

Ecology of a sympatric pair of coregonid fish:
Species interactions and temperature

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2008

Dissertation for the degree of *philosophiae doctor*



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*Series of dissertations submitted to the
Faculty of Mathematics and Natural Sciences, University of Oslo
Nr. 795*

ISSN 1501-7710

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Cover: Inger Sandved Anfinsen.
Printed in Norway: AiT e-dit AS, Oslo, 2008.

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ACKNOWLEDGEMENTS

First, I wish to thank my supervisors Thomas Mehner and Asbjørn Vøllestad. Thomas, without you this work would never have become what it is today. Thank you for always being available and willing to spend your time on planning, guiding me and commenting carefully on all the texts I have written. I know that not all PhD-students have supervisors as supportive as you have been. I highly appreciated that you always made sure that I had access to technicians and other colleagues for my field and lab work, to make my PhD run smoothly from the very beginning. Asbjørn, I also wish to thank you for always being there whenever I had a question, even though I did not include you much in the project the first part of my PhD. Your calmness, constructive advices and fast e-mail replies were always appreciated, whether I needed scientific advices or guiding through the bureaucratic university regulations. I regret that I did not get to spend more time at CEES with you and your colleagues.

Second, I wish to thank all the technicians at IGB that have helped me with field and lab work, especially Christian Helms, Alex Türck, Titus Rohde, Karna Kuntze and Henrik Zwadlo. Your expertise is invaluable and without your help most of my data would never have been collected. Thanks also to all the students, “eco girls” and trainees, especially Josefine Stiller, that have spent shorter or longer periods at IGB, for helping me with all the frozen fish.

I have also gotten lots of support from the other members of the coregonid group at IGB; many thanks to Jörg Freyhof, Jan Ohlberger, Susan Busch, Georg Staaks and Franz Hölker. Thanks also to Kirsten Pohlmann and Peter Kasprzak in Neuglobsow. Not only have you all contributed to my work and data collections, but you have also been a large part of the social and scientific pleasure in my everyday working environment. Thanks for all the discussions and contributions during the years.

I want to thank the PhD students at Department IV; Susan Busch, Katrin Daedlow, Malte Dorow, Markus Faller, Volker Huckstorf, Thomas Klefoth, Christian Lewin, Jan Ohlberger, Torsten Schulze and Silva Uusi-Heikkilä, other IGB students; Nadja Neumann, Veronica Huber and Susann Wilhelm, and all the other colleagues at Department IV. You

have all been an important part of my life in Berlin, on the border between science and social life. Thanks for all the science during the day and social activities during the nights – or vice versa. A very special thank you to Silva – I have been grateful for having you only a few footsteps away and for knowing that I could always come to you, be it in your aquarium room or your apartment.

Outside IGB I want to thank everybody at “Limnologen” at Lund University for giving me a great time during winter 2007. Especially, I thank Lynn Ranåker – I surely hope we will keep in touch both in science and privately. I also want to thank everybody at “Akvatisk” at NINA - First, for fostering my growing interest in science already during my MSc in 2004, and secondly for making me feeling so welcome when I returned to Trondheim after the years in Berlin. Thanks to Anders G. Finstad for always showing interest and support, even when I was far away.

Other people have also contributed to the results of this thesis, and I want to thank my co-authors; Chris Harrod, Catriona Clemmesen and Christoph Petereit. I always appreciated talking to you and our discussions gave me motivation beyond the papers we wrote together.

Finally, thanks to Jan Ohlberger and Torbjørn Forseth for commenting on the draft of my thesis synopsis, and to Ida Nilstad Pettersen for helping with proof reading.

Trondheim, October 2008

Ingeborg Palm Helland

ABSTRACT

A major interest in evolutionary ecology is to understand the ecological forces behind evolution and coexistence of closely related sympatric species. Sympatric fish in postglacial lakes frequently display resource polymorphism and segregate available niches. In the dimictic Lake Stechlin (north Germany) two coregonid fish coexist; vendace (*Coregonus albula*) and the dwarf-sized lake-endemic Fontane cisco (*C. fontanae*). The two species are reproductively isolated by differential breeding times and it has been suggested that the species pair may have evolved in sympatry since the last glaciation. It was assumed that coexistence of the two was facilitated by segregation in benthic and pelagic niches, a pattern typical for sympatric pairs of postglacial fish. However, my thesis shows that the sympatric species pair in Lake Stechlin does not follow the expected form of niche segr

In spite of only weak segregation along habitat and diet niche axes, the two species differ consistently in morphology and adult size. Furthermore, segregation in microhabitat within the pelagic area was found. Fontane cisco has a deeper and colder average depth distribution than vendace, in accordance with their apparent thermal preferences. Hence, species-specific thermal adaptations probably contribute to ecological divergence. Additionally, temperature as factor for spatial distribution has consequences for predator-prey interactions, because of different thermoselective behaviour of the coregonids and their zooplankton prey. The spatial overlap between the coregonids and zooplankton changes with seasonal changes in lake temperature, and thermal predator avoidance of their prey influences the diet of vendace and Fontane cisco.

I conclude that segregation in metabolic and reproductive traits is the most likely reason for the coexistence of vendace and Fontane cisco. First, the vertical gradient in water temperature probably facilitates microhabitat segregation within the pelagic area through physiological adaptations. Furthermore, dissimilar spawning times and growth rates result in a displaced size-distribution of Fontane cisco compared to vendace, which may keep similarly sized individuals and similar life history stages of both species from occurring together. The combination of these factors may sufficiently reduce competition and allow coexistence of the two closely related fish species.

