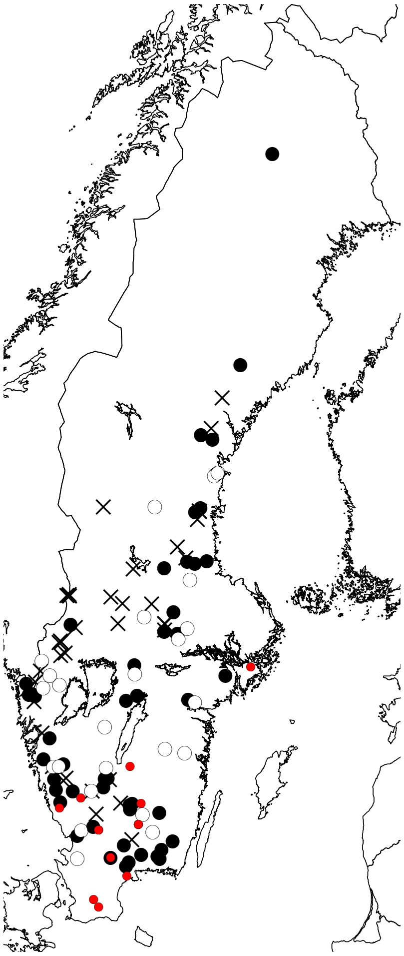


Figure 2. Map of Sweden with locations of lakes used in Paper I (lakes with perch = ×, with perch and roach = •, and with perch, roach and vendace = ○), and in the study of (Persson *et al.*, 1991) (red circles).

1.7 Underlying mechanisms for habitat selection

Using experiments both to investigate sensitivity to predation, and relative competitive abilities as well as energetic gain in competing species, will aid in understanding the relative importance of these factors when looking for explanations for the habitat distribution patterns in the field. In Paper II, I therefore performed both predation and feeding experiments on roach and vendace to study the mechanisms underlying their trade-off in mortality risk to energy gain in different habitats.

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, b; 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 different prey items. I therefore used perch predators in an open water environment to study the relative sensitivities of roach and vendace to predation, as well as their evasive behaviour (Paper II).

Individual foraging abilities and the effects of environmental factors may efficiently be studied in controlled environments using laboratory experiments (Persson, 1988; Bergman, 1988; Diehl, 1988). To better understand mechanisms underlying competition and patterns of relative abundance of roach and vendace across different lake habitats, I therefore designed laboratory experiments where temperature and light were used as abiotic factors (Paper II). The relative efficiency of vendace as a zooplankton predator compared to e.g. roach has so far not been quantified, although metabolic information has been collected for both species separately (Hölker, 2003; 2006; Ohlberger *et al.*, 2007). I used experiments in aquaria to investigate the relative foraging capacities in different temperature and light treatments, as well as collecting swimming speed data, to calculate estimates of species- and size-specific metabolism as well as net energy gain in different temperatures (Paper II).

2 Objectives

Increased understanding of ecological interactions and habitat preferences of species can be used to predict how changes in the environment may affect species specifically, which in turn is necessary to be able to foresee the effects of management measures or other human impact on fish communities.

The goal with this thesis is to increase the knowledge and understanding of freshwater lake systems by studying the habitat selection of three common fish species in lakes: perch, roach, and vendace. I examine patterns of habitat distribution and population dynamics observed in lakes, and experimentally study biotic interactions between these three species, searching to explain the mechanisms by which the outcome of these interactions are manifested through habitat selection.

The major questions I address in this thesis are:

- How do habitat distribution patterns differ between the species?
- Do the population structures of perch and roach differ depending on whether vendace is present or not?
- If roach and vendace are the main species occurring in the pelagic habitat, what are the mechanisms that can explain their habitat use?
- How can the trade-off between risks of being eaten versus energy intake be understood by these mechanisms?
- Can the mechanisms found in the study further help in understanding the habitat distribution of species?

3 Materials and methods

3.1 Habitat use of perch, roach and vendace

To investigate the habitat distribution of the three studied fish species in two habitats, I used data from 115 lakes (Paper I). Size structures as well as relative abundance in the littoral-benthic and pelagic habitats were compared among lakes having: only perch; perch and roach; or perch, roach and vendace. Based on results from previous studies regarding competitive abilities of roach and perch as well as population dynamics (Svanbäck & Persson, 2004), four hypotheses were tested:

(1) Habitat choice in roach 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 (hypothesis 3). This is expected to lead to a higher mortality for small-sized roach from perch predation, resulting in a higher proportion of larger roach, as larger size confers a refuge from predation by perch.

3.2 Underlying mechanisms for habitat distribution patterns

To study the relative sensitivity of roach and vendace to predation from perch in an open water environment, I performed predation experiments in pond enclosures lacking vegetation, with mean water depth 1.1 m (Figure 3, Paper II). I used perch as predators and either roach or vendace as prey, as well as a mixed prey treatment with both species. Behaviour of predators and evasive behaviour of 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.

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 & Persson, 1986; Persson *et al.*, 1991; Mehner *et al.*, 2007, Paper I), where they would have a predation refuge from perch, I predicted that vendace would be more susceptible than roach to predation from perch.

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

To study competition between roach and vendace, I performed laboratory experiments in aquaria, measuring relative foraging capacities as well as swimming speeds of roach and vendace in different temperature and light conditions (Figure 4, Paper II). In the experiments, roach and vendace were foraging on different densities of zooplankton to investigate their functional response under varying light and temperature conditions. Furthermore, I used the recorded swimming speed data in bioenergetic models for each species, respectively, to test whether estimated net energy gain could explain the habitat distribution of the two species in the field (Paper II).

