Interplay Between Environment and Genes on Morphological Variation in Perch – Implications for Resource Polymorphisms

JENS OLSSON
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Abstract

Recent research has suggested that individual specialization within populations could be substantial and more common than previously acknowledged. Eurasian perch is one of many species of fish in lakes of postglacial origin that displays a morphological and dietary variation tightly coupled to the littoral and pelagic habitats of the lake. The occurrence of such resource polymorphisms might have important consequences for local adaptation and might also be an important initial step in speciation.

I have investigated the importance of a number of factors for the development of resource polymorphisms using perch as a study organism. I found a weak genetic basis for morphological differences, and the environmental influence on morphology was of such a magnitude that an induced morphology could be reversed. The results nevertheless suggested that genetic differentiation could be substantial at small spatial and temporal scales, even within habitats. Several environmental factors were shown to influence the morphological development, and the results also suggest that behavioral differences could mediate a morphological response. I also found evidence for that competition-driven divergence might only occur when divergence in resource use is favoured at the same time as growth rates are kept sufficiently high for character divergence to be effective. The results finally indicate that divergence in the gut length of individuals might co-occur with habitat and diet use in resource polymorphic populations. This might enhance habitat fidelity and possibly also facilitate the persistence of resource polymorphisms since individuals should experience a cost of switching diets due to a too specific digestive system.

Based on these findings I conclude that small scaled genetic differentiation might be more common than currently acknowledged, that more multi-factorial studies are needed if we are to fully understand the mechanisms behind trait diversity, and that competition not always favors divergence.

Keywords: Perch, Resource polymorphism, Genetic differentiation, Phenotypic plasticity, Morphology, Competition, Character divergence, Behavior, Growth rate, Resource level, Gut length

Jens Olsson, Department of Ecology and Evolution, Limnology, Norby 20, Uppsala University, SE-75236 Uppsala, Sweden

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For all the perch that died during the course of this thesis

“It’s a long way to the top if you wanna rock n’ roll” (Young-Young-Scott, 1975)
List of papers

This thesis is based on the following papers, which will be referred to by their Roman numerals.


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Introduction

General background

The way organisms behave and look is seldom the result of stochastic processes. Rather, the behavioral and morphological attributes expressed in populations are usually a response to the environmental conditions experienced. For example, in birds, the beak is the primary tool used in feeding. As such, in the famous Darwin’s finches there is substantial variation in beak morphology between species coupled to the preferred diet of the species. Within the monophyletic family of ground finches (Geospiza), species specialized on hard and large seeds have deeper beaks compared to those species preferentially feeding on smaller and softer seeds (reviewed in Schluter 2000). This results from that the depth of the beak determines an individual’s efficiency in handling seeds of different size (reviewed in Freeman & Herron 2004). Another good example of the tight relationship between morphology and the environmental condition is the wide array of body shapes found in fishes. Species living in structurally complex habitats feeding on attached prey usually develop a deep-bodied and laterally-compressed morphology with large pectoral fins (Webb 1984; Webb & Weihs 1986). In contrast, species found in open waters feeding on widely dispersed prey usually develop more streamlined bodies with narrow caudal peduncles and small pectoral fins (Webb 1984; Webb & Weihs 1986). The functional significance of these extreme morphologies is that fish with large pectoral fins and deep and laterally-compressed bodies are superior in maneuvering, whereas species with a streamlined morphology with small pectoral fins in turn are better cruisers (Webb 1984; Webb & Weihs 1986).

Intraspecific polymorphisms

Further good examples of the tight correlation between the environment and the phenotype are the numerous cases of intraspecific polymorphisms found across a wide range of animal taxa (Skúlason & Smith 1995; Smith & Skúlason 1996). In nature, generalist populations usually consist of individuals specialized on a subset of the resources utilized by the population, and this form of individual specialization in resource use is proposed to be more common than currently appreciated (Bolnick et al. 2003). Since there usually is a strong link between resource utilization and morphological expression,
individual resource specialization might result in a resource polymorphism (Skúlason & Smith 1995; Smith & Skúlason 1996). Other potential outcomes might be the development of an ecological sex dimorphism (Shine 1989, 1991; Bolnick & Doebli 2003) or ontogenetic resource segregation (Polis 1984; Werner & Gilliam 1984). Sometimes the intraspecific differences in resource polymorphisms might exceed the variation seen between conventional species (Werner & Sherry 1987; West 1986, 1988; Ehlinger & Wilson 1988). However, at least as likely as discrete resource specialization is the occurrence of a more continuous and subtle distribution of phenotypes in the population where the major differences are found between the average individual from each resource specialist category (Ehlinger & Wilson 1988, Robinson et al. 1993; Via et al. 1995). Such subtle phenotypic variation could hence possibly account for the fact that new examples of resource-based differentiation in morphology steadily increases among animal taxa.

Much effort has been put into studying intraspecific polymorphism during recent years, but we still know relatively little about the underlying mechanisms. However, as suggested by the examples of differences in beak morphologies in Darwin’s finches and body shapes of fishes, a fitness trade-off between the divergent forms in different environments is hypothesized to be one of the major causes (Schluter 1993; Smith & Skúlason 1996; Robinson et al. 1996; Schluter 2000; Svanbäck & Eklöv 2003, 2004). Individuals should hence be superior competitors on the resources they are adapted to, while being less effective in novel environments due to a less optimal behavior and/or morphology. For example, a fish that is morphologically adapted for cruising over large distances capturing widely dispersed food is generally a poor competitor in a structurally complex habitat with cryptic prey attached to the structure (Webb 1984, 1988). If the theory of trade-offs holds, a fish adapted to the structurally complex environment should at the same time be a poorer competitor in the non-structured open environment. In the absence of trade-offs, no partitioning of resources and resulting variation in morphology between individuals would exist. Instead, we would find a superior, single phenotype in all environments. The combination of increased intra-specific resource competition and availability of open and underutilized new niches is hypothesized to be the major driver of niche expansion in natural populations (Robinson & Wilson 1994; Smith & Skúlason 1995; Bernatchez & Wilson 1998; Schluter 2000). Evidence of this comes from a few theoretical (Roughgarden 1972; Wilson & Turelli 1986) as well as empirical studies (Smith 1993; Schluter 2000; Bolnick 2001). Individuals should, according to these theories, via the influence of disruptive selection switch to novel and/or sub optimal resources in order to escape competition during periods of increased intraspecific competition. A prerequisite for this to happen is that the switching part of the population gains higher fitness after the niche-shift. The shift to exploitation of new resources may in turn expose individuals to new selection regimes leading to character divergence.
In Eurasian perch (*Perca fluviatilis*), there is evidence that increased competition could drive exploitation of novel resources (Svanbäck & Persson 2004). Svanbäck & Persson (2004) studied a perch population with intrinsically driven population dynamics over a 9 year period, and found that at low perch densities (i.e. relaxed intraspecific competition) the majority of the population was found in the littoral habitat whereas at high perch densities (i.e. intense intraspecific competition), a large proportion of the adult perch performed a habitat switch into the less preferred pelagic habitat.

Not only competition but also predation is potentially a diversifying force. Several studies have shown that predators could have large influences on the behavior and morphology of their prey populations (reviewed in Lima & Dill 1990; Werner & Anholt 1993), though the role of predation in character divergence has received less attention (Langerhans *et al.* 2004). Some recent findings have, however, highlighted the importance of predation during the process of divergence (e.g. Brönmark & Miner 1992; Relyea 2002; Abrams 2003; Langerhans *et al.* 2004; Nosil 2004; Eklöv & Svanbäck 2006; Eklöv & Jonsson, *In press*). Predators could either directly influence prey via their mere presence (Brönmark & Miner 1992; Eklöv & Jonsson *In press*), induce habitat shifts subjecting their prey to novel selection regimes and thereby indirectly affect trait diversity (Eklöv & Svanbäck 2006), or directly select for traits via killing (Vamosi 2002).

