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# The influence of trophic polymorphisms on habitat coupling in aquatic food webs

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### **Abstract**

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Trophic cascades, together with other indirect interactions are important aspects in shaping the composition and abundance of species in the food web. Theoretically, movement of energy between systems, and coupling between habitats by mobile predators have been suggested as being important for food web stability and evenness. Individual diet specialisations have been shown to be widespread in many animal taxa. Although not widely studied, some studies have indicated that mobile predators that display individual specialisations, may have a reduced ability to couple habitats.

In this thesis, by using field studies and an experimental study, my aim was to assess the individual specialisation displayed by Eurasian perch (*Perca fluviatilis*) and its influence on the ability of the perch to couple habitats. In the experiment, we also investigated the effect of habitat coupling, or the lack of habitat coupling, on the dynamics and stability of the resources in the ecosystem.

We show that habitat diversity and resource availability influenced perch individual specialisation and morphological variation. We found that the perch total niche width decreased with decreasing habitat switching ability. We demonstrate asymmetrical habitat coupling ability in perch across pelagic and littoral habitats, providing evidence that not all individuals within a species respond in the same way when it comes to spatial coupling and thereby providing stability within a food web.

Our results expand on previous work and suggest that habitat coupling ability can influence individual specialisations and niche width. Furthermore, we show the importance of individual specialisations in relation to habitat coupling. Finally, we provide evidence for the theory that a food web dominated by a food specialist should exhibit more variable resource dynamics than a food web dominated by a generalist predator by showing a greater indirect effect of predation on the phytoplankton levels when no habitat coupling occurs. While many models and theoretical concepts have proposed a stabilising effect of cross movement of energy and mobile predators, little empirical evidence exists that confirms this mechanism.

In conclusion, my thesis gives some support for the theoretical predictions that habitats coupled by a generalist predator should be more stable.

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"It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth..."

Charles Darwin - On the Origin of Species



# List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

- I Marklund, MHK., Svanbäck, R., Zha, Y., Scharnweber., Eklöv, P. The influence of habitat accessibility on the dietary and morphological specialisation of an aquatic top predator. *Manuscript in revision*
- II Marklund, MHK., Svanbäck, R., Eklöv, P. Habitat coupling mediates trophic cascades in an aquatic community. *Manuscript*.
- III Scharnweber, K., Strandberg, U., Marklund, MHK., and Eklöv, P. (2016). Combining resource use assessment techniques reveals trade-offs in trophic specialization of polymorphic perch. *Ecosphere* 7(8):e01387. 10.1002/ecs2.1387
- IV Marklund, MHK., Svanbäck, R., Faulks, L., Breed, M., Scharnweber., Zha, Y., Eklöv, P. Asymmetrical habitat coupling of a top predator. *Manuscript*

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# Glossary

Bottom-up control	Control of food web from the bottom up; i.e. from the primary producers to the top predators where the herbivores are limited by the production of food
Habitat coupling	Feeding on resources from multiple habitats
Indirect effects	An effect of one species on another that occurs through links with a third species in a food web (e.g. trophic cascades)
Omnivory	Feeding on multiple trophic levels and multiple resources
Stability	How variable dynamics are in an ecosystem. Higher variability is less stable, lower variability is more stable
Top-down control	Control of food webs from the top down; i.e. from the predator to the producers where the herbivores are limited by predation
Trophic cascade	The change in density or biomass in the same direction of a species/group as that of a species/group an even number of trophic levels above
Trophic level	Position of an organism in the food web



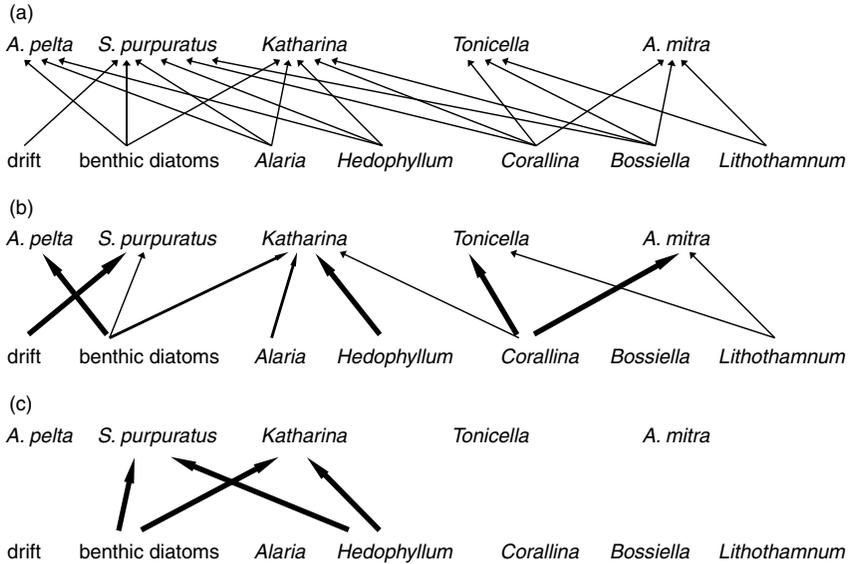
# Introduction

## Food webs

Every species interacts with other species around it, such as prey or predator organisms. The description of these interactions and the network are commonly referred to as a food web or, as Charles Darwin called it in *The Origin of Species*, the “entangled bank”. Generally, food web describes the feeding relationships among species, and tells us about the structure by describing the complexity and how many trophic levels there are in the food web. Diagrams of a food web can help us understand and describe feeding links (i.e. topological web), the movement of energy from one species to another in the food web (i.e. energy flow webs), and the linkages that regulate the trophic structure (i.e. functional web) (Figure 1) (Paine 1980). This information is important for our understanding of the dynamic, persistence and the stability of food webs (Moore and de Ruiter 2012) as well as the understanding of interactions over larger spatial scales (i.e. over habitat and landscape scale).

Elton (1927) was the first to describe the shape of a food web using his pyramid of numbers, with fewer individuals at the top of the food web compared to the bottom. Another fundamental conclusion that Elton came to was that food chains are short and usually have four or five trophic levels. Elton and Lindeman (1942) held the view that the structure, control of resources, and production of food webs were regulated from the bottom up - from the primary producers to the top predators. Lindeman hypothesised that the shorter food chain length was due to there being only about 5-15% of energy transferred between trophic levels at each step in the food web because of usage by individual organisms and inefficient energy transformation.

The alternative view is that food webs can be regulated from the top down, where herbivores are rarely limited by food but rather by predators - predation regulates the levels below (Hairston et al. 1960). The top-down hypothesis was developed by Hairston in the 1960s (Hairston et al. 1960) and later termed the ‘green world hypothesis’. Fretwell (1977) extended the ideas of Hairston et al (1960) by looking at food chain length, primary productivity and ecological efficiency in different ecosystems. Fretwell (1977) stated that ‘not all worlds are green’, arguing that predation effects will vary depending on the production of the ecosystem. He further suggested that in odd-linked food webs, plants will be food limited, and in even-linked food webs, plants will be grazer limited.



