Ecology and Evolution of Adaptive Morphological Variation in Fish Populations

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Abstract
The work in this thesis deals with the ecology and evolution of adaptive individual variation. Ecologists have long used niche theory to describe the ecology of a species as a whole, treating conspecific individuals as ecological equivalent. During recent years, research about individual variation in diet and morphology has gained interest in adaptive radiations and ecological speciation. Such variation among individual niche use may have important conservation implications as well as ecological and evolutionary implications. However, up to date we know very little about the extension of this phenomenon in natural populations and the mechanisms behind it.

The results in this thesis show that the extension of individual diet specialization is widely spread throughout the animal kingdom. The variation in diet is mainly correlated to morphological variation but not always. Furthermore, this variation in diet and morphology among individuals could be both genetically determined and environmentally induced and it mainly comes from trade-offs in foraging efficiency between different prey types.

The results from a number of studies of perch also show that individual perch differ in morphology and diet depending on habitat, where littoral perch has a deeper body compared to pelagic perch. This difference in morphology corresponds to functional expectations and is related to foraging efficiency trade-offs between foraging in the littoral and pelagic zone of a lake. The variation in morphology in perch is mainly due to phenotypic plasticity but there are also small genetic differences between the littoral and pelagic perch. Two separate studies show that both predation and competition may be important mechanism for the variation in morphology and diet in perch.

In conclusion, the results in this thesis show that individual variation in diet and habitat choice is a common phenomenon with lots of ecological and evolutionary implications. However, there are many mechanisms involved in this phenomenon on which we are just about to start learning more about, and only further research in this area will give us the full insight.
LIST OF PAPERS

This thesis is based on the following papers that will be referred to by the corresponding Roman numerals


IV  Svanbäck, R. and Eklöv, P. Genetic variation and phenotypic plasticity: causes of morphological variation in Eurasian perch. Manuscript

V  Eklöv, P. and Svanbäck, R. Predation favors adaptive morphological variation in perch populations. Manuscript


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Ecology and Evolution of Adaptive Morphological Variation in Fish Populations

Introduction

"Natural selection … leads to divergence of character, for more living beings can be supported on the same area the more they diverge in structure, habitat and constitution”

(Darwin, C. 1859)

If intra-specific competition is strong, then an individual that is able to efficiently use a new resource may experience reduced intra-specific competition and gain higher fitness (Wilson and Turelli 1986). Expansion of the population niche width and adaptations to novel resources has theoretically been shown to be one of the causes of resource polymorphisms and ultimately sympatric speciation (e.g. Smith and Skúlason 1996, Dieckman and Doebeli 1999, Doebeli and Dieckman 2000). The expansion of the population niche width is thought to be due to increased intra-specific competition or reduced inter-specific competition, and support for this stems largely from observational studies of character release and displacement (Grant 1972, Robinson and Wilson 1994, Robinson and Schluter 2000).

In the late forties, Svärdson (1949) observed that habitat variation in a species is low when inter-specific competition is dominant whereas if intra-specific competition dominates then habitat variation is much greater. In the mid sixties, Van Valen (1965) developed the “niche variation hypothesis”. Both Svärdson and Van Valen proposed that niche expansion in the absence of inter-specific competition was achieved by increased between-individual variation in resource and habitat use. Roughgarden (1972, 1974) provided further support for the role of between-individual variation by theoretical work. After a few supportive (e.g. Rothstein 1973, Grant et al. 1976, Bernstein 1979), and a few negative tests (e.g. Soulé and Stewart 1970, Soulé 1972, Patterson 1983), the discussion of individual variation trailed off in the 1980s. However, the discussion of intra-specific niche variation has recently revived with renewed interest in resource polymorphism, adaptive radiation, and ecological speciation (e.g. Smith and Skúlason 1996, Doebeli and Dieckman 2000, Mousseau et al. 2000, Schluter 2000).

Between-individual niche variation can occur in several ways, including ecological sex dimorphism (e.g. Shine 1989, 1991), ontogenetic niches (e.g. Polis 1984, Werner and Gilliam 1984), and discrete polymorphisms (e.g. Smith and Skúlason 1996). These cases of niche differentiations are correlated to discrete morphological differences between the foragers. Between-individual niche variations have also been shown to occur where there are no obvious discrete morphological differences between the foragers, and such “individual
specialization” may sometimes exceed differences between conventional species (e.g. Werner and Sherry 1987, West 1986, 1988, Ehlinger and Wilson 1988).

The feeding specialization among individuals may to some extent reflect morphological and behavioral constraints (e.g. Wainwright 1988, Ehlinger and Wilson 1988) but they may also be a consequence of learning (e.g. Heinrich 1976, Werner and Sherry 1987). The morphological and behavioral constraints in handling time efficiency and search efficiency give rise to foraging efficiency trade-offs (e.g. Lewis 1986, Milinski 1987, Ehlinger and Wilson 1988, Robinson 2000). The trade-offs in foraging on different food resources that may lead to phenotypically divergent populations are hypothesized to be a primary cause of trophic polymorphisms and adaptive radiations (e.g. Ehlinger and Wilson 1988, Schluter 1993, Smith and Skúlason 1996, Robinson et al. 1996). For example, observations on a Galapagos finch species, the medium ground finch (Geospiza fortis) has revealed that individuals with different beak sizes feed in different ways. The efficiency that the medium ground finch display in cracking seeds varies depending on beak size, and in the dry season, when food supply is likely to be limiting and most mortality to occur, they feed on seeds of different sizes and hardness in proportion to their beak sizes (Grant et al. 1976, Price 1987). The same correlations between beak size and diet has been found for other seed-eating finches elsewhere (Smith 1987, 1993, Benkman 1993, Diaz 1994,). The foraging efficiency trade-offs leading to differential energy intakes will have consequences for the foragers’ fitness. It is hypothesized that the functional trade-offs in handling seeds of different sizes and hardness are responsible for the adaptive radiation in Galapagos finches and other seed eating finches elsewhere (e.g. Grant 1986, Smith 1987).

Genetic divergence between populations due to local adaptations or environmentally induced morphological changes are the two processes that have been ascribed to cause differences in trophic morphology. Genetic divergence through local adaptations have long been recognized to create great morphological variation, but that plasticity may be a major component of phenotypic variation has just recently attracted much attention. Many organisms can modulate their morphology in response to environmental cues. Such plasticity is thought to be an important adaptive strategy for populations experiencing variable environments (Stearns 1989, Scheiner 1993), and it is likely that phenotypic plasticity plays an important role in diversification (West-Eberhard 1989). For example, if the positive correlation between the trait and fitness is exclusively due to nonheritable environmental component, the trait may appear to be under directional selection and yet not evolve. Such cases have been suggested for life history traits (Price et al. 1988, Price and Liou 1989) and morphological characters (van Noordwijk et al. 1988, Alatalo et al. 1990). This has important consequences for our ability to predict phenotypic changes when measuring natural selection.
"In an extremely small area ... and where the contest between individual and individual must be severe, we always find great diversity in its inhabitants.”

(Darwin, C. 1859).

As Darwin wrote in the “Origin of Species”, more recent models of so-called "competitive speciation” hypothesize that competition is diversifying, (Rosenzweig 1978, Pimm 1979, Dieckmann and Doebeli 1999), i.e. that the gradual expansion into a new niche occurs in response to competitive pressure within the old niche. Trophic resource polymorphisms in fishes for example, are believed to have arisen through intra-specific competition via character release (Robinson et al. 1993, Robinson and Wilson 1994, Skulason and Smith 1995). Due to the absence of other species such as competitors and predators, intra-specific competition has forced individuals to inhabit new niches and thereby broaden the species’ niche width.

Just as competition is diversifying, predation is also an important selective force in most natural communities. Besides its obvious impact on abundance and size structure of prey populations, predation has commonly selected for ecological, behavioral and morphological traits in prey (Lima and Dill 1990, Harvell 1990). Various morphological structures in prey organisms’ function as efficient adaptations against predation, and these morphological defenses could be either constitutive or environmentally induced. Furthermore, recent findings have shown that predation may be involved in creating variation within a species (Vamosi 2002, Abrams 2003).

So in order to understand the evolutionary ecology of a population or a species, then individual differences are important to document, for it is the variation among individuals that is the raw material on which natural selection acts.

Morphological variation and habitat use in fish populations
Many aspects of a fish’s ecological niche can be indicated from its morphological features. For example, body shape and fin dimensions are good indicators of the habitat preference and swimming behavior of fishes (e.g. Keast and Webb 1966, Webb 1984). There are three main categories of locomotion in fish that are highly dependent on the body form of the fish (Webb 1984, Webb and Weihns 1986). The three categories are cruisers, maneuverers and accelerators. Each of these has a distinct structure and form optimal for the special activity. Most fish however, have body and fin forms intermediate among those of specialists (Webb 1984). Therefore, most fish are locomotor generalists in that they perform well in several areas of locomotor patterns, although performance in each area is lower than that of the relevant specialist. The locomotor pattern of cruisers is optimal for exploitation of widely dispersed food (Webb 1984) and the optimal morphology of a cruiser includes a fusiform shaped body with a slim caudal peduncle (Webb 1984, Webb and Weihns 1986). Performance in maneuvers is affected by body and fin morphology (Howland 1974, Webb 1976, 1983), and the optimal design for maneuvering is to have a short, deep laterally compressed body with mid-lateral pectoral fins (Webb 1982, 1984, Webb and Weihns 1986). In lake fish communities, deep-bodied species are usually found in the more structurally complex littoral...
habitat, whereas pelagic fish show more streamlined body morphology (e.g. Keast and Webb 1966, Watson and Baloon 1984, Motta et al. 1995). Predators of locally abundant and evasive prey require maximal acceleration (Webb and Skadsen 1980, Rand and Lauder 1981, Vinyard 1982) to minimize the duration of interaction. The optimal body form of an accelerator is characterized by *Esox* and consists of an elongated body shape with a deep caudal peduncle and a large muscle mass (Webb 1984, Webb and Weih 1986).

Many fish species exhibit considerable intraspecific variation in morphology. This intraspecific variation can be divided into intra- and inter-population variation. Inter-population variation is considered to be correlated with differences in the availability of resources either through competition with other species (Lindsey 1981, Magnan 1988) or by system specific differences in resource conditions (e.g. Lavin and McPhail 1985, 1986, Mittelbach et al. 1992, Walker 1997). Intra-population variation in morphology of fish on the other hand is thought to be correlated with habitat choice of individuals (Smith and Skúlason 1996), where intraspecific competition is thought to give rise to the pattern of correlation between morphology and habitat choice (Wilson and Turelli 1986).

Resource polymorphisms in fish have attracted a lot of attention in the past decade where most examples reflect segregation between the littoral and the pelagic habitats of lakes (Smith and Skúlason 1996). In the cases of a littoral-pelagic segregation of individuals it has been found that the littoral individuals have a deeper body (e.g. Ehlinger and Wilson 1988, Snorrason et al. 1994, Robinson et al. 1996), and longer pectoral and pelvic fins (Ehlinger and Wilson 1988, Bourke et al. 1997, Dynes et al. 1999). The pelagic fish on the other hand have a more streamlined body with shorter pectoral and pelvic fins (Ehlinger and Wilson 1988, Robinson et al. 1996, Bourke et al. 1997, Dynes et al. 1999).

The differentiation in morphology between the littoral and pelagic habitats range from a more normal distribution of phenotypes where only the mean values differ between the littoral and pelagic habitat (e.g. Ehlinger and Wilson 1988, Robinson et al. 1993, 1996) to clear bimodal non-overlapping morphologies between the habitats (e.g. Mann and McCart 1981, Hindar and Jonsson 1982, Pigeon et al. 1997). These stages of differentiation in morphology might represent intermediate stages in speciation (Smith and Skúlason 1996) and in some cases it has been found that the morphs differentiate not only morphologically but also genetically (e.g. Hindar et al. 1986, Foote et al. 1989, Vuorinen et al. 1993).
Objectives

Despite the long history of the “niche variation hypothesis” we still lack knowledge about the mechanisms that drives the population niche width. For example, trade-offs in foraging efficiency are thought to be a mechanism behind differential resource use but still we know little about the mechanisms behind the trade-offs. The concept of character release predicts that the population niche width (or at least the morphological variation) will increase in the absence of a competitor. However, empirical studies of character release and polymorphisms in fish have only considered the ontogenetic end stages, whereas most fish species grow several orders of magnitude during their life. Furthermore, theories of competitive speciation suggest that intra-specific competition is important in expansion of the population niche width. Up to date, the theories of competitive speciation describes a situation when the population is at a numerical equilibrium despite that most populations in nature fluctuate in numbers through time. This has lead to that when character release/displacement and resource polymorphisms are studied, analyzed and discussed, this is performed in the absence of a population dynamic perspective. Furthermore, the strong focus on competition as the driving force has led to an ignorance of predation as a factor in driving niche variation.

The main objective of this thesis was to gain deeper knowledge about individual variation in diet and habitat choice. More specifically, the ecological and evolutionary causes and consequences of individual variation. The main questions addressed in this thesis are:

- How common are the patterns of individual diet specialization in nature and what are the theory behind the mechanisms of individual specialization (I)
- Is the individual diet and habitat specialization related to morphological variation (I, II and III)
- Is the morphological variation within and between habitats related to foraging efficiency trade-offs and if so how do they relate to growth rates in nature (III)
- Is the morphological variation between habitats related to genetic difference or to phenotypic plasticity (I, and IV)
- It is known that predation can influence habitat choice of the prey but what is the effect of predation risk on individual diet specialization and morphological development in prey (V)
- Competition is said to be diversifying but what is the effect of population dynamical feedbacks on individual diet choice (VI)
Methods

To study the ecology and evolution of adaptive individual variation several different methods were used. This thesis consists of a review (paper I) and studies on different temporal and spatial scales such as snap shot and long-term field surveys (paper II, III, and VI), aquaria experiments (paper III), and outdoor pond and common garden experiments (paper IV and V). Paper I was designed to investigate the general pattern in nature whereas the other papers were designed to answer more specific questions. To answer the more specific questions, Eurasian perch (*Perca fluviatilis*) was chosen as study organism, based on the vast background knowledge of the species’ ecology.

Species studied
Eurasian perch is one of the most common fish species in Eurasia (Svärdson 1976, Johansson and Persson 1986). Perch is an ontogenetic omnivore and undergoes two diet shifts over its life span. Perch spawn in the littoral zone and the 5-7 mm long, newly hatched larvae shift habitats to the pelagic zone within a day (Byström *et al.* 2003). As the larval perch grow they get pigmented and develop into juveniles at a size of approximately 20 mm. Due to their small size, juvenile perch are very vulnerable to predation and therefore they shift back to the littoral zone after a few weeks (Byström *et al.* 2003). Larval and juvenile perch mainly feed on zooplankton (Craig 1978, Guma’a 1978, Coles 1981, Byström *et al.* 1998). With an increase in size, perch gradually shift to macroinvertebrate feeding and finally as large become piscivorous (Fig. 1) (Persson 1988). As adults, perch occupy both the littoral and pelagic habitats of lakes and movements between these habitats are relatively restricted (Eklöv 1997).

![Figure 1](image_url)

Figure 1. Graphical description of the major diet categories and ontogenetic diet shifts in perch.

Defining Individual Specialization
Roughgarden (1972, 1974) provided a quantitative framework for thinking about intrapopulation niche variation. Roughgarden (1972) suggested that the size
component of the total niche width (TNW) of a population could be broken down into two components; the variation in resource use within individuals (within-individual component, WIC), and the variance between individuals (between-individual component, BIC) so that $TNW = WIC + BIC$. Roughgarden developed this framework for a single continuous variable such as prey length, but later Roughgarden (1979) proposed a measure that uses the Shannon-Weaver index as a proxy for variance in discrete data. In both continuous and discrete cases, the relative degree of individual specialization (IS) can be measured as the proportion of TNW explained by within-individual variation ($WIC/TNW$). If all individuals utilize the full range of the population’s niche this value approaches 1, whereas smaller values indicate decreasing inter-individual overlap and hence higher individual specialization. Originally Roughgarden developed this framework for within- and between-phenotype variation (or between-sex variation, Ebenman and Nilson 1982), but it can also be applied at the individual level (Bolnick et al. 2002).

As mentioned, intrapopulation niche variation can occur by subdividing the population’s niche in a number of different ways, for example into sex, age, or obvious distinct morphs. The goal of paper I was to demonstrate that there also could be important niche variation among individuals. Therefore we defined an “individual specialist” as an individual whose niche is substantially narrower than its population’s niche for reasons not attributable to its sex, age, or discrete (a priori) morphological group. Note however that individual specialization is characterized not by a low WIC per se but by a low WIC relative to TNW. Thus, in paper I we surveyed the literature for examples of individual specialization on resources, such as prey taxa, host plants or oviposition sites. When possible we noted the morphological distribution, if it had a genetic basis, the timescale of consistency and if there were any trade-offs associated with the individual specialization. Papers II, III, IV, V and VI all intend to investigate various components and mechanisms behind individual variation outlined from paper I.
Major results and discussion

“Hence I look at individual differences ... as being the first step towards such slight varieties as are barely thought worth recording in works on natural history. And I look at varieties which are in any degree more distinct and permanent, as steps leading to more strongly marked and permanent varieties; and at these latter, as leading to sub-species, and to species.”

(Darwin, C. 1859).

As Darwin mention in the “Origin” (though not talking directly about diet variation), individual diet specializations and discrete resource polymorphisms may provide important stepping-stones for speciation. However, most empirical and theoretical studies of resource use treat conspecific individuals as ecological equivalent. Recently, ecological segregation with correlations between phenotype and resource use has been documented in resource polymorphisms where we have discrete morphs specializing on different resources (reviewed in Wimberger 1994, Skúlason and Smith 1995, Smith and Skúlason 1996). Parallel to the research on resource polymorphisms, researchers have documented cases where individuals specialize on different resources without any distinct differences in morphology. In paper I, we review the literature on individual specialization and found evidence for individual specialization for 93 species distributed across a broad range of taxonomic groups (Table 1). Although few studies actually had quantified the degree to which individuals were specialized relative to their population, the between individual variation sometimes comprised the majority of the population’s niche width (paper I), where feeding behavior within a population can span those of several families (e.g. Werner and Sherry 1987).

Table 1. Summary table of the number of species in each taxonomic group where individual specialization have been noted (data from paper I, table 1).

<table>
<thead>
<tr>
<th>Taxonomic group</th>
<th>Number of Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gastropods</td>
<td>5</td>
</tr>
<tr>
<td>Crustaceans</td>
<td>5</td>
</tr>
<tr>
<td>Insects</td>
<td>18</td>
</tr>
<tr>
<td>Fishes</td>
<td>29</td>
</tr>
<tr>
<td>Reptiles and amphibians</td>
<td>5</td>
</tr>
<tr>
<td>Birds</td>
<td>20</td>
</tr>
<tr>
<td>Mammals</td>
<td>11</td>
</tr>
</tbody>
</table>

Why would a group of individuals end up using different resources despite sharing a common environment? The answer closest to hand is that individuals will use different resources if they have different resource-use
efficiencies, reflecting variable morphological, behavioral or physiological capacities to search and handle alternative resources. According to this, most of the foraging specialization can be associated with morphological variation independent of the magnitude (Robinson and Wilson 1994, Skúlason and Smith 1995, Smith and Skúlason 1996, paper I). Yet, this poses a second problem; why does phenotypic variation result in efficiency variation? In many cases where individuals of different morphologies specialize in different niches, evidence has been found for efficiency trade-offs between the alternate niches (e.g. Ehlinger and Wilson 1988, Ehlinger 1990, Smith 1990, Robinson et al. 1993, Schluter 1993, 1995, Huckins 1997, Paper I, III). Without such trade-offs constraining efficiency on different resources, phenotypic variation would not produce functional variation, and all individuals would be equally capable of using all resources (Taper and Case 1985).

Most cases of resource polymorphism and adaptive variation within fish populations show that the segregation occurs between the littoral and pelagic habitats. So in order to investigate the relationship between morphology and habitat/diet specialization in perch we sampled perch from the littoral and pelagic habitats of Lake Trehörningen (papers II and III). Lake Trehörningen is situated in central Sweden (latitude 64° 00’ 50” N, longitude 20° 08’ 00” E) with a lake area of 2.37 km², and a maximum depth of 17 m. In addition to perch, Lake Trehörningen also contains roach (Rutilus rutilus), pike (Esox lucius), and vendace (Coregonus albula).

We have found in Lake Trehörningen and other lakes that perch individuals from the littoral zone are deeper bodied and forage on littoral prey types compared to the more streamlined individuals that forage on pelagic prey types and are found in the pelagic zone (Paper II, III, Eklöv and Svanbäck unpublished data). This difference in morphology corresponds to functional expectations for fish species that occupy these habitats (e.g. Webb 1984). The difference in morphology and diet of perch between the two habitats have also been shown to reflect morphology dependent foraging efficiencies, where deeper bodied individuals caught in the littoral zone had higher foraging efficiency in experiments with structure. The more streamlined individuals from the pelagic zone on the other hand had higher foraging efficiency in open water trials (paper III).

The foraging efficiency trade-offs found in paper III were due to behavioral differences in both searching for and attacking prey. The littoral perch used slower search velocity than pelagic perch when foraging in open water, and their search velocity was not much affected by foraging in vegetation. The search velocity of the pelagic perch was on the other hand much affected by foraging in vegetation, and pelagic perch thus ended up with slower search velocity in vegetation trials compared to littoral perch. For pelagic prey types a higher search velocity was related to a higher detection rate whereas for littoral prey types a slower search velocity was related to higher detection rate (Svanbäck and Eklöv 2004). Furthermore, the littoral perch used a slower attack velocity while attacking
prey than pelagic perch did (paper III). For the pelagic macroinvertebrate 
(*Chaoborus* sp.) in the vegetation trials and the littoral prey type used (mayfly 
larvae) in both vegetation and open water, a slower attack speed was related to a 
higher capture success whereas a higher attack speed was related to a higher 
capture success in open water trials for *Chaoborus* sp. (Svanbäck and Eklöv 2004). 
Overall, the differences in behaviors between littoral and pelagic perch resulted in 
the differences in foraging efficiencies in perch from the two habitats (paper III, 
Svanbäck and Eklöv 2004). The foraging efficiency results found in perch are 
similar to those found in other fish species (Schluter 1993, Ehlinger 1990) and such 
trade-offs in foraging efficiency has been suggested to be important in creating 
intraspecific differences between morphologies in resource and habitat use (e.g. 

Other studies emphasize the importance of learning for foraging 
specialization (e.g. Lewis 1986, Pietrewiez and Kamil 1979, Heinrich 1976, 
Partridge 1976). For example, in a laboratory study of *Pieris rapae*, the cabbage 
butterfly, Lewis (1986) found that the time required for individuals to find the 
source of nectar in flowers decreased with successive attempts and that learning to 
extract nectar from a second species inferred with the ability to extract nectar from 
the first. There is no reason why learning should not aid in creating individual diet 
specialization in perch and as such, learning should work in concert with 
morphological variation.

**The ontogeny of foraging specialization**

A fundamental biological reality among most organisms is that they grow in size 
during their ontogeny. The increase in size will affect fundamental ecological 
properties such as energy demand, the ability to find and process food and the 
ability to avoid predators (Werner 1988, Persson 1988). In fish, the increase in size 
will affect morphological and behavioral properties. For example, as fish are gape-
limited predators, a fish will be restricted in its prey use by the size of its gape 
(Wainwright and Richard 1995). Whereas the habitat-morphology relation in paper 
III only concerns the overall difference in morphology between the two habitats, 
paper II analyzed the role of adaptive variation during ontogeny in perch. More 
specifically, in paper II we investigated if there were any differences in 
morphological trajectories during the ontogeny of perch collected from the two 
habitats of Lake Trehörningen and how the diet choice related to the morphology. 

We found in paper II that perch get relative deeper body morphology as 
they grow. Such change in morphology during ontogeny will make larger perch 
more adapted to benthic/littoral feeding compared to the smaller more streamlined 
young perch (paper III). These factors affecting resource intake in fish may in turn 
result in that only a small portion of the available resource spectra can be 
processed.

The above discussion is reflected in the resource use of perch from Lake 
Trehörningen. At small size classes, perch of both littoral and pelagic origin are 
feeding on zooplankton (paper II). This makes the degree of individual 
specialization very low (IS ~ 1, Fig. 2). The perch in the littoral zone then starts to
feed on macroinvertebrates at intermediate sizes, whereas the pelagic perch keeps on feeding on zooplankton (paper II) which makes the degree of individual specialization increase (Fig. 2). At the largest size classes of perch caught in Lake Trehörningen, all individuals in the littoral zone fed on fish whereas the pelagic individuals fed either on fish or zooplankton keeping the degree of individual specialization high. In other lakes we have found the same pattern of size and individual specialization as in Lake Trehörningen. However, at larger size classes than those caught in Lake Trehörningen, both littoral and pelagic perch fed on fish, which therefore lowered the degree of individual specialization again (Svanbäck and Eklöv, data).

![Figure 2. The degree of individual specialization in perch from lake Trehörningen depending on size class. Note that high IS (i.e. IS close to 1) means low degree of specialization. The degree of individual specialization is calculated according to equations 1 and 2 in paper VI.](image)

**Divergent natural selection**

In paper III we found strong effects of morphology on foraging efficiency of perch in the laboratory (see also Svanbäck and Eklöv 2004). What evidence is there that these effects are important for trophic polymorphism and fitness among fish populations in the field? Divergent natural selection between and within populations exploiting different resources is hypothesized to be a primary cause of trophic polymorphisms and adaptive radiation (Lack 1947, Schluter and Grant 1984, Grant 1986, Schluter 1993, 1995, Skúlason and Smith 1995, Robinson et al. 1996, Smith and Skúlason 1996). An easy but weak test of this hypothesis has been to look for correlations between morphology and resource use. This is a pattern that we have found in many lakes for perch and other fish species like roach (paper II and III, Eklöv and Svanbäck, data, Fransson, Eklöv and Svanbäck, data),
and there are several other studies showing a similar relationship (e.g. Grant 1986, Smith 1987, Schluter and McPhail 1992, Hjelm et al. 2000). Furthermore, we found correlations between, and trade-offs within morphology and resource use efficiency (paper III, Svanbäck and Eklöv 2004), which is another criterion for divergent natural selection (e.g. Smith 1987, Ehlinger 1990, Losos 1990, Benkman 1993, Schluter 1993). The resource use efficiency found in perch (paper III, Svanbäck and Eklöv 2004) is hypothesized to give rise to the environment-dependent correlation between morphology and growth (fitness) that we observed in paper III (Robinson et al. 1996, Schluter 1993, 1995).

In paper III, we found that the deeper bodied individuals from the littoral zone grew faster than the more streamlined individuals whereas the opposite pattern was found in the perch from the pelagic zone. Even though growth is not a direct measure of fitness, growth rate is an important component of fitness in fishes because size is correlated with a number of fitness components such as increased reproductive success, reduced vulnerability to predation, increased over-winter survival and increased success in competition (e.g. van den Berghe and Gross 1989, Ridgway et al. 1991, Mittelbach 1981, 1984, Lundvall et al. 1999, Werner and Hall 1988, Post and Evans 1989, Merrett 1994). This finding would suggest that the fitness trade-off appears to be concave, which would favor the evolution of specialist phenotypes in each habitat (Schluter 1995, Robinson et al. 1996), although factors such as temporal variation in resource abundance can influence this outcome (Wilson and Yoshimura 1994). Similar patterns of growth has also been found in pumpkinseed sunfish (Lepomis gibbosus) where the deeper bodied individuals from the littoral zone grew faster than the more streamlined individuals whereas the opposite pattern was found in the pumpkinseed sunfish from the pelagic zone (Robinson et al. 1996).

**Phenotypic plasticity and genetics in adaptive morphological variation**

In forming a phenotype, two interacting processes act on the developmental programme; the genome and the environment (Scheiner 1993). Genetic variation for a fixed phenotype has been hypothesized to be favored in stable environments (Hori 1993, Smith 1993) whereas phenotypic plasticity can be an important adaptive strategy for coping with environmental variability (Stearns 1989, Scheiner 1993). In stable environments the selection regimes are rather constant (Dieckmann and Doebeli 1999, Doebeli and Dieckmann 2000) which would favor genetic variation for a fixed phenotype (DeWitt et al. 1998). Paper IV attempts to measure the relative importance of genetic differences versus phenotypic plasticity in perch from Lake Trehörningen. We performed a common garden experiment were adults from the two lake habitats spawned separately and their offspring were raised in enclosures with either open water or vegetation in an artificial pond.

In paper IV we found that the morphological variation in perch to a large extent was determined by environmental factors and that the genetic variation only contributed to a small amount to the morphological variation. In a similar experiment, Robinson and Wilson (1996) showed that environment determined most of the morphological variation for pumpkinseed sunfish, though the genetic
component influenced the variation more than in perch. Furthermore, in paper IV we also found that the trade-offs in foraging efficiency found in paper III not only have a morphological basis, but also that it might have a genetic basis. Perch from littoral parents had a higher proportion of littoral prey types in their diet compared to perch from pelagic parents independent of the environment they were grown in. This fact might suggest that there are behavioral differences between littoral and pelagic perch that is not transformed into morphological differences during one season of growth. It might also suggest that the structural component of the habitat have a bigger effect on morphological variation than the prey items have. Correspondingly, Olsson and Eklöv (manuscript) have shown in an experiment, combining structural complexity and diet, that structure had a bigger effect than diet on morphological development in perch.

How come phenotypic plasticity dominates genetic variation in forming perch body morphology? As discussed above, in size-structured populations, it is common for individuals to exploit several niches sequential in the course of their life history (Werner and Gilliam 1984). Because perch potentially undergoes two niche shifts during its lifetime, i.e. from zooplanktivory to benthivory and then from benthivory to piscivory (e.g. Persson 1988, Hjelm et al. 2000, paper II) and the optimal morphology related to planktivory, benthivory and piscivory are not related to each other (Webb 1984) it might be necessary to compromise between the optimal forms in order to perform well in all three niches. Some degree of plasticity will then aid in adapting to the new niche that the individual experience.

In addition to ontogenetic influences on diet choice, variation in resource levels in both habitats will influence the diet choice of individuals. Such variations in resource levels can be from fluctuating intensity of intra- and inter-specific competition (Persson et al. 2000, paper VI), or due to environmental variations (Grant 1986, Grant and Grant 2002). Furthermore, predation can be a major selective factor (e.g. Reznick et al. 1990, Vamosi 2002) and besides selecting for different morphologies, the presence of predators has shown to induce habitat shifts in prey individuals (e.g. Eklöv and Diehl 1994, Persson and Eklöv 1995). The density of predators or the predation pressure might also vary within or between seasons (e.g. Persson et al. 2000, Eklöv and Svanbäck data). So not only might intra-specific competition and inter-specific competition change through time, predation pressure might also fluctuate through time.

However, we have in paper IV, but also in other studies of perch (paper V, Hjelm et al. 2001, Olsson and Eklöv manus) shown that the response to the environment is fast. These findings about phenotypic plasticity in perch corroborate the results of paper II that the differences in morphological growth trajectories between the littoral and pelagic perch might be due to phenotypic plasticity.

The effect of predation on adaptive variation and diet specialization
There has been a long-standing debate whether intra-specific competition can be a mechanism driving phenotypic divergence among species and also a process of speciation. This debate has led to extensive research in this area and the evidence
so far support that this is a likely outcome (e.g. Schluter 2000, Bolnick 2001). However, the debate has also lead to a neglect of other important ecological factors for the adaptive divergence of species, such as the presence of predators (see Abrams 2000, Abrams and Chen 2002). Predation has been shown in numerous theoretical and empirical examples to have strong direct and indirect effects on ecological interactions, but also on evolutionary important traits of organisms (Sih et al. 1985, Lima and Dill 1990, Lima 1998, Vamosi 2002). Such direct and indirect responses could for example involve morphological and behavioral adaptations that reduce vulnerability to predators (Lima and Dill 1990, Brönmark and Miner 1992). Furthermore, a reduction of competitors could potentially change the selective regime connected to resource competition (Rundle et al. 2003). However, the role of predation during resource polymorphisms and adaptive variation has received limited attention.

The major aim with paper V was to experimentally test the prediction that variation in predation risk could cause adaptive changes in phenotypic traits in a fish population without necessarily affecting intraspecific competitive interactions. The prediction lean on the assumption that food resource types varies among habitats, and that a predator induced habitat shift in the prey would lead to differential resource use and consequently shifts in adaptive characters.

A behavioral response to the presence of predators is to shift habitat to a less risky habitat (Eklöv and Diehl 1994, Persson and Eklöv 1995). However, the optimal habitat for escaping predation might not be the optimal habitat for foraging. The prey individual might thereby end up in a safer habitat but with morphology maladapted for foraging. In such a situation, it would be adaptive for the prey individual to change its morphology to become more adapted to the new feeding environment. The results of paper V suggest that the presence of predators may be important for trophic polymorphisms. When the predation risk was higher in one habitat, the prey fish shifted to the other habitat and fed on the specific food resources found in this habitat. The restricted diet did in turn affect the phenotype of the prey fish in a predicted way. When the open water environment was safer the prey fish foraged in the open water and changed to a more streamlined morphology, whereas the fish fed littoral preys and got deeper body morphologies when the vegetated habitat was safer. There was no difference in prey mass increase across treatments, indicating that the competition for resources was probably weak and that the differential resource use of the prey fish probably resulted from the restricted habitat use due to predation risk.

The restriction in habitat also reflected the diet and degree of individual specialization. When the prey was restricted to one habitat due to differences in predation pressure they all fed on the same food resource. In treatments with equal predator densities in both habitats individual specialization was high, since some individuals fed littoral resources and others pelagic resources. As a result of differences in diet specialization among treatments we found that in treatments with high degree of individual specialization, there was also a higher degree of morphological variation. Thus, if there are unequal predation pressures among habitats then morphological variation might be constrained in the same sense as a
competitor species would do (character displacement, see Robinson and Wilson 1994).

**Density dependent changes in individual diet specialization**

Theoretical analyses and empirical studies of diet choice, polymorphism and sympatric speciation are usually restricted to only consider populations at numerical equilibrium (e.g. paper I, Skúlason and Smith 1995, Smith and Skúlason 1996, Dieckman and Doebeli 1999; Doebeli and Dieckman 2000). In contrasts, many populations fluctuate in density over time in relation to resource levels (e.g. Grant 1986; Mittelbach et al. 1995; Smith et al. 1999; Persson et al. 2003; Grant and Grant 2002; Klemola et al. 2002). Fluctuations in resource levels have been related to external environmental factors (e.g. Grant and Grant 2002) or intrinsically driven dynamics (e.g. Persson et al. 2003).

In paper VI, we studied a perch population that experienced intrinsic cycling due to size-dependent inter-cohort competition and cannibalism, involving a more than twenty fold change in the density of adult individuals (Person et al. 2000, 2003). The purpose of paper VI was to analyze the effect of intra-specific competition on individual diet specialization in a population dynamical context. The study was carried out in Lake Abborrtjärn 3, a small (9.3 ha, maximum depth 12 m) lake in central Sweden (latitude 64° 29’ N, longitude 19° 26’ E). In this paper we focus on two main issues behind individual specialization. First, we investigate the mechanisms (WIC and TNW) that may give rise to differences in individual specialization. Second, we investigate the effect of population density on diet choice in perch including feedbacks of perch consumption on resource levels.

When adult perch density was low, the abundances of benthic invertebrate and YOY perch were high and dominated the diet of adult perch, whereas the density of zooplankton was low due to predation from YOY perch. Thus at low densities of adult perch the degree of individual specialization was low. At high adult perch densities, benthic invertebrate abundance was lower and zooplankton level was higher and some perch switched to feed on zooplankton increasing individual specialization. This corroborates the results of Persson et al. (2000) where it was found that adult perch were all found within the littoral zone at low densities and with an increase in the adult population a larger proportion of the population used the off-shore habitat as the preferred prey types (YOY perch and macroinvertebrates) were scarce.

The results of paper VI show that individual specialization may fluctuate with population density through feedback mechanisms via resource levels. Expansions of population niche width and adaptations to novel resources have been suggested to be one of the causes of resource polymorphisms and ultimately sympatric speciation for equilibrium conditions (Smith and Skúlason 1996; Dieckman and Doebeli 1999; Doebeli and Dieckman 2000; Claessen and Dieckman 2002). However, there are only a few empirical studies that have looked at the combination of population dynamics and evolutionary dynamics (for
examples see Tamarin and Krebs 1969; Gaines and Krebs 1971; Sinervo et al. 2000).

Fluctuations in density may have profound implications on the evolution of resource polymorphisms. In our studied perch population all adult perch were found within the littoral habitat at low adult densities (Persson et al. 2000). This means that deeper bodied individuals will have the highest fitness in this phase (Fig. 3) (Robinson et al. 1996; paper III). In contrast, at high adult densities the same fitness scenario will be true for the ones staying in the littoral zone whereas the slender-bodied individuals will have the highest fitness in the pelagic zone (paper III) (Fig. 3). Thus, the fitness landscape for the adult population will fluctuate with population density and depend on both density and frequency of different phenotypes (Wilson and Turelli 1986, Svanbäck and Bolnick manuscript). The fluctuating fitness landscape scenario therefore suggest that selection will favor phenotypic plasticity rather than genetically determined morphologies in this perch population as found in paper IV.

Figure 3. Hypothesized fitness landscapes for perch at low and high densities. At low densities perch occupy only the littoral habitat whereas at high densities perch occupy both habitats (Persson et al. 2000). The fitness should thus follow fluctuations in densities between the right and the left graph, with many stages in between.

Concluding remarks and future perspectives

Although plenty examples of trophic polymorphism and adaptive variation in freshwater fishes exist, we still know very little about the mechanisms that drive this pattern. The most common explanation for trophic polymorphism is that this is caused by a release in interspecific competition (Robinson and Wilson 1994,
Schluter 1994, Skúlason and Smith 1995). However, in the natural environment both predation and competition is probably involved and it is likely that the phenotypic response is affected by a trade-off between foraging gain and predation risk. The trade-off between foraging and predation risk has been shown to be the major factor influencing species interactions in ecological communities (Werner and Anholt 1993, Lima 1998) and theoretical analyses show that this trade-off may also lead to evolutionary branching and ultimately speciation (Abrams 2003).

In reality, individual variation and polymorphism are ends of a continuum of increasingly discrete variation. This thesis focuses on the less discrete end of this continuum, in which individuals cannot clearly be assigned to distinct morphotypes. In this thesis I have shown that the occurrence of individual diet specialization in nature is a widely distributed phenomenon and that it to a large extent depends on trade-offs in foraging efficiency on alternate resources. I have also shown that this trade-off in foraging efficiency is connected to morphological characteristics of the forager. Furthermore, in a common garden experiment I have shown that the morphological variation in perch connected to diet and habitat choice in nature was mainly a result of phenotypic plasticity and only to a small degree to genetic variation. The reason for such a large degree of phenotypic plasticity in perch might be due to fluctuations in the level of competition or changes in predation pressures through time.

In this thesis I have only grazed over a number of potential mechanisms that might influence morphological variation and diet choice of individuals. However, each paper in itself raises a couple of interesting questions for further research. For example;

1) Paper II focuses a lot on the ontogenetic aspect of adaptive variation. Is ontogenetic niche shifts a mechanism that promotes phenotypic plasticity in adaptive characters? In a recent paper, Claessen and Dieckmann (2002) found that diversification and speciation could occur along the axis of optimal size for ontogenetic niche shift. Further research on ontogenetic niche shifts in adaptive variation could possibly determine the effect and importance of ontogenetic niche shifts in diversification.

2) The indication of disruptive selection in paper III raises the question; how common is this pattern among fish populations in general and particularly in perch populations? This aspect is interesting on its own, but also competitive disruptive selection is supposed to be the main mechanism behind resource polymorphisms and could eventually lead to sympatric speciation.

3) Genetically determined phenotypes or phenotypic plasticity? Paper IV and other research in this area show that there can be a varying degree to which these two factors determine the phenotype of an individual. But what are the proximate mechanisms behind this variation in adaptive variation and resource polymorphisms?

4) Research on the effect and importance of predation in adaptive variation and resource polymorphism is in its infancy. Paper V focuses on
behavioral responses and morphological changes in the prey as a function of differences in predation pressure among habitats. However, there are other ways predator-prey interactions can influence resource polymorphisms. Predation may actually select for certain morphology as a consequence of differences in escape ability between preys of different morphologies. If so, is the escape ability – morphology correlation equal among habitats, or are different morphologies adapted to escape predators in different habitats? Furthermore, a prey individual can change its morphology in response to the presence of predators as has been found in crusian carp (Brönmark and Miner 1992). How would such morphological response influence resource intake rate and how does it influence resource polymorphisms and adaptive variation.

5) Population dynamics and evolutionary dynamics. Paper VI suggests that population dynamics can influence the evolutionary dynamics in a population. Other recent papers have suggested that evolutionary dynamics can influence the population dynamics (Yoshida et al. 2003). However, the interplay between population dynamics and evolutionary dynamics is also in its infancy. Could the observed population dynamics in paper VI explain the low degree of genetic variation found in perch (paper IV), or are there other mechanisms driving the evolution of phenotypic plasticity? These questions can only be answered with further empirical and theoretical studies.

The occurrence of resource polymorphism is supposed to be higher in regions with species poor faunas (Robinson and Schluter 2000). However, in lake Trehörningen there are only a few other species present, but still we find the same kind of adaptive variation in more species rich lakes in the Uppland region (Eklöv and Svanbäck data). Moreover, both in Lake Trehörningen (Svanbäck data) and in lakes in Uppland (Fransson, Eklöv and Svanbäck data) where we find differences in morphology between littoral and pelagic perch, we also find similar differences between littoral and pelagic roach. To spice it up even more, in Lake Erken I have found evidence for that three different fish species show the same pattern of adaptive variation at the same sampling time (Svanbäck data). So the real challenge for future research in this area is to merge individual variation, population and community dynamics, and evolutionary dynamics.

“Natural selection, as has just been remarked, leads to divergence of character and to much extinction of the less improved and intermediate forms of life. On these principles, I believe, the nature of the affinities of all organic beings may be explained”

(Darwin, C. 1859).
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