



Living in a predation matrix

Studies on fish and their prey in a Baltic Sea coastal area

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Abstract

This thesis was written within the framework of a biomanipulation project where young-of-the-year (YOY) pikeperch (*Sander lucioperca*) were stocked to a Baltic Sea bay to improve water quality through a top-down trophic cascade. The aim of my doctoral studies was however focused on a broader ecological question, namely predation (the main driving force in a biomanipulation). Hence, this thesis consists of four papers where we study the interactions between predator and prey using fish and zooplankton and how these interactions can be measured.

In *paper I* we evaluated the performance of different diet analysis methods by individual based modelling and found that when having a nutritional gain perspective, mass based methods described diets best. *Paper II* investigated how the explorative, foraging and anti-predator behaviour of the YOY pikeperch used for stocking were affected by their rearing environment (pond vs. tank rearing). The more complex and varied environment in the semi-natural ponds seemed to promote a more flexible and active behaviour, better equipping young fish for survival in the wild. For *paper III* we studied the diel vertical migration in the six copepodite stages of the zooplankton *Acartia* spp. and *Eurytemora affinis* in relation to fish biomass, phytoplankton abundance and temperature. Both species migrated and in addition showed increased migration range with size within species, indicating evasion from visual predators. *Paper IV* addressed the movement of littoral Eurasian perch (*Perca fluviatilis*) via stable isotope signatures (^{13}C and ^{15}N) and body condition. We found clear indications of sedentarity and intra-habitat dietary differences. Interactions between predators and prey are complex and affected by both physiological and environmental characteristics as well as behavioural traits. The results in this thesis suggest that different species and even different life stages pursue different strategies to survive.

List of papers

- Paper I** Ahlbeck, I., Hansson, S. and Hjerne, O. (*Manuscript*)
Evaluation of diet analysis methods by individual based modelling. Submitted to *Canadian Journal of Fisheries and Aquatic Sciences*.
- Paper II** Ahlbeck, I. and Holliland, P.B. (*In press*) Rearing environment affect important life skills in pikeperch (*Sander lucioperca*). *Boreal Environment Research*. ISSN 1797-2469 (online).
- Paper III** Holliland, P.B., Ahlbeck, I., Westlund, E. and Hansson, S. (2012) Ontogenetic and seasonal changes in diel vertical migration amplitude of the calanoid copepods *Eurytemora affinis* and *Acartia spp.* in a coastal area of the northern Baltic Proper. *Journal of plankton research* 34: 298-307.
- Paper IV** Ahlbeck, I. Hansson S. and Karlöf, O. (*Manuscript*)
Sedentarity in Eurasian perch (*Perca fluviatilis*) in a coastal Baltic Sea area. Submitted to *Ecology of Freshwater Fish*.

My contribution to the studies:

Paper I: Part in planning the model, responsible for programming, analyzing model output and evaluating method performance. Writing the manuscript together with my co-authors.

Paper II: Planning experiments and executing them together with co-author Per Holliland. Responsible for data analysis. Main author of manuscript.

Paper III: Part in zooplankton sampling, responsible for sampling and analyzing fish biomasses. Commenting on the manuscript.

Paper IV: Part in data sampling (responsible for sampling in Himmerfjärden) and data analysis. Main author of the manuscript together with co-author Sture Hansson.

All the accepted papers are reprinted with kind permission from the publishers; paper II – Boreal Environment Research Publishing Board, paper III – Oxford University Press.

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Introduction

Predation describes a biological interaction where a predator feeds on its prey (Begon *et al.* 1996). Predators affect the abundance and distribution of their prey, and vice versa. The positive effect on the predator may seem obvious, but there are also positive effects on the prey population such as increased growth rate, reproduction and offspring survival as competition for limited resources decrease (Begon *et al.* 1996). The negative effect on the individual prey being killed is of course apparent and the number of anti-predator strategies that prey have evolved suggests that predation is a strong selective force (Stiling 2002). Both physical and behavioural defences such as aposematic colouration, camouflage, mimicry, chemical defence, intimidation displays and advertising unprofitability have evolved to protect the prey. Even separation of predator and prey in time or space is used to escape predation.

