

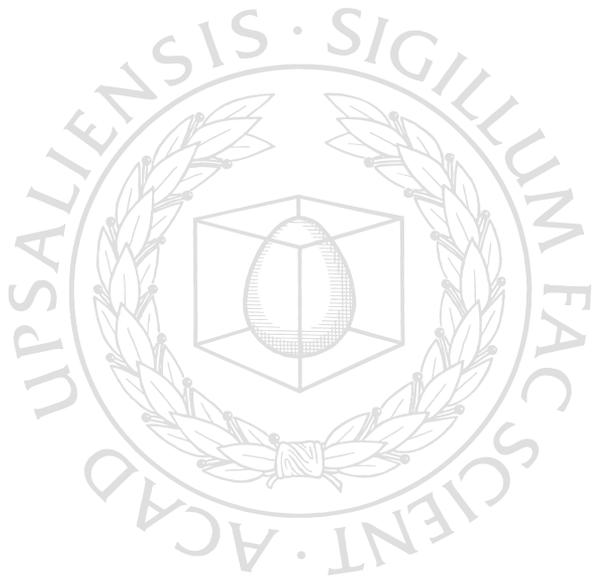


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Phenotypic Processes Triggered by Biological Invasions

PHILIPP E HIRSCH



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Abstract

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Individuals within a single population can vary widely in their phenotype e.g. in their body shape. These differences are an important source of biodiversity and they can precede evolutionary divergence within a population.

In this thesis we use the biological invasion of the zebra mussels into Swedish lakes to investigate which processes create or maintain phenotypic diversity within populations of the two native fish species perch and roach and the mussel itself. Both fishes have specially adapted body shapes that depend on whether they feed in the near-shore or open-water habitat of lakes. This habitat-specific divergence was more pronounced in lakes with zebra mussels, probably because resources in both habitats were in higher supply due to the mussels' effects on the lakes. Divergence in perch body shapes between habitats was also higher in lakes with a higher water clarity, suggesting that visual conditions can affect the resource use and thus also the expression of a habitat-specific body shape.

When investigating the diversity of body shapes in the mussel itself we found that mussels from one lake changed their shell shape when exposed to different predators: fish predators induced a more elongated shell shape while crayfish predators induced a rounder shell. These specific shell shapes probably serve as two alternative predator defenses protecting the mussel from predation.

We conclude that the availability and use of distinct resources is an important source of diversity within populations. Abiotic conditions can play a previously underappreciated role by promoting or impairing the use of the distinct resources thus affecting the divergence. The diversity of shell shapes we found in the zebra mussels complements our study by demonstrating that not only consumer responses to resources but also resources' responses to predators can generate phenotypic diversity.

Keywords: Resource polymorphism, phenotypic plasticity, phenotypic divergence, anti-predator responses, *Perca fluviatilis*, *Rutilus rutilus*, *Dreissena polymorpha*

Philipp E Hirsch, Uppsala University, Department of Ecology and Genetics, Limnology, Norbyvägen 18 D, SE-752 36 Uppsala, Sweden.

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To my family

Envelope pictures: Zebra mussel-colonized footbridge with perch in Lake Långsjön

List of Papers

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

- I Svanbäck R., Hirsch P.E., Bartels P. and Eklöv P. Different venues, different menus: causes and consequences of disruptive selection in natural populations
(*manuscript*)
- II Hirsch P.E., Eklöv P. and Svanbäck R. Indirect trophic interactions with an invasive species affect phenotypic divergence in a top consumer
(*in revision*)
- III Hirsch P.E., Eklöv P., Reyes M., Quevedo M., Fransson R. and Svanbäck R. Replicated divergence in two consumer species affected by resource availability
(*manuscript*)
- IV Bartels P., Hirsch P.E., Svanbäck R. and Eklöv P. Visibility drives intra-population divergence in Eurasian perch (*Perca fluviatilis*)
(*manuscript*)
- V Hirsch P.E., Cayon D. and Svanbäck R. Plastic responses of an invasive prey to multiple predators – an experimental and field study
(*manuscript*)

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Prologue

Progress in science

One common way of progressing science is through falsification of hypotheses. The process of falsification typically starts with the formulation of a hypothesis which is a proposed explanation of a natural phenomenon. Researchers test the hypothesis by studying how well it can explain observations of nature. Failure to explain the natural phenomena, i.e. observations that contradict the hypothesis, leads to the falsification and modification of the hypothesis. A modified hypothesis then explains nature better. Over time, researchers will improve their ability to explain nature by constantly testing and modifying hypotheses so that they account for ever more observations. In this thesis I aim to contribute to this form of scientific progress. I will do that by formulating a number of hypotheses and by testing whether these hypotheses can explain the observations I (and other researchers) have made in nature. For a critique and alternative accounts of scientific progress see Chalmers (1999).

Introduction

Motivation of this thesis

Fifteen years ago when walking along the beach I found a large number of jellyfish that were washed ashore. At closer inspection, I found only the lower part of the animal resembled a jellyfish. On top of a soft body part with tentacles, the animal featured a small, boat-like structure with a sail spanning from one side to the other. At home, when consulting a field guide I learned these jellyfish indeed use their sail-like structure for wind-dispersal across the sea. Even more mesmerizing was the guide's information that some individuals of this species have left- while others feature right-oriented sails. This diverging pattern would secure a population's passive dispersal by enabling it to sail with different wind directions (Woodcock 1956). Then and now I wondered what the origins of this peculiar variation in morphology might be, and to a large extent this curiosity led to this thesis. Today I know that the jellyfish (*Velella velella*) displays a prominent form of morphological variation named 'polymorphism'. Which factors determine the divergence in left- and right-oriented sails in this elusive species remains debated (Bieri 1959, Woodcock 1997). The knowledge of factors leading to variation however, is not only an inspiring source of motivation to a young scientist, but also relevant for scientific knowledge.

Within every species, and even within every natural population, there is some degree of variation in morphology or other traits among individuals. Such variation is the raw material from which natural selection selects out certain individuals. Those individuals whose traits constitute the best fit to the environmental conditions will be able to reproduce while those with a less optimal fit will be selected out. Over time, individuals favored because of certain traits become reproductively isolated. Through this process of speciation their advantageous traits become the fixed characteristics of a certain species. These species make up the diverse entities that we term 'biodiversity' (West-Eberhard 2003). Understanding the processes leading to variation between individuals in the first place can help us to understand how environmental factors in general can generate diversity. Regardless of whether such variation between individuals ultimately leads to the formation of new species, understanding the factors that lead to such differences will allow us to better explain nature.