**Phenotypic plasticity and heritable differences**

Two opposing but sometimes interacting processes could account for an intraspecific polymorphism: either heritable genetic differences between individuals or environmental induction and phenotypic plasticity (Scheiner 1993). Phenotypic variation in relatively unstable environments is thought to be influenced by phenotypic plasticity (Stearns 1989; Pfennig 1992; Scheiner 1993), whereas such variation occurring in stable environments is hypothesized to be under strong genetic control (Hori 1993; Smith 1993). Theory predicts that phenotypic plasticity should evolve when alternative phenotypes are favored in heterogeneous environments (e.g. Via & Lande 1985; Moran 1992; Via *et al.* 1995), but if selection regimes are rather constant, genetically fixed traits should due to the associated costs with plastic phenotypes evolve (DeWitt *et al.* 1998). Despite that phenotypic plasticity is a common feature of many intraspecific polymorphisms (e.g. Day *et al.* 1994; Lindsey 1981; Meyer 1987; Wimberger 1992; Robinson & Wilson 1995, 1996; Mittelbach *et al.* 1999; Svanbäck & Eklöv 2006), there are also reports of genetically differentiated intraspecific morphs (e.g. Hindar *et al.* 1986; Foote *et al.* 1989; Smith 1993; Vuorinen *et al.* 1993; Bernatchez *et al.* 1996, 1999; Gislason *et al.* 1999; Taylor 1999; Hendry *et al.* 2000, 2002; Rundle *et al.* 2002). Furthermore, sometimes a polymorphism within the same species could be caused by heritable genetic differences in one system,
whereas in other systems it could be driven by phenotypic plasticity (Nordeng 1983; Gislason et al. 1999). The two processes forming an individual’s phenotype are thus not mutually exclusive. The formation of a polymorphism could instead be governed by heritage from the parental genotype with adaptive plasticity playing a proximate role in fine-tuning the phenotypic expression (Smith & Skúlason 1996). Moreover, the amount of gene flow between closely situated populations is thought to be substantial (Wright 1943; Epperson 2003; Rousset 2004), and gene flow should counteract local differentiation (Wright 1931; Slatkin 1985; Lenormand 2002). The different morphs in resource polymorphisms are commonly found at relatively small spatial scales with large potential for homogenizing gene flow. Examples of genetically differentiated intraspecific morphs might therefore suggest that genetic differentiation could be substantial at scales smaller than commonly acknowledged.

Most alternative morphs influenced by phenotypic plasticity are conditional and non-reversible, but in a few cases they have been shown to be reversible (Meyer 1989, 1990; Pfennig 1992; Proulx & Magnan 2004). One reason for why not all organisms exhibit such an “infinite and perfect” phenotypic match to the environment experienced is the hypothesized costs associated with possessing a plastic phenotype (DeWitt et al. 1998; Agrawal 2001). The constraints to infinite plasticity might for example come in the form of costs of maintaining and producing an optimal phenotype, costs of having a developmentally instable phenotype, genetic constraints for expressing an optimal phenotype, and costs associated with acquiring information about changes in the environment (reviewed in DeWitt et al. 1998; see also Van Buskirk 2000; Relyea 2002). If these constraints cause an organism with a plastic phenotype to exhibit lower fitness when expressing the same mean trait value as an organism with a fixed phenotype, a cost of plasticity is indicated. Despite that costs of plasticity have important ecological and evolutionary consequences, they have in comparison to the benefits of plasticity rarely been studied (DeWitt et al. 1998). An explanation for this might be the difficulty to empirically measure the embedded costs of expressing an induced character (Van Buskirk 2000). Most studies investigating constraints of plasticity have so far been confined to systems where predators induce a plastic trait response in their prey (e.g. Petterson & Brönmark 1997; DeWitt 1998; Van Buskirk 2000; Relyea 2002), and more studies are therefore needed in systems where the response is induced by other forms of environmental heterogeneity.

Phenotypic plasticity has been recognized to slow down evolutionary divergence (reviewed West-Eberhard 1989, 2003), since an environmentally-induced trait that enhances its bearer’s fitness is less likely to become established in a population compared to a genetically fixed trait. There has, however, lately been a revived interest in the idea of plasticity as a diversifying factor in evolution (West-Eberhard 1989, 2003; Pigliucci & Murren 2003;
Price et al. 2003). Phenotypic plasticity might actually contribute to the origin of novel traits and alter the directions of change (West-Eberhard 1989, 2003). Furthermore, evidence for genetic variation and heritability of phenotypic plasticity is currently accumulating, suggesting that selection might thus act upon plasticity just as it does on any other phenotypic character (reviewed in Pigliucci 1996; Svanbäck & Eklöv 2006). The traditional view of the speciation process where genetic and phenotypic changes between diverging groups is thought to develop after the evolution of barriers for interbreeding (West-Eberhard 2003) has also been challenged by the theory of genetic assimilation. Here characters originally acquired by environmental induction become genetically fixed where after evolutionary branching and speciation follows as a result of reproductive isolation between divergent forms (Pigliucci & Murren 2003; West-Eberhard 2003). Phenotypic plasticity thus enables populations to more easily move between adaptive peaks. However, whether or not evolutionary divergence follows plasticity-driven divergence should depend on the level of plasticity. At low levels of plasticity, an inability to develop appropriate phenotypes in novel environments could impede colonization and therefore prevent subsequent divergence (Pigliucci & Murren 2003; Price et al. 2003). Likewise, at too high levels of plasticity, genetic variation might not get exposed to novel selection regimes and no further divergence will therefore follow. Divergence is therefore expected to be highest at intermediate levels of plasticity. Despite that little work is done in this area of research, there is substantial and convincing evidence for that a genetically fixed phenotypic response initially could be formed by environmental induction (reviewed in Pigliucci & Murren 2003). More empirical studies are nevertheless needed before the role of plasticity in evolution could be firmly established.

The role of behavior during divergence

So far I have mainly focused on morphological responses to environmental heterogeneity, but adaptive behavioral differences might also develop between populations inhabiting different geographical areas (reviewed in Foster 1999). For example, guppies (Poecilia reticulata) from locations with different predation regimes have been shown to have different mating behaviors (Endler 1995), different ecotypes of white fish (Coregonus clupea-formis) have a genetic basis for different swimming behaviors (Rogers et al. 2002), and differences in behavior have been hypothesized to play an important role in speciation among Lake Malawi Cichlids (reviewed in Stauffer et al. 2002). Furthermore, whereas morphological traits are relatively conservative to change, it has been suggested that behavioral traits are more flexible (reviewed in Rogers et al. 2002). Behavioral differences have therefore been postulated to precede morphological differences during the process of diversification (e.g. Mayr 1963; West-Eberhard 1989; Price et al. 2003), since
flexibility in individual behavior is more likely to result in favorable adaptations. Adaptive variation in behavioral traits might thus be a potent force in initiating new directions in the process of adaptive radiation.

The role of resource polymorphisms in evolution

What is then the point of investing money and time in studying intraspecific polymorphisms? To me a good reason is that an individual variation in morphology coupled to resource use has been considered to be of great evolutionary significance as the build-up of reproductive isolation between genetically differentiated morphotypes might represent an initial step in a speciation process (West-Eberhard 1989; Smith & Skúlason 1996; Doebeli & Dieckmann 2000; Figure 1).

Figure 1. Schematic view showing potential steps and mechanisms leading to resource polymorphisms and eventually speciation, according to Smith and Skúlason (1996).