LIST OF INDIVIDUAL PAPERS

This thesis is based on the following papers, which are referred to in the text by their roman numbers (I-V):

- Paper I **Helland, I. P.**, C. Harrod, J. Freyhof and T. Mehner. 2008. Co-existence of a pair of pelagic planktivorous coregonid fish. *Evolutionary Ecology Research*. **10**:373-390.
- Paper II **Helland, I.P.**, L. A. Vøllestad, J. Freyhof and T. Mehner. Morphological differences between two ecologically similar sympatric fish species. *Submitted to Journal of Fish Biology*.
- Paper III **Helland, I. P.**, J. Freyhof, P. Kasprzak, and T. Mehner. 2007. Temperature sensitivity of vertical distributions of zooplankton and planktivorous fish in a stratified lake. *Oecologia*. **151**:322-330. DOI: 10.1007/s00442-006-0541-x
- Paper IV Mehner, T., **I.P. Helland**, S. Busch, C. Riese, P. Kasprzak and J. Freyhof. Opposite thermal refuges from vertically migrating planktivorous fish in two coexisting *Bosmina* species. *Submitted to Oecologia*.
- Paper V **Helland, I.P.**, C. Clemmesen, C. Petereit, T. Mehner. Starvation does not explain abundance decline during early larval stage of vendace (*Coregonus albula*). *Manuscript*.

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INTRODUCTION

Ecological divergence and coexistence of competitors

A fundamental topic in evolutionary ecology is to understand the mechanisms of species diversity and coexistence. Organisms are adapted to their surroundings as a result of natural selection on morphological, behavioural and physiological traits, since different traits are favoured in different environments. The environment includes both abiotic factors (e.g. climate, physical properties, resources) and biotic factors like species interactions (e.g. predation, competition, mutualism). The ecology of an organism is a response to these environmental variables and species occupy different ecological niches in the ecosystem. According to classical competition theory, coexistence of ecologically similar species is only possible through segregation of the available niches (Hardin 1960, Dayan and Simberloff 2005). Niche segregation is believed to contribute to species richness and biological diversity (Resetarits and Chalcraft 2007). Reduction of the competition pressure increases fitness and can be achieved in two main ways; (i) by niche specialisation, where a broader niche

is divided into two or more narrower niches, or (ii) by niche invasion, which is when the previous niche is expanded into new or underexploited resources (Schluter 2000). This ecological divergence may result from competition both within and among species (Gray et al. 2005, Svanbäck and Bolnick 2007). It can be hard to know whether observed segregation between species is due to present competition or evolutionary history. When species have different resource preferences due to adaptations that have evolved over time it is called selective segregation, in contrast to interactive segregation, which may be caused by present exploitation or interference competition (Nilsson 1967, Bøhn and Amundsen 2001). Competition can be asymmetric, such that only one species is restricted by the presence of the other (Jonsson et al. 2008). Closely related lineages are of special interest when studying competition and ecological divergence, since observed resource preferences do not result from taxonomic differences.

Ecological partitioning of competitors is often accompanied by changes in morphological characters. The most famous example of ecological divergence resulting from competition is probably

Darwin's finches on Galapagos, where feeding efficiency is closely coupled to beak morphology and specialisations on different types of seeds (Grant and Grant 2006). Furthermore, adaptive divergence in resource use can be followed by differences in life history traits, often in relation to body size (Fraser et al. 2008). Segregation of populations because of divergent or disruptive selection is believed to be an important process in speciation, since reproductive isolation may arise as a by-product (Dieckmann and Doebeli 1999, Coyne and Orr 2004). There is an ongoing debate concerning how adaptive divergence can operate when gene flow is present and hybridisation may occur (Hendry and Taylor 2004, Gow et al. 2007). Gene flow may constrain adaptive divergence since phenotypes that otherwise would have segregated into different ecological environments are kept as one gene pool. However, gene flow may also support adaptive divergence by increasing the genetic variation and by spreading of advantageous alleles. Finally, the gene flow may be reduced due to adaptive divergence and evolution of reproductive isolation (Räsänen and Hendry 2008).

Freshwater fish in postglacial lakes

Many species of freshwater fish in northern postglacial lakes repeatedly display segregation in niche use among sympatric morphs (Skulason and Smith 1995, Robinson and Parsons 2002). Coexistence of such sympatric forms is facilitated mainly by specialisations to either benthic or pelagic niches, typically with smaller planktivorous fish residing in pelagic habitats and larger benthivores living in littoral or profundal zones (Amundsen et al. 2004). Sometimes more than two forms may coexist (Jonsson and Jonsson 2001). This resource partitioning is usually coupled with morphological adaptations to the preferred habitat, for example in structures of the mouth and gill raker apparatus. Typically the benthivorous forms have few gill rakers while the pelagic type has dense gill rakers and mainly feed on zooplankton (Kahilainen et al. 2004). Additionally, the different strategies are often associated with differences in life history, such as growth rate, size and age at maturation and spawning time or place (Jonsson and Jonsson 2001, Fraser et al. 2008).