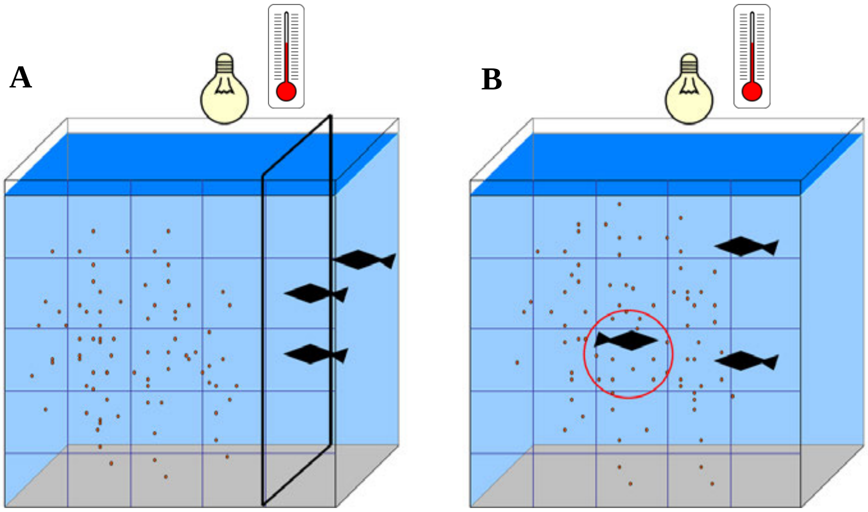


Figure 4. Schematic picture of aquarium experiment (Paper II). A) Before fish were released, and B) recording the capture rate and swimming speed of one randomly selected individual when eating zooplankton (*Daphnia magna*) during the experiments.

In the laboratory experiment, I used a combination of natural temperature and light conditions in thermally stratified lakes, to be able to elucidate possible mechanisms explaining competition-driven patterns of habitat use as well as relative abundance of roach and vendace. The size of fish in the foraging experiments matched the predominant size interval of roach found in the pelagic zone in lakes. I chose temperature treatments according to a standard situation in temperature stratified lakes during summer (Paper II). At a temperature corresponding to the epilimnion (above the thermocline), where the two species coexist in the pelagic zone of lakes, I used two different light treatments. I chose light treatments as to resemble normal light levels in the epilimnion during daylight, and during dusk or dawn.

I predicted that both species increase capture rates as well as swimming speeds with increased temperature. Based on spatial distribution patterns observed in lakes, where vendace is normally found in deeper (Northcote & Rundberg, 1970; Dembinski, 1971; Hamrin & Persson, 1986; Persson *et al.*, 1991; Mehner *et al.* 2007; Paper I), and thus colder and darker water than roach, I predicted that a) the capture rate of vendace would be less affected by low light levels than it would be for roach, b) vendace would have higher metabolic costs compared to roach in warmer waters, and c) the net energy gain of vendace would be higher than for roach at lower temperatures, while d) the net energy gain for roach at the highest temperature would be higher, than for vendace.

4 Results and discussion

4.1 Habitat distribution patterns

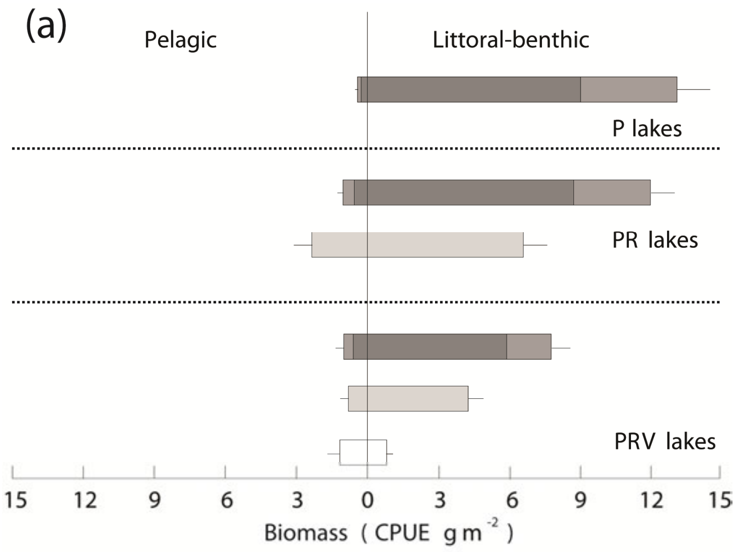
The distribution of the three species differed between the pelagic and littoral-benthic habitats, and depended on the presence of the other species (Paper I). Roach biomass was lower in lakes with vendace, and roach used the pelagic habitat to a relatively less extent in the presence of vendace (Figure 5a). 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 (Figure 5b). This suggests that competition from the specialized zooplanktivorous species vendace has a clear negative effect on roach. 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. Vendace were found mostly below 6 m in the pelagic zone, which indicates that vendace, in contrast to roach are able to explore the zooplankton resource in the deeper part of the pelagic zone (Paper I). As zooplankton can perform diel horizontal migrations and move into deeper waters to avoid predation (Lampert, 1993), the predation pressure for zooplankton may be stronger when vendace is present, as a refuge for zooplankton in deeper water might be lacking. In support of this view, vendace has been shown to strongly deplete the zooplankton resource (Helminen & Sarvala, 1997), which suggests a potential strong effect of their zooplankton consumption for competing species in the pelagic zone.

In this study, relative biomass of perch in the pelagic habitat was higher in lakes with zooplanktivores, i.e., only roach, or both roach and vendace, compared to lakes with only perch present (Paper I, Figure 5b). This may be explained by intra-specific competition for perch in the littoral-benthic habitat in lakes with roach, or in lakes with both roach and vendace, leading to that perch use the pelagic zone to a greater extent with competing species present.