Resource polymorphisms

More common in nature than the peculiar case of the jellyfish are resource polymorphisms. In resource polymorphisms, variation within a population is driven by differences in resource use. Resource polymorphisms arise when not all individuals of a population feed on each resource type to the same extent. This is common in nature and subsets of a population frequently use different resources (Skúlason and Smith 1995, Smith and Skúlason 1996). Often, this differential resource use entails a modification of the phenotype, commonly in the form of morphological traits that are specially developed to feed on specific resources. For example, in the diverse group of African estrildid finches the beak size is the main morphological trait determining which seeds the respective species feeds on. The beak size determines the efficiency with which a bird can handle a seed i.e. finches with large beaks feed more efficiently on hard seeds while finches with small beaks perform better on soft-seeds (Smith 1990). These different specializations are one factor leading to phenotypic diversification: finch populations exhibit a resource polymorphism in the form of small and large beak sized morphs.

Phenotypic divergence

As the beak polymorphism in finches illustrates, differences in resources can lead to different consumer phenotypes. These phenotypic differences are the first step towards phenotypic divergence within a population. For phenotypic divergence to occur, the environment should offer distinct rewards in form of distinct resources (Schluter 2000). It is the difference in rewards between habitats or along an environmental gradient that generates trade-offs among different phenotypes. Only if there are distinct rewards there is no one phenotype that can perform best across the entire spectrum of environmental conditions (Marnocha et al. 2011). Many environments feature distinct habitats which provide different resources to consumers. For example, lakes can be divided into a near shore-line littoral and an open-water pelagic habitat. For consumers like fish the resources and hence the form of resource use are distinctly distributed between these habitats (Robinson and Wilson 1994). Littoral resources are patchily distributed and physical structures such as stones and macrophytes affect foraging. Pelagic resources, in contrast, consist of widely dispersed organisms in the open-water column which is devoid of physical structure. Therefore, efficient foraging on either littoral or pelagic resources requires different swimming behaviors which can in turn lead to different morphologies. The bottom-living prey of the littoral zone needs to be slowly approached and picked selectively, requiring a deeper body which minimizes turning radius while maximizing maneuverability. Free-swimming widely dispersed prey, in contrast, needs to be searched for

by persistent swimming. Persistent swimming requires a slender body that minimizes drag forces (Pettersson and Hedenström 2000). Thus, no single morphology will be equally efficient in foraging in both habitats of a lake. Between the habitats the optimal phenotypes will differ, leading to phenotypic divergence within a fish population. This form of divergence into deeper-bodied littoral and streamlined-bodied pelagic forms occurs in a large number of freshwater fish species and has become a textbook example for the study of phenotypic divergence (Robinson and Wilson 1994).

Disruptive selection

An important factor generating and maintaining resource polymorphisms is disruptive selection (Skúlason and Smith 1995). Disruptive selection, in this context, is based on trade-offs in resource use efficiency of different phenotypes. Say the individuals within a population vary in some traits connected to foraging. If resources differ in the environment, some individuals will be feeding with higher efficiency on some resources but lower efficiency on others. This also means that individuals need to trade-off efficiency in feeding on one resource against the efficiency in feeding on another. For example, if a finch with a small beak switches to feeding on hard seeds it will be less efficient than an individual with a large beak. Such trade-offs in feeding efficiency are thought to be connected to fitness trade-offs (Hendry et al. 2009).

It is safe to assume that feeding efficiency and thus nutritional status is positively related to an individual's fitness. A better match between the expressed morphology and the one required to efficiently feed on a specific resource will ultimately lead to higher fitness. This should then favor specialized phenotypes with a high phenotype-resource match. Intermediate phenotypes not specifically matching any resource have an intermediate foraging efficiency and are hence disfavored compared to the specialized phenotypes. Support for this hypothesis comes from experiments which compare the feeding efficiency of individuals with different phenotypes. For example, sticklebacks show a pronounced resource polymorphism, with a deeper bodied morphology feeding predominately on bottom-living prey and a slender bodied morphology feeding on widely dispersed prey in the open water. When two individuals with a specialized phenotype were artificially crossed, the offspring had an intermediate morphology. Feeding efficiency of this intermediate phenotype was lower on both, bottom-living and open-water prey (Schluter 1995). A reduced feeding efficiency lead to a slower growth (Schluter 1995) and hence the fitness of this intermediate phenotype should be lower compared to the specialized individuals. Disruptive selection, then, is thought to select against these intermediate individuals

because of their lower fitness while at the same time favoring extreme phenotypes. The extreme phenotypes will have the highest feeding efficiency and the highest fitness. Disruptive selection is therefore believed to lie at the root of phenotypic divergence within populations (Schluter 2000). The stronger the disruptive selection is, the stronger should be the divergence between subsets of a population. Studying which factors influence the strength of disruptive selection and phenotypic divergence hence allows us to follow the process of diversification within a population.

Phenotypic plasticity

The stickleback example of an intermediate phenotype resulting from a cross between extreme phenotypes implies that there was a heritable determination of the feeding morphology. Variations in phenotypes however, need not always have a genetic basis. Frequently they result from phenotypic plasticity. Phenotypic plasticity describes an individual's ability to produce different phenotypes in response to different environmental conditions (West-Eberhard 2003). For example, the spadefoot toad's tadpoles can develop different trophic morphs depending on available resources. Most commonly, these tadpoles are omnivorous. However, when shrimp are present in the pond where they hatch, they can develop an alternative carnivorous morph which efficiently preys on shrimp. Together with tadpoles that develop the original omnivorous morph, this plasticity leads to a resource polymorphism in tadpoles populations (Pfennig 1992).

The above discussed examples investigated how consumers respond to resources and how that can lead to phenotypic diversity. However, many, if not most, species are not only consumers but are themselves a resource for predators. To avoid their predators many prey species can modify their phenotypes. Different predators can vary in their feeding tactics and different predator tactics might require different prey defense phenotypes. Many prey species have no way of predicting which predator will pose the biggest threat to them. Tadpoles, for instance, may encounter either actively hunting fish predators or sit-and-wait dragonfly predators. Which of the two predators will pose the larger threat is not predictable for individual tadpoles at the time of hatching. The threat of predation is not constant through space and time, with predators and their prey fluctuating in density. To overcome this unpredictability, the tadpoles can plastically express one of two different anti-predator tail shapes. A longer tail allows to escape from actively hunting fish predators and a deeper tail allows to quickly evade attacking sit-and-wait predators by a quick burst swim (Teplitsky et al. 2004).