*Figure 1.* Examples of the 3 different approaches for depicting trophic relationships in a food web: (a) Topological food web describing feeding relationships between organisms, (b) Energy flow web describing the transfers of energy or matter between species (the thickness of the arrows indicates the rate of flow: thicker line = greater flow; thinner line = lesser flow), and (c) Functional web describing the strength of interactions among species (From Paine 1982).

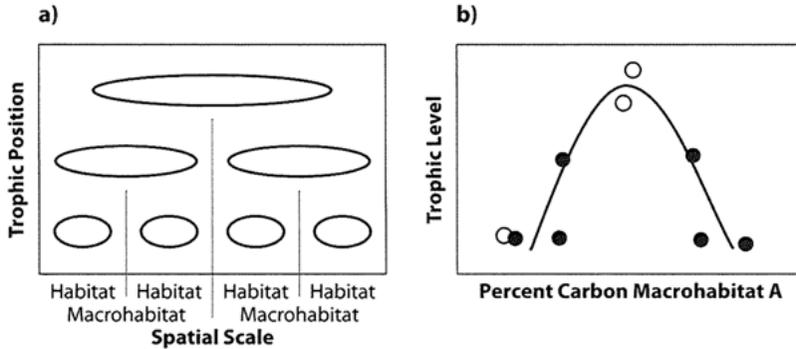
Trophic cascades often occur when a predator in a food web suppresses their prey, thereby releasing the next trophic level down from predation (Carpenter et al. 1985, Pace et al. 1999, Polis et al. 2000, Borer et al. 2005), which in turn changes the biomass or abundance in every non-adjacent level in the food chain (Persson 1999). For example, planktivorous fish can induce a trophic cascade by feeding on zooplankton and consequently indirectly elevating levels of phytoplankton and other smaller bodied zooplankton (McQueen et al. 1989). Trophic cascades, together with keystone predation, apparent competition and apparent predation, constitute one of several other possible indirect interactions that can alter the abundance of species (Menge 1995).

## Body size, habitat coupling and scale

Body size tends to increase with trophic position (Elton 1927, Woodward et al. 2005, Arim et al. 2010). It is proposed that body size is one of the most important traits that differentiate individuals in a community (Woodward et al. 2005). Larger organisms tend to be more mobile and, therefore, their ability to move and forage over larger spatial scales is higher compared to

smaller organisms (McCann et al. 2005, Arim et al. 2010). Subsequently, smaller organisms tend to be more isolated. As a result, these larger mobile predators could potentially link spatially separate habitats (for example littoral and pelagic habitats) (Figure 2a). That is, the organisms low in the food web hierarchy would utilise one set of carbon (e.g. zooplankton would utilise resources mainly from the pelagic, and benthic macroinvertebrates would utilise resources mainly from the littoral habitat), while further up the food web organisms use carbon from a wider range of diet sources. Consequently, the further up the trophic food chain an organism is, the higher its mobility and the more habitats it will be able to cover (McCann et al. 2005) (Figure 2b). Consumers can thereby couple habitats at different scales, from microhabitats to macrohabitats to landscape scales, which are coupled by larger and larger consumers (McCann 2012). For example zooplankton might couple the dissolved organic carbon and the phytoplankton pathway within the pelagic subwebs (Sherr and Sherr 1991). But when looking at the whole lake ecosystem separate littoral and pelagic subwebs in a lake might be coupled by fish (Vadeboncoeur et al. 2002, Zanden and Vadeboncoeur 2002). Finally, there are larger mobile consumers such as birds and mammals that are able to couple over larger landscape scales, for example between terrestrial and aquatic environments (Hebert et al. 2008).

Ecological models have shown that these larger mobile consumers should have a stabilising effect on food webs. This stabilising effect is created by individual predators foraging over a larger range than their prey, thereby linking the ranges of several individual prey items. When one of the ecosystems is perturbed, populations in the other ecosystem can respond and allow for recovery in the prey population of the first ecosystem (Rooney et al. 2006). For this stability of the ecosystem to occur, the maintenance of distinct and separate food chains with their differing production and turnover rates is vitally important (Rooney et al. 2006). But there must also be a quick response from the predator to any fluctuations in the prey populations (McCann et al. 2005, McCann 2012). Predators that switch between prey populations should therefore dampen oscillations and fluctuations at lower trophic levels and stabilise ecosystems (McCann et al. 2005).



*Figure 2.* Figure of a hierarchical food web and the end point of carbon originating from distinct habitats. Organisms low in the food web are isolated compared to the organisms higher up the food web that couple both habitats, having carbon originating from both habitats. (a) Depiction of the spatial scales the organism covers and the trophic position it occupies. (b) Description of the pathway of the carbon for the average consumer at a given trophic level. Dots represent species and the line represents the average trend across all species in the food web (McCann 2012).

## Niche space and morphological adaptations

Since Van Valen (1965) proposed the niche variation hypothesis, ecologists have recognised that individuals can substantially differ in resource use. The degree of individual specialisation, where individuals use a small subset of the population's resource base, has been shown to be widespread in many vertebrate and invertebrate taxa (Roughgarden 1974, Svanbäck and Eklöv 2002, Bolnick et al. 2003, Svanbäck and Eklöv 2003, Araújo et al. 2009, Newsome et al. 2015, Snowberg et al. 2015). The specialisation usually depends on an individual's preference for resources, intra- and interspecific competition, efficiency related to morphology and/or behavioural and physiological ability to use the resources in question (Van Valen 1965, Bolnick et al. 2003, Svanbäck and Bolnick 2007, Bolnick et al. 2010, Araújo et al. 2011).

Trophic polymorphism has been found to be especially common in fish (Smith and Skúlason 1996). There are examples of different morphs of several fish species such as arctic charr (Snorrason et al. 1994, Jonsson and Jonsson 2001), sticklebacks (Schluter and McPhail 1992) and sunfish (Ehlinger and Wilson 1988), exhibiting multiple morphs, often one categorised as littoral and one pelagic, with differing feeding patterns. Usually foraging in structurally complex habitats such as in the littoral zone with vegetation is thought to require a high manoeuvrability assisted by having a deeper body morph (Ehlinger and Wilson 1988, Smith and Skúlason 1996). Foraging in the open pelagic zone is instead associated with feeding on more

spatially dispersed prey where long distance swimming is required and therefore a more fusiform body shape is favourable (Ehlinger and Wilson 1988). These morphological adaptations to the habitat improves the feeding efficiency of the individuals, and there are studies showing that fish with intermediate morphologies have lower growth rates than the specialised morphotypes (Robinson et al. 1996, Svanbäck and Eklöv 2003). Therefore, the benefits of specialisations may be a net increase in energy and/or reproductive success, both of which would lead to variation in individual fitness within populations (Bolnick et al. 2003).

Some studies have demonstrated that this local morphological specialisation, which can lead to high intraspecific niche partitioning, can also influence the way fish couple habitats. High niche partitioning can lead to a reduced ability of the mobile predators to effectively switch between differing habitats (Quevedo et al. 2009, Knudsen et al. 2010). This reduced ability to switch between habitats suggests that there may be a cost imposed on specialised phenotypes shifting between habitats that can influence the movement of energy and nutrients across spatially separated food webs. So far, there is little empirical evidence demonstrating how coupling of habitats, or the lack of it, influences diet specialisations and the stability in food webs.

# Aims of the Thesis

The overall aim of this thesis is to study how individual specialisations and morphological variation interact with predator mobility to influence community dynamics. More specifically, the thesis chapters focus on:

- How individual and morphological specialisations in a top-predator are influenced by habitat availability and the ability to couple habitats (**Paper I**).
- How a predator's ability to couple habitats influences the dynamics and stability of the primary producers and prey (**Paper II**).
- Understanding individual diet and morphological specialisations obtained by combining multiple resource use methods (**Paper III**).
- The extent to which perch couple littoral and pelagic habitats, and how the ability to couple habitats is related to individual and morphological specialisations and genetic variation in a natural environment (**Paper IV**).

# Methods

Eurasian perch (*Perca fluviatilis*) was used as the model organism. The Eurasian perch (hereafter perch) is a common, omnivorous top predator in aquatic ecosystems in Sweden. As larvae, perch feed on zooplankton in the pelagic zone. With increased body size they also start to feed on macroinvertebrates (Persson 1988, Byström et al. 2003) and later, they become piscivorous (Persson 1988). Perch have known resource polymorphisms, where littoral individuals feed more on littoral resources (benthic macroinvertebrates) and have a deeper body shape, whereas individuals in the pelagic habitat feed more on pelagic resources (zooplankton) and have a more streamlined body shape (Svanbäck and Eklöv 2003, Olsson and Eklöv 2005, Eklöv and Svanbäck 2006).

## Design of pond experiments

An experimental approach was used to explore the influence of habitat switching and habitat availability on the dietary and morphological specialisation of perch (**Paper I**), and the resulting effects on the dynamics in the food web (**Paper II**).

Ponds with natural sediment were used, allowing for a semi-natural setting, with resource populations originating from the sediment and the lake water in the ponds. The access of perch to different habitats was manipulated to determine niche use and specialisations depending on habitat availability. Before the start of the experiment, the ponds were emptied of water and the vegetation was removed. Each pond was divided into the same number of experimental enclosures (ca. 4.5 x 6 m) using nets (mesh size 4 mm). Each enclosure contained a pelagic and benthic habitat of equal area and each pond contained all the four different treatments. The pelagic environment was created by covering the substrate with plastic, restricting resource acquisition to the open water. The other half of the pond consisted of the benthic habitat, where the fish had full access to benthic resources. The treatments were as follows:

- (1) Open (no net between habitats) – the perch could move freely between pelagic and benthic habitats

- (2) Switched (net between habitats) – perch were manually moved between the two habitats giving them access to alternating pelagic and benthic habitats every 2 weeks (half of the population was moved from the benthic habitat to the pelagic habitat and the other half was moved from the pelagic habitat to the benthic habitat)
- (3) Closed (net between habitats) – half of the population only had access to the pelagic habitat, whereas the other half only had access to the benthic habitat during the whole experimental period
- (4) Control – no perch in the treatment.

The experiment was run for 8 weeks. At the end of the experiment perch were removed from the enclosures, killed using an overdose of phenoxy-ethanol, frozen and taken to the laboratory for later analysis. Chlorophyll *a* (as a proxy for phytoplankton biomass), zooplankton and macroinvertebrates were sampled at the start of the experiment, thereafter every 2 weeks, and at week 8 at the termination of the experiment.

Phytoplankton biomass, was determined by filtering 500 ml of water from each enclosure which was then frozen until further processing in the laboratory. Chlorophyll *a* was later extracted from the filters using standard methods with ethanol extraction and measured spectrophotometrically at 665 and 750 nm.

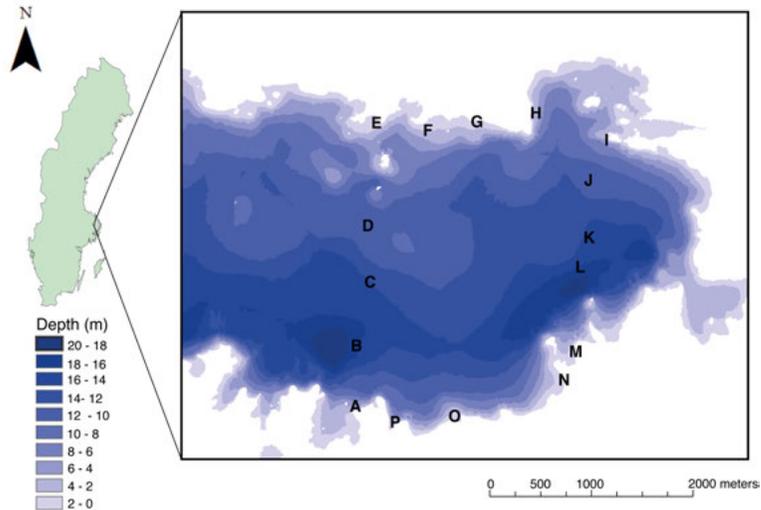
Zooplankton was sampled using a 100  $\mu\text{m}$  mesh net which was pulled horizontally through approximately 2 metres of water in each enclosure. Samples were immediately preserved with lugol solution. Later in the laboratory, the zooplankton were identified, counted and measured using an inverted microscope.

Macroinvertebrates were sampled with a Willner core sampler (core diameter 65 mm). Four samples were taken from each enclosure on the benthic side where the sediment surface was exposed to assess spatial variability. Samples were sieved using a mesh size of 0.5 mm, preserved in 70% ethanol and stained with bengal rose. In the laboratory, the macroinvertebrates were subsequently counted and identified.

## Field studies

**Papers III** and **IV** describe field-based studies investigating niche space, morphological variation and habitat coupling in natural systems. Gill nets of standard survey-link type (littoral nets 30 x 1.5 m and pelagic nets 27.5 x 6 m) were used to catch the fish which were subsequently investigated to determine the dietary and morphological specialisations by combining several resource use techniques (**Paper III**). In **Paper IV** the relationship between individual specialisations, morphological and genetic variation on the ability to couple habitats was investigated. For **Paper III**, three clear water lakes

were sampled in littoral and pelagic habitats. For **Paper IV**, one large clear water lake was sampled at 16 sites (Figure 3) in both littoral and pelagic habitats. The nets were set in the evening and retrieved in the morning. Fish were removed from the nets and stored on ice until further processing.



*Figure 3.* Map of Lake Erken, Sweden, and location of sampling sites for **Paper IV**. Littoral north sites = E, F, G, H, I, littoral south sites = A, M, N, O, P, pelagic west sites = B, C, D, pelagic east sites = J, K, L. © Lantmäteriet Gävle (2012). Permission i2012/921

## Niche space and morphology

### Resource usage

Resource utilisation of perch was estimated in three ways; using stomach content analysis (**Papers I, III, IV**), stable isotope analysis of muscle tissue (**Papers III, IV**), and fatty acid analysis (**Paper III**).

Analysis of stomach contents gives a detailed picture of resource use immediately before sampling. By contrast, stable isotope analysis is a more indirect measure of the diet of a consumer where the food of the consumer is ingested, broken down and assimilated into its tissue. Therefore, stable isotope analysis provides a better estimate of the resource usage of the consumer over a longer period of time (e.g. months, rather than days for the stomach content analysis). Fatty acids include lipids in cell membranes and are important for many physiological processes (Brett and Müller-Navarra 1997, Parrish 2009). Many fatty acids cannot be synthesised by consumers and are therefore a direct signature of prey (Tocher 2003, Iverson 2009). Fatty acids can also provide information about the functional importance of specific

dietary items and the quality of resources. Fatty acid analysis can also be a useful tool for specifying resource use since some primary producers have characteristic fatty acid compositions, which will be reflected in the tissue of the consumer (Dalsgaard et al. 2003, Kelly and Scheibling 2011).

For the stomach content analysis, prey items were quantified using a dissecting microscope. The length of the first 10 randomly selected prey of each diet category was measured to the nearest 0.1 mm. The average length was then converted to biomass (mg dry weight) using length/weight regressions. For **Papers I, III and IV** various diet indices were calculated to determine the niche space and individual diet specialisation. For **Paper III**  $PS_i$  was utilised and for **Papers I and IV**,  $IS$ ,  $BIC$ ,  $TNW$  and  $WIC/TNW$  indices were used (Schoener 1968, Roughgarden 1972, Roughgarden 1974, Bolnick et al. 2002).  $PS_i$  measures the diet overlap between individual  $i$  and the population as:

$$PS_i = 1 - 0.5 \sum_j |p_{ij} - q_j|$$

Where  $p_{ij}$  is the frequency of the diet category  $j$  in the individual  $i$ 's diet,  $q_j$  is the average frequency of the diet category  $j$  in the entire population. For individuals that consume resources in proportion to the population as a whole,  $PS_i$  will equal 1.  $PS_i$  was used to calculate the level of individual specialisation ( $IS$ ) in the population as a whole and is expressed by the average  $PS_i$  :

$$IS = \frac{\sum_i (PS_i)}{N}$$

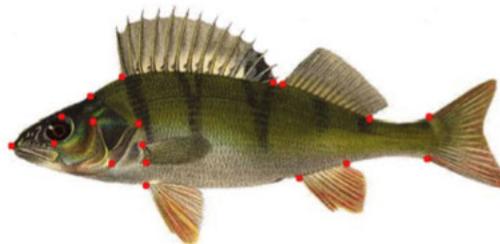
$WIC/TNW$ , is a measure of the relative degree of individual specialisation in the population (Roughgarden 1972, Roughgarden 1974, Bolnick et al. 2002). This ratio is based on the total niche width of a population ( $TNW$ ) which is composed of a within, and between individual component ( $TNW = WIC + BIC$ ). The  $WIC$  (Within Individual Component) is the diet variation found within individuals, whereas  $BIC$  (Between Individual Component) is the variation in resource use between individuals.  $PS_i$ ,  $IS$  and  $WIC/TNW$  range from 1, when all individuals use the full range of the population's niche, to 0 when each individual only uses a single prey type (Roughgarden 1972, Roughgarden 1974, Bolnick et al. 2002).

In the stable isotope analyses (**Papers III, IV**), the isotopes  $\delta^{13}C$  and  $\delta^{15}N$  were used to evaluate the resource usage and niche width in perch. Carbon isotopes vary substantially between different primary producers with dissimilar energetic pathways. Consequently,  $^{13}C$  can be used to determine the source of the carbon for a specific individual or group (Layman et al. 2012).

Carbon signals in lakes generally have more negative  $\delta^{13}\text{C}$  values in pelagic species and more positive  $\delta^{13}\text{C}$  values in littoral species (France 1995). However, the nitrogen isotope  $^{15}\text{N}$  is enriched stepwise with trophic transfer and is therefore a way to estimate the trophic position of the consumer in the community (Post 2002, Layman et al. 2012). The ratio of stable isotopes should vary in accordance with the diet niche, but in cases where the consumer is not feeding on a specific diet (e.g. if the consumer feeds on both plants and animals), the stable isotopes will not reflect the composition of the diet but rather an average of the diet eaten by the individual over time (Layman et al. 2012).

## Morphological assessment

Landmark-based thin-plate spline analysis of perch morphology was used to characterise shape variation. The left side of each perch was photographed using a bright background under constant light conditions. Using TPS-dig2 a number of landmarks were digitised from the photographs, which captured the x and y coordinates of the landmarks (Rohlf 2015b)(Figure 4). For **Papers I, III and IV** tpsRelw (Rohlf 2015a) was used to calculate relative warp scores from the digitised landmarks. The relative warp scores were then used to calculate Euclidean distances (ED) in morphological space of each perch individual (**Papers I, IV**). ED is a distance metric between two points, which here represents the variation in morphological shape between individual perch and the average shape of perch within the population. Relative warp scores were used to visualise body form changes of perch in **Papers I, III and IV** using MorphoJ (Klingenberg 2011). Canonical Variate Analysis (CVA) and Discriminant Function Analysis (DFA) were run to assess significance (Mahalanobis distances) of shape differences between treatments (**Paper I**), between littoral and pelagic perch for each lake (**Paper III**), and between habitats and regions in the single lake (**Paper IV**).



*Figure 4.* The position of the 18 landmarks used for analysing perch morphology in **Paper I** and **IV**.

## Genetic analyses

Population differentiation over smaller spatial scales than the dispersal ability of the fish has previously been found in several studies (Smith and Skúlason 1996, Gerlach et al. 2001, Behrmann-Godel et al. 2006, Bergek and Björklund 2007). This could have consequences for the habitat coupling ability of predators. For **Paper IV** we were interested in investigating if constraints in habitat coupling were related to individual specialisation, morphological or genetic variation. Genetic variation using previously developed primers from nine microsatellite loci was determined (Borer et al. 1999, Wirth et al. 1999, Leclerc et al. 2000). Fin clip DNA was extracted using a modified salting out method (Paxton et al. 1996) and type-it Microsatellite PCR Kits were used for PCRs (QIAGEN, California, USA). PCR products were then screened on an ABI3730XL and scored with GeneMarker v 2.40 (Hulce et al. 2011). Peaks were binned automatically and manually checked. Genotyping errors due to allelic dropout and null alleles were screened using MICRO-CHECKER v 2.2.3 (Van Oosterhout et al. 2004). Linkage disequilibrium and deviations from Hardy-Weinberg's equilibrium were assessed in GENEPOP (<http://genepop.curtin.edu.au>) (Raymond and Rousset 1995, Rousset 2008), using sequential Bonferroni correction for multiple testing where appropriate.