Finding prey

As for all animals, finding food is a continuous task for fish and selection pressure on adaptations to the foraging tasks is intense; as a result different physiological and behavioural adaptations have evolved. Physiological adaptations are e.g. evident from the fish's phenotype. Trophic polymorphism has been described in at least nearly 100 species (Robinson and Wilson 1994, Smith and Skúlason 1996) and demonstrates that fish have adapted to different micro-environments within their surroundings e.g. pelagic and littoral morphs (e.g. Svanbäck and Eklöv 2003, 2004). When these specialised morphs are tested outside their environment they perform worse than within "their own" environment, with hybrids performing intermediately (Schulter 1993). As for behavioural adaptations, many fish migrate in a diel pattern, both vertically (e.g. Narver 1970, Blaxter 1973, Begg 1976) and horizontally (e.g. Hobson 1972, Baumann 1974, Bohl 1980, Krumme 2009) following their preys migrations.

Although some species forage alone (e.g. Nursal 1973), most species forage in the presence of con- and hetero-specifics, which adds complexity to foraging behaviour. When feeding with others fish need to compete. To reduce competition morphological differentiation (as discussed above)

within and between species may occur as fish with similar morphology is expected to compete more than those that are morphologically distinct. Group foraging however also adds a positive aspect of facilitation between foragers and protection against predators. Fish foraging in groups can base their decision on private information (learned responses or prior experience from non-social interactions, e.g. Milinski 1994) or social information where information about the location or quality of a food source is transmitted from more informed individuals (e.g. Reader *et al.* 2003, Valone and Templeton 2002).

Avoiding predators

The ability to assess and respond to changes in predation risk is the key to successful predator defence. Fish use smell and vision among other senses, to assess their environment and detect predators associated with certain cues (Pitcher 1986). The predator can provide chemical cues informing prey about the predator's recent hunting habits (e.g. Hirvonen *et al.* 2000, Vilhunen and Hirvonen 2003) and the concentration of odour may reveal the proximity of the predator and hence the predation risk (e.g. Kusch *et al.* 2004). Visual cues such as body shape, posture and mouth size may reveal identity and hunger level of the predator (Karplus *et al.* 1982, Magurran and Girling 1986, Helfman 1989). In addition, fish may also gain information by associating with other prey. Both con- and hetero-specifics produce chemical (e.g. Chivers and Smith 1998, Wisebden *et al.* 2004) and visual cues (e.g. Verheijen 1956, Krause 1993) in response to increased predation risk or injury and this can stimulate others to increase their level of vigilance or engage in anti-predator behaviours such as avoidance, shoaling, skittering, movement towards substrate, freezing or a reduction in activity (Chivers and Smith 1998, Brown *et al.* 2004).

To limit predator encounter rates, even in the absence of predation cues, prey seek localities where predators are less abundant or have reduced foraging efficiency. Predator mediated change of habitat use is most evident in studies of presence/absence of predators in a system, where juvenile fish often relocate from the unprotected pelagic to the littoral, where they can hide in vegetation in presence of predators (e.g. Brabrand and Faafeng 1993, Diehl and Eklöv 1995, Romare 2001). Many fish reduce encounter rates by diurnal migration, where fish move between habitats, both vertically and horizontally (Bohl 1980, Moore *et al.* 1995, Krumme 2009), to find food in one habitat and shelter from predators in the other. This allows them to optimize the trade-off between foraging and predation risk (e.g. Clark and Levy 1988).

It is not only fish that try to avoid predators through migration. Predation evasion is considered the major biotic factor driving zooplankton diel vertical migration (DVM) (e.g. Lampert 1993, Hays 2003). DVM is triggered or altered by the presence of predator kairomones (Haney 1993) and is specific to visual predators such as fish, making zooplankton avoid higher light levels at the surface during the day reducing the risk of detection by visual predators (e.g. Zaret and Suffern 1976, Hays 2003). Reverse DVM (avoiding deep waters during day) is also attributed to predation (e.g. Ohman *et al.* 1983), specifically by invertebrate predators.

Aim of thesis

When starting my doctoral studies the aim of my project was to investigate if biomanipulation with pikeperch could be a complement to traditional water treatment in the Baltic Sea bay Himmerfjärden, by improving water quality through a top-down trophic cascade. However, due to different practical reasons the pikeperch stockings that were supposed to trigger the trophic cascade were delayed; hence the effects of the stocking will be beyond the reach of this thesis. The aim of my doctoral studies was therefore redirected to focus on a broader ecological question, namely predation (the main driving force in a biomanipulation). Hence, this thesis consists of four studies concerning interactions between fish and zooplankton in Himmerfjärden and how this can be measured.