For example, increased intraspecific competition might govern exploitation of novel resources, exposing individuals to new selection regimes in turn leading to character divergence and finally to the evolution of different species (Rosenzweig 1978; Doebeli & Dieckmann 2000; Figure 1). Hence, by studying intraspecific polymorphism we can increase our knowledge about
the factors creating natural diversity and understand the processes important in speciation. Schliewen et al. (1994) showed that in two different crater lakes in Cameroon, 11 and 9 different species, respectively, of cichlids have evolved in sympatry, probably as a result of competition for resources and habitats. Furthermore, in a recent study, Barluenga and co-authors (Barluenga et al. 2006) presented convincing evidence that an initial divergence in resource use in a population can lead to future speciation. The authors studied two species of fish from the Midas cichlid species complex (Amphilopus citrinellus and A. zaliosus) from Lake Apoyo, a small and young crater lake in Nicaragua. The lake was colonized in a single event by A. citrinellus. A. zaliosus was then shown to have evolved within the lake from the ancestral A. citrinellus colonizers in less than 10,000 years. Disruptive ecological selection in resource use is thought to have played an important role during the speciation event since the two species are morphologically differentiated from each other and additionally differ with respect to food preferences and habitat use. The above examples suggest that systems harboring heritable polymorphisms should be considered as "evolutionary hotspots" that merit special attention for conservation since they might represent an arena for future speciation (Bernatchez & Wilson 1998).

Resource polymorphisms and character release in postglacial fish

To date, one of the best example of intraspecific differentiation in morphology coupled to divergent resource use, are the replicated resource polymorphisms found across several families of fish from lakes in previously glaciated areas of the Northern hemisphere (Robinson & Wilson 1994; Schluter 1996; Robinson & Parsons 2002). Populations of these species have for long been known to show intraspecific variation in morphology, with the evidence originating from old anecdotes of local fishermen, later confirmed in scientific reports (e.g. Ekman 1912). It was, however, not until the eighties and nineties that the phenomena received increased interest of students in evolutionary ecology (Skúlason & Smith 1995; Smith & Skúlason 1996). The lakes in which these resource polymorphisms are found were formed and colonized after the last glaciations about 10,000 years ago (Robinsson & Wilson 1994) which resulted in relaxed interspecific competition and availability of open niches (Robinsson & Wilson 1994; Schluter 1996; Robinson & Parsons 2002). The morphological variation in postglacial species of fish occurs repeatedly and is associated with the discrete resource distributions in the different habitats of the lakes (Robinsson & Wilson 1994; Schluter 1996; Robinson & Parsons 2002). For example, one typically finds benthivorous individuals having blunter snouts, longer upper jaws, larger pectoral fins and
more deep-bodied morphologies in the vegetated and shallow littoral habitat, whereas the deeper and non-structured pelagic zone usually is inhabited by a planktivorous morph with a more pointed snout, equally sized jaws, usually longer and more numerous gill rakers, and a more fusiform body form (e.g. Malmquist et al. 1992; Schluter & McPhail 1992, 1993; Robinson et al. 1993; Robinson & Wilson 1994; Snorrason et al. 1994; Svanbäck & Eklöv 2002, 2003). The habitat-specific morphologies seem to be adaptive since a few studies have demonstrated a fitness trade-off in optimal morphology between habitats (Ehlinger 1990; Schluter 1993; Robinson et al. 1996; Robinson 2000; Svanbäck & Eklöv 2003, 2004). The differences between morphotypes can be rather extreme, and in some instances up to four different morphs within the same lake have been recorded (Jonsson & Jonsson 2001). More commonly, however, the morphological differences are rather subtle and therefore easily overlooked.

As in most cases where resource polymorphisms have been documented, we still know relatively little about the mechanistic background behind the intraspecific differentiation in morphology in postglacial fish. There might, however, be multiple selective factors operating on the development of fish morphology. Several studies have, for example, demonstrated that both the food type and predation regime could influence the morphological expression of fish from different habitats (Meyer 1990; Robinson & Wilson 1995; Day & McPhail 1996; Mittelbach et al. 1999; Vamosi 2002; Abrams 2003; Andersson 2003; Stauffer & Gray 2004; Eklöv & Svanbäck 2006; Eklöv & Jonsson In press). Less is, however, known about how differences in food density and quality as well as the physical structure of the habitat affect the morphological development. Phenotypic plasticity is important in forming the morphological differentiation within postglacial fish species (e.g. Robinson & Parsons 2002), and despite that evidence of additive genetic variation for plasticity has accumulated (reviewed in Robinson & Parsons 2002), little is known about the limits of the plasticity. Nevertheless, due to the replicated pattern, the large influence of plasticity, and good knowledge of functional morphology, resource polymorphisms in postglacial fish species offers a great opportunity for studying important processes during divergence.
Aims of this thesis

The focus of this thesis is on the mechanistic background of the evolution of resource polymorphisms and morphological diversity. The majority of the studies have focused on plastic responses in morphology to a heterogeneous environment, but the degree of genetic differentiation between individuals from contrasting as well as similar environments was also investigated. More specifically, this thesis focuses on the following issues and specific questions addressed:

The role of phenotypic plasticity and genetic differentiation in resource polymorphisms.
- Could an induced morphology be reversed (paper I)?
- What is the degree of genetic differentiation between individuals from different/similar habitats (paper II)?

Factors influencing the development and plasticity of polymorphic populations.
- What is the influence of habitat complexity and divergent feeding modes on the development of resource polymorphisms (paper I)?
- What are the effects of resource abundance and habitat type on behavioral and morphological plasticity (paper III)?
- Could resource competition via reduced growth rates constrain morphological plasticity and divergence (paper IV)?

Divergence of internal morphological attributes in resource polymorphisms.
- Could different food resources cause differentiation of the digestive system (paper V)?
- What are the implications of divergent digestive systems for the occurrence of resource polymorphisms (paper V)?
Relevance of the thesis

I believe that the most important thing when doing science is to ask yourself, “What’s the relevance of my studies?” Despite that this is an obvious question, it is not always that easy to come up with a reasonable answer for the things you are doing. This is especially true when some of your findings originate as by-products of studies originally intended to investigate something completely different. I will here try to prove the relevance of my findings and put them into a broader context both in light of basic research and applied science.

When it comes to basic research, I believe that the main relevance of this thesis is that studies of intraspecific variation in morphology and resource polymorphisms might, as already stated, give us insights about the very early stages of the process of diversification and speciation. Furthermore, the world around us is, due to global warming, currently changing at a pace that has never been seen before. The resulting environmental change could be that some biotopes and habitats are destroyed whereas others are created. By studying phenotypic plasticity we can increase our understanding of several ecological interactions since the degree of plasticity has profound influences on the ability to track environmental change. For example, competitive interactions between species might be altered if one of the competitors has a highly plastic morphology that enables it to efficiently utilize a wider range of resources than would otherwise be possible. From a more applied perspective, studies of phenotypic plasticity will increase our understanding of whether it is enough to preserve single and unique populations and environments as opposed to a wide range of different environments in order to allow for intraspecific character expansion, and thus the evolution of unique populations and species. Furthermore, the degree of genetic differentiation between populations has for long been thought to be scale-dependent where the exchange of migrants, and hence also genes, between populations determines the degree of differentiation. Pronounced differentiation is therefore thought to be confined to situations where populations are separated by large geographic distances with limited migration between populations. Detecting genetic structures over small spatial scales such as differentiation between sympatric morphs in a polymorphism will therefore increase our understanding of how populations are structured in nature. Moreover, systems with genetically determined polymorphisms should merit special attention in conservation since they might harbor a large potential for future speciation. Fi-
nally, if we wish to preserve genetic variation in nature and are to accept that differentiation occurs at smaller scales than previously acknowledged, then studies investigating the genetic structures of natural populations at a wide range of spatial scales are definitely needed.
Study species and methods