This possible explanation is supported by results from Svanbäck *et al.*, (2008), who suggested that intra-specific competition was more important than inter-specific competition for the habitat use of perch. It can be expected that inter-specific competition from other zooplanktivorous species should also increase intra-specific competition for non-piscivorous perch in the littoral-benthic zone by reducing the available zooplankton resource. Increased competition in the littoral-benthic habitat may explain why perch use the pelagic habitat to a greater extent when competing species are present in the system.

When comparing the lake group with perch and roach to the lake group with perch, roach and vendace, there was no significant difference in the ratio of pelagic perch (total) biomass to littoral-benthic perch (total) biomass (ANOVA, P=0.390). Furthermore, there were no significant differences in the ratio of pelagic to littoral-benthic biomass of piscivorous (ANOVA P=0.568), or non-pisccivorous perch (ANOVA, P=0.290) between lake groups. For non-piscivorous perch, this pattern may primarily be explained by relative foraging efficiencies on the zooplankton resource, where roach is more efficient than perch (Persson 1983c). Competition from roach may then lead to that perch would gain less energy in the pelagic zone. In this case, the pelagic habitat would already be less profitable for perch even if only roach were present. Therefore, it is unlikely that the additional effect of vendace as a superior competitor in the pelagic zone would be clearly manifested regarding the habitat use of non-piscivorous perch (Paper I). This may be a result of an indirect effect of increased competition in the littoral-benthic habitat. If roach are forced out from the pelagic zone by the presence of vendace, thus increasing the competition in the littoral-benthic zone, this may lead to that the relative profitability of the two habitats may be similar for non-piscivorous perch, irrespective of whether vendace is present or not.

For piscivorous perch, the lack of differences between lake groups in habitat use may indicate indirect interactions resulting in altered habitat use of suitable prey fish. Because of competition from vendace, resulting in altered habitat use of roach and/or non-piscivorous perch, which may in turn affect availabilities of prey fish, could lead to a similar relative profitability for piscivorous perch in both habitats. However, to understand the relative habitat profitabilities for perch depending on the presence of vendace would require detailed studies of food availability and perch diets in different systems.



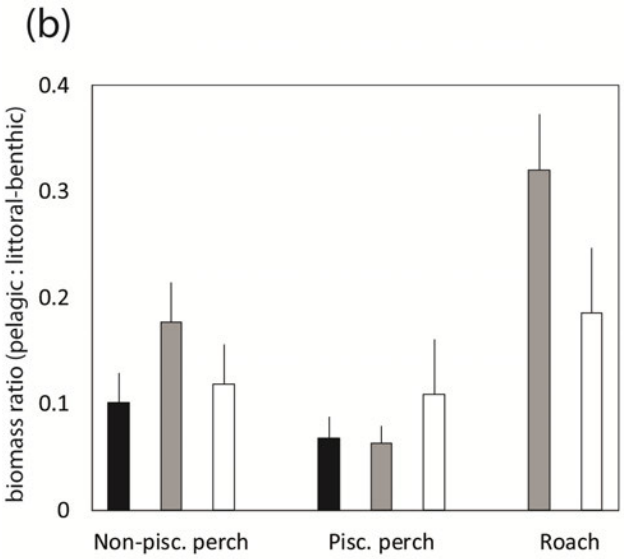


Figure 5. (a) Biomasses ± 1 S.E. in the littoral-benthic and pelagic habitats of three groups of lakes. P, perch; PR, perch and roach; PRV, perch, roach and vendace. Top bar in each lake group=perch biomass; middle bar=roach and lowest bar=vendace. For perch, darker shading indicates the piscivorous 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.

4.2 Effects on population structures in perch and roach

Results from the field study (Paper I) shows that the biomass of piscivorous perch in both the littoral-benthic and the pelagic habitats was positively related to the biomass of zooplanktivorous fish, but when controlling for total biomass, the relationship was not significant. Thus, in contrast to predictions, neither the relative amount of perch piscivorous biomass, nor the non-piscivorous perch biomass showed any significant relationship to the biomass of roach and vendace, i.e., when controlling for total biomass.

Persson *et al.* (1991) predicted that the higher proportion of piscivorous perch, which they found in lakes with vendace, could be explained by indirect biotic interactions favouring perch populations. The arguments regarding relative habitat qualities for perch, with suggested indirect effects of habitat utilization by foremost roach (see Section 4.1), as well as the assumption that intra-specific interactions are important for perch (Svanbäck *et al.,* 2008), are supported by observed patterns of individual growth in perch (Paper I). In the smallest size class (<60 mm), individual growth of perch was lower in lakes with roach and vendace, compared to in lakes without vendace, indicating a higher competitive pressure for small perch in lakes with vendace. However, in the 150–180 mm and 180-210 mm size classes, individual growth of perch in lakes with perch, roach and vendace was higher than in lakes with only perch and roach (Paper I). This is in accordance with previous studies, showing that a high competition for small perch can be released by intra-guild predation (Claessen *et al.,* 2000; Persson & De Roos, 2012). There may be increased predation possibilities for perch in lakes with vendace, either by access to an alternative prey species, or generally increased access to prey fish. An increased access to prey fish could in this case be explained by the higher competitive pressure, in accordance with previous studies where higher risk taking behaviour in hungry prey organisms was found (Jakobsen *et al.,* 1987; Godin & Smith, 1988). Furthermore, high individual growth for larger perch and a faster turnover rate of piscivorous perch biomass may also provide an alternative explanation to a large proportion of piscivorous perch in the population.