Unpredictable threats from different predators are assumed to favor individuals that are able to plastically change their defense phenotypes, whereas individuals that express the same phenotypes regardless of predation threat, should be disfavored. Because most defenses come with energy costs the decision to express the defense has consequences for the prey's energy budget. Efficiency in sensing and plastically responding hence improves not only the survival but also the energy optimization of the prey (Agrawal 2001). Selection favoring individuals that are plastic in their phenotype expression also means that phenotypic plasticity itself is a trait that can evolve (Van Buskirk and Relyea 1998). Phenotypic plasticity should not be seen as opposed to evolutionary divergence but much more as one important component for the creation of diversity (West-Eberhard 2003).

An agenda to study the origins of phenotypic diversity

Given the variety of factors that lead to phenotypic diversification an agenda is needed for studying the origin of this diversity. The question of how the diversity of life is created and maintained is one of the central questions of biology, unifying disciplines like ecology and evolutionary biology (Matthews et al. 2011). Following Darwin's seminal work on this question (Darwin 1859), generations of naturalists have advanced his ideas to explain the origins of diversity. This has led to a synthesis termed 'the ecological theory'. The ecological theory posits that phenotypic and ultimately evolutionary divergence results from disruptive selection which itself stems from differences in the environment (Schluter 2000). In a recent book, Schluter (2000) re-evaluated the ecological theory in light of the evidence that has accumulated since its formulation. He proposes that the study of which factors lead to phenotypic divergence should follow two aims. The first is to clarify whether disruptive selection qualifies as the source of phenotypic divergence i.e. if selection truly favors extreme and selects against intermediate phenotypes. The second aim is to identify the factors that influence phenotype expression and lead to disruptive selection.

In my intention to contribute to the study of diversity I will follow this agenda. Yet, studying these factors is difficult because most species are embedded in complex food webs. Within this food web they directly and indirectly interact with not only their resources but also with predators and competitors. As Matthews et al. (2011) imagined in an elegant analogy, individuals can be considered actors whose roles (phenotypes) change in response to many different influences from peer-actors and the audience (forces of selection). The actors' roles (phenotypes) also change because they act on a stage of abiotic ecological conditions. These abiotic conditions constitute the structural components of the theatre which affect the roles the actors play but can themselves be influenced by the actors (species

interactions changing abiotic conditions). The life of actors is complex. And following this analogy we have to admit that disentangling the factors that determine the degree of phenotypic diversification can be a daunting task. One possible way of tackling this, is to use biological invasions as natural experiments (*in sensu* Stockwell et al. 2003).

Biological invasions as experiments

Biological invasions typically start with a species entering an ecosystem which it would not have reached by its natural means of dispersal. Upon the usually human-mediated arrival, the species can establish a founder population within the new ecosystem. From a successful founder population, the species then further spreads and flourishes with notable effects for the ecosystems' native species. This is when a newly established species is labeled as invasive (Lockwood et al. 2007). The success of many invasive species implies that they are able to rapidly adapt to new environmental conditions. The rapid adaptation in some invading species has changed our picture of phenotypic divergence and evolution as a process requiring thousands of generations (Huey et al. 2000). Investigating invasive species' responses to the new environment could therefore allow us to study which factors affect phenotypic diversification.

Many biological invasions come with drastic effects for the invaded ecosystems' species. For the native community each invasive species constitutes a new predator, a new prey or a new competitor, or even all of those at once. Invasive species can thus be considered a new interaction component 'added' to the pristine ecosystem. By comparing invaded and pristine systems we have the possibility to investigate how different species interactions affect the magnitude and occurrence of phenotypic diversification.

In some cases the effects of invasive species also change the abiotic conditions in the invaded environment. For example, invasive crayfish can drastically change the bottom structure of small rivers by moving large amounts of sediment when digging their burrows (Statzner et al. 2000). Biological invasions can thus also serve as natural experimental manipulations of the abiotic conditions. Studying the differences in phenotype expression and the degree of divergence under different abiotic conditions then allows further investigating the factors that create or maintain diversity within populations.

Model species

The zebra mussel

A prominent invasive species with demonstrable effects on biotic and abiotic conditions in the invaded ecosystems is the zebra mussel (*Dreissena polymorpha*). Native to the Ponto-Caspian area the mussel has colonized a wide variety of lakes and watercourses on both sides of the Atlantic (Higgins and Vander Zanden 2010). Where it has established, it occurs in densities not normally reached by any native species and usually dominates the benthic fauna in terms of biomass (Ward and Ricciardi 2007). In invaded lakes zebra mussels can have drastic effects on the near shore littoral and open water pelagic resources (Higgins and Vander Zanden 2010). Zebra mussels are efficient bottom-living filter feeders and their filtering activity augments the biomass production by shunting pelagic nutrients to the benthic zone. Benthic organisms not only benefit from the increase in pelagic food but also from the zebra mussels' shells which provide a surplus of structure and thus habitat (Figure 1). Taxa living on the sediment increase in density where zebra mussel occurs because the mussels' shells increase the foraging grounds for both invertebrate prey and predators. Benthic invertebrates living in the sediment, however, suffer from the mussels sealing off the sediment (Ward and Ricciardi 2007).

The phytoplankton mostly decreases in density due to the zebra mussels' filtering activity (Higgins and Vander Zanden 2010). In lakes where phosphorus is not limiting phytoplankton growth, the presence of zebra mussels can trigger shifts in zooplankton community composition. The mussels' incurrent siphons limit the size of ingestible zooplankton allowing the mussel to filter out only smaller sized zooplankton and phytoplankton (MacIsaac 1994). However, when phosphorus concentrations are sufficient to sustain rapid phytoplankton growth this can compensate for the loss by mussel foraging and maintain a stable but lower phytoplankton biomass. The larger sized zooplankton taxa which could escape mussel ingestion can feed and flourish on the remaining phytoplankton stock. This mechanism is likely underlying the shifts towards larger-sized zooplankton taxa in some zebra mussel invaded lakes (Idrisi et al. 2001).

Perch and roach

As model consumer species whose phenotypes could be affected by the zebra mussels we studied perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*). Both species occur in most lakes in Sweden and together they constitute the main part of the biomass of the total fish community (Brunberg and Blomqvist 1998).

Both species show resource polymorphisms between littoral and pelagic habitats with deeper-bodied littoral and streamlined-bodied pelagic individuals (Figure 2). Experimental and field studies demonstrated that deeper-bodied morphs are more efficient in feeding on bottom-living invertebrates while slender-bodied morphs are more efficient in feeding on widely dispersed zooplankton prey (Hjelm et al. 2003, Svanbäck and Eklöv 2003). Both, roach and perch thus satisfy the condition that different phenotypes have different feeding efficiencies on different resources.