In **Paper IV**, to explore genetic differentiation between sites,  $F_{ST}$  was estimated using GenoDive v 2.0b27 (Meirmans and Van Tienderen 2004). As long-term isolation between sites is not expected, pairwise relatedness ( $r$ ) (Lynch and Ritland (1999) was also calculated using GENALEX v 6.5 (Peakall and Smouse 2006, Peakall and Smouse 2012). Mean relatedness within sites was estimated in GENALEX. To further explore whether habitats were reducing gene flow, the distributions of relatedness between pairs of individuals within (i.e. pelagic-pelagic; littoral-littoral) and between habitats (i.e. pelagic-littoral) were visually compared. If habitats were a barrier to gene flow, a higher proportion of related individuals would be expected within habitats compared to between.

## Statistical analyses

Several different statistical approaches were used to analyse the data. **Papers I, II and IV** were studies with nested factors. In the pond experiments (**Papers I, II**) treatments were nested in ponds, and in the field study (**Paper IV**) stations were nested in region, as such nested analyses were run using the lme4 package in R version 3.2.3 (R Development Core Team 2016). In **Papers I and IV** the RInSp package, version 1.2 (Zaccarelli et al. 2013) in R was used to calculate diet indices. A nested ANOVA was run on the diet

indices to investigate the treatment effect (**Paper I**) and habitat and regions effect (**Paper IV**) on diet specialisation.

In **Papers I** and **IV** PERMANOVA (nonparametric MANOVA) (Clarke and Gorley 2015) and nested ANOVA were used to evaluate dietary and morphological variation. In **Paper II**, PERMANOVA, nonmetric multidimensional scaling (NMDS), and repeated measure ANOVA with nested design were used to evaluate species abundance, size and compositional change over time. In **Paper III**, PERMANOVA and NMDS were used to assess fatty acid composition, and similarity percentage routine (SIMPER), to show which fatty acid contributed the most to the observed differences between the resources and perch in the littoral and pelagic habitats. Also, in **Papers III** and **IV**, stable isotope data were analysed using Bayesian mixing models in the package MixSIAR (Stock and Semmens 2013) in R to determine the proportions of resources used from the littoral or the pelagic habitats of perch.

# Results and Discussion

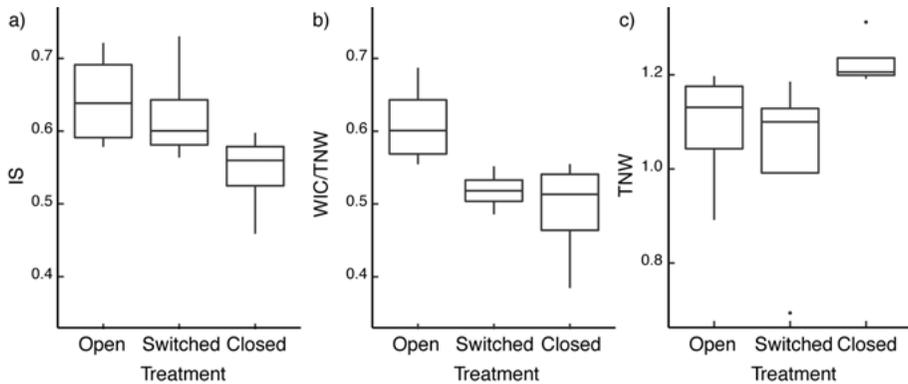
## Habitat coupling, individual specialisations and community stability

Generalist dominated food webs with many weak interactions are considered to be more stable than specialist dominated food webs with a few strong interactions (McCann et al. 1998). In **Paper I**, we showed that individual dietary and morphological specialisations in perch can influence their habitat coupling ability. Furthermore, a high individual diet specialisation for the perch in the closed treatment where the perch could not couple habitats was found (Figure 5a). These results together with the less stable chlorophyll *a* values in **Paper II**, support the theory by McCann et al. (1998) that a food web dominated by a food specialist should exhibit more variable resource dynamics than a food web dominated by a generalist predator.

Ecosystems can be destabilised by removal of energy channels, a reduction in ecosystem heterogeneity, and removal of mobile predators (Rooney et al. 2006). A major prediction of the hypothesis of McCann et al. (2005) is that small fragmented habitats, such as lake or island food webs, should be more prone to destabilising top-down cascades. Instead, a mobile consumer could increase the stability of the overall food web by allowing the predator to utilise and couple desynchronised resources and couple fragmented landscapes (McCann et al. 2005, Rooney et al. 2006, McCann and Rooney 2009). In **Papers I** and **II**, the largest predation influence is shown on the prey resources in the decoupled and fragmented treatment. This provides further evidence for the stabilising potential of a mobile general consumer coupling fragmented habitats (McCann et al. 2005).

Competition is often a strong driving factor for variation in diet and phenotypic traits within populations (Roughgarden 1972, Svanbäck and Persson 2004, Svanbäck et al. 2008). However, no difference in competition between treatments for the perch in the pond experiment was found (**Paper I**). At the same time the total niche width (*TNW*) was not significantly different between the treatments (Figure 5c), indicating that the population's niche width was not influenced by habitat accessibility. Layman et al. (2007) showed that the population niche width decreased with habitat fragmentation because predators were constrained in their ability to choose potential prey items, resulting in a lower chance for specialisation. However, a decreasing individual niche use in relation to the populations' total niche (*WIC/TNW*) from

the open to switched to closed treatments was found to occur (Figure 5b), which indicates a decreased generalisation and decreased habitat coupling with decreased habitat accessibility. Thus, it seems that variation in habitat and resources resulted in individuals becoming either diet generalists or specialists depending on habitat accessibility.



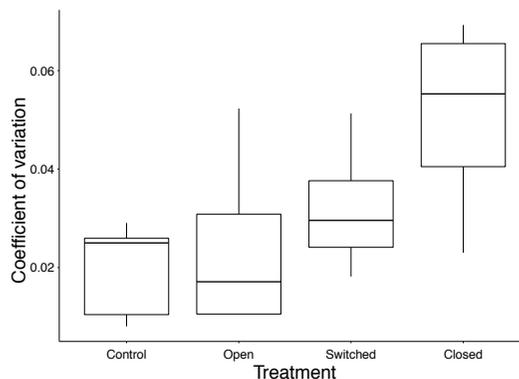
*Figure 5.* Box and whisker plots showing the diet niche width metrics for each treatment in the pond experiment in **Paper I** (a) Individual Specialisation ( $IS$ ) for the population as a whole,  $IS$  ranges from 1, when all individuals are generalists and use the full range of the population's niche, to zero when each individual uses only a single prey type. (b)  $WIC/TNW$ , which quantifies the relative degree of individual specialisation and the population niche width. As  $WIC/TNW$  approaches 1, all individuals in the population utilise the full range of the population niche. (c)  $TNW$ , which quantifies the total niche width of the population.  $TNW$  can be broken down into two components, the variation in resource use within individuals ( $WIC$ ), and the variance between individuals ( $BIC$ ). Dots indicate outliers, i.e. points located further than 1.5 times the interquartile range.