This benthic-pelagic pattern has been shown in for example charr (*Salvelinus alpinus*, Knudsen et al. 2007),

three-spined stickleback (*Gasterosteus aculeatus*, Gow et al. 2008), sunfish (*Lepomis gibbosus*, Jastrebski and Robinson 2004), perch (*Perca fluviatilis*, Svanbäck and Eklöv 2004) and whitefish (*Coregonus lavaretus*, Kahilainen et al. 2007). It is assumed that these pairs are results of competition, either by segregation of a generalist ancestor into resource specialists (i.e. niche specialisation), or by increased phenotypic variance and adaptations to under-utilised niches (i.e. niche invasion). Some of the cases have been suggested as examples of sympatric speciation, since the ecological divergence allows coexistence and has led to reproductive isolation between the populations (Gislason et al. 1999, Knudsen et al. 2006). Due to the recent formation of the postglacial lakes the divergence in these species pairs are considered to have evolved fast, i.e. within less than 15,000 years (Taylor 1999).

One of the most ecologically diverse groups of north temperate fish is the genus *Coregonus*, which consists of species of whitefish, vendace and cisco. A wide variety of sympatric coregonid forms coexist (reviewed by Hudson et al. 2007), for examples within the species complexes *C. artedi* and *C. clupeaformis* in North

America (Turgeon and Bernatchez 2003, Bernatchez 2004), and *C. lavaretus* and *C. albula* in Europe (Schulz et al. 2006, Østbye et al. 2006). Differences are repeatedly found in diet, habitat, life history, morphology, behaviour and genetics. Most of these populations follow the typical benthic-pelagic pattern, but other separations are also found, such as segregation in pelagic water depth (shallow vs. deep), degree of anadromy and time or location of spawning (Hudson et al. 2007). The coregonids in Quebec, North America, provide good examples of parallel phenotypic evolution of such benthic and pelagic forms. Here, populations of *C. artedi* are pelagic planktivores, while the sympatric populations of *C. clupeaformis* usually are benthic. However, in areas where *C. artedi* does not occur, *C. clupeaformis* has repeatedly diverged into a dwarf-form and a normal form, where the dwarf occupies the underutilised pelagic niche of the absent *C. artedi* (Derome and Bernatchez 2006). Also for European *C. lavaretus* the general trend in several lakes is the use of benthic and limnetic niches among sympatric populations (Østbye 2005).

Temporal and spatial patterns of habitat use

Niche partitioning in lakes often involves segregation in habitat and depth distribution. However, many aquatic organisms migrate between different water depths during day and night. This diel vertical migration has been demonstrated for both zooplankton and fish (Scheuerell and Schindler 2003, Winder et al. 2004). Also several populations of coregonid fish perform diel vertical migration (Hrabik et al. 2006, Mehner et al. 2007a). It is believed that the migration is a result of trade-offs between prey availability and predation risk. By hiding in deeper and darker water during day and ascending to shallow water to feed only during night, prey species can avoid visual predators. Furthermore, the migration between depth layers involves crossing different thermal zones. The energy-efficiency hypothesis predicts that diel vertical migration is connected to this variation in temperature, and that animals have energetic advantages when feeding in warmer food rich layers and digesting in deeper and colder water (Sims et al. 2006).

Temperature is one of the main factors determining the abiotic environment of animals because it affects the rate

of chemical reactions (Wootton 1998). Thermally stratified lakes consist of two distinct habitats, separated by the steep thermal gradient of the thermocline; the circulating warmer water in the upper epilimnetic layer and the cold and stable hypolimnetic layer below (Brönmark and Hansson 2001). Because animals are adapted to certain thermal regimes, water temperature is involved in regulating their habitat choice. It has been suggested that temperature is a part of an animal's multi-dimensional niche and should be treated as an ecological resource (Magnuson et al. 1979). This way temperature can also be a part of resource segregation between closely related competitors. Furthermore, differences in thermal requirements influence species interactions on all trophic levels, such as between fish, zooplankton and phytoplankton (Edwards and Richardson 2004, Pincebourde et al. 2008).

Many fish species perform habitat changes during their ontogeny, for example by occupying the littoral zone during the larval phase and switch to a fully pelagic life later on (e.g. Næsje et al. 1986). The larval stage is considered the most vulnerable period of a fish's life and the high mortality among larvae is regulated by growth rate, food availability and predation

risk (Houde et al. 1997). Because time of spawning varies among fish species, their larvae may occupy different temporal and spatial niches. In temperate regions larvae from autumn- or winter-spawners usually hatch right after ice-off and spring temperatures are important for successful recruitment. Several fish species show fluctuating year-class strengths (Karjalainen et al. 2000, Axenrot and Hansson 2003). One of the suggested explanations for these fluctuations is the match-mismatch hypothesis, which predicts high larval recruitment when the hatching of fish larvae matches the plankton bloom and thus gives good access to food (Hjort 1914, Cushing 1990). It has been suggested that recruitment success of autumn-spawning fish is more vulnerable to yearly variations in climatic variables than the recruitment of spring-spawners, because the latter more easily can adjust their spawning to right temperatures (Nyberg et al. 2001).

The coregonids in Lake Stechlin

Lake Stechlin is a dimictic oligo-mesotrophic lake situated 120 km north of Berlin, Germany (53°10'N, 13°02'E). It is a postglacial lake formed less than 12,000 years ago, with a surface area of 430 ha (Koschel and Adams 2003). The lake is one of the deepest in its region with

maximum depth 69 metres and a mean depth of 22.8 metres. *Coregonus* spp. are the dominant fish species in the pelagic area with more than 95% of the total fish abundance, while roach (*Rutilus rutilus*), perch (*Perca fluviatilis*) and bleak (*Alburnus alburnus*) are common in the littoral area and surface layers (Mehner and Schulz 2002, Anwand et al. 2003).