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 and/or behaviours of roach and perch, the pike populations may increase, and the consumption of perch and/or 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, may indicate a higher predation pressure in the littoral-benthic habitat, causing this size range of roach to use the pelagic habitat more, in spite of a hypothesized higher competitive pressure in the pelagic zone with vendace present. Pike is a common fish predator in lakes, and was documented from test-fishing data in 66% of the 115 lakes in 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 & 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 (Figure 6a, Paper I). One possible explanation for this can be 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.

Perch in the size range 120–150 mm were relatively less common, while perch in the size range 180–210 mm were more common in lakes with only perch, compared to the other lake groups (Figure 6a). This pattern could appear as a result of the type of population dynamics common to allopatric perch populations, often resulting in shifts between periods when perch populations are stunted in growth, and periods with perch populations dominated by larger cannibalistic perch (Claessen *et al.*, 2000; Persson *et al.*, 2000). As I selected perch lakes on the basis of abiotic factors, as to resemble lakes where vendace were present, and not based on perch population characteristics, it is likely that a proportion of these lakes were in the phase with a large proportion of cannibalistic perch.

According to predictions, size distributions of roach were skewed toward larger sizes in lakes with vendace (Paper I, Figure 6b). Roach in the size range 60-90 mm were less common and in the size range 180-210 mm were more common in the littoral-benthic habitat in lakes with vendace. One explanation for this was inherent within the prediction that piscivorous perch were expected to be more abundant in perch-roach-vendace lakes, as larger size would confer a refuge from predation from perch, and also from pike. However, the prediction regarding a higher proportion of piscivorous perch in lakes with vendace, or differences in the habitat use of piscivorous perch depending on the presence of vendace, was not supported by results (Paper I). As relatively fewer small roach were present, and there was an over-representation of roach in a size refuge from predation in lakes with vendace, these results indicate that the lack of support regarding perch population structure may require alternative explanations related to high growth of piscivorous perch, and/or apparent competition through pike, as given above. The arguments regarding alternative explanations may then also be applicable to explain the size structure of roach in lakes with vendace.

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. 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 more detailed studies using time series data of single lakes.

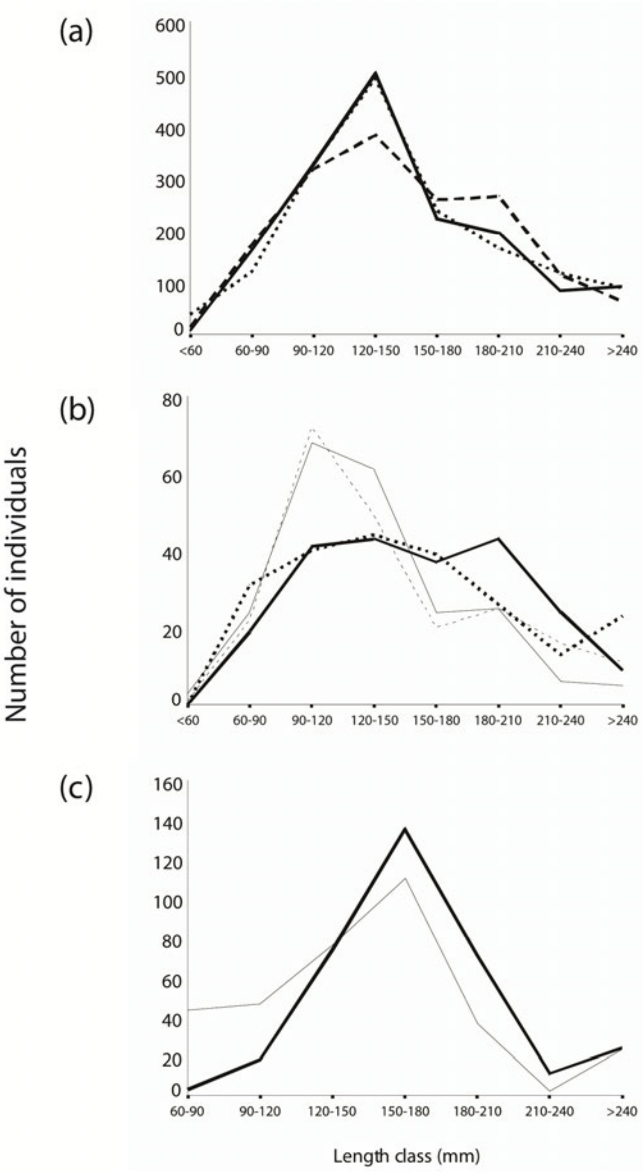


Figure 6. Number of individuals in 30 mm length classes of (a) perch from the littoral-benthic habitat (72 lengths randomly selected from each of 22 lakes); (b) roach from the littoral-benthic and pelagic habitats, respectively, in nine lakes with vendace and nine lakes without vendace (24 lengths randomly 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.

4.3 The effect of predation

The field study showed that there were differences in the size distributions of roach and vendace among habitats (Paper I, Figure 6b, c). There was a significant over-representation of roach in the size range 90-120 mm in the pelagic zone compared to the littoral-benthic zone (Figure 6b). This indicates that the pelagic habitat for roach in the size-range 90-120 mm is profitable, when balancing energy gain and predation risk. For smaller roach, on the other hand, it is likely that the pelagic habitat is less safe to be able to avoid predation, because of the lack of vegetation. It can be hypothesized that the trade-off in predation risk to energy gain changes markedly with size for roach.

Indeed, roach in the size-range 60-90 mm were relatively less common in the littoral-benthic habitat of lakes with vendace than in lakes without, indicating a possible higher predation pressure in those lakes. The different size distributions of vendace and roach among habitats can be explained by a suggested effect of size-dependent habitat selection, as well as behavioural traits affecting the sensitivity to predation in different ways. For example, the evasive behaviour of roach may be more adapted to a habitat with vegetation, while the opposite may hold for vendace. The susceptibility of roach and vendace to predation in an open habitat was therefore experimentally investigated (Paper II).

In contrast to roach, small vendace in the size range 60-120 mm were under-represented in the littoral-benthic zone compared to the pelagic zone (Figure 6c, Paper I). This can be explained by that the littoral habitat is shallow and warm, being a part of the epilimnion. Vendace, being a salmonid species and thus generally more adapted to colder temperatures, can be expected to utilize the temperature refuge in the hypolimnion of the pelagic zone. However, as also deeper parts of the benthic zone is included in the littoral-benthic habitat, where small vendace are very scarce, a habitat closer to the shore and bottom may be less suitable for small vendace. Explanations for this pattern may be sought in behavioural adaptions to avoid predation.

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 use of either habitat; roach which is predominantly found in more shallow habitats in or near to vegetation, and vendace in the "true" pelagic zone with a deep water column.

In contrast with the prediction, which was that vendace would be more sensitive than roach regarding sensitivity to predation by perch, there was no significant difference between treatments with only roach or only vendace prey (ANOVA p=0.226, Figure 7). In the mixed treatment, the difference in number of prey caught depending on species was also non-significant (ANOVA p=0.168, Figure 7). This suggests that there is no difference between roach and vendace in their sensitivity to predation by perch, although there was a slight, non-significant tendency towards that vendace might be more sensitive. The lack of corroboration indicates that the main reason for differences in habitat use between roach and vendace may be explained by other mechanisms than predation, e.g. competition and/or metabolism, in the trade-off between mortality and energy gain for the two species.

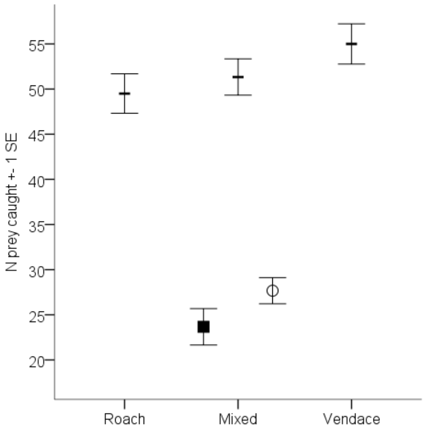


Figure 7. Captured prey (mean N ± 1 SE) in pond enclosure experiments with perch used as predators and roach (black squares) and vendace (white circles) used as prey (six replicates of each treatment). Horizontal bold bars represent total number of prey caught in each treatment.

4.4 Net energy gain explains habitat use of competitors

Ectothermic species are differently adapted to forage efficiently in different temperatures, and also have different adaptions 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 compare their competitive abilities, I calculated estimates of 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, the capture rates increased with temperature in both roach and vendace (Paper II), showing that foraging efficiency generally increases with temperature within the applied temperature range. The capture rate of vendace was higher than for roach at all temperature and light treatments. Thus, in contrast to predictions, roach capture rate was lower than for vendace also at 18°C. However, the temperature-dependent, generally higher foraging efficiency of vendace compared to roach, does not explain why roach are actually found in the pelagic zone, and why the two species are spatially separated, so that vendace mainly use the deeper, and roach use the shallow water.

Because light affects the foraging success of many species, it could be predicted that light as additional factor could explain the habitat distribution of roach and vendace. However, the prediction that vendace capture rate would be relatively less affected by low light levels than for roach 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. Thus, different light levels could not further explain the distribution of vendace and roach in the field. Furthermore, vendace are not primarily found in the shallow water with more light, although their foraging abilities were greater in warm temperatures and in higher light levels.

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. However, the swimming performance when not foraging, measured at 18°C without prey, was similar between species. These results indicate that active metabolic rate, including energy expenditure from swimming when foraging, may be an important factor to determine the relative competitive abilities of roach and vendace.

From modelled net energy gain based on results from the foraging experiment (Paper II), I found that the net energy gain of roach was equal to that of vendace at the highest temperature and in the lowest light level. This explains why roach does only use the upper, warm water in summer. It also explains why roach, as shown in earlier studies, migrate out to the pelagic zone at night to eat zooplankton, as roach then in fact are similar to vendace in their net energy gain. The surprisingly high metabolic costs of roach in low temperatures, in combination with relatively low foraging efficiency, may explain why roach avoid the deeper, colder water.

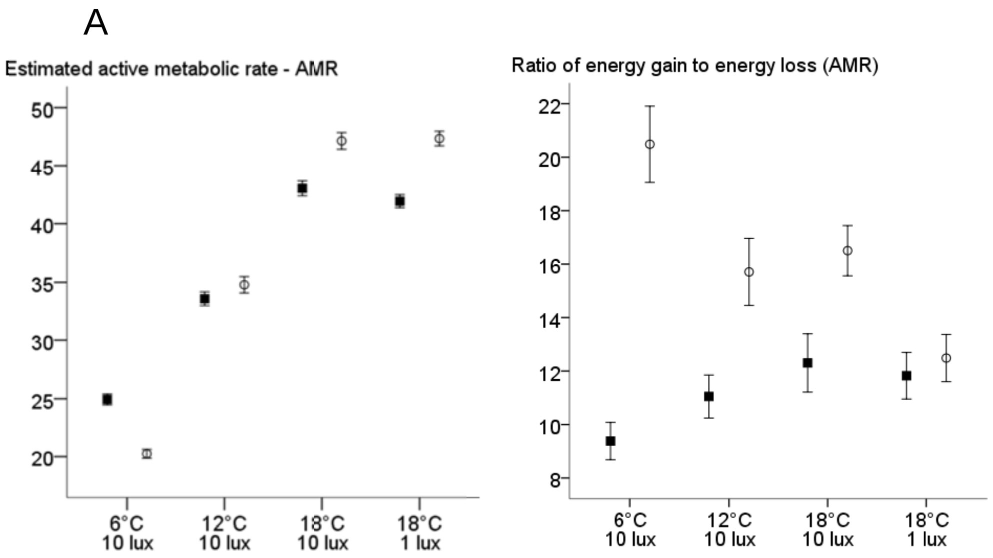


Figure 8. A) Estimated active metabolic rate (AMR, Joules · h^{-1}) and B) ratio of energy intake from capture rate (prey · s^{-1} converted to Joules · h^{-1}) to estimated active metabolic rate (mean ± 1 SE) for roach (black squares) and vendace (white circles) in different temperature and light treatments when foraging on *Daphnia magna* (pooled data from different prey densities, six replicates of each density). 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.

To conclude, by applying metabolic models using both capture rate and swimming speed across temperatures, competitive abilities of the two species could be better understood in connection to patterns of habitat distribution in the field. In future studies of habitat selection of ectothermic organisms, it is important to include metabolism as the central factor regulating habitat use. In fisheries management, as several fish species may both interact and use different habitats, it is important to understand the role of metabolism of different species and sizes when regulating fisheries, or planning for efficient recovery of depleted stocks.

5 Conclusions and future perspectives

This thesis shows how habitat use can be understood in terms of the trade-off between mortality and net energy gain. By experimentally studying effects of predation and competition, and also including modelled metabolism, the underlying mechanisms for observed patterns in the field are identified. The thesis has a broad scope in that it includes three species, of which the complex interactions of two of them are particularly well-studied. Broadening the scope to explore how these interactions interplay and are linked between two habitats, through the presence of a third species, adds to the complexity of the studied system. However, by both including field monitoring data from a wide selection of lakes, as well as experiments where factors may be regulated, makes it possible to find the patterns, then to explore the underlying mechanisms, for the further understanding of observed situations in nature.

First, this thesis explored patterns and tested hypotheses concerning biotic interactions for habitat distribution of three fish species, using data from a comparatively large number of lakes. One species (roach) diminished the use of the pelagic habitat in the presence of a competitor (vendace), which resulted in a lower biomass of the first species. This is an expected effect of inter-specific competition. Concerning the competing and/or predator species perch, the patterns were less clear. In conclusion, results did not support the prediction that perch populations would benefit from the presence of vendace. However, support was found for that an increased competitive pressure for perch could be released by increased possibilities for predation, including cannibalism, as found in previous studies. Results presented in this thesis show that this release of competition may be mediated by the presence of a species specialized for one habitat (vendace). By affecting the habitat use of roach, and in turn, affecting competition for small perch, vendace may also increase the possibilities for predation for perch. Species interactions, including indirect interactions, e.g., apparent competition, are shown to be important for the habitat distribution of different species. Observed patterns may thus be explained in terms of more complex biotic interactions in the food web, involving habitat use, caused by the presence of a species specialized for one habitat.

Second, field data indicated that small individuals of one competing species (roach) could be more sensitive to predation in one habitat, while the opposite was indicated for the other competing species (vendace). I conducted a predation experiment to illustrate the trade-off between growth to mortality for these competing species. As the experiment showed no clear differences in sensitivity to predation by perch in the open water habitat, this indicated that the use of the pelagic habitat is mostly governed by the possibilities of energy intake. However, the two species also showed different evasive behaviours, which aids in explaining their habitat use.

Third, I experimentally quantified relative competitive abilities of competing species (roach and vendace), and how these abilities 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. However, by also applying species-specific metabolic models, using swimming speed to estimate temperature-dependent metabolic costs, the net energy gain in different temperature and light conditions was found to be a mechanism which could explain competitive abilities in terms observed patterns of habitat distribution of the competing species in the field.

This thesis will contribute to an increased understanding of interactions among freshwater fish species. Apart from increasing the knowledge of the studied species in temperate lakes, these results may further elucidate 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. The conceptual Figure 9 shows how habitat use is a central link in ecosystems and food-webs. 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. Even within the fundamental niche, however, 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 such biotic interactions, i.e. intra- and inter-specific competition, and predation. However, biotic interactions and resulting density-dependence also depend on habitat use (Figure 1), 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.

Based on this purpose, future studies could increase our knowledge of how environmental change and biotic interactions may affect the net energy intake and habitat use of different species. 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 can help us in designing the management and planning our use of natural resources, to avoid the risk of losing sensitive species.

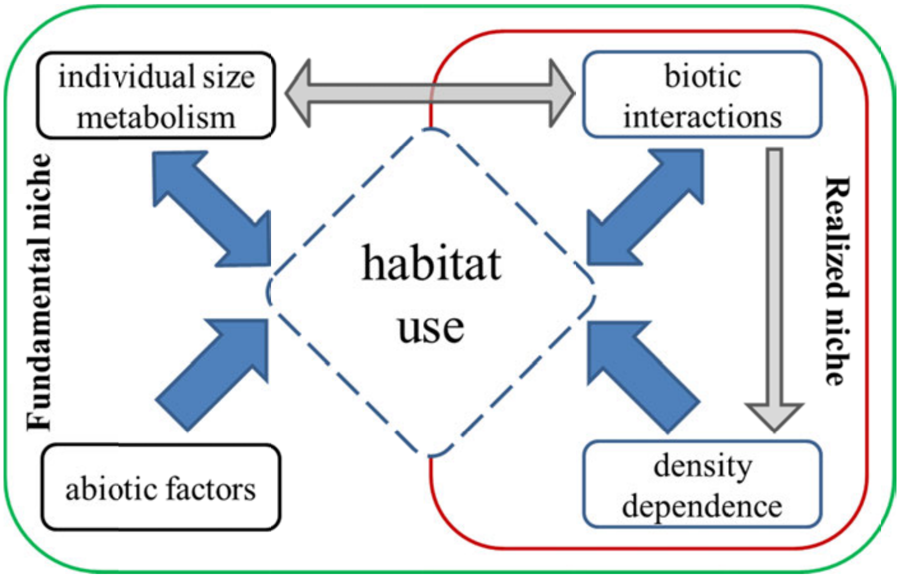


Figure 9. Conceptual figure of ecological components, with habitat use linking a) individual characteristics (size and metabolism) to b) abiotic factors, c) density dependence, and d) biotic interactions (predation, competition). Abiotic factors as well as individual limitations concerning size and metabolism set the borders for the fundamental niche of organisms. Adding density dependence effects and biotic interactions sets the borders for the realized niche.