In general, the results from the diet of the perch indicate that individual diet specialisation can be context dependent. Habitat characteristics can influence composition and relative abundance of prey, which can then cause variation in individual specialisation and niche variation (Newsome et al. 2015). In **Paper I**, a strong connection between morphological and dietary specialisations was not found. These results are supported by studies that have shown that morphology is not always a good predictor of diet (Holbrook and Schmitt 1992, Bolnick et al. 2007, Araújo et al. 2009, Snowberg et al. 2015).

Traditionally it is thought that ecological release from competition will lead to a niche expansion, increasing the population's niche width and morphological variability within the population (Van Valen 1965). The absence of connection between morphological variation and dietary specialisations may be due to the absence of a biomechanical trade-off, if one morph is not more beneficial in the habitat, there would be no strong reason for a connection between morphology and diet. Morphological variation was higher in the population that utilised the full population niche space. That is, morpho-

logical variation seemed to be reduced with increased dietary specialisation. While it is generally thought that higher levels of ecological opportunity should favour individual specialisations (Roughgarden 1974), there are studies that show that when ecological opportunity (i.e. spatial heterogeneity) is reduced no diversification in morphology is observed (Rainey and Travisano 1998). This suggests that the increased among-individual morphological variation observed in the open treatment might be influenced by the heterogeneous habitat available in this treatment which is consistent with the character release hypothesis (Bolnick et al. 2010), and also consistent with other studies (Rainey and Travisano 1998, Nosil and Reimchen 2005, Parent and Crespi 2009). We also show that niche variation and the individual specialisation of an active predator is influenced by the opportunity and ability to couple habitats.

Since habitat coupling has been suggested to promote stability in food webs (McCann et al. 2005, Rooney et al. 2006, McCann 2012), we were interested in further investigating the influence of habitat switching by the predator in **Paper I** on the stability of primary producers (i.e. chlorophyll *a* used as a proxy for phytoplankton biomass) and primary consumers (zooplankton and macroinvertebrates) in **Paper II**. In **Paper II**, greater indirect effects from predation on primary producers were found, with stronger top-down control resulting in higher population dynamics of the primary producers when no habitat coupling occurred (Figure 6).



*Figure 6.* Box and whisker plots showing the coefficient of variation of chlorophyll *a* from the pond experiment in **Paper II** which indicates the stability of primary consumers. Top and bottom of the boxes are first and third quartiles, the line median, with whiskers extending to  $\pm 1.5 \times$  interquartile range.

These results are in line with predictions from earlier studies (McCann et al. 2005, Rooney et al. 2006, McCann 2012) and provide empirical support to the theoretical hypothesis that lack of habitat coupling should have a destabilising effect on food webs. Whilst a difference between the treatments in chlorophyll *a* results was seen, the zooplankton and macroinvertebrate re-

sults were not as clear. No significant difference in zooplankton and the macroinvertebrate abundances between the fish treatments (i.e. open, switched and closed treatment) was found. However, a change in the composition of zooplankton between the fish treatments and the control, from a dominance of larger cladocerans (such as Daphniidae) to a dominance of smaller cladocerans (such as *Bosmina* spp. and Chydoridae) in the fish treatments was apparent.

It is currently unclear why a significant difference in effect between closed and control treatments on chlorophyll *a* levels but not on zooplankton and macroinvertebrate abundances took place. There was possibly an effect of predation on the zooplankton community composition that was not detected or measured, such as an increase in abundance of other groups (e.g. rotifers and naupli) with a potential competitive release from the larger cladocerans (Kirk 1991, Pace et al. 1998).

Although a strong predation effect on zooplankton abundance was seen, there was very weak or no effect of predation on the macroinvertebrate abundances. A slight change of abundances over time was seen, which seemed to be due to a slight increase in macroinvertebrate abundances of mainly Ephemeroptera and benthic Diptera. If anything, a decrease in abundance in some groups in the fish treatments such as Ephemeroptera, Ostracoda and Chironomidae would have been expected, since these groups are sensitive to predation and perch are known to heavily feed on these groups (Diehl 1992). As some of the macroinvertebrate groups emerge in the autumn (Diehl 1992), and our experiment ran until early autumn, emergence of macroinvertebrates may have obscured potential treatment effects.

## Niche space and morphological variation

Niche space and morphological variation was analysed in **Papers I, III** and **IV**. For **Paper III** we combined three different resource use approaches to acquire a more detailed description of niche space and trophic specialisations of perch in three different lakes. Stomach contents and stable isotope studies have been extensively used to assess resource use, however fatty acids have not been used to the same extent, but can be useful in providing more information about the quality of the resources assimilated. By using all three of these techniques (fatty acids, stable isotopes and stomach contents), a broader more detailed picture of the trophic divergence displayed in perch was obtained. Stomach contents revealed high variation in resource use between lakes, but only in one of the three lakes was there a significant different resource use within the lake. In the other two lakes, there was a high overlap of resource use between the pelagic and the littoral perch.

Since stomach contents analysis gives a snap-shot in time estimate of resource use, only giving information about the most recently consumed or-

ganisms, it might not accurately reflect the longer term (seasonal) diet of the organism in question. This was evident in one of the lakes studied, where perch had previously been sampled and their stomach contents analysis carried out in a similar fashion. This study (Bartels et al. 2012) showed a much lower percentage of littoral prey consumed for littoral perch than we observed (**Paper III**). While stomach contents gave a detailed picture of the resource use at the time of sampling, stable isotope analysis provided a more detailed picture of the general resource use over a longer time frame.

The fatty acid analyses showed that the composition of fatty acids in the resources consumed by perch varied greatly between pelagic and littoral habitats. Littoral perch had more abundant littoral fatty acids in their tissue, and pelagic perch had more abundant pelagic fatty acids. An exception was one fatty acid (22:6n-3) which is especially important in neural development (Parrish 2009), and is typically abundant in pelagic resources like copepods (Persson and Vrede 2006). This fatty acid showed very similar patterns in both littoral and pelagic perch, despite it being found in low levels in the littoral resources. A possible explanation for this is that littoral perch also feed in pelagic habitats to some extent. Alternatively, perch might be able to convert some other fatty acids to this essential one (Xu and Kestemont 2002, Tocher 2003, Murray et al. 2014), but probably at a metabolic cost. Either way it is possible that there is a requirement for littoral perch to feed to some extent on pelagic resources due to essential fatty acids not being found to the same extent in the littoral habitat.

We generally found perch in littoral habitats were deep bodied and perch in pelagic habitat were more fusiform in shape, which is consistent with previous work (Svanbäck and Eklöv 2002, Quevedo et al. 2009, Bartels et al. 2012). While such general trends were present, we nevertheless found a large variation in morphology within habitats, with one lake exhibiting very low variation in the morphology between the pelagic and the littoral perch. Such a finding provides further evidence that morphology in perch is a highly plastic trait that can be induced and altered depending on factors such as intraspecific and interspecific competition and risk of predation (Svanbäck and Eklöv 2003, Olsson and Eklöv 2005, Eklöv and Svanbäck 2006).