Vendace (*Coregonus albula*) is a common species in Fennoscandia and the Baltic region, with its southernmost distribution in north Germany. The species is planktivorous, usually lives in cold and well oxygenated water and is known to perform diel vertical migration (Hamrin 1986, Mehner et al. 2007b). The occurrence of two types of coregonids in Lake Stechlin was first noted by G. Bauch in 1953 and later the coexistence of a dwarf-sized spring-spawning population in addition to the normal winter-spawning population of vendace was demonstrated by Anwand et al. (1996). This spring-spawning *Coregonus fontanae*, or Fontane cisco, was described as a separate endemic species in 2003, based on morphology and the dissimilar breeding time (Schulz and Freyhof 2003). Initial genetic analyses based on AFLP (amplified fragment length polymorphism) technique have confirmed

genetic differences between the vendace and Fontane cisco (K. Pohlmann, J. Freyhof, T. Mehner, unpublished results). Furthermore, mitochondrial DNA and microsatellite loci have shown a strong genetic discrimination between Fontane cisco from Lake Stechlin and another spring-spawning endemic species in a lake nearby, namely the *Coregonus lucinensis* in Lake Breiter Luzin (Schulz et al. 2006). Hence, the evolution of spring-spawning populations of coregonids seems to have happened independently in the two north German lakes. It was assumed that the spring-spawning Fontane cisco in Lake Stechlin was a deep-water species which mostly utilised benthic food and that it did not perform diel vertical migration like sympatric vendace (Anwand et al. 1996, Schulz et al. 2003). However, few ecological comparisons have been done between the two sympatric populations after they were distinguished as two separate species.

AIM AND STRUCTURE OF THESIS

The objective of my thesis is to evaluate the ecological differences between

vendace and Fontane cisco in Lake Stechlin, in order to elucidate the mechanisms of evolution and coexistence of the two populations. It was expected that coexistence of the two was facilitated primarily by segregation in diet and habitat following the benthic-pelagic pattern. The main questions to be answered in my thesis are as follows:

- Do sympatric vendace and Fontane cisco segregate in diet and habitat? (**Papers I and III**)
- Do vendace and Fontane cisco differ in morphology over all adult size-classes and water depths? (**Paper II**)
- Does Fontane cisco perform diel vertical migration like vendace? (**Paper III**)
- What determines depth distribution and diel vertical migration of the coregonids and their main prey? (**Papers III and IV**)
- Does starvation of newly hatched larvae regulate year-class strength of coregonid populations? (**Paper V**)
- What is the ecological basis for evolution and coexistence of vendace

and Fontane cisco in Lake Stechlin?

(Thesis synopsis)

The main findings of the five papers are summarised in the result part. Detailed discussions of the results can be found in each of the attached papers, while in this synopsis I will focus on the overall picture. I will allow myself to include some speculations beyond the results available at present, to try to understand the co-existence of the sympatric pair of coregonids in Lake Stechlin.

RESULTS IN SUMMARY

Paper I: Coexistence of a pair of pelagic planktivorous coregonid fish

The aim of this paper was to investigate trophic segregation between vendace and Fontane cisco. We hypothesized that dietary specialisation reduces competition and is the main facilitator of the coexistence of the two closely related species. However, a combination of stomach content analyses and stable isotope analyses of individuals collected at different depths over ten months, revealed surprisingly small differences in diet between the two species.

There were significant diet differences between individuals collected at different depths and between differently sized individuals, but little trophic segregation between vendace and Fontane cisco. There were, however, indications that individuals of Fontane cisco captured in deep water feed at a higher trophic level than both conspecifics captured in shallower water and vendace at all depths. The main conclusion was that both coregonid species are planktivores and hardly segregate in their diet. Due to a substantial overlap in food sources, other specialisations should support their coexistence.

Paper II: Morphological differences between two ecologically similar sympatric fish species

Morphology of fish is often connected to resource use. However, different morphological adaptations to diet between vendace and Fontane cisco are not likely since both species are pelagic planktivores (paper I). Still, other morphological adaptations may facilitate their coexistence, and due to differences in life history, growth rate and swimming-related physiology we expected the two species to vary in external morphology. Earlier

morphological description of the coregonids in Lake Stechlin was only based on spawning females sampled at dissimilar localities and times. Therefore, this paper expanded the previous comparison by including individuals of both sexes over a range of body sizes and capture depths. Moreover, the sampling was prolonged to several months to minimise erroneous species differences due to seasonal variation in gonad size, because the two species have dissimilar spawning times and gonad development influences body shape (i.e. larger abdomen). The results from landmark-based geometric morphometrics confirm that the two coregonids differ significantly in overall body shape, in spite of being rather similar in external morphology to the human eye and showing large ecological overlap. While vendace has similar shape in all sizes, the morphology of Fontane cisco changes with body-size. As the dwarf-sized Fontane cisco grows larger it becomes morphologically more similar to vendace. The ecomorphological explanation for different body-shapes of the two species is not straightforward, but may be related to different metabolic strategies in the two species. Furthermore, temporal segregation in spawning and growth patterns influences

the ecology and life history of vendace and Fontane cisco differently, and may have consequences for both ecological and morphological traits.