In this thesis Eurasian perch was used as a model organism to answer the postulated hypothesis. Eurasian perch is widely distributed in fresh and brackish waters in Northern Eurasia (Thorpe 1977a), and is one of the most common species of fish in Sweden (Svärdsson 1976; Johansson & Persson 1986). The spawning time of perch is in late spring during a period of accelerating increase in water temperature and usually takes place in shallow waters (reviewed in Thorpe 1977b). To date, there is no evidence for mate choice in perch. Instead, a female typically sheds all her eggs at once in a continuous connected egg strand into the surrounding vegetation or structure followed by fertilization by several males (reviewed in Thorpe 1977b). The eggs hatch after about 25-27 days and the 5-7 mm long larvae migrate out to the pelagic habitat within a day and start shortly to feed on zooplankton (Hjelm et al. 2000). After a few weeks in the pelagic habitat, the juvenile perch shift back to the littoral zone and, due to their larger size, start feeding on macroinvertebrates (Byström et al. 2003). Perch usually become piscivorous later in life with increasing size (Persson 1988), but recent studies have reported that this final stage could be reached surprisingly early in the ontogeny (Beeck et al. 2002; Quevedo & Olsson 2006). Despite that perch usually go through two ontogenetic habitat shifts one typically finds individuals from all size classes both in the littoral and pelagic habitats of lakes (Svanbäck & Eklöv 2002). The movement of individuals between these two habitats seems to be relatively restricted (Eklöv 1997), and like many other species of fish inhabiting postglacial lakes of the Northern Hemisphere, perch from the two habitats differs in morphology and resource use (Robinson & Schluter 2000; Svanbäck & Eklöv 2002, 2003). Typically, perch caught in the littoral habitat are mainly feeding on benthic and littoral prey and have a more deep-bodied and downward bent morphology compared to pelagic perch which mainly feed on pelagic prey and is more streamlined with an upward bent morphology (Figure 2). Many of the studies reporting such resource polymorphisms in fish show distinct morphotypes between littoral and pelagic habitats of lakes (reviewed in Smith & Skúlason 1996), but in perch the variation in morphology are more continuous and overlapping between the habitats (Svanbäck & Eklöv 2002; Figure 2a).
Figure 2. Morphological differences between perch from the littoral and pelagic habitats of lakes. A) Perch from Lake Erken, and B) cartoon of the extreme morphologies found in each habitat.

Furthermore, the morphological development of perch seems to be independent of sex (Peter Eklöv & Richard Svanbäck, unpublished data), and the habitat-specific morphologies seem to be adaptive (Svanbäck & Eklöv 2003, 2004). For example, individuals with the most extreme morphologies have the highest growth rates in their natal habitat (Svanbäck & Eklöv 2003; Eklöv & Svanbäck 2006), and littoral fish have higher foraging success on littoral food types in trials with vegetation (Svanbäck & Eklöv 2003, 2004). The opposite pattern was found for pelagic perch (Svanbäck & Eklöv 2003, 2004). The differentiation in morphology coupled to resource use seems to be common in perch, and has to date been recorded in about 20 different lakes (Peter Eklöv et al. unpublished data). However, the degree of differen-
tiation and overlap in morphology differs between lakes (Peter Eklöv et al., unpublished data), suggesting that factors like, for example, lake morphology and differences in intra- and interspecific competitor biomasses are affecting the morphological expression in natural populations (Lindsey 1981; Magnan 1988; Smith & Skúlason 1996; Jastrebski & Robinson 2004; Peter Eklöv & Richard Svanbäck, unpublished data).

Methods

To study the mechanistic and genetic background to the observed variation in morphology in perch, I used a combination of laboratory experiments and field studies. In the laboratory experiments I typically used young-of-the-year (YOY) perch housed in aquaria and exposed to different combinations of habitat structures, feeding modes and food levels. All fish used in these experiments were at an age of about two months old and caught in the littoral zone. At this age perch have already migrated back from the pelagic habitat and are typically found in both habitats (Svanbäck & Eklöv 2002) with little exchange of individuals between the habitats (Eklöv 1997). Therefore, I believe that most of the experimental fish were of a common littoral origin.

To quantify the morphology of the fish in both experiments and field studies I used landmark-based geometric morphometrics (see for example Zelditch et al. 2004). This is a powerful, flexible and easily interpreted multivariate technique to measure shape differences among specimens (Marcus et al. 1996). In contrast to traditional morphometrics, which are based on linear distances between landmarks, geometric morphometrics also incorporates changes in shape over the whole object that is often best described by non-linear relationships. The procedure I used involved thin-plate spline analyses where a number of homogenous landmarks were digitalized on a photo of each fish. I used the software TpsDIG32 (Rohlf 2005) to capture the x and y coordinates of the landmarks and the resulting data were then transferred to TpsRelw (Rohlf 2005). Here the shape variation resulting from differences in position and size of the specimen are excluded (Zelditch et al. 2004), and the treatment effects are calculated by comparing the landmark configuration of all specimens. Based on the shape variation in the data set, TpsRelw (Rohlf 2005) calculates the shape of the consensus (i.e. average) specimen to which it then relates the shape of each single object in data set. The deviation in shape of each object from the consensus specimen is then decomposed into a unique set of variables called non-uniform scores or partial warps and uniform scores. The partial warps describe small shape changes (local deformations) between the objects such as for example the position of a fin, whereas the uniform scores map shape changes along the whole body axes such as twisting or bending of the body. Since TpsRelw
produces a number of partial warps where each usually explains a fraction of the total variation, I used a Discriminant Function Analyses (DFA) as described in Svanbäck and Eklöv (2003, 2006) and Jastrebski and Robinson (2004) to facilitate efficient interpretation of the morphological differences between treatment groups. In the DFA the partial warps and uniform scores were used as independent variables and treatment as grouping variable. The morphological parameters entered into the DFA are combined into a few discriminant functions with a unique value (morphological index) for each individual. The morphological index (MI) of each function maximally discriminates between the predefined groups and describes the shape of each individual. The individual MI’s obtained from the DFA were then used as parameters in further analyses. An obvious advantage with geometric morphometrics is that it is simple to visualize the morphological variation in the data set. I used the software TpsRegr (Rohlf 2005) to visualize differences in morphology between treatment groups. This program performs a regression between the landmark coordinates original captured by TpsDIG32 and the morphological indexes obtained from the DFA. In paper II I instead used relative warps obtained from TpsRelw (Rohlf 2005) as variables in the morphological analyses. Relative warps represent principal-component vectors in a multivariate shape-space and was used to compare morphological and genetic differentiation (see paper II for further details).

In order to elucidate whether differences between populations are due to environmental induction (i.e. phenotypic plasticity) or heritable genetic differences, one can either raise individuals of known origin in similar and/or different environments (i.e. perform a common garden experiment) or directly analyze differences in the genetic architecture of individuals. In this thesis I used the latter technique by looking at the individual variation at a number of microsatellite loci. Microsatellites are tandem repeats of 1-6 nucleotides at a high frequency in the nuclear genome (Selkoe & Toonen 2006). A locus typically varies in length between 5 and 40 repeats and microsatellites are species specific (Selkoe & Toonen 2006). One of the reasons for why microsatellites are frequently used as population genetic markers are their high mutation frequency which generates enough genetic diversity to enable studies of processes acting on ecological time scales (Selkoe & Toonen 2006). Thus, it is relatively easy to genotype different individuals in a population by using several variable microsatellite loci, and the data set becomes more reliable when including more loci. Another reason for using microsatellites as population genetic markers are their assumed neutrality, but evidence is accumulating that this is not always the case (reviewed in Selkoe & Toonen 2006; John Gilbey, unpublished data). For example, several human diseases are directly caused by mutation at microsatellite loci and a microsatellite might sit adjacent to a gene under selection and thereby be passed on by hitchhiking. Whether microsatellites should be assumed to represent neutral population genetic markers is still an open question, but the
most common methods for estimating gene flow between populations (e.g. $F_{ST}$, rare alleles and maximum likelihood) have been shown to be relatively robust to at least weak selection (Slatkin & Barton 1993).
Results and Discussion

I will here try to summarize the major results of my thesis, discuss potential implications of my findings and also put them into a broader context in light of what has been done in previous studies in this area of research.