6 Summary

To increase the knowledge and understanding of freshwater lake systems, I have studied the habitat selection of perch, roach, and vendace. These three fish species use both the pelagic and the littoral-benthic habitats to different extents. Perch is an omnivore which also becomes piscivorous at a certain size. Roach is an omnivorous species and a relatively efficient zooplanktivore. Vendace is a pelagic species specialized in eating zooplankton. Vendace can be expected to affect the habitat use and biotic interactions of roach and perch, both directly and indirectly. Based on previous studies, I investigated whether perch populations could benefit from the presence of vendace. I also conducted experiments to elucidate mechanisms behind patterns of species distributions, as well as direct and indirect interactions among the study species.

I used monitoring data from lakes to examine differences in the species distributions among habitats, as well as population structures, depending on the species composition. Results show that roach used the pelagic habitat less in the presence of vendace, and the biomass of roach was less in lakes with vendace. This is an expected effect of inter-specific competition. Furthermore, roach used mainly the 0-6 m depth zone in summer time, in both the pelagic and the littoral-benthic habitat. Also, the size interval of roach found in the pelagic zone indicated that the trade-off between energy intake and predation risk is similar in both lake types. The smallest roach avoided the pelagic zone, which indicated that the littoral zone is safer for small roach to avoid being eaten by predators. In contrast, vendace size distributions indicated that this species was most sensitive to predation in the littoral-benthic habitat.

The observed patterns were more unclear regarding perch. In lakes with only perch, perch used the pelagic habitat less compared to in lakes without roach and/or vendace. In lakes with vendace, the habitat use of perch was variable compared with other lake groups. Furthermore, results did not support the prediction that perch populations would be comparatively larger in biomass in the presence of vendace, as size structures of perch did not differ from lakes with perch and roach, and perch biomass was not higher in lakes with vendace. However, the growth of small perch was slower in lakes with vendace, while the growth of perch in the size range where they become piscivorous was faster. This supports previous results, where an increased competitive pressure for perch was shown to be released by increased possibilities for predation, including cannibalism. The release of competition for perch may be mediated by the presence of vendace. Vendace affected the habitat use of roach, thereby indirectly affecting competition for small perch, as well as possibilities for predation in lakes with vendace. A lack of corroboration for the prediction that perch populations would increase from the presence of vendace may be explained by cannibalism mediated by apparent competition. Intermediate-sized perch may then more easily become piscivorous in lakes with vendace, which was supported by this study. Observed patterns may thus be explained by complex biotic interactions in the food web, involving apparent competition and changed habitat use, caused by vendace.

In a predation experiment, I examined the relative predation sensitivity as well as evasive behaviours of roach and vendace in an open water habitat, with piscivorous perch used as predators. The results showed no clear differences in sensitivity to predation by perch in the open water habitat, indicating that the use of the pelagic habitat is mostly governed by the possibilities of energy intake. However, the two species also showed different evasive behaviours, which may aid in explaining their habitat use.

In foraging experiments in aquaria, I quantified foraging efficiencies and swimming performance of roach and vendace eating zooplankton in different temperature and light treatments. I then applied metabolic models to compare the net energy gain of these species in different treatments. Based on their higher consumption rates in all treatments, vendace may be interpreted as competitively superior to roach. However, by applying metabolic models, competitive abilities of the two species could be better understood as mechanisms to explain patterns of habitat distribution in the field. Only at the highest temperature and in the lowest light level was the net energy gain of roach similar to that of vendace. Net energy gain can explain why vendace do use the cold water in the hypolimnion, and why roach use the upper, warm water during periods of the day with low light levels.

The thesis shows that habitat use is a central link in lake ecosystems and food-webs. Also, a general mechanism for observed patterns of habitat distribution of ectothermic organisms is net energy gain, taking the species- and size-specific metabolism of co-occurring species into account. Such knowledge can aid in producing scenarios for expected changes in fish communities as a result of environmental change.

7 Sammanfattning

För att öka kunskapen om och förståelsen av hur sjöar fungerar som ekosystem studerade jag habitatval av abborre, mört och siklöja. Dessa arter är ganska vanligt förekommande i sjöar men finns i olika hög grad i den öppna, fria vattenmassan eller i den strand- och bottennära zonen. Abborre är allätare som kan bli fiskätande vid en viss storlek. Mört är också allätare och ganska effektiv när det gäller att fånga och äta djurplankton. Siklöja är en art som är specialiserad på att äta djurplankton i den öppna vattenmassan där den ofta finns relativt djupt. Därför kan man förvänta sig att siklöja både direkt och indirekt skulle påverka interaktionerna konkurrens och predation (betyder här då en fisk äter annan fisk) i ekosystemet, delvis genom ändrat habitatval hos abborre och mört. Baserat på vad som föreslagits i tidigare studier undersökte jag om abborrpopulationer kunde gynnas av att arten siklöja fanns i samma sjö. Jag gjorde även experiment för att belysa ekologiska mekanismer som skulle kunna förklara arternas fördelningar mellan olika habitat.

Jag använde miljöövervakningsdata från 115 sjöar för att undersöka om det fanns skillnader, dels i arternas fördelning mellan olika habitat, dels i deras storleksstruktur, beroende på sjöarnas fiskartsammansättning. Resultaten visade att mört använder den öppna vattenmassan i mindre utsträckning samt att mörtens biomassa var relativt mindre i sjöar med siklöja. Detta är ett förväntat resultat av konkurrens mellan mört och siklöja. Mört använde mest relativt grunt och varmt vatten (0-6 m) i sjöar sommartid, i båda habitaten. Storleksintervallet av mört som fanns i den pelagiska zonen var ungefär detsamma oavsett om siklöja fanns i sjön eller inte. Detta indikerar att mörtens avvägning mellan möjligheter till att hitta mat och risken att bli uppäten var ungefär samma i sjöar med eller utan siklöja. De minsta mörtarna undvek den öppna vattenmassan, vilket indikerar att den strandnära zonen är säkrare för små mörtar när det gäller att undkomma predatorer. Små siklöjor undvek i stället den strand- och bottennära zonen.

När det gäller abborre var mönstren inte lika tydliga. I sjöar med bara abborre använde abborre den öppna vattenmassan i mindre utsträckning jämfört med i sjöar där även mört fanns, eller i sjöar med både mört och siklöja. I sjöar med abborre och mört, men utan siklöja, fanns det en viss tendens att icke fiskätande abborre (mindre än ungefär 15 cm) använde det fria vattenmassan mer än i andra sjöar. I sjöar med siklöja varierade abborrens habitatutnyttjande mer än i andra sjöar. Det som förväntades, baserat på vad som föreslagits av andra forskare, var att stora abborrar skulle vara relativt vanligare och abborrbiomassan större i sjöar med siklöja. Men resultaten visade inte detta. Abborrens storleksstruktur skilde sig i stort sett inte beroende på om siklöja fanns i sjön eller inte, jämfört med om det bara fanns mört. Trots bristen på stöd för hypotesen om mer abborre i siklöjesjöar, visade data att små abborrar växte långsammare i sjöar med siklöja. Abborrar i det storleksintervall då de brukar bli fiskätande växte i stället bättre i sjöar med siklöja. Detta stöder tidigare resultat som tagits fram av andra forskare. De har visat att ökad konkurrens för liten abborre kan motverkas av ökade möjligheter att fånga fisk för större abborrar, vilket inkluderar kannibalism. Denna kompensation i abborrpopulationer kan alltså åstadkommas genom att siklöja finns i sjön, men det behöver inte innebära att abborrpopulationerna blir relativt större i sjöar med siklöja. Siklöja påverkar mörtens habitatval så att mörtar i viss utsträckning trängs bort från den fria vattenmassan. Därför ökar konkurrensen indirekt för små abborrar i den strand- och bottennära zonen. Detta kan däremot öka möjligheterna för fiskätande abborrar att hitta bytesfisk, så att abborrpopulationen ändå påverkas positivt. Dessa interaktioner inbegriper så kallad ”apparent competition”, vilket innebär att en predator kan gynnas av att det tillkommer en ytterligare bytesart. Predatorarten kan därmed bli mer talrik, vilket gör att ännu fler fiskar blir uppätna och mängden bytesfiskar minskar. Denna minskning som i första hand kan verka bero på konkurrens mellan bytesarterna är i själva verket en effekt av att predatorerna blir fler. De observerade mönstren i sjöar med eller utan siklöja kan alltså förklaras med relativt komplexa artinteraktioner i födoväven.

Predationsexperimentet som utfördes i ett öppet habitat visade ingen tydlig skillnad i hur känsliga mört respektive siklöja var för predation från abborre. Detta indikerar att deras avvägning för att befinna sig i den fria vattenmassan i första hand gäller möjligheter till att hitta mat där. Arterna hade olika beteenden för att komma undan abborrar. Mörtar hoppade över ytan medan siklöjor gick ihop ännu tätare i ett stim och rörde sig mot botten. Dessa olika beteenden kan ytterligare förklara varför arterna utnyttjar olika habitat i olika hög grad.

I akvarieexperiment jämförde jag hur effektivt mört och siklöja kunde äta djurplankton i olika temperaturer och ljusstyrkor, och hur fort de simmade. Sedan använde jag matematiska modeller framtagna av andra forskare för att räkna ut hur mycket energi mört respektive siklöja förbrukade, dels beroende på hur fort de simmade, dels på vad det var för temperatur i vattnet. Då fick jag ett mått på nettoenergiintaget, genom att också räkna in hur mycket energi fiskarna fick i sig per tidsenhet. Vid första anblicken verkade siklöja vara den överlägsna konkurrenten eftersom den åt djurplankton snabbast i alla temperatur- och ljusbehandlingar. Med stöd av detta gick det inte att förklara varför mört fanns alls i det öppna vattenmassan, eller varför siklöja mest fanns i djupare vatten och inte bara i det varmaste vattnet där den åt snabbast. Genom att i stället jämföra nettoenergiintaget hos arterna gick det att förklara varför siklöja fanns på olika djup och gärna i det djupa, kalla vattnet. Det gick också att förstå varför mört, enligt tidigare vad tidigare studier visat, ofta vandrar ut i den fria vattenmassen på natten och varför mört undviker kallt vatten.

Denna avhandling visar att arters habitatval är en central länk i ekosystem och födovävar. Dessutom är nettoenergiintag en generell mekanism som kan förklara fördelningen av populationer mellan olika habitat. Sådan kunskap kan vara värdefull om man vill kunna göra förutsägelser när det gäller effekter av miljöförändringar för fisksamhällen.

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