Study area

Baltic Sea

The Baltic Sea is one of the world's largest brackish water bodies. It has an area of nearly 387 000 km² (SMHI 2003) and the drainage area is densely populated with over 85 million inhabitants (Rönnberg and Bondorff 2004). There is a strong north-south salinity gradient with a 10 psu unit difference between the Danish trait and the northern Bothnian Bay (Berns 2005), and also significant environmental variations between the coastal areas and the open sea (Rönnberg and Bondorff 2004). The water volume is small compared to its drainage area, consequently the Baltic receives several hundredfold larger quantities of pollutants than oceans in general (Berns 2005). The large drainage area, long retention time and the low water temperatures increase the strength of human influences. The low salinity also results in low species diversity, which sometimes have been proposed to make the food web extra sensitive to disturbance.

Himmerfjärden

Himmerfjärden is a bay on the west coast of the northern Baltic proper, situated in Stockholm's southern archipelago. The inner Himmerfjärden basin is approximately 11km long, with an average depth of 17m and has a salinity of 6-7‰ (Engqvist 1996). The bay receives discharge from a municipal waste water treatment plant that processes waste waters from about 0.25 million people. Due to the denitrification taking place in the sewage treatment plant, the discharged water is comparatively rich in ¹⁵N, resulting in a pronounced gradient in the relationship between ¹⁴N and ¹⁵N in the bay. The pelagic fish community of Himmerfjärden is dominated by herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) and the littoral by perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*). The zooplankton biomass is dominated by the copepods *Eurytemora affinis* and *Acartia* spp. (Johansson 1992).

During 2008-2011 approximately one million YOY pikeperch were stocked to the bay in a biomanipulation experiment, where the increase in piscivorous fish is expected to result in a decrease in zooplanktivorous fish biomass, an increase in herbivorous zooplankton and a decrease in phytoplankton biomass. The behaviour of these stocked fish is investigated in Paper II. Data for papers III and IV were collected in Himmerfjärden; paper IV also contains data from Näslandsfjärden and Hallsfjärden, which are northward extensions from Himmerfjärden (Fig. 1). Paper I is an *in silico* study.

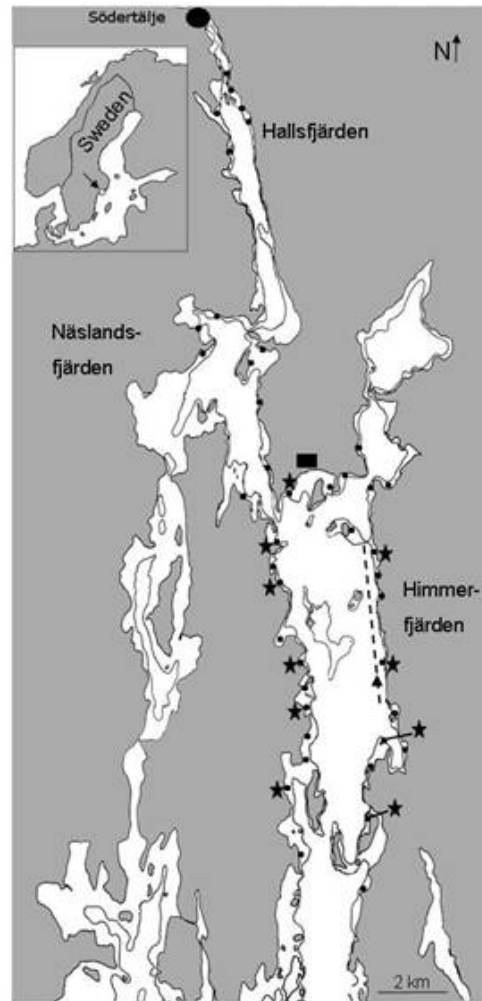


Figure 1. Study area. The dots indicate the location of littoral fishing stations and the stars are indicating stations where stable isotope data were collected. The zooplankton sampling station is indicated by the triangle and the hydro acoustic sampling was conducted along the broken line. The waste water treatment plant is indicated by the black square. The 10m isobath is shown.

Methods

Below, the methodology for each study is briefly described. For a more detailed description please see corresponding papers.

Paper I

To evaluate different methods used for fish diet analysis, an individual based model of a foraging fish was constructed to create fish with known diets but with inter-individual variation in stomach content. The virtual stomachs were analyzed with both basic stomach analysis methods (frequency of occurrence, dominance, numeric, mass, and points) and composite indices (%Index of Relative Importance, Comparative Feeding Index). To explore the behaviour of the different methods and which ones produced the most reliable diet estimates, the result from each method was compared to the “true” diet of the fish.

Paper II

Aquaria experiments were conducted to study the effects of rearing environment on the behaviour of YOY pikeperch used for stocking in Himmerfjärden. Three behavioural tests were performed on fish from three different facilities producing fish for stocking (one tank facility and two semi-natural ponds). All tests were run during late September and early October 2010, when fish were four months old. We used 50L test aquaria and observed the fish from behind a black screen. All fish were randomly selected from the breeders. Explorative behaviour was measured by recording the time it took until a fish left a start box and then recording its position in the aquarium every 15 seconds for ten minutes. Foraging behaviour was measured by recording the time until the first attack on a prey for each fish in the group. Anti-predator behaviour was measured by recording the behaviour of the pikeperch every 15 seconds during ten minutes when in visual contact with a perch.

Paper III

Zooplankton sampling was carried out day and night, monthly from May through October 2009. Samples were collected with a 25 L transparent acrylic glass tube sampler. Sampling started at the surface and was repeated every 2.5 m down the water column to 32.5 m. The collected water was filtered through a 20 μm sieve and preserved *in situ* with borax buffered formalin. Each zooplankton sample was counted using a dissection microscope. Fish abundance was measured with sonar surveys conducted the consecutive night to the zooplankton sampling, using a scientific echo sounder along a transect that passed close to the zooplankton sampling site.

Paper IV

Fish were collected with Nordic gill nets (Appelberg 2000) in Himmerfjärden (30 stations) and in Näslandsfjärden and Hallsfjärden (six stations each, Fig. 1). Fishing took place annually in late August–early September during the years 2008–2011 in Himmerfjärden and 2000–2010 at the other sites. Each fish were weighed and photographed at site, and total length measured from the photographs to calculate body condition. Isotope analyses were conducted for samples collected in Himmerfjärden in 2011. Samples from muscle and dorsal fin were collected from eight 1+ perch (*Perca fluviatilis*) from ten stations evenly distributed along the shoreline (Fig. 1). Samples were analyzed at UC Davis Stable Isotope Facility, University of California, Davis, for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope composition.

Summary of papers

Paper I

Much of our understanding of ecology, both at species level and food web level, stems from studies of diets based on stomach content analysis. Studies of fish's consumption indicate predator-prey interactions and are important to understand the effects of fish on the structure and function of aquatic food webs. Diet analysis is a series of choices about sample type, sampling regime, identification and treatment of prey remains and quantification of prey importance, each step with several possible method options. Concerning calculation of prey importance, numerous methods have been developed (Pierce and Boyle 1991, Hyslop 1980, Hynes 1950) and the usefulness of various methods is debated (e.g. Hynes 1950, Hyslop 1980, Cortés 1997, Hansson 1998). Hence, we evaluated how well 27 diet analysis methods described the energetic gain of fish by using individual based modelling to compare diet compositions derived with these methods with the "true" long term diet of the fish, something that is difficult to obtain from naturally feeding fish. We chose to express true diets in terms of energetic/nutritional composition, as this is a common objective in diet analysis and also basic input data in e.g. quantitative food web analyses and frequently used in models such as Ecosim/Ecopath (Walters *et al.* 1997). The basic diet methods are based on numbers, biomasses/volumes and frequency of occurrence of prey, but composite diet indices, integrating data from two or more methods have been developed to compensate for assumed biases associated with the basic methods (e.g. Cortés 1997, Christensen 1978). The effects of fish characteristics, prey characteristics, sampling regime and treatment of prey remains on method output were investigated.

We found that prey preference, prey size and evacuation rates were important factors influencing the performance (i.e. similarity with true diet) of the diet analysis methods. The frequency of occurrence, dominance method, numeric method, mass method, and points method performed on average better than the composite indices, %Index of Relative Importance and Comparative Feeding Index. The frequency of occurrence, dominance method and numeric method described the true diet surprisingly well, despite

the true diet being expressed in mass. However, frequency of occurrence and numeric methods shifted in performance in relation to the other methods, producing results most similar or least similar to the true diet depending on fish type. The mass methods and points methods produced on average diet compositions most similar to the true diet and were most robust, producing diet estimates similar to the true diet both across different fish types and across samples of the same fish type, indicating that mass based methods should be used for diet analyses of energy/nutrition.