The role of phenotypic plasticity and genetic differentiation in resource polymorphisms.

Phenotypic plasticity seems to be ubiquitous in populations of fish (e.g. Lindsey 1981; Meyer 1987; Wimberger 1992; Robinson & Wilson 1996; Robinson & Parsons 2002), and the genetic diversity between alternative forms seems to be remarkably low (reviewed in Schluter 1996; Bernatchez & Wilson 1998). However, the genetic basis behind many resource polymorphisms is in general poorly understood (Smith & Skúlason 1996), and the role of polymorphisms during the process of evolutionary branching and speciation remains controversial.

Despite that plasticity seems to be influential in the morphological development of fish, little is known about the limits of this plasticity. Whether or not an induced trait is reversible or not could have profound influences on several evolutionary and ecological outcomes. The competitive interactions between species might for example be altered if one of the species exhibits a reversible morphology that enables it to efficiently utilize a wider range of resources than would otherwise be possible. Also, the potential for character divergence and evolution might change if populations as a result of reversible plasticity are able to more easily move between adaptive peaks in the fitness landscape (West-Eberhard 2003). Paper I showed that YOY perch to some extent were able to reverse an induced morphology in such a short time as four weeks. Little is known about reversible plasticity in animals and especially so in species with resource polymorphisms (but see Meyer 1989, 1990; Pfennig 1992; Proulx & Magnan 2004). To the best of my knowledge only two studies (Meyer 1987; Proulx & Magnan 2004) have previously demonstrated that an induced morphology could be reversed during a relatively restricted amount of time. Neither of these studies did, however, demonstrate such a fast response as found in paper I. The importance of phenotypic plasticity in the development of perch morphology is now well estab-
lished (Hjelm et al. 2001; Svanbäck & Eklöv 2006; Eklöv & Svanbäck 2006; Paper I, III, IV), and there might be several reasons for perch to exhibit a highly plastic phenotype. For example, perch likely experience an ontogenetic trade-off in optimal morphology since each niche experienced over ontogeny favors a unique and non-compatible morphology (e.g. Webb 1984, 1988; Ehlinger & Wilson 1988; Ehlinger 1990; Schluter 1993; Svanbäck & Eklöv 2003, 2004). By displaying a plastic and to some extent reversible instead of genetically fixed morphology, perch might have the ability to track the optimal morphology of each niche and hence experience a higher fitness during all ontogenetic stages. Furthermore, populations of perch might experience intense population dynamics (Persson et al. 2000; Svanbäck & Persson 2004). By having a plastic phenotype perch might successfully respond to the temporal changes in the optimal morphologies favored at different population densities.

After establishing that perch morphology was highly plastic, I wanted to estimate the degree of genetic differentiation between fish from different habitats (paper II). A recent common-garden experiment reported that only about 2 % of the morphological variation between littoral and pelagic perch was explained by the parental type (Svanbäck & Eklöv 2006). The influence of heritage on morphology could however have been underestimated in this study since the authors did not use a complete sib design in the experiment. In paper II the resolution of genetic differentiation was increased by using molecular methods.

![Figure 3](image_url)

**Figure 3.** Map over the three sites sampled in Hjulstafjärden, Lake Mälaren. The habitat characteristics of Site 1 were of a pelagic type, whereas sites 2 and 3 were more littoral like.
The focus in studies of resource polymorphisms has almost exclusively been on differences between individuals utilising contrasting environments and/or habitats. Evidence is, however, accumulating of that morphological differentiation could be significant between environments with similar habitat characteristics (Ruzzante et al. 2003; Webster M, Hart P, Olsson J, Ruxton G & Eklöv P, submitted manuscript). Therefore, perch from two neighboring littoral sites (Figure 3) were also included in paper II. The sampling procedure was also repeated (in May during perch spawning and in August the same year) to study the consistency of differentiation. The results indicated significant genetic differentiation between the pelagic and the two littoral sites at both sampling dates, and the overall differentiation was actually larger in August compared to May. To my surprise differentiation was substantial also between the two closely situated littoral sites at both sampling events. The spatial scale on which these differences have evolved is strikingly small, where two of the sites are situated less than 400 meters from each other (Figure 3). Gene flow is thought to counteract local differentiation (Wright 1931; Slatkin 1985; Lenormand 2002), and closely situated populations are via extensive migration thought to exchange genes frequently (Wright 1943; Epperson 2003; Rousset 2004). In line with a few recent studies (Van Oppen et al. 1997; Arnegard et al. 1999; Barluenga et al. 2006; Senar et al. 2006), the pattern found in paper II challenge this view by suggesting that differentiation over small spatial scales could be substantial despite the potential for homogenizing gene flow. When comparing the temporal replicates at each of the three sites studied in paper II it was evident that temporal differentiation was substantial (Figure 4). Whereas there is evidence for genetic differentiation over small spatial scales, comparably little empirical work has been done on differentiation at the temporal scale. The findings in paper II do, however, corroborate the results found by Dannewitz and co-authors (2005) suggesting that temporal genetic differentiation might make a significant contribution to the overall genetic structuring of natural populations. The driving mechanism behind the temporal differentiation found in previous studies are sampling of different cohorts derived from parents that differ in allele frequencies (Jorde & Ryman 1995; Dannewitz et al. 2005). Paper II might be unique in demonstrating temporal differentiation within such a short time scale as one year, and I am confident that sampling of genetically differentiated cohorts are not driving the pattern. For example, the sampled fish at each site and sampling date spanned over a substantial and overlapping size range representing several cohorts of perch, and in August the fish were clearly differentiated between sites despite no size and age differences.
Figure 4. Genetic similarity between the six different groups of perch sampled. The plot is based on a Principal Component Analysis in PCAGen (Goudet 1999) of the variation at the 8 microsatellite loci used. The two first principal components (PC) explained 47.8 and 22.7% respectively of the variation.

Another potential explanation for the small scaled differentiation found in paper II is that perch caught at the different sites were morphologically differentiated from each other and that the morphological differences were heritable. There was a temporal effect on morphology corroborating the pattern of genetic differentiation between May and August. There was also a spatial effect on morphology in August where the genetically more related perch caught at Site 2 and 3 (Figure 4) also were morphologically more similar to each other compared to the morphologically and genetically more differentiated fish caught at Site 1. In May, however, the pattern of genetic and morphological differentiation did not corroborate each other. As in August, there was a pattern of isolation by distance with higher gene flow between the closely situated Site 2 and 3 compared to the more distantly situated Site 1 (Figure 4), but we found no differences in morphology between sites. Hence, the overall genetic basis for morphological in our study did not seem to be very strong. Instead, the morphology of these fish was likely influenced by differences in the environmental conditions at the site of (see also Hjelm et al. 2001; Svanbäck & Eklöv 2006; Paper I). There might be several other explanations for the small scaled differentiation in this study, but we found indications of that the majority of the sampled groups consisted of individuals that were more related to each other than expected by chance alone. Hence, in addition to a minor genetic basis for the morphological differences, the pattern of small scaled genetic differentiation could have been influenced by limited gene flow between groups of perch that consisted of close relatives. We do, however, not know whether kin preference and/or
recognition have evolved in the sampled population, but other studies have reported that shoals of perch might consist of individuals that are full- and/or half sibs (Gerlach et al. 2001). Juvenile perch have also been demonstrated to prefer to associate with related fish in front of non-kin (Behrmann-Godel et al. 2006), and it is known for long that perch is a relatively sedentary species that exhibit strong site and shoal fidelity (e.g. Kipling & Le Cren 1984; Imbrock et al. 1996).

Mechanisms influencing the development and plasticity of polymorphic populations.