Paper III: Temperature sensitivity of vertical distributions of zooplankton and planktivorous fish in a stratified lake

In stratified lakes water temperature creates a strong vertical gradient which determines the environmental conditions for organisms that inhabit the lakes. Here we studied the depth distributions of vendace and Fontane cisco and their zooplankton prey in relation to water temperature over the year. The night-time average depth distribution (i.e. centre of gravity) of vendace, daphnids and copepods were found to be significantly correlated to the average water temperature. During the warmer period in summer they occurred closer to the lake surface. However, the biological explanation for the preference of shallow water during the warmer months was not clear. The paper also shows that both vendace and Fontane cisco perform diel vertical migration and usually do not cross the thermocline. The coregonids generally stay below 30 metres during day, ascend to

shallower water layers during dawn and descend again during dusk. Both vendace and Fontane cisco are truly pelagic species, but in spite of a large overlap in the depth distribution, the two populations differ significantly in their average depth distribution. Fontane cisco stays on average deeper than vendace during all months and thereby also experiences lower temperature.

Paper IV: Opposite thermal refuges from vertically migrating planktivorous fish in two coexisting *Bosmina* species

Prey organisms can find refuges by occupying different habitats than their predators. Since the habitat of the coregonids as well as their zooplankton prey were shown to be correlated to water temperature (paper III), we hypothesized in this paper that zooplankton avoided predation by selecting other thermal zones than the coregonids. Moreover, the paper investigates the functional explanation for the different vertical distribution over the season, by comparing species-specific depth distribution to the buoyancy stability. This variable reflects the changes in the upper water layers over the seasons, including the vertical shift of the location

of the thermocline, the steepness of the thermal gradient, and the location of the isothermal layers. The coregonids in Lake Stechlin perform diel vertical migration and probably feed mostly in shallower water during crepuscular hours and night, while the distribution of their main prey *Bosmina longirostris* and *B. coregoni* does not change between day and night.

The buoyancy stability of the upper 20 metres in the lake significantly explained the depth distribution of the coregonids and the two *Bosmina* species. While the coregonids and *B. coregoni* moved upwards when the lake was stratified, *B. longirostris* moved to deeper waters. Hence, the two zooplankton species have opposite patterns and *B. coregoni* have a higher habitat overlap with predators. This corresponds to the higher amount of *B. coregoni* in the diet of the coregonids (paper I). The thermal refugia were highly efficient since the proportion of *Bosmina* in the diet of the fish was correlated with the temperature distance between predator and prey. The main conclusion was that both zooplankton species selected habitats outside the diel vertical migration amplitude of the fish. *B. coregoni* occupied the epilimnetic layer in a warmwater refuge, while *B. longirostris* occupied the

lower hypolimnion in a cold-water refuge. Furthermore, the coregonids remain in an isothermal layer during the whole stratification period, and the move into shallower water during summer (paper III) is probably a reflection of where the preferred water layer is vertically located.

Paper V: Starvation does not explain abundance decline during early larval stage of vendace (*Coregonus albula*)

Vendace has fluctuating year-class strength and high mortality during the first four weeks of life in many lakes, but the factors that determine the mortality are not fully understood. In this paper we compared growth and starvation of larval vendace from Lake Stechlin with a starvation threshold derived from laboratory-reared larvae under controlled feeding and temperature regimes, to evaluate whether starvation modified the density of newly hatched larvae. Based on larval RNA:DNA ratio, gut content and growth (length and weight) from the first four weeks after hatching, we showed that none of the individuals captured in Lake Stechlin were in a starving condition, in spite of a strong decline in larval abundance after two weeks. Simultaneously to

the decrease in larval abundance, the condition and food consumption of the remaining larvae increased, and the survival seemed to be size-independent. We concluded that extrinsic mortality (starvation and predation) are not stringent enough to regulate the abundance of larval vendace in Lake Stechlin, even if some predation may occur. Therefore, we speculate that intrinsic mortality (i.e. individual quality differences) may be more important, for example through failure of physiological development and transitions during the larval phases.

DISCUSSION

The results of my thesis show that the sympatric species pair of coregonids in Lake Stechlin does not follow the expected pattern of niche segregation along the benthic-pelagic axis. Both species are truly pelagic and both species utilise the same planktonic food source, as shown in **paper I**. Furthermore, in contradiction to earlier assumptions by Anwand et al. (1996) and Schulz et al. (2003), **paper III** reveals that also Fontane cisco performs diel vertical migration. For a summary of investigated differences and similarities of vendace and Fontane cisco, see Table 1.

Ecology of a sympatric pair of coregonid fish

It is difficult to understand how two closely related species can live in sympatry with such little segregation in niche, without one species being out-competed by

the other. Therefore, lack of dietary specialisation indicates that other mechanisms of segregation are involved in the coexistence in Lake Stechlin.

Table 1. Summarised comparisons of vendace and Fontane cisco from Lake Stechlin.

Trait	Vendace	Fontane cisco	Source
Body size (mm)*	Average	97.9	94.9
	Maximum	162	144
Morphology	Shorter and deeper caudal peduncle	Larger eye, longer head, more posterior pectoral fin	Paper III
Trophic position	$\delta^{15}\text{N}$	6.9	7.5
	$\delta^{13}\text{C}$	-24.8	-24.8
Spawning period	December	April - July	Paper I
Hatching time	December	April - July	Schulz and Freyhof 2003
Night-time population depth (m)*	March-April	Unknown	Paper V
	April	14.4	27.1
	August	13.2	13.0
	December	15.2	24.4
Metabolic optimum temperature ($^{\circ}\text{C}$)	> 8	< 8	Paper III
Temperature preference ($^{\circ}\text{C}$)	> 8	< 8	Ohlberger et al. 2008b
Temperature preference ($^{\circ}\text{C}$)	9.0	4.2	Ohlberger et al. submitted

* Note that individuals <50 mm and water depths >35 m in the lake are not included in the calculations in paper III, due to methodological limitations of data collection with trawl.

Vertical segregation and temperature

Even though vendace and Fontane cisco both live in the pelagic area, **paper III** shows that the two species segregate in their vertical distribution. There is a large overlap and separation by depth is not complete, but there is probably a microhabitat segregation within the vertical pelagic zone. A similar pattern is found for coexisting vendace and whitefish (*Coregonus lavaretus*) in Lake Skrukkebukta (northern Norway) (Gjelland et al. 2007). Ecological segregation based on pelagic habitat depth is less frequently reported than the benthic-pelagic divergence, but is nevertheless described for some sympatric forms of Arctic charr (*Salvelinus alpinus*), cisco (*Coregonus* spp) and lake trout (*Salvelinus namaycush*) in very deep lakes in North America (Turgeon et al. 1999, Power et al. 2005, Zimmerman et al. 2007).

The deeper average depth distribution of Fontane cisco compared to vendace indicates that Fontane cisco experiences less favourable conditions, since food abundance and light intensities in Lake Stechlin decrease with depth (Mehner et al. 2005). It has therefore been hypothesized that Fontane cisco com-

pensates for this through higher feeding efficiency. This was, however, recently rejected when no differences in feeding behaviour between the two species could be demonstrated at natural light and food densities (Ohlberger et al. 2008a). The disadvantage of unfavourable habitat could be involved in the lower growth rate of Fontane cisco (Schulz and Freyhof 2003). However, bioenergetic comparisons of sympatric dwarf and normal North American whitefish (*C. clupeaformis*) have showed that the slow growth of dwarf fish was related to higher metabolic rate, rather than low food consumption (Trudel et al. 2001).

The results presented in **papers III** and **IV** indicate that temperature is an important factor in coregonid ecology. Interestingly, the deeper and colder average depth distribution of Fontane cisco compared to vendace shown in my thesis, corresponds strongly to recent physiological findings of the species pair. Laboratory experiments with temperature-regulated shuttle-box system have revealed that while vendace prefers temperatures around 9°C, the preferred temperature of Fontane cisco is 4°C (Ohlberger et al. submitted). In accordance with this Fontane cisco have lower metabolic

swimming costs at 4°C, but higher costs compared to vendace when the temperature increases to 8°C or more (Ohlberger et al. 2008b). Therefore, temperature-related physiological adaptations seem to have contributed to an ecological divergence between the two closely related species. Hence, substantial differences in diet preference may not be needed for their coexistence. Furthermore, the differences in swimming-related physiology may be involved in the morphological differences presented in **paper II**, although functional links are not yet tested.

Temperature can be treated as an ecological resource involved in resource specialisations (Magnuson et al. 1979). In some ant communities resource partitioning has been demonstrated to be primarily based on specialisations in temperature tolerance (Cerda et al. 1998). Furthermore, thermal preferences involved in habitat segregation have also been found for sympatric species of Australian lizards (*Ctenophorus* spp., Daly et al. 2008). It has been speculated that coexistence of native Barrens topminnow (*Fundulus julisia*) and the invasive western mosquitofish (*Gambusia affinis*) may be permitted by interspecific difference in growth rate at certain water temperatures (Laha and

Mattingly 2006). Similarly, Fontane cisco probably is the strongest competitor in colder water, while vendace performs better above a temperature threshold of around 8°C. It has been suggested that the lower metabolic requirements and smaller body-size of Fontane cisco may be an adaptive strategy to live in deeper waters (Ohlberger et al. 2008a).

Temperature has been suggested to be an important part of the diel vertical migration of coregonids in Lake Stechlin, because feeding in warm food rich layers during night followed by digestion in deep and cold water during day can maximise the growth rate (Mehner et al. 2007a). Additionally, temperature shapes the interactions between the two coregonid fish and their prey species, as showed in **papers III and IV**. The depth distribution of Lake Stechlin coregonids seems to be determined by physical stability in the water column, more specifically the seasonal location of the thermocline. This is seen from the correlation between the vertical distribution of fish and the calculated buoyancy stability in the lake. The average depth distribution of the coregonids is situated in similar temperature layers during the whole period of stratification. This indicates that the fish try to remain in

their preferred thermal zone, probably due to metabolic requirements. There are, however, species-specific differences in both vertical distribution and thermal preference. These differences are not only found between the closely related coregonids (**paper III**), but also between the closely related zooplankton species *Bosmina coregoni* and *B. longirostris* (**paper IV**). This illustrates that it can be important to focus on single species when studying adaptations and species interactions. A recent comparison of congeneric and morphologically similar species of sunfish (*Enneacanthus* spp.) also concluded that each species interacts differently with the environment, probably due to different metabolism or different predation efficiency (Resetarits and Chalcraft 2007). This corresponds to the niche theory that species coexistence is permitted by ecological divergence and that sympatric species cannot be too similar (Dayan and Simberloff 2005).

Temporal segregation

A clear segregation between vendace and Fontane cisco is the spawning season. Such a temporal isolation reduces gene flow. Isolation by time is expected to

be frequent in nature because reproductive time often is heritable and selection usually varies throughout the reproductive season (Hendry and Day 2005). Therefore, temporal isolation is assumed to be an important feature of many systems, but only few examples among animals have been properly demonstrated, including storm petrel (*Oceanodroma castro*, Friesen et al. 2007), periodical cicadas (*Magicicada* spp., Simon et al. 2000) and Pacific salmon (*Oncorhynchus* spp., e.g. Ramstad et al. 2003). Coexisting fish populations with completely separated spawning times are also found for dwarf-sized and normal Arctic charr (*Salvelinus alpinus*) in Lake Fjellfrøsvatn (Knudsen et al. 2006) and Lake Sirdalsvatn (Hesthagen et al. 1995) in Norway. These charr populations are additionally segregated in littoral and profundal habitat and diet, in contrast to the Lake Stechlin coregonids. In sympatry the development of reproductive isolation simultaneously requires the ability of the divergent populations to coexist (Coyne and Orr 2004). We know little about the processes that have initiated the reproductive isolation between the sympatric coregonids in Lake Stechlin. However, my thesis indicates that temperature-mediated ecological segregation may be a strong

force in maintaining the coexistence of the two populations. This is probably operating through microhabitat segregation within the pelagic zone, together with adaptations in metabolism and growth rate.

Asynchrony in timing of spawning and hatching may contribute directly to the coexistence of sympatric species, through temporal partitioning of resources and habitat. Competition may be strongest between individuals of comparable sizes or at comparable life history stages, because of overlapping resource requirements (Werner and Gilliam 1984). Hence, inter-specific competition between vendace and Fontane cisco may be reduced along a temporal axis, by avoiding simultaneous occurrence of similar individuals. While **paper V** demonstrates that larval vendace inhabit the littoral zone in April and May, we were unsuccessful in detecting the hatching time and larval habitat of Fontane cisco. Therefore, we can only speculate about possible differences in early life history between the Lake Stechlin coregonids. Nevertheless, based on the spawning period of Fontane cisco (April to July) it can be assumed that the larvae hatch in late summer or even autumn. Hence, larvae of the two species probably experience highly dissimilar environments

(e.g. temperature, predation risk, food abundance) during their first weeks of life (Nyberg et al. 2001). This indicates that the ecological differences between vendace and Fontane cisco are strongest during the first year of life, even if adults show large ecological overlap. In correspondence with this assumption, **paper II** shows that the morphological differences between the two are larger for younger adults than for older fish. If the hatching time of Fontane cisco is as prolonged as the spawning time, there could also be a substantial difference in the strength of intraspecific interactions (e.g. food competition and shoaling behaviour) for larvae of Fontane cisco compared to the more synchronised vendace population. **Paper I** gives indications that differently sized individuals utilise different food sources, and that this size-effect on trophic position (i.e. $\delta^{13}\text{C}$) is stronger for Fontane cisco than vendace. Similarly, **paper II** shows that adult morphology of Fontane cisco changes with body size, while this is not the case for vendace. When put together, this could indicate that Fontane cisco has larger ontogenetic niche shifts than vendace. If this was true, the reason could perhaps be the differences in seasonal growth pattern because of the different spawning and hatching time.

However, these possible differences between young stages are so far only speculations.

Under certain circumstances coexistence of sympatric species can be maintained through temporal dynamics where the competitors differ in their sensitivity to environmental fluctuations. For example are closely related tree species in a tropical forest able to coexist because the less sensitive species is more successful during harder conditions, while the sensitive species is the strongest competitor during good periods (Kelly and Bowler 2005). Perhaps related temporal dynamics exist for the coexistence of the spring- and winter-spawning strategies in Lake Stechlin, since recruitment and year class strength may be highly dependent on the match-mismatch between larvae and favourable environmental conditions. It has been suggested that spring-spawning fish are less vulnerable to climatic variation in spring, such as timing of ice-break and plankton bloom, compared to winter-spawning species (Nyberg et al. 2001). Thus, the hatching of Fontane cisco during summer may be beneficial also in years when vendace recruitment is low due to starvation and mismatch of vendace larvae in spring. However, the results of **paper V**

show that larval vendace were not subjected to starvation, at least not in the year studied. Our results indicated that other factors than starvation and predation are more important for recruitment. Nevertheless, this is the first study evaluating larvae of the coregonids in Lake Stechlin and therefore the results are only preliminary. At present, we do not know how this one year relates to other years or how the recruitment of larval Fontane cisco is in comparison to vendace. The prolonged spawning time of Fontane cisco may be a bet-hedging strategy, which minimise the risk of mismatch with food abundance and predation risk by a temporal spreading in the hatching of larvae, and thus increases the chances of successful recruitment (Stearns 1992). Long-term data on recruitment of vendace and Fontane cisco are not available, but hydroacoustics have indicated that the total coregonid abundance in Lake Stechlin varies between years (Mehner et al. 2008). Clearly, more information on the larval stage of both species is needed to understand the Lake Stechlin system. In fact, few studies of resource partitioning among sympatric fish in postglacial lakes have focused on early life history stages. However, Chouinard and Bernatchez (1998) found little trophic

niche partitioning between larvae of North American lake whitefish (*Coregonus clupeaformis*), even when adults were strongly segregated into pelagic and benthic niches. Nevertheless, larvae hatching in different habitats or at different times are at least segregated at this age, and Lecomte and Dodson (2004) concluded that such temporal and spatial segregation among larvae contributes to coexistence of two populations of rainbow smelt (*Osmerus mordax*) in an estuarine.

We have no apparent explanation for how the temporal segregation in reproduction between vendace and Fontane cisco has evolved, in spite of the demonstrated differences in microhabitat, temperature preference, growth and morphology. One possibility is that strong competition pressure either among reproducing individuals or their young offspring has led to divergence in reproductive traits directly. This could happen even if adults of both species have rather similar ecology. Temporal difference in breeding can be a mechanism of reducing competition, both inter- and intra-specifically. For example is food competition among young hermit crabs (*Pagurus* spp.) expected to be reduced by temporal segregation in larval production

(Wada et al. 2000). Similarly can interspecific differences in timing of breeding potentially relax competition for spawning habitat among riverine fish (Grabowski and Isely 2007). Vendace populations spawn in autumn or winter in most lakes, and the shift in spawning time and evolution of spring-spawning coregonids seem to have happened independently in the two north German lakes Lake Stechlin and Lake Breiter Luzin (Schulz et al. 2006). However, it is known from several coregonids that they show flexibility in reproductive traits and that coexisting forms may show different spawning habitats or spawning time (Hudson et al. 2007).

To sum up, the most likely reason for the coexistence of vendace and Fontane cisco is segregation in metabolic and reproductive traits. First, different temperature preference and physiological adaptations creates microhabitat segregation within the pelagic area. Second, different spawning times and growth rates result in a displaced size-distribution of Fontane cisco compared to vendace, which may keep similar-sized individuals and similar life history stages of both species from occurring together. The combination of these factors may sufficiently reduce

competition and allow coexistence of the two closely related species.

CONCLUSIONS

Based on the questions asked in the introduction, the main conclusions to be drawn from my thesis are:

- The sympatric pair of coregonids in Lake Stechlin does not follow the expected segregation along the benthic-pelagic axis. Both vendace and Fontane cisco are truly pelagic and utilise similar food resources.
- There is an overlap in depth distribution, but nevertheless a microhabitat segregation within the pelagic habitat. Fontane cisco occurs on average deeper than vendace, and therefore experiences colder water.
- Vendace and Fontane cisco differ consistently in external morphology at all adult sizes and all water depths. Younger and smaller individuals of Fontane cisco are more morphologically different

from vendace than larger and older individuals are.

- Both species perform diel vertical migration.
- Temperature is a strong factor in determining habitat and prey availability of coregonids in Lake Stechlin.
- The coregonids in Lake Stechlin occupy an isothermal layer of the lake during the stratified period. Their habitat choice and vertical distribution over the year appear to be a response to the location of the thermocline.
- The main prey species of vendace and Fontane cisco avoid predation by inhabiting other thermal zones than their predators. Because the closely related *Bosmina coregoni* and *B. longirostris* have opposite thermal strategies they have different extent of habitat overlap with the predators, and hence occur in different amounts in the coregonid diet.
- Starvation is not a major threat to larval vendace the first weeks after hatching.

- Differences in temperature-related physiology and timing of reproduction are the most likely reasons for coexistence of vendace and Fontane cisco. The combination of these factors may sufficiently reduce competition and allow coexistence of the two closely related species.

FUTURE PERSPECTIVES

Many questions regarding the ecology and interactions between vendace and Fontane cisco are not yet answered. Comparisons of these coregonids have just started, since separation of the two only recently became possible. Generally, the Lake Stechlin coregonids are worth of future studies because the system is unique. First, my thesis shows that closely related lacustrine fish can coexist also when specialisations into benthic and pelagic diet and habitat are not present. Hence, less visual niche adaptations like metabolism and microhabitat can be important and should be evaluated also in other coexisting fish populations. Second, in spite of many examples of ecological partitioning among sympatric fish populations in postglacial

lakes, most systems do not have such strong temporal segregation in reproduction as vendace and Fontane cisco. As discussed in my thesis this temporal segregation may be very important for their coexistence. To understand the reasons for and mechanisms of such a large shift in spawning time can be beneficial for fish evolutionary ecology, as well as for studies of speciation processes. More knowledge about vendace and Fontane cisco may give insights into other sympatric pairs and contribute to understanding divergence among competitors.

My thesis and other studies over the last few years have given some indications on how vendace and Fontane differ from each other and which adaptations they have to their niches. However, no study has so far demonstrated that the two species actually compete with each other. Tests of competitive interactions can be done for example by comparing differences between allopatric and sympatric situations. Hence, in this case, vendace in Lake Stechlin could be compared to vendace populations in nearby lakes, where no spring-spawning coregonid exists. If the Lake Stechlin vendace has a compressed niche compared to allopatric vendace populations this would indicate that Fontane cisco restricts

vendace. Whether vendace restricts Fontane cisco is harder to test in nature, since Fontane cisco is endemic to Lake Stechlin. However, comparisons of the coregonids in Lake Stechlin and Lake Breiter Luzin may shed light on competitive interactions, since both lakes contain both spring- and winter-spawning populations of coregonids.

Competition can also be tested with experimental approaches, for example in common garden experiments. It would be very interesting to compare similar-sized individuals of both species under identical conditions in aquarium. This has partly been done with respect to functional response for adults (Ohlberger et al. 2008a), but not under competitive conditions, and not for larvae or juveniles. To study this would require controlled hatching times of the eggs, to enable simultaneous occurrence of larvae of both species. Furthermore, artificial production of hybrids would allow for testing whether hybrids show intermediate performance of vendace and Fontane cisco, and hence which traits that may have a genetic basis.

In my opinion, future research on the Lake Stechlin coregonids should focus more on early life history stages. All

comparisons have so far been done between adults and the available information indicates that the differences may be larger between young vendace and Fontane cisco than for older. Furthermore, few details are available on the reproductive cycle of both species, such as gonad investment, spawning habitat, egg development and hatching time. Knowledge on growth and age patterns as well as long-term abundance estimates of both species would also be valuable, to understand the interactions and dynamics between the two.

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