## Individual specialisations influence habitat coupling

In **Paper IV**, we show that perch present asymmetrical habitat coupling. Perch in the littoral habitat were feeding from both the littoral and the pelagic habitats. However, in clear contrast, perch in pelagic habitats were primarily using resources from the pelagic habitat (Figure 7).

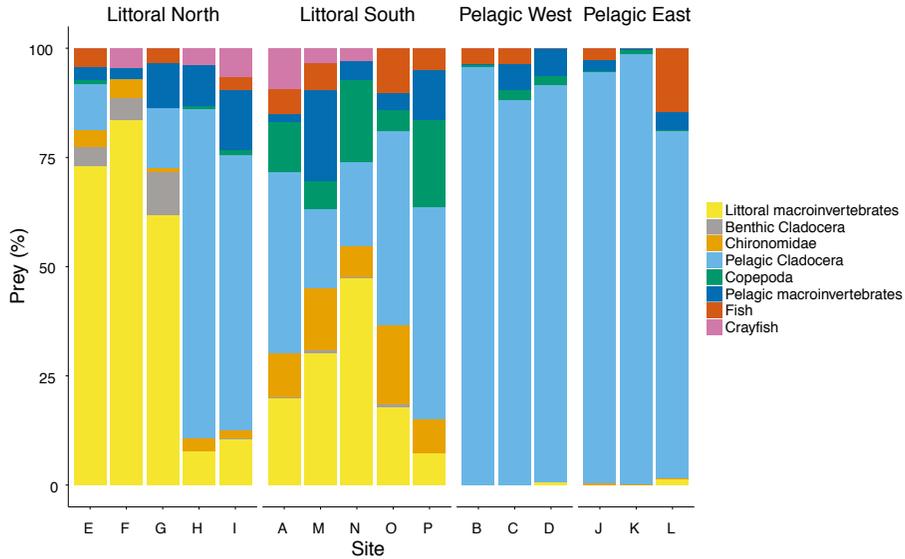


Figure 7. Resource usage of perch at the different sites and regions of lake Erken based on gut content analyses in **Paper IV**. Terrestrial prey was found to have been consumed in one perch in site A (1% of diet) and was excluded.

A generalist predator is expected to be able to couple habitats to a higher degree than a specialist predator (McCann et al. 2005, Rooney et al. 2008, McCann and Rooney 2009). In this study, we show that there were constraints in the ability of some individuals to couple habitats, which has consequences on the ability of predators to stabilise food webs. Asynchronous resource dynamics have been recognised to potentially dampen variation and promote stability (McCann et al. 2005, Rooney et al. 2006). However, most research effort has focused on whether turnover rates of different energy channels can be stabilised by mobile predators, and not the stabilising effects of mobile predators as a result of resource preference.

The littoral perch described in **Paper IV** had the highest individual diet specialisations, but also exhibited the largest niche width. Although this seems counterintuitive, assuming that specialisation equals narrow niche, we show that the littoral perch also had a high between individual component (*BIC*). That is, they strongly divided resources among individuals within the population. A potential explanation for this pattern is that it resulted in a reduced intraspecific competition (Lister 1976, Bolnick et al. 2010, Faulks et al. 2015). Our stable isotope analyses corroborated the gut contents data in **Paper IV**, providing evidence of longer term separation of habitat use and a higher niche width in the littoral habitat. These results also support an earlier theory that suggests that higher resource diversity (ecological opportunity) should favour individual specialisations (Roughgarden 1974). Niche width is often positively correlated with morphological variation (Van Valen 1965,

Roughgarden 1972, Snowberg et al. 2015), and fish show habitat specific morphological adaptations with deeper bodied fish often found in the littoral habitat, and more fusiform fish in the pelagic habitat (Day et al. 1994, Smith and Skúlason 1996). While general support was found for morphological adaptations to the habitat and a larger niche space with higher morphological variation, this was not the case in one of the littoral regions (littoral north). Perch from this region diverged from this pattern and displayed a large niche space but narrow morphological variation. This pattern may have been due to the composition and the accessibility of resources, where the range in habitat heterogeneity and presumably resource diversity in this region was lower compared to the other littoral region. Linking lower habitat heterogeneity to increased individual specialisation and lower morphological variation was also found in **Paper I**. Habitat heterogeneity might counteract intraspecific competition and increase individual niche expansion. Since no correlation between individual diet specialisation and intraspecific density between habitats was found, it is possible that habitat heterogeneity plays a major role in determining individual diet specialisation and morphological variation (**Paper IV**).

A stable environment is predicted to result in the development of different and specialised genotypes eventually leading to polymorphism and speciation (Day 2000, Rueffler et al. 2006). In contrast, in a variable environment phenotypic plasticity is predicted to be favoured in order to be able to adjust and change to changing environmental conditions (Siepielski et al. 2009). In **Paper IV**, we also investigated whether there was a genetic component to the individual diet and morphological variation. However, no evidence was found to support genetic differentiation based on habitat type or morphology. Although fine-scale genetic structure has previously been found between pelagic and littoral perch populations (Bergek and Björklund 2007), the main component of morphological adaptation and variation is believed to be driven by phenotypic plasticity (Olsson and Eklöv 2005, Svanbäck and Eklöv 2006).

While we found no genetic structure in **Paper IV**, individual specialisations were found to influence habitat coupling in unexpected and asymmetrical ways. We provide evidence that the ability of top predators to couple habitats can be dependent on the individual specialisations they express, and that habitat coupling is not always symmetrical within a population. Consequently, the influence of individual specialisations and niche space on the ability of individual predators to couple habitats needs to be considered in future studies.

## Concluding remarks

Overall, this thesis shows that individual specialisation can be influenced by the use of habitat and niche space. This can have implications for food web dynamics by impacting the predators' ability to couple habitats. The main conclusions from this study are as follows:

- Individual specialisation and niche width can impact on the ability of mobile predators to couple habitats (**Papers I, IV**).
- The observed habitat coupling by perch is not always symmetrical across pelagic and littoral habitats, littoral perch could couple littoral and pelagic habitats to a higher degree than pelagic perch (**Paper IV**).
- By using several methods for diet assessment, the resolution of resource use was improved and provided evidence for a broader niche width of littoral perch and an inclusion of pelagic prey for littoral perch (**Paper III**), providing further evidence that top predators might not always couple habitats symmetrically (**Paper IV**).
- By controlling the habitat switching ability of perch, evidence was provided that a habitat not coupled by a mobile predator had a less stable resource dynamics than a coupled habitat (**Paper II**).
- Evidence for the destabilising potential of a specialist predator on the resource dynamics in a fragmented community was also presented (**Paper II**).
- Finally, it is important to consider individual variation since this can influence the ability of the predator to couple spatially separate habitats (**Papers I, III, IV**).

This thesis highlights the importance of considering individual variation within a species. Lower adaptive capacity by some individuals resulting in reduced habitat switching can have implications for community dynamics and stability which, on a broader scale, can have important implications on the food webs. This in turn is important to consider for future management of aquatic communities.

# Sammanfattning på svenska

Varje art påverkar och samspelar med andra arter, antingen som byte eller som rovdjur. Beskrivningen av dessa interaktioner, och nätverket det skapar, kallas näringsväv. Med en näringsväv kan man beskriva hur många arter som finns i ett ekosystem och vilka födorelationerna är, dvs vem som äter vem. Näringsvävar har flera trofiska nivåer där en trofisk nivå beskriver hur högt i näringskedjan organismen befinner sig. Toppredatorer har den högsta trofiska nivån medan producenter som t.ex. alger är längst ner. Ofta beskrivs näringsvävnader genom diagram för en enklare förståelse av de potentiella länkar som kan förekomma. Näringsvävar och de dynamiska processer som förekommer i näringsvävar kan vara väldigt komplexa. För att på ett grundligt sätt kunna studera näringsvävar och populationsdynamik över tid krävs att man samlar in och mäter organismernas förändring i antal och tillväxt relaterat till varandra över en längre tid, helst flera generationer. På grund av den stora insats som skulle krävas har mycket få empiriska tester av populationsdynamik och näringsvävar gjorts. Det är generellt accepterat att bara ca 5-15% av all energi som finns på en trofisk nivå överförs till nästa steg, detta anses vara en av anledningarna till att man generellt i naturen observerar relativt korta födokedjor, bara mellan 4-5 nivåer. Av samma anledning har det föreslagits att näringskedjor har möjlighet att bli längre i produktiva områden med mycket näring.

Reglering av näringsvävar och näringskedjor kan ske uppifrån och ned eller nedifrån och upp. Reglering uppifrån och ned (top-down) är när predatorer högt upp i näringskedjan äter betare (konsumenter) vilka då frigör alger och växter (d.v.s. primärproducenter) från betning vilket gör att de i sin tur ökar. Reglering nedifrån och upp beskriver processer där konsumenterna är begränsade av vad som kan produceras av primärproducenterna. Det vill säga hur mycket växtlighet som kan produceras reglerar hur mycket föda som finns för konsumenterna, som i sin tur reglerar hur många bytesdjur det finns för predatorerna.

Storleken av en organism är viktig eftersom det avgör vad den kan äta, som exempel, en större fisk har ofta en större mun som gör att den då kan äta större byten. En större organism har ofta också kapaciteten att förflytta sig längre sträckor än en mindre organism, på detta sätt kan den äta och använda större rumsliga skalor än mindre organismer. Detta innebär också att de har möjlighet att koppla och länka separata habitat som t.ex. fisk som ibland kopplar strandnära och öppna pelagiska habitat i en sjö. Samma gäller för

fåglar och större däggdjur, där större individer har större kapacitet att koppla över de största spatiala skalorna mellan habitat i vatten och land. Toppredatorers möjlighet att koppla habitat har ansetts vara stabiliserande för födoväven, men hittills har inte många empiriska studier lyckats bekräfta dessa teorier.

Individer inom samma art har visat sig kunna ha distinkta skillnader i resursutnyttjande. Vissa individer använder bara en liten del av det totala nischutrymmet som arten har tillgång till. Orsaken till denna individuella specialisering är ofta konkurrens mellan individer eller individens resurspreferens, men det kan också vara på grund av att vissa individer morfologiskt (kroppsform) anpassar sig till habitatet de lever i. Denna morfologiska specialisering har visat sig vanlig för vissa arter och den kan innebära att individer använder en mycket mindre del av den nisch den har totalt tillgång till, vilket i sin tur skulle kunna innebära en mindre möjlighet för dessa individer att koppla separata habitat.

Det övergripande syftet med denna avhandling var att öka förståelsen av individuell specialisering och morfologiska anpassningar och hur detta kan påverka predatorers (såsom fisk) rörlighet och hur detta i sin tur kan påverka födoväven.

Jag använde mig av abborre (*Perca fluviatilis*), en vanlig fisk i svenska sjöar, som studieorganism. När abborren är ett yngel äter den zooplankton (Djurplankton). När den blir lite större övergår den till att äta mera macrovertebrater (d.v.s. ryggradslösa djur såsom maskar, iglar och insekter som lever i och nära vattnet) för att senare i livet med en större kroppsstorlek övergå till att äta fisk. Som fullvuxen är abborren ofta en toppredator i våra svenska sjöar. De abborrar som uppehåller sig i det littoralala habitatet nära strandkanten, har ofta en högruggad kroppsform och äter ofta mer organismer som förknippas med de strandnära habitaterna (macrovertebrater) medan de som uppehåller sig i det öppna, pelagiska habitatet har en mer strömlinjeformad kroppsform och äter organismer som förknippas med det öppna habitatet (zooplankton).

För min avhandling utförde jag dels ett dammexperiment där jag undersökte hur abborrarnas tillgång till olika habitat och möjlighet att byta mellan habitaterna påverkade deras morfologiska och diet (nische) specialisering. Jag undersökte också abborrarnas predationseffekt på födoresurserna, d.v.s. på primärkonsumenterna (macrovertebraterna och zooplankton), samt deras påföljande påverkan på primärproducenterna (d.v.s. växtplankton). Jag utförde också två fältstudier. I båda fiskade jag abborre med hjälp av fisknät från både det strandnära littoralala och det öppna pelagiska habitatet. I dammexperimentet fann vi större indirekta effekter av predation från fisk på växtplanktonen när habitaterna inte var kopplade. Detta överensstämmer med modeller som tidigare utförts av andra forskare som undersökt habitats koppling av predatorer. Våra resultat tillför empiriska data till modellernas förutsägelser om predatorers stabiliserande potential vid habitats koppling. Vi fann

också att möjligheten för abborre att koppla habitat delvis beror på den individuella dietspecialiseringen av abborre och habitatets komplexitet. Både i dammexperimentet och i fältstudien visar vi att abborre med en större nischebredd har bättre möjlighet att koppla habitat. Dessa resultat i samband med en mindre stabil växtplanktondynamik (förändring över tid) i dammexperimentet, stödjer tidigare teorier om att när en näringsväv domineras av en dietspecialist som predator, så uppvisar näringsväven en större och mer varierande dynamik (förändring över tid), än när en näringsväv är dominerad av en generalist (mer allätande) predator.

Sammanfattningsvis så visar min avhandling att enskilda individers specialisering kan påverka födoväven och kopplingar mellan olika organismer på ett sätt vi inte tidigare har tagit hänsyn till. Denna studie förbättrar vår förståelse av individuell specialisering och illustrerar komplexiteten av födovävar och hur individuell specialisering kan påverka topp-predatorers möjlighet att koppla habitat.

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