Despite the recent advances in studies of the process of diversification, more research is needed in order to fully understand what factors that influence the development of resource polymorphisms. The environment an organism experience is often heterogeneous with numerous variables and a wide range of selective factors potentially influencing the phenotypic expression. By studying the trait response from several environmental variables acting in concert we can gain insights in how the environment affects the divergence of species. Furthermore, intense competition over resources has been hypothesized to drive divergence (Roughgarden 1972; Wilson & Turelli 1986; Schluter 2000), but the empirical examples among non-microbial systems are few (see references in Schluter 2000; Bolnick 2001, 2004). We hence know little about limits and constraints of competition driven divergence.

Although there have been several studies on trait plasticity in fishes, there are to the best of my knowledge only one previous multi factorial study looking at the trait response from several environmental variables acting in concert (Andersson et al. 2006). Since natural populations generally undergo strong population dynamics (e.g., Krebs et al. 1995; Hanski et al. 2001; Mittelbach et al. 1995; Persson et al. 2003; Svanbäck & Persson 2004) resulting in fluctuations in resource abundances and optimal habitat choices of individuals, paper III investigated how differences in resource levels influenced behavioral and morphological plasticity of perch subjected to two simulated habitat treatments. The behavioral component studied was activity. The activity of an individual plays the key role in various fitness components such as the foraging rate, growth rate, mortality rate and predation risk (Werner & Anholt 1993). The resource level influenced plasticity in both activity and morphology, and the resource level also affected individual growth rates. Behavioral differences have been hypothesized to precede morphological transitions since they due to larger flexibility are more likely to result in favorable adaptations (Dill 1983; West-Eberhard 1989). I suggest that the morphological response to different resource levels in paper III to some
extent was mediated via differences in activity and individual growth rates. The habitat type also affected morphological plasticity but to a lesser extent, and there was no effect on activity from habitat type. Furthermore, the resource level experienced explained 44.3 %, habitat type 22.1 %, and the resource level x habitat type interaction 21.4 % respectively of the total variation in morphology. Thus, these results suggest that both resource levels and habitat type are important factors influencing trait plasticity in perch, but potentially do so with different magnitudes.

In paper I the impact of several variables acting in concert on trait plasticity was further explored. More specifically the impact of divergent habitat complexities and feeding modes on the morphological development of perch was studied. Both these variables differ between the littoral and pelagic habitats of lakes and could potentially influence the morphological radiation found in perch and other species of postglacial fish. For example, the littoral habitat typically has a physical structure consisting of vegetation, and fish usually picks prey attached to the vegetation or the bottom substrate. Pelagic fish on the other hand experience an open and non-structured habitat and feeds on widely dispersed planktonic prey in the open water column. The results of paper I are in accordance with other studies showing that divergent diets and/or feeding modes can trigger a morphological response (see for example Robinson & Wilson 1995; Day & McPhail 1996; Meyer 1990; Mittelbach et al. 1999; Andersson 2003; Proulx & Magnan 2004). We also found that the habitat structure explained 40.7 % of the morphological variation, whereas the feeding mode only explained 4.9 % and the interaction between the two explained 30.2 %. Thus, the effects of divergent habitats structure on morphology were dramatically superseding that of differences in feeding modes. A likely explanation for this pattern could be that the experimental design rendered different exposure times of the two variables tested. The perch were only fed once a day, and the effects of divergent feeding mode were therefore restricted to short periods of time once a day, whereas the effects of structure were present all of the time. Despite this bias, paper I is to the best of my knowledge the first to demonstrate that the physical complexity of the habitat could trigger a morphological response.

According to theory, intense resource competition within a generalist population could generate disruptive selection where individuals specialized on rare resources escape competition and should thereby experience an increase in fitness (Roughgarden 1972; Wilson & Turelli 1986). If the level of competition is kept constant at a high level the generalist population might split into two or more subpopulations each consisting of individuals specialized on a subset of the resources available. In the long run, selection might also favor evolutionary branching (Doebeli & Dieckmann 2000). This scenario of competition-driven divergence is only true as long as individuals are not constrained from developing the traits needed for successful exploitation of alternative resources. A number of studies have, however, highlighted that
organisms could be constrained from morphologically tracking and responding to changes in selection regimes (e.g. Björklund & Merilä 1993; Baker & Wilkinson 2003; Stauffer & Gray 2004). In paper I indications was found of that variation in individual growth rates could influence reversibility of an induced morphology, and an ignored but potential constraint to morphological plasticity might thus be limitations in growth. Individual growth rates are usually negatively related to the density of the population (e.g. Petranka 1989; Persson et al. 2000; Bolnick 2004), and at high population densities the level of intraspecific competition is high. Paper IV therefore investigated if there was a connection between competition, growth rate and morphological plasticity. In an aquarium experiment we demonstrated that morphological plasticity in perch exposed to contrasting habitat types was growth dependent in that morphological differentiation was confined to treatments with high growth rates (Figure 5a). At lower growth rates there was no divergence in morphology between the different habitat treatments (Figure 5a). Despite that a wide span of growth rates was covered in the aquarium experiment, it is hard to translate these results to natural conditions since there is a wide array of environmental variables that potentially could influence morphological differentiation between littoral and pelagic habitats of lakes (Paper I and III). Nevertheless, a reasonable assumption is that perch in the natural environment show a negative relationship between competitor biomass and divergence if they are constrained by density dependent growth. In this respect we found a corroborating pattern in a field study of 10 lakes since there was a negative correlation between morphological divergence between the littoral and pelagic habitats in each lake and the intraspecific biomass in the lake (Figure 5b). Intraspecific competitor biomass is frequently used as a proxy of intraspecific competition (e.g. Bolnick 2001, 2004; Svanbäck & Persson 2004), and the results of paper IV hence suggest that a reduction in growth rates due to intense competition might slow down and/or constrain morphological plasticity and likely also divergence between contrasting environments. The underlying mechanisms behind this pattern are to date not known, but it might be that at low growth rates all energy available is used for metabolic maintenance and no surplus energy is therefore available for morphological modulation.
Figure 5. The relationship between morphological divergence and competition. A) Morphology was positively related to the individual growth rate, and differentiation between habitat types (filled symbols indicate littoral habitat type and open symbols pelagic habitat type) was confined to treatments with high growth rates (triangles). Individual growth rates usually decrease with increased levels of competition, and no differentiation was found between habitat treatments at intermediate (squares) or low (circles) growth rates. B) The degree of morphological differentiation (y-axis) between littoral and pelagic perch decreased with increasing levels of intraspecific competition (perch biomass, CPUE) in 10 sampled lakes.

Divergence of internal morphological attributes in resource polymorphisms.

Whereas most studies conducted on resource polymorphisms have focused on divergence in external morphological features and their functional implications (e.g. Smith & Skúlason 1996; Svanbäck & Eklöv 2003, 2004),
little is known about differences in other phenotypic traits. It is well established among several vertebrate taxa that the digestive demands of the food utilized influence the digestive system (reviewed in Piersma & Lindström 1997; Starck; 1999). For example, individuals feeding on low quality food usually have larger digestive tracts compared to those feeding on more easily digested food resources (Sibly 1981). A larger digestive systems allow longer transit times and a larger diameter per unit body for food processing, hence facilitating a more efficient utilization of the energetic content of the food (Sibly 1981; Magnan & Stevens 1993). The proposed cost of having a large digestive tract is increased requirements of nutrients and energy for maintenance of the tract (Sibly 1981; Moss 1983), and animals are thus expected to trade-off the size of their digestive tracts between the digestive requirements of their food and the costs involved in maintaining a large organ system. We would therefore expect to find plasticity in the morphology of the digestive organs among animals experiencing temporal or spatial differences in food quality (Hammond 1993; Magnan & Stevens 1993; Piersma & Lindström 1997). Since organisms seldom display infinite plasticity, it might be costly for individuals with a specialized digestive system to switch to food types with novel digestive requirements. The diverse array of food types found in the different habitats utilized by resource polymorphic populations likely differ in quality. Divergent digestive requirements of these food types could thus hinder individual movement between habitats and in the long run hence facilitate stability and persistence of resource polymorphisms. In paper V a difference in the length of the gastrointestinal tract between perch in the littoral and pelagic habitats of a lake was found. Perch caught in the littoral habitat had on average relatively shorter guts compared to fish from the pelagic habitat (Figure 6a). A likely cause for these differences could be divergent resource use as indicated by the differences in stable isotope signature (δ¹³C and δ¹⁵N isotopes). At present we do not know whether littoral and pelagic food resources differ in digestibility and/or energy content, but a subsequent aquarium experiment suggested that this might actually be the case. Perch was shown to exhibit considerable plasticity in their digestive system, where fish adjusted their gut length to match the digestive requirements of the food. Individuals fed a food types that was hard to digest developed longer guts compared to those that were fed more easily digested food (Figure 6a). Furthermore, the littoral zone is hypothesized to be the preferred habitat of perch (Svanbäck & Persson 2004), and the food types found in the littoral habitat might be of higher energy content, digestibility and/or quantity compared to the pelagic habitat. A similar pattern was found by Magnan and Stevens (1993) where brook charr (Salvelinus fontinalis M.) feeding on their less preferred diet, zooplankton, were shown to have longer pyloric caeca compared to charr feeding on their preferred diet of macro-invertebrates. This pattern was hypothesized to be caused by a lower energetic value of zooplankton compared to macro-
invertebrates (Magnan1989). To study whether it was costly for perch conditioned on a specific food type to switch to a novel food type, paper V also investigated the change in body condition of fish whose diets were switched to either be of higher or lower digestibility. In accordance with the predictions the body condition of perch drastically decreased when the new food were of comparably lower digestibility (Figure 6b).

**Figure 6.** A) Gut length of perch exposed to either easy digested or less digestible food (Experiment: left panel). The right panel represents gut lengths of perch caught in the littoral and pelagic habitat of Lake Söderningen. B) Change in body condition of perch experiencing a switch in the quality of their food. The body condition of perch initially fed easily digested food (black squares) drastically decreased after the diet switch. Perch initially fed less digestible food (open squares) did, however, experience an average increase in body condition after the diet switch.
The body condition of perch initially fed less digestible food did, however, increase slightly after the diet switch (Figure 6b). Furthermore, the decrease in body condition for fish switching to less digestible food was only temporal (Figure 6b), suggesting that there might be a time constraint on the development of an optimal digestive system in perch. Despite the proposed cost when switching to a suboptimal diet, we do not know at present whether the observed decrease in body condition was associated with a cost of modulating the gastrointestinal tract, a cost of developing new digestive enzymes or simply a cost of switching to a diet with lower energetic value. Nevertheless, the approximately 40 days it took for fish exposed to a suboptimal diet to recover a higher body condition represent a substantial part of the growth period of perch at this latitude. Hence, if the observed pattern of a decrease in body condition when switching food types applies to natural conditions, this likely has large fitness consequences for perch. For example, individuals in suboptimal condition might be inferior competitors, take higher risks when foraging and thus increase their susceptibility to predators (Werner & Anholt 1993). Furthermore, fish in poor condition likely have lower growth rates compared to fish in good condition and as suggested in paper IV, a decrease in the growth rate should constrain perch from expressing an optimal morphology. This would in turn decrease an individuals’ competitive ability and thereby further decrease its fitness. Thus, based on the results of paper V, I propose that the shape of internal structures such as the digestive system might co-vary with food preference in resource polymorphic populations, and despite that this response could be highly plastic it might enhance habitat fidelity.
Conclusions and Perspectives

Despite that the work in this thesis only has touched upon a minor frac-
tion of those numerous mechanisms and factors that potentially shape an
individual’s phenotype, I hope that my results will help to fill some of the
gaps in our knowledge about what factors contribute to form the diversity of
organisms. In this section I will summarize the major findings of the thesis,
and based on my findings raise a number of issues that might be worth con-
sidering in future studies.

In light of what has been found in previous studies of fish, it is perhaps
not that surprising that perch morphology is highly plastic. More surprising,
at least to me, was the finding that an induced morphology to some extent
could be reversed. We know relatively little about the limits of morphologi-
cal plasticity, and these findings suggest that predictions of various evolu-
tionary and ecological interactions, such as for example the potential for
character divergence and competitive interactions between species, might be
altered if reversible plasticity is common in the natural environment. In line
with this result I found a rather weak heritable basis for perch morphology
but detected genetic differentiation at strikingly small spatial and temporal
scales. Something that might have contributed to form these patterns could
be that perch aggregate in genetically differentiated groups consisting of
close relatives. Since there also was substantial genetic differentiation be-
tween habitats of similar characteristics, I think that it is important to widen
the perspective in future studies to also consider the potential for differentia-
tion within similar habitats, especially so when studying the replicated mor-
phological variation found in post-glacial fish species. Whether small scale
genetic differentiation is common in perch is an open question. For example,
a recent study (Sara Bergek & Mats Björklund, unpublished manuscript)
found evidence for genetic differentiation at a similar scale as found in paper
II, whereas there were no genetic structures between littoral and pelagic
perch from a relatively smaller lake (Olsson et al., unpublished data). It
might be that small scale genetic differentiation in perch is lake dependent,
since both lakes where genetic structures were detected were comparably
large. A recent theoretical study also suggested that evolutionary branching
is more likely in populations of large sizes (Claessen et al. In press). A pre-
requisite for genetic differentiation might also be that perch from different
parts of the lake have separate spawning grounds (see e.g. Hendry et al.
2000). Nevertheless, our results suggest that if we overlook the potential for
temporal differentiation and only collect samples at a single occasion, we may get a biased picture of the level of population differentiation that actually exists.

Despite that it has rarely been addressed in empirical studies of fish, the finding that a number of different environmental variables could affect the phenotypic expression in populations is, to me, rather straightforward. Nevertheless, if we are to establish what factors that are important in promoting divergence in nature, more multi-factorial studies on the phenotypic expressions are needed. Furthermore, a long standing paradigm that has little empirical support is that behavioral changes should precede morphological transitions during the process of divergence. I suggest that the finding of a plastic response in both behavior and morphology to the resource level experienced might indicate that morphological differentiation, in at least perch, could be driven by behavioral responses to a heterogeneous environment. Natural populations are seldom at numerical equilibrium (Krebs et al. 1995; Hanski et al. 2001; Mittelbach et al. 1995; Persson et al. 2003; Svanbäck & Persson 2004). Rather, their densities fluctuate over time, something that in turn might affect the amount of resources available. The finding of that a difference in resource levels could impact both behavioral and morphological development of perch hence suggests that population dynamics might influence diversification.

I also propose that intense competition could constrain morphological divergence since the morphological development might be influenced by differences in growth rates. I do, however, still believe that intraspecific competition might play an important role in the process of divergence, but during somewhat more limited conditions than previously thought. Competition driven divergence might actually be restricted to situations where divergence in resource use is favored at the same time as individual growth rates are kept sufficiently high for plasticity-driven divergence to be effective. For example, at low levels of competition, growth rates are sufficiently high for morphological modulation, but disruptive selection is weak, and so utilization of novel environments is therefore not favored. The potential for plasticity-driven divergence should, on the other hand, not be favored during the most intense forms of competition, despite strong disruptive selection, since individual growth rates might be too low. The results of paper IV also suggest that selection might be more effective on heritable rather than plasticity-induced morphological traits during high levels of competition.

Finally, paper V suggested that adaptations in the digestive system might co-vary with the morphological and dietary divergence of individuals in resource polymorphic populations. Despite that differences in the outline of the digestive tract might be the result of a plastic response to the quality of the current food types, these results also suggest that individuals adapted to a specific food type might experience a fitness-associated cost when switching to food types of lower digestibility. Several studies on postglacial fish spe-
cies have documented a trade-off in optimal morphology between the habitats utilized, something that might prevent random mixing of individuals and hence enhance habitat fidelity. Since the quality of food resources in different habitats likely differ, the proposed cost of having a too specific digestive system could at least theoretically reinforce habitat fidelity and in turn favor the persistence of resource polymorphisms.

During the course of this project I have, based on my findings, raised a number of questions that hopefully will be answered in the future. In my opinion, a few of these that potentially could be worth addressing in coming studies are:

- How common is reversible plasticity in nature and is the potential for it dependent on the size and age of the individual? Since a sufficient growth is required for the modulation of morphology (Paper I and IV), and individual growth rates decrease with increasing size, reversible plasticity is perhaps restricted to the high growth rates significant for small sizes and juvenile stages.

- How common is genetic differentiation at small scales and what is the mechanistic background? A related question is what environmental conditions and life-history characteristics are required for small scale differentiation to evolve?

- To what extent could we expect to find local adaptations between environments with similar habitat characteristics? It might actually be that differentiation within environments supersedes differentiation between contrasting environments (Paper II).

- Which environmental variables are important in trait plasticity and divergence in populations? Paper I and IV show that such diverse factors as the physical complexity, the feeding mode and the resource abundance of a habitat could influence the behavioral and morphological development of individuals. It is thus obvious that similar multi-factorial studies are needed if we are to understand the mechanisms important during divergence. Furthermore, the role of population dynamics in diversification should also attract the attention of students in evolutionary ecology.

- Paper III suggests that competition-driven divergence might be restricted to somewhat more limited conditions than previously thought. It would therefore be interesting to know if our findings are general and applicable to other taxa. Since little empirical work is done in this area of research, more studies are needed to confirm that increased levels of competition generally lead to character divergence.
At last, despite that paper \textsuperscript{V} suggests that divergence in the morphology of the digestive system might co-vary with habitat and diet choice in resource polymorphic populations, we do not know the limits of gut length plasticity, whether an induced response is reversible or not, or the heritability of gut length. Furthermore, the suggested cost of having a too specific digestive system might enhance habitat fidelity and in the long run also facilitate the stability and persistence of resource polymorphisms. We do, however, know little about this and it would therefore be interesting to conduct similar studies in other taxa in order to elucidate the generality of this hypothesis.

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Summary in Swedish (Sammanfattning)

Bakgrund


En av de djurgrupper där resurspolymeromfismer inom en och samma population är vanligt förekommande, är fiskar från sjöar i områden på norra halvklotet som var täckta av is under den senaste istiden. Hos dessa fiskarter förekommer resurspolymeromfismer i ett upprepat mönster kopplat till de olika habitaterna i en sjö. Abborren är en av de arter som uppvisar en sådan inomartsvariation i födo- och habitatsutnyttjande. Abborrar fångade i litoralen (den grunda strandzonen) är vanligtvis mer höglyggade, har en nedåtriktad mun och livnär sig främst på bottendjur. Individer från det pelagiala habitatet (det öppna vattnet) är å andra sidan mer ström- linjeformade, har en uppåtriktad mun och har specialiserat sig på att äta djurplankton. Vid större storlek börjar båda formerna även att äta fisk. Tidigare studier har indikerat att litorala och pelagiala abborrar är sin ursprungsmiljö trogen. Det förekommer nämligen ett begränsat utbyte av fisk mellan de två habitaterna. De habitatspecifika anpassningarna har även visat sig vara fördelaktiga då de
möjliggör den effektivaste bytesfångsten och rörelsesättet i de respektive habitaten. För personer med bakgrund som fritidsfiskare är det antagligen ingen nyhet att abborrar från olika habitat ser olika ut, med de mer högryggade "nate-abborrarna" och de mer "slanka" fiskar man får på grund mitt ute i sjön. Trots detta är det först på senare år som man har börjat studera kroppsformsvariationen hos abborre ur ett mer vetenskapligt perspektiv.

Varför studera resurspolymorfismer?


Vad jag kommit fram till

Resultaten från den inledande studien i denna avhandling visade att en abborres kroppsform är mycket plastisk och att ett förutbestämt utseende kunde ändras och även reverseras under en så kort tidsrymd som fyra veckor. Detta resultat tyder på att abborrar mycket snabbt kan svara på plötsliga miljöförändringar, i alla fall med avseende på dess kroppsform. I en uppföljande studie i Mälaren så undersökte det om det även finns några genetiska skill-
nader mellan abborrar från olika habitat. För att studera om abborrar från habitat med samma karakterer kan vara genetiskt differentierade från varandra, så undersöktes även två närliggande litorala lokaler. Provfisket utfördes både under abborrens lek (tidig maj) och i augusti, och det fanns tydliga genetiska skillnader mellan den pelagiala och de litorala lokalerna. Skillnader fanns även mellan de två närliggande litorala lokalerna under båda provtagningstillfällena. Något som var slående var att det även förelåg en genetisk differenceringen mellan de två provfisketillfällena inom varje lokal. Abborrarna från de olika habitaten uppgivade tydliga skillnader i kroppssform, men det fanns endast en svag koppling mellan dessa skillander och graden av genetisk differencerering. I enlighet med vad den inledande studien i avhandlingen visade, så verkade de genetiskt isolerade abborrgruppernas utseende istället vara styrt av en plastisk respons till de rådande miljöförhållandena på fängstlokalen. Mer detaljerade analyser visade att abborrarna inom de olika grupperna bestod av närbesläktade individer med begränsat utbyte av gener mellan grupperna. Sammantaget indikerar resultaten av dessa två studier att abborrar kan bilda genetiskt differentierade stim med nära släktningar, där utseendet är ett resultat av en plastisk respons till den rådande miljön.


I det avslutande arbetet i denna avhandling så undersökte vi om en abborrens tarmssystem är anpassat till och påverkas av de olika sorters föda som man hittar i de litorala och pelagiala habitaten i en sjö. En fältstudie indikerade att det finns en skillnad i tarmlängd mellan individer från de två habitaten. Litorala abborrar hade kortare tarmar än pelagiala abborrar. Ett uppföl- jande akvarieexperiment visade att denna skillnad i tamlängd kan vara kopplad till kvaliteten på födan som erbjuds. I enlighet med vad man tidigare sett i studier hos andra djur så utveckalde de individer som fick föda av låg kvalitet längre tarmar än de som fick föda av högre kvalitet. Det är i tarmarna som det största näringsupptaget sker, och genom att förlänga sina tarmar så får en individ ett mer effektivt näringsupptag om den främst livnär sig på föda av låg kvalitet. En trolig anledning till att inte alla individer maximerar längden på sina tarmar är att om man äter föda av hög kvalitet så överstiger kostnaderna med att bilda och underhålla ett extra stort tarmssystem vinsterna med det samma. Trots att utseende på abborrens tarmssystem verkar vara plastiskt så är det möjligt att kopplingen mellan tarmlängd och födokvalitet kan påverka en individs benägenhet till att byta habitat. Vi fann nämligen att kroppskonditionen sjönk drastiskt hos abborrar som tvingades byta till en föda av lägre kvalitet. Ett rimligt antagande är därför att en abborre som har ett tarmssystem väl anpassat till högkvalitetsföda i det litorala habitatet inte bör vara benägen att byta habitat till följd av kostnaden (dvs en försämrad kroppskondition) med ett dåligt anpassat matspjälkningsystem. En sådan kostnad av ett habitatskifte torde öka troheten mot ursprungshabitatet hos...
abboorre och således även möjliggöra upprätthållandet av resurspolymorfismen.

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