Paper II

In Sweden, YOY pikeperch are often stocked to natural waters in the late summer or autumn to strengthen natural populations, Himmerfjärden being one such area. This study came about as behavioural differences were observed between fish from different breeders when fish were stocked for the biomanipulation project. The question arose about how rearing environment was affecting pikeperch behaviour, and hence their chances of survival after stocking. In order to survive the stocked pikeperch have to be able to avoid predators as well as act as such in the new environment.

Fish in artificial rearing environments often lack ontogenetic experiences required for proper behavioural development (Kelly *et al.* 2005), likely affecting their survival after stocking to natural waters. Behaviours such as explorative behaviour, foraging behaviour and predator avoidance are strongly influenced by the physical and social properties of the rearing environment (Magnhagen *et al.* 2008). Reared fish can be trained prior to release, to improve such behaviour, but results from training are equivocal (e.g. Berejikian 1996, Maynard *et al.* 1996). Instead, the rearing environment can be designed to facilitate the development of adequate behaviours. Increased environmental complexity has been proved to positively influence behavioural plasticity and learning in fish (e.g. Braithwaite and Salvanes 2005, Strand *et al.* 2010), increasing chances of survival after stocking.

Prior to this study, no studies have been presented on how pikeperch is influenced by differences in rearing conditions even though it is a commonly stocked fish. We compared several important behaviours likely to affect survival directly after stocking among YOY pikeperch that had been reared in one indoor facility and two different semi-natural ponds. These behaviours were exploration of a new environment, feeding on a novel live prey and responses to a predator. We found clear behavioural differences between the rearing environments. Whilst there were no significant differences between pond and tank reared fish in reluctance to enter a new environment, pond reared fish exhibited clearer exploration behaviour and

spent significantly more time in macro-vegetation after entrance to the new environment. Pond reared fish were significantly faster to start foraging on a live prey (*Neomysis integer*) that they had not encountered before. Pond reared fish were also significantly more active in their anti-predator response than tank reared fish. The tank reared fish had a very passive and uniform behaviour compared to the pond reared fish in all tests, suggesting that the tank fish are less suitable for stocking. In addition to the differing behaviour there were considerable differences in size between the rearing environments, where the tank reared fish were considerably larger. Generally it is considered better to be bigger, but a more refined behaviour may outweigh this advantage. There are many factors differing between the tank and pond environments and it is impossible to distinguish how much each factor affects the behaviour. Nevertheless, the physical and behavioural differences are present at the stocking occasion and may very well impact the success rate when stocking YOY pikeperch to natural waters. The results also challenge the present tendency of replacing the traditional rearing of pikeperch in semi-natural outdoor ponds with more intensive indoor hatchery production.

Paper III

Diel vertical migration is performed by many aquatic species, most commonly descending during day and ascending during night. DVM is influenced by various abiotic and biotic factors such as light, clines, temperature, food availability and predation. Predator evasion is suggested to be the major biotic factor driving zooplankton DVM (e.g. Lampert 1993, Hays 2003), affected by the abundance of zooplanktivorous fish. DVM becomes more pronounced when abundance of zooplanktivorous fish increases (Bollens and Frost 1989, Frost and Bollens 1992), e.g. with the increase of YOY fish in the spring (Ringelberg *et al.* 1991). The reverse, i.e. reduced migration amplitude or ceased migration, has also been observed when predation pressure has been reduced by zooplanktivorous fish removal in biomanipulation (Dini *et al.* 1993). Hence we explored the seasonal changes in DVM of *Acartia* spp. and *Eurytemora affinis* in relation to the seasonal variation in zooplanktivorous fish abundance.

We found trends in depth distribution and DVM behaviour of *Acartia* spp. and *E. affinis*, but no clear correlation with night length, zooplanktivorous fish biomass or phytoplankton abundance. Temperature may have influenced DVM as both species migrated up to the thermocline at night. The lack of response to fish density is surprising and prevents us from using zooplankton DVM as a predation indicator. That the migration amplitude of *Acartia* spp. and *E. affinis* in this study seems unrelated to fish biomass suggests that the

kairomone concentration, used for predator detection (Ringelberg, 2010), always exceeds the level causing maximum migration. The link between DVM and fish biomass has previously been studied by comparing, i.e. absence/presence of fish (Gliwicz, 1986; Horppila, 1997), but in Himmerfjärden there is no period free from fish, possibly making the influence of fish biomass difficult to detect.

However, both species did perform DVM and in addition showed size related differences in DVM within species. Larger and hence more conspicuous individuals generally migrated further than smaller ones, nevertheless indicating a relationship between DVM and predator evasion. With the exception of females, all *E. affinis* copepodite stages performed migrations of over 10 m with a slight increase in DVM range with copepodite stage. Adult female *E. affinis* however remained at depth throughout the diurnal cycle, with only slight upward movement at night. *Acartia spp.* had a weaker DVM than *E. affinis* and resided closer to the surface during day. In *Acartia spp.* DVM amplitude increased with copepodite stage and size more clearly than in *E. affinis*, suggesting an ontogenetic shift in behaviour. As DVM is considered an evasion strategy from visual predators the similar size of the two species would suggest them to have similar DVM, but as this was not the case there are probably several factors affecting DVM behaviour. We suggest it is related to differences in hydrodynamic sensitivity, fecundity and reproductive strategy (sac carrying or broadcast spawning). Our results also clearly show that ontogeny has an important role in governing DVM. The ontogenetic migration differences raises caution against analyzing samples of mixed stages.

Paper IV

Finally, we wanted to investigate how stationary perch are in our study area. Migration of Eurasian perch (*Perca fluviatilis*) is generally limited (e.g. Fry *et al.* 2011). This sedentary behaviour may lead to intra-population differentiation (e.g. Hansson 1985, Bergek and Björklund 2009). It is for example well known that morphological differences exist between perch inhabiting littoral and pelagic habitats respectively (Hjelm *et al.* 2001, Svanbäck and Eklöv 2003), but variation within the same habitat is, on the other hand, less known. Since the characteristics of the littoral can vary greatly between sites, local variation in physical condition and dietary habits could be expected provided that the fish are reasonably sedentary and that feeding conditions vary spatially. To explore sedentarity of littoral perch we combined measures of stable isotope data (^{13}C and ^{15}N) and fish body condition.

There were significant differences in isotope signatures between sampling stations in Himmerfjärden, particularly in $\delta^{15}\text{N}$, clearly indicating sedentarity, with a significant southward trend in the bay for $\delta^{15}\text{N}$, mirroring the isotopic gradient from the sewage treatment plant. If fish had moved along the stretch of the bay no isotopic differences would have been detected. For $\delta^{13}\text{C}$ there was a significant difference between the eastern and western side of the bay. Perch caught on the western side of the bay had significantly higher $\delta^{13}\text{C}$ values than those from the eastern side, indicating a more pelagic diet on the eastern side and fish at eastern shore stations were also leaner, possibly indicating a more pelagic adaptation. These indications of sedentarity and intra-habitat differences in feeding conditions are further strengthened by the significant condition differences found between bay sides and even within bay sides for young fish.

For such differences in condition and isotope signature to arise fish need to be site faithful. Both isotope and condition measurements show that even in areas where no obvious barriers exist, there are sub-groups in the perch population. Prey tend to avoid habitats where they have previously encountered predators (Utne-Palm 2001) and juvenile fish has been shown to change their habitat use in presence of predators from the unprotected pelagic to the littoral, where they could hide in the vegetation (e.g. Brabrand and Faafeng 1993, Romare 2001, Diehl and Eklöv 1995). This can be one explanation to why 1+ perch are sedentary, but our results indicate that also larger, less vulnerable, individuals stay site faithful. Several studies have shown that fish prefer to associate with individuals with the same recent habitat exploitation as this may facilitate spread of social information on prey availability (e.g. Ward *et al.* 2004, Webster *et al.* 2007), possibly also explaining site fidelity. Hence, both environmental and behavioural factors may have led to the differences in body condition and isotopic signature seen in this study.

Concluding remarks

Predation is undoubtedly an important force in nature. Interactions between predators and prey are complex phenomena affected by both physiological and environmental characteristics as well as behavioural traits. The results in this thesis suggest that different species and even different life stages pursue different strategies in finding prey and avoiding predation. Perch show a sedentary behaviour possibly governed by foraging and anti-predation advantages, while zooplankton migrate to avoid predation with clear within species differences in DVM depending on ontogenetic stage. Ontogenetic differences are also partly evident in perch, as the sedentarity seems more widespread in younger fish. We can also see that different behavioural strategies develop depending on ontogenetic experiences, as evident from the YOY pikeperch. The tank reared fish clearly developed a more passive behaviour and seemed more indifferent to what happen around them compared to the pond reared fish indicating that pond reared fish would be better equipped as both predator and prey in the wild. For us to be able to study these predator-prey interactions it is important to critically evaluate the methods we use to measure this.

Sammanfattning

Denna avhandling är skriven inom ramen för ett biomanipulationsprojektet där årsungar av gös (*Sander lucioperca*) satts ut i en Östersjövik för att förbättra vattenkvaliteten genom en så kallad trofisk kaskad. Studierna i min doktorandutbildning har dock fokuserats på en bredare ekologisk fråga, nämligen predation (den viktigaste drivkraften i en biomanipulation). Därför består denna avhandling av fyra artiklar där vi studerar samspelet mellan rovdjur och bytesdjur med hjälp av fisk och djurplankton och hur dessa interaktioner kan mätas.

I *studie I* använde vi individuell modellering för att utvärderade hur väl olika dietanalysmetoder presterade ur ett näringsmässigt perspektiv och fann att massabaserade metoder beskrev dieten bäst. *Studie II* undersökte hur juvenila utsättningsgösars explorativa, foragerings- och antipredatorbeteende påverkades av deras uppfödningssmiljö (damm- contra tankuppfödning). Den mer komplexa och varierade miljön i de semi-naturliga dammarna verkade främja ett mer flexibelt och aktivt beteende hos fisken och rusta dem bättre för överlevnad i det vilda. För *studie III* studerades hur diel vertikal migration i de sex tillväxtstadierna hos djurplanktonarterna *Acartia* spp. och *Eurytemora affinis* beror av fiskbiomassa, växtplanktonförekomst och temperatur. Båda arterna migrerade och visade dessutom ökat migrationsspann med ökad kroppsstorlek inom art, vilket tyder på undvikande av visuellt jagande predatorer. Den sista studien, *studie IV*, kvantifierade migration hos littoral abborre (*Perca fluviatilis*) via stabila isotoper (^{13}C och ^{15}N) och kondition. Vi fann tydliga indikationer på att abborren är platstrogen och att dietskillnader inom habitatet förekommer. Interaktionerna mellan predator och bytesdjur är komplexa och påverkas av både fysiologiska och miljömässiga egenskaper samt beteendemönster, där olika arter och till och med olika livsstadier använder olika strategier för att överleva.

Acknowledgment

So here I am, already at the end of my PhD studies. It's quite a surreal feeling. It all went by so fast, even though some projects really seemed never ending...

But I wouldn't be here if it wasn't for all the great people around me. First of all I would like to thank my supervisor Sture Hansson for taking me in and for your everlasting enthusiasm and patients. You have been a great tutor, always having your students' best interest at hand, and a reliable co-author. Thanks Olle Hjerne for being a supportive and encouraging co-supervisor and co-author. I am also grateful to Börje "MacGyver" Larsson for making field equipment from nothing and taking care of us no matter the hour, Per-Erik Erlandsson and Bertil Svangren for assistance and supply of field equipment and to all fishing right owners. Thanks to Lina Enhus, Callis Amid, Maria Jalmlöv, Karl-Magnus Johansson, Katja Landeström, Oliver Karlöf and Caroline Ek for helping out with sampling. Data on fish from Hallsfjärden and Näslandsfjärden were provided by the consultancy company Akvatisk Miljöforskning AB. I would also like to thank Aquaria Vattenmuseum for great help and service during the pikeperch study and to all the pikeperch breeders.

I also feel a tremendous gratitude towards the wonderful friends I have gained. Thank you for being there, for lighting up the workday, for all the friendly words, the laughs and the encouragements. Thank you for being an inspiration and for putting things into perspective. Thank you for all the coffee breaks, lunches, evenings out, conference journeys and generally great moments. You will always be in my heart! But there is one person I owe more to than anyone else for being here today. Pelle, I can not even explain how much you have meant to me during these years. Sture may have taken me in, but you made me stay when things were tough. I could never have done this without you!

Finally I want to acknowledge my beloved family. Thank you Björn, mum and dad for your endless love and support and occasional rescue operations! You make me stand strong! I love you!

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