In combination with the zebra mussels' demonstrable effects on lakes' littoral and pelagic resources these model species make up a suitable system for investigating which factors influence phenotypic diversity.

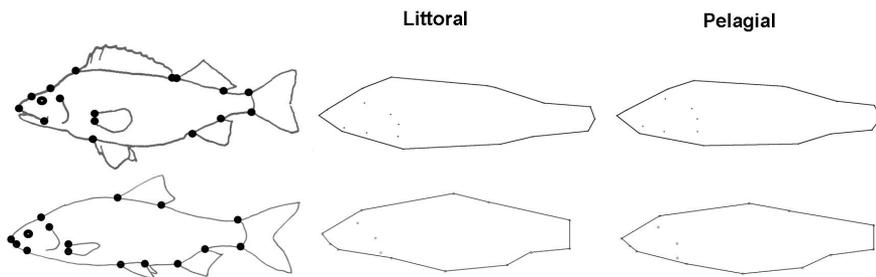


Figure 2. Morphology of perch (top) and roach (bottom). The outlines depict the average variation in shape between littoral and pelagic habitats that were derived from the morphological landmark analysis using the landmarks indicated on the fish bodies to the left.

Objectives and hypotheses of the thesis

In my thesis I aim to investigate a number of factors potentially influencing phenotypic expression and diversification by using the biological invasion of the zebra mussel as a natural experiment.

I first aim to clarify whether disruptive selection truly favors extreme phenotypes and whether that leads to phenotypic divergence. For that I put forward the following hypothesis:

1. The fitness of an individual is determined by how well its morphology matches its resource use. Differences in resource use within a population therefore lead to disruptive selection and morphological divergence (paper I)

Given that the use of distinct habitat-specific resources is tightly coupled to the morphology of an individual I then ask whether different resource availabilities influence the magnitude of divergence between habitats. I formulate as a second hypothesis:

2. The availability of profitable and discrete resources in habitats affects the magnitude of morphological divergence between habitats (paper II, paper III)

After having addressed these important biotic conditions I continue by asking whether also abiotic conditions can influence phenotypic diversification. I hypothesize:

3. The use of discrete resources and thus the magnitude of divergence can be changed by visual conditions (paper IV, paper I)

Because not only consumers react to resources but also resources to consumers I end by investigating how an invasive species responds to predators in a newly invaded system. Specifically, I propose as a last hypothesis:

4. Phenotypic plasticity in an invasive species allows specific responses to predators in a newly invaded system (paper V)

Methods

Study lakes

This thesis is based on experimental and field data collected on two spatial scales: a detailed survey in one lake and surveys including between five and 14 lakes.

The detailed survey and the experiment with zebra mussels were conducted at Lake Erken. Lake Erken is a meso-eutrophic lake situated in Southeastern Sweden. Zebra mussels were first recorded in the lake in 1975. Shortly before, signal crayfish (*Pacifastacus leniusculus*) were also introduced, replacing the extinct naturally occurring noble crayfish (*Astacus astacus*) (Naddafi et al. 2007). The lake holds a native population of roach and perch.

At nine sites within Lake Erken and in several other lakes we sampled benthic invertebrates and zooplankton to measure the resource availability for roach and perch. Roach and perch were caught with standardized littoral and pelagic nets that allow the catch of all size classes of a population (except very small larval fish).

The lake surveys across several lakes made use of the isolated nature of lake ecosystems in a landscape which allows to utilize lakes as replicate units. To assess the effect of zebra mussels on the lakes' resources and consumers we compared invaded lakes and pristine lakes. In detail, we studied the divergence in roach and perch from similar lakes situated in the Uppland region in Southeastern Sweden. Detailed limnological and ecological analyses indicated that the lakes with zebra mussel do not show any directional differences in ecological conditions that could confound the effect of the zebra mussels. A recent ecological model aimed at predicting in which waters the zebra mussel can potentially occur found that all the Uppland lakes in our study could theoretically host zebra mussels (Hallstan et al. 2010).

Morphology of fish

Morphology was measured using geometric morphometrics based on landmark positions known to differ between littoral and pelagic fish (Figure 2). For this, pictures were taken and the landmarks were digitized using special software (paper I). The relative positions of the landmarks were used as data input into a multivariate discriminant function analysis to determine the maximal discrimination between littoral and pelagic individuals. A subsequent canonical analysis revealed a single score for each individual. The score indicates each individual's position in the littoral-pelagic morphology spectrum. The divergence was assessed by calculating the difference between the average of all pelagic and littoral individuals' scores.

Short and long term diet overlap

As a measure of short-term diet overlap we analyzed the gut content of littoral and pelagic fish and expressed the overlap as the proportion of shared diet items between both forms (paper IV).

As a long-term measure of diet overlap we used stable isotope analyses. The trophic role of littoral and pelagic fish in lakes is typically estimated using the ratios of heavy to light carbon and nitrogen isotopes. The heavy carbon isotopes are less likely to be taken up by pelagic primary producers compared to bottom-living primary producers which accumulate relatively more heavy carbon isotopes. This difference is reflected in higher consumers carbon isotope ratios and allows to position an individual into the littoral or pelagic feeding ground (France 1995). The heavy nitrogen isotopes also

react more slowly than lighter ones. This leads to an increased accumulation of heavy nitrogen with higher trophic levels of the food web. The heavy nitrogen isotopes therefore allow to determine the trophic position of an individual in a food web (Fry 2006). When putting up a carbon and nitrogen stable isotope biplot each individual can be given a point which depicts its position in this two-dimensional niche space. As a measure of diet overlap between littoral and pelagic forms of roach and perch we used the convex hull area overlap (Quevedo et al. 2009). The convex hull is the area occupied by all littoral or pelagic individuals in the two-dimensional (carbon-nitrogen) space.

Fitness measure and disruptive selection

We use the condition factor as proxy for fitness as it is highly correlated to food intake and growth rate, which are important for survival and reproduction (Persson et al. 2000, Persson et al. 2004). The condition factor was calculated as the weight of an individual divided by its length whereby the length is put in relation to the average length increase in each population to account for differences in growth between populations.

The direction of natural selection is measured using selection gradients which are standardized descriptive statistics for the relation between fitness and factors influencing fitness (Lande and Arnold 1983). Directional selection means that a single phenotype is favored or disfavored. Divergent selection describes selection for divergent phenotypes whereby disruptive selection favors the extreme ends of a phenotypic spectrum (Rueffler et al. 2006). We estimated the standardized selection gradients by linear and quadratic regression of our fitness proxy (condition factor) against the phenotype (morphological score of each individual). The presence and magnitude of disruptive selection was then measured by the curvature of the quadratic relation between fitness and morphology. If the curvature is positive then individuals at the two extreme ends of the morphology spectrum have the highest fitness whereas intermediate phenotypes have lower fitness.

Zebra mussels' phenotypic responses to predators

Phenotypic anti-predator traits in zebra mussels were assessed measuring morphology and strength of the shells. To characterize shell morphology we used elliptic Fourier descriptors. This method compares the outline of a shell to a same-sized ellipse and extracts principal components that can be visualized and allow to discriminate between rounder and more elongated shells (Iwata and Ukai 2002). To assess the shell strength we used a force gauge that measured the shells resistance to breakage at the place of the shell where it is usually crushed by shell crushing mussel predators.

Results and Discussion

Disruptive selection leads to phenotypic divergence

Ecological theory attributes the origin of diversity to different selective pressures resulting from different environmental factors. Our search for the origins of diversity within our model species therefore begins with an empirical test for different selective pressures in different environments. Specifically, we tested disruptive selection as the source of divergence in fourteen populations of perch that all diverged into a littoral and pelagic form. The discreteness of littoral and pelagic resources suggests that only a specialized pelagic or a littoral morphology can best exploit the habitats' resources. We would then expect morphologically divergent individuals to share fewer diet items than morphologically similar individuals. Indeed, in line with our expectations, we found that diet overlap between perch decreased with increasing morphological distance between individuals (paper I, paper IV). Long-term diet choice inferred from stable isotope analyses further confirmed the connection between resource use and morphology. When roach and perch had a high morphological divergence between littoral and pelagic habitats then also the niches between individuals inhabiting the two habitats were divergent, i.e. there was a low long term diet overlap (Quevedo et al. 2009, paper III, figure 3). This indicates that morphology is tightly connected to the resource use but more importantly this means that the fitness of extreme phenotypes should be higher than that of intermediate ones. In perch and roach and many other fish species it has been shown that morphology determines feeding efficiency in littoral and pelagic habitats (Robinson and Wilson 1994, Svanbäck and Eklöv 2003). Individuals with intermediate morphologies and hence intermediate feeding efficiencies should be selected against while individuals on both extreme ends of the morphology spectrum should be favored. We actually found that with increasing match between resource use and morphology an individual's fitness was higher (paper I, figure 2). The lower fitness of intermediate phenotypes should promote phenotypic divergence and we could show that morphological divergence was positively related to the strength of disruptive selection (paper I, figure 1). In other words: the higher the fitness of the extreme phenotypes compared to the intermediate ones, the more the phenotypes differed from each other between habitats.

Disruptive selection stemming from different environments is one of the most prominent explanations for phenotypic and ultimately evolutionary divergence (Smith and Skúlason 1996, Hendry et al. 2009). Yet, empirical evidence for the divergent forces of such different selection pressures is surprisingly scarce (but see e.g. Carlsbeek and Smith 2008). Our results confirm our expectations and provide empirical support for the idea that selection favoring extreme phenotypes can lead to phenotypic divergence within a population.

Replicated phenotypic divergence

How do we make sure that the factors we assume to influence phenotypes are of general nature and not specific to only one focal species or one study system? When the same pattern of diversification is observed in more than one species and more than one system then we can infer that the factors leading to that diversification are of a general nature (Ruehl et al. 2011). For example, all mammals that permanently live underground have evolved stronger forelimbs for digging. Because this morphological trait is found in such diverse groups as placental and marsupial mammals it is thought to be a common response to a general selective pressure (Nevo 1979). If different habitats pose different selective pressures in general, then individuals of several species should show a similar direction of divergence between habitats. Indeed, in fish, the divergence into a littoral and pelagic morphotype has been demonstrated in a variety of species (Robinson and Wilson 1994, Skúlason and Smith 1995). Few studies, however, have considered testing for divergence in more than one species in the same replicated systems (but see Langerhans et al. 2003, Ruehl et al. 2011). Such a test would be particularly compelling because system- and species-specific differences can be accounted for when using more than one species and several systems as replicate units.

We therefore studied the morphological divergence between littoral and pelagic forms in both roach and perch in five lakes in the same geographical region and found that both roach and perch diverge into a littoral and pelagic form (paper III, figure 1). In both species the littoral forms had a deeper body whereas the pelagic forms were more slender-bodied (paper III, figure S3). Roach and perch are similar in the resources they consume and the way how they consume them. Yet, they are very distant phylogenetically, belonging to Perciformes and Cypriniformes, respectively which are two different orders of the class of ray-finned fishes (Actinopterygii). Our results hence highlight that habitat differences generally result in similar selective pressures leading to phenotypic divergence in freshwater fish.

Resource availability driving divergence

We now know from perch that morphological divergence is likely a result of disruptive selection and we could confirm that a second species shows the same divergence in the same systems. This knowledge is a suitable starting point for asking which factors lead to morphological divergence in both roach and perch. We could illustrate that the relation between resource use and morphology influences divergence in perch (paper I, paper IV). We therefore studied the relative importance of resource availability for phenotypic divergence in both perch and roach. We did so by using the zebra mussels' demonstrable effects on lake ecosystems' resources. Lakes with zebra mussels have higher densities of large benthic invertebrates and large zooplankton (paper II, figure 3,4). Perch and roach prey selectively and with higher energy gain on large invertebrates and large zooplankton (Persson 1986). We hypothesized that the availability of distinct resources would influence the magnitude of divergence in consumers. When testing this hypothesis using the zebra mussels effects on lakes we found roach and perch to have a higher morphological divergence in lakes with zebra mussels. We propose this increased divergence to be a response to the zebra mussel-mediated increase in resources. A surplus of discrete resources would further increase the fitness gain of expressing a specialized phenotype relative to an intermediate phenotype. Increasing morphological specialization to one habitat's resources could hence explain the augmented phenotypic divergence.

We found that zebra mussels did not change the presence or absence of habitat-specific resources but they increased their availability and their quality (paper II, figure 3,4). Our results thus highlight the importance of distinct rewards across a spectrum of environmental conditions for generating phenotypic diversity within populations.

The role of competition

Competition is believed to be an agent of disruptive selection and as such central to phenotypic and evolutionary divergence (Losos and Pringle 2011). When resources are limited, individuals with similar feeding preferences will compete for those resources. To mitigate this competition a competing individual can modify its phenotype so that its feeding efficiency on the limited resources is increased relative to its competitors. This can lead to divergence between subsets of a population or between species competing for the same resource. For example, when two different species of Darwin's finches occur on islands alone they have similar beak sizes to prey on seeds. But when they occur together and compete for seeds one develops large

beaks whereas the other one develops smaller beaks. The phenotypic divergence between the two finch relatives is believed to have originated from individuals specializing on different parts of the limited resources (Grant and Grant 2006). Perch and roach are not related but forage mainly on the same resources. Previous research has shown that they can compete for these shared resources (e.g. Persson 1986). Our data did not allow to disentangle the mechanisms of how competitive interactions between roach and perch affect phenotypic divergence in either of the species. We could demonstrate however, that the morphological divergence in the two species was actually positively correlated. When perch showed a high divergence between littoral and pelagic forms then roach did as well (paper III, figure 1). Clearly, how the interaction between the two species affects divergence is a question that deserves further study.

Competition between roach and perch has been assumed to be less important than competition within individuals of the same species, at least in determining which habitat both species occupy (Svanbäck et al. 2008). In general, competition among individuals of the same species should be much fiercer than between different species. A conspecific will most likely be more similar in its resource use and phenotypic specialization and as such a stronger competitor than another species (Bolnick et al. 2003). Interestingly, experimental work and field data suggest that high competition from conspecifics restricts rather than promotes phenotypic divergence in perch (Olsson et al. 2006, 2007). This can be mainly attributed to differences in the growth rate which is lower under high competition. With many competitors and lower growth rate there seems to be less energy left to invest into modulation of the morphology (Olsson et al. 2006, 2007). Our data supported the positive relation between growth rate and magnitude of divergence in perch (paper II, figure 6).

Yet, the density of intra-specific competitors did not emerge as a consistent factor influencing divergence in roach or perch (paper I, figure S6, S7; paper II, table S1; paper IV, table S2). A possible explanation for these inconsistent results can be found in a difference in the effective resource availability: for competition to act as a selective force the resources must be limited. Testing whether resources are truly limited is difficult and is seldom attempted (Gurevitch et al. 1992). Resource availability as such is rarely measured (Schluter 2000) and the majority of studies use the density of competitors as a proxy for the intensity of competition. Our results underscore the importance of including both resource availability and competition intensity measures in the search for which factors affect divergence.

Direct and indirect interactions affecting divergence

Direct predator-prey or competitor interactions are commonly used to explain phenotypic divergence within populations (Nosil and Crespi 2006, Losos and Pringle 2011). However, in the case of perch a direct interaction with zebra mussels is precluded because perch cannot prey on zebra mussels. From our data the picture emerges that zebra mussels mediate the morphological divergence in perch through changing perch resources rather than through directly interacting with them (paper II, paper III). The ubiquity of indirect species interactions in nature is undisputed and indirect species interactions can have large ecological effects (Schmitz et al. 2004). For example, predators can indirectly reinforce populations of primary producers through preying on herbivores and thus controlling the primary producers' predators (Polis and Strong 1996). Our results point to the possibility that indirect interactions can also affect phenotypic divergence.

In contrast to perch, roach are well-known and efficient predators of zebra mussels and can hence directly interact with this invasive species as a new food source (Prejs et al. 1990, Nagelkerke and Sibbing 1996). In fact, in Lake Erken we found that morphological divergence in roach was decreased when zebra mussel density increased (paper III, figure 2). This contradicts the pattern from the comparison of lakes with and without zebra mussels. Lake Erken holds the highest densities of zebra mussels of all our studied lakes. We propose that this high density of zebra mussels lead to roach consuming zebra mussels and that this direct interaction accounts for this contradiction. With increasing density of zebra mussels, roach in the pelagic zone expressed a more deep-bodied morphology, suggesting an increased use of littoral resources including zebra mussels (paper III, figure S4). We used stable isotope data to assess the long term diet overlap between littoral and pelagic roach and to estimate how much of the diet of roach stems from the pelagic energy pathway. Both littoral and pelagic roach tended to rely more on the pelagic energy pathway and therefore the long term diet overlap increased with increasing zebra mussel density (paper III, figure 3). Because the body morphology of littoral roach did not change we assume that roach from both habitats increasingly consumed zebra mussels. Zebra mussels are bottom-living organisms but are filter-feeders of pelagic nutrients. Roach in both habitats seem to profit from the mussels' shunting of pelagic energy into the littoral and develop both a littoral morphology and a pelagic isotope signature. The overall morphological and diet divergence between littoral and pelagic roach therefore decreased.

Initially, the augmented availability of resource increased divergence in both perch and roach probably by increasing the profitability of distinct rewards and hence the specialization on them (paper II, paper III). Interestingly,

when a resource couples previously distinct energy pathways and is available in high densities, some consumers seem to follow this coupling. For roach, the zebra mussels constitute a rewarding new food source supplied in high availability. This exemplifies that direct interactions with a new food source can decrease phenotypic divergence in previously separated forms.

Visual conditions affect phenotypic divergence

As can be concluded from the relation between morphological divergence and resource use it appears that direct and indirect consumer-resource interactions affect phenotypic divergence (paper I - paper III). The environment of an organism however, is not merely defined by the presence of resources, predators or competitors. Each organism is also exposed to abiotic conditions of its environment much like it is exposed to predators or competitors. Abiotic conditions can influence the performance of individuals thus changing the outcome of interactions between individuals. For example, for visually oriented animals the accessibility of resources is determined by visual conditions. Owls can efficiently hunt for mice in moonlight but their capture rate decreases sharply in moonless nights (Clarke 1983). When visual conditions influence the interaction between consumer and resource the question then becomes whether different visual conditions can affect phenotypic divergence.

To elucidate the role visual conditions play for consumer-resource interactions we related divergence in perch to the water clarity in fourteen populations of perch. We found that morphological divergence increased with increasing water clarity (paper I, figure S8). Interestingly, we found that density and community composition of littoral and benthic resources was unrelated to water clarity in the seven lakes where resource data was available (paper IV). This result seemingly contradicts our previous conclusions that resource availability determines divergence. The apparent contradiction, however, becomes resolved when we look at the resource use of perch. Diet analyses showed that the overlap in diet between littoral and pelagic perch was higher in turbid lakes (paper IV). This indicated a change in resource use to less discrete and more indifferent feeding of individuals in both habitats.

A clear distinction between the foraging behaviors in the littoral and pelagic zone is fundamental to the divergence in foraging morphology. Foraging in the littoral zone generally requires a slow search velocity to increase foraging rates on patchy distributed cryptic prey. Foraging on conspicuous prey types in the pelagic zone requires a higher search velocity to increase foraging rates on widely dispersed open water prey (Ehlinger and Wilson 1988, Svanbäck and Eklöv 2003). Higher water clarity leads to higher

detection rates which, in combination with increased prey density, allows for higher swimming speed in the pelagial (Marchand et al. 2002). We found that lakes with zebra mussels provide both a higher availability of large zooplankton and higher water clarity (paper III). The combination of high search velocity and high energy gain from the detected food should thus facilitate the expression of a morphology matching the pelagial. When visual conditions diminish, e.g. in the absence of zebra mussels, pelagic prey might get more cryptic and search velocities will then be reduced (Park et al. 2007). The pronounced distinction in swimming behavior and morphology between the two habitats will then decrease.

The majority of studies on the origins of diversity have focused on species interactions as e.g. competitive interactions. We hypothesized that visual conditions can influence diversification by changing the interactions between resources and consumers. We could establish a clear link between the use of distinct resource and the magnitude of divergence. Our data on the role of abiotic conditions suggest that visual conditions that affect the resource use, can influence the magnitude of diversification in a visually-oriented forager. This highlights the previously underappreciated role of abiotic factors in determining phenotypic diversity.

Phenotypic plasticity in invasive zebra mussels

So far we have investigated the role of resources for consumer divergence. Phenotypic diversification within a population however, can also be generated by factors other than resource use. Most consumers are themselves resources and as such exposed to predation. This predation pressure can elicit anti-predator phenotypes that can lead to pronounced differences among individual phenotypes (Beadman et al. 2003).

To investigate the role of plastic anti-predator responses for phenotypic diversity we can again make use of the zebra mussel invasion, specifically into Lake Erken (paper V). In Lake Erken, the zebra mussel encounters roach and signal crayfish. Roach and crayfish are two different predators with the documented ability to forage efficiently but with different feeding modes on zebra mussels. Roach ingest whole mussels and are hence limited in feeding on mussels by the size of their mouth. Crayfish crush the shells prior to consuming the soft tissue and are hence limited by the force needed to overcome the shell strength (Nagelkerke and Sibbing 1996, Schreiber et al. 1998). Being sessile, the mussel's main defense against these predators is its shell. We therefore conducted experiments in which we exposed zebra mussels from Lake Erken to crayfish and roach and analyzed the mussels' shell shape and strength as response variables.

We found that when exposed to either a single roach or single crayfish zebra mussels expressed a shell phenotype that would provide protection against the prevailing predator's feeding mode: an elongated but weaker shell to avoid being swallowed by roach and a round and hard shell to prevent being crushed by the crayfish (paper V, figure 1).

We hypothesized that plasticity allows an invasive species to express specific responses to new predators. While we cannot conclusively unravel the co-evolutionary history of roach, crayfish and zebra mussels we think it is plausible that this specific predator-prey system was established in Lake Erken within contemporary timescales. Because neither of the predators had direct contact with the mussels but mussels still developed different shell phenotypes, we can conclude that individual mussels can sense the prevailing predation threat and express suitable defense phenotypes. This plasticity might well contribute to the zebra mussels' invasion success as it seems to allow for appropriate responses to predation threats also in newly colonized systems.

I began this thesis by asking which processes can explain the striking diversity we can see in nature. Since we now know that the plastic response to predators profoundly affects the shape of zebra mussels we used zebra mussels as a model to test whether predation pressure in the wild can explain the variation in their shapes.

We therefore tested for relationships between the shell shape and strength of zebra mussels and several environmental factors in Lake Erken. The mussels phenotypes were not significantly influenced by the density of crayfish or roach predators (paper V, figure S3,S4). Instead, phenotypes were related to intra-specific population density and bottom substrate in the form of stones (paper V, figure 6).

This observation contradicted our experimental findings which suggested that phenotype expression in zebra mussels is predominantly a result of anti-predator responses. Nonetheless, there is valuable insight to gain from our field study because it demonstrates that even if directional differences in expression of phenotypes are found under controlled conditions, other factors can determine the phenotype expression in the field.

Conclusions

In summary, the following can be concluded from this thesis:

1. Disruptive selection favors extreme phenotypes on opposite ends of the phenotype spectrum and thus leads to morphological divergence.
2. The recurrent divergence between habitats in two species suggests that the selective forces leading to this divergence are of general nature.
3. The magnitude of phenotypic divergence between habitats can depend on the availability of profitable habitat-specific resources.
4. Visual conditions can affect the phenotypic divergence by changing the consumer-resource interactions.
5. An invasive species can be able to plastically respond to predators even in a contemporary established predator-prey system. However, these responses do not necessarily explain the phenotypic diversity observed in nature.

Outlook and Perspectives

Plasticity or genetically determined?

One obvious question is whether the phenotypic divergence between habitats in perch and roach results from phenotypic plasticity or has a genetic basis. Previous research on perch showed that the morphological response to feeding on different habitats predominantly results from plastic responses of individuals (Svanbäck and Eklöv 2006). For roach we do not have information concerning the genetic determination of morphological divergence. However, the lack of genetic pre-determination of trophic morphologies does not necessarily mean that there is no genetic basis of phenotypic divergence. Phenotypic plasticity is a trait that can also evolve (West-Eberhard 2003). In our case, the ability of the fish and the zebra mussel to modify the morphology based on the resource use could well be considered an evolvable trait. Future studies should therefore address the relevance of plasticity for divergence as e.g. whether individuals from populations with higher divergence are faster in switching their morphology from intermediate to littoral and pelagic and back.

How are we humans affecting diversity?

Virtually all ecosystems globally are affected in one way or another by human activities that can also change the abiotic conditions in affected ecosystems. For example, habitat-alteration by humans can flatten ecological gradients and thus lead to the loss of phenotypic diversity (Freedman et al. 2010). Many aquatic ecosystems show an increased turbidity due to increased nutrient input resulting from human land-use areas like e.g. agriculture or deforestation (Ficke et al. 2007). From our finding of decreased divergence with decreasing water clarity we can anticipate that such human effects could lead to the loss of biodiversity by impairing the processes that lead to or maintain divergence. Introductions of invasive species have led to an unprecedented loss of biodiversity over the past decades (Sala et al. 2000). We could illustrate that the invasion of the zebra mussels can also increase phenotypic divergence and thus maintain diversity in nature. I therefore want to emphasize that despite the increase in divergence in some consumers the zebra mussels invasions contribute to the

homogenization of faunas by making all invaded lakes less unique in their species compositions.

What is the role of predation?

Another important species interaction influencing morphology and hence also divergence in morphology in fish is predation. For example, carp have been shown to develop a deeper body in the presence of pike predators (Brönmark and Miner 1992). A deeper body improves the chances of survival under predation pressure of gape-size limited predators. Carp populations exposed to gape-size limited predators have a deeper-bodied morphology than populations not exposed to predators (Brönmark and Miner 1992). In perch, the risk of predation has been shown to affect habitat choice and thus morphology (Eklöv and Svanbäck 2006). Also roach can change their morphology in response to predators by shifting the location of their fins to the caudal body parts possibly allowing higher escape speeds (Eklöv and Jonsson 2007). As mentioned at the beginning of this thesis, most predators and consumers, and also roach and perch, are prey themselves. To which extend phenotypic responses to predation pressure influence the degree of divergence between littoral and pelagic roach or perch in our lakes however, remains unknown and clearly warrants further study. One could, for example, test experimentally how the presence of predators changes the morphological divergence between littoral and pelagic forms of both perch and roach.

Implications for food webs?

Recent theoretical work points towards the function mobile consumers like fish have for the coupling of spatially separated energy pathways in food webs. By moving between and foraging in different habitats fish could compensate density fluctuations in lower trophic levels in either of the habitats (McCann et al. 2005, Rooney et al. 2006). Our study showed that the divergence into habitat-specific morphs is a recurrent phenomenon within fish communities. Using resources in another habitat than the phenotype is matching will be disadvantageous due to e.g. decreased feeding efficiency (Knudsen et al. 2010). Divergence should therefore restrict the coupling of habitats by fish by preventing them from moving between and foraging in both habitats. How consumers' coupling of energy pathways affects the function and stability of food webs has yet to be empirically tested. Future research testing the coupling between habitats should consider that intra-population divergence can affect the coupling.

How is ontogeny affecting divergence?

Both roach and perch change resource use and morphology throughout their ontogeny. By comprising all size-classes of both species in our analyses we put the focus on divergence affecting the total population. The obtained results can be applied to the total population and are more easily understandable and interpretable. I acknowledge however, that this is a simplification. Changes in resource use during ontogeny can affect phenotypic responses (Hjelm et al. 2001). Thus, different life stages of roach and perch might well be differently affected by zebra mussels or visual conditions. Future studies should therefore incorporate detailed investigations of different life phases of both fish species. An exemplary question could be whether the zebra mussels' consumption of small zooplankton can lead to competition with pelagic fish larvae.

Can we speak of adaptation?

Throughout the thesis I used the term adaptation with caution. I did this because adaptation is a loaded term that implies cross-generational fitness benefits. Yet, we cannot provide direct evidence for the increased survival and reproductive output for neither of the fish morphologies or zebra mussel phenotypes. Nevertheless, the evolutionary relevance of the phenotypic variations is evident as they provide the raw material for selection to act upon. Above that, our empirical support for the presence of disruptive selection indicates that fitness differences are clearly associated with the phenotypes. However, future work on phenotypic responses should aim to test the adaptive value of the expressed phenotypes. For example, experiments how the different induced phenotypes of zebra mussels perform in surviving under different predators' direct predation could give further insight into the adaptive value of such plastic responses.

What can be done better?

Obviously, a lot. But more constructively, I want to conclude by giving some ideas of how future researchers can learn from my mistakes and this thesis' shortcomings. In this thesis, the invasion of the zebra mussels was used as a natural experiment. As becomes evident from the previous points in this section however, there is a lot to learn from more controlled experiments. An experimental validation of the factors that influence divergence would require large scale experiments under semi-natural conditions. Results from these experiments will complement the field observations and allow a more

in-depth study of the mechanisms underlying differential phenotype expression.

Finally, I want to advocate that an ideal contemporary ecological monitoring should include some measures of phenotypic traits in native species. The effect of zebra mussels on lake's resources is a securely established fact. Pre- and post-invasion data on phenotypic divergence however, would make it easier to attribute changes in the native species' divergence to the effects of the invasive species.

Epilogue

In this thesis I aimed at progressing science by testing the hypotheses I posed in the beginning. Based on observations of nature I could partly find support for the hypotheses. That means I could not falsify them.

Now one might ask: is this really true? Is it true that zebra mussel develop different shell shapes in response to predators? To this kind of questions I can simply reply that I do not know whether it is true or not; I can only assume that, based on the testing of the hypotheses, it is not false up to the present day. Or in other words: it is not falsified yet. One important next step in scientific progress would now be to continue testing the hypotheses. These tests should include more species and more systems to scrutinize the generality of the hypotheses. Future reformulation of the hypotheses should then make them more general, so that they explain even more observations of nature. In the 'Outlook and Perspectives' section I gave some ideas on further explanations that modified hypotheses could comprise. Future tests will show whether the hypotheses withstand the falsification attempts based on new observations. They might turn out to be fallible or remain unfalsified. In any case, they constitute the raw material in the form of new knowledge acquisition that science can proceed from; much like the phenotypic variations constitute the raw material selection can act upon.

Another question typically raised at this point concerns the relevance of this thesis. To me, scientific relevance is a term that is largely defined by the opinions of groups and individuals (e.g. editors of scientific journals). As such it is liable to the zeitgeist. Regardless, I would like to think that this thesis constitutes more than just a collection of observation-based facts. The results and implications of this thesis can contribute to our understanding of nature. In particular, they can help to explain why life around us is as diverse as we see it. My contribution to this explanation, how ever small it may be, certainly was worth my efforts - hopefully also those of the reader.

Sammanfattning på svenska

Att förstå vilka faktorer som styr livets biodiversitet är en grundläggande del i biologers arbete. Den mest påtagliga och omtalade biodiversiteten är skillnaderna och mångfalden av arter i ett ekosystem, men det finns även biodiversitet inom en art och till om med inom en enda population.

Att studera vilka faktorer som leder till att fysiska skillnader ökar hos individerna inom en population kan bidra till vår förståelse av generella faktorer som leder till biodiversitet.

Vi undersökte vilka faktorer som begränsar variation i kroppsform inom en population genom att följa vandringsmusslans etablering i svenska sjöar. Vi använde oss av musslans effekter på en sjös ekosystem. Dessa effekter gav oss möjligheten att studera hur tillgängligheten till resurser och grumlighet påverkar kroppsformen för två inhemska fiskarter (mört och abborre). Habitaterna där dessa två fiskarter lever formar deras utseende. Individerna längs strandzonen har en djupare kropp som är bättre anpassad för att livnära sig på bottenlevande organismer. Individerna i öppet vatten har en strömlinjeformad kropp som är lämplig för att simma snabbt och uthålligt när de jagar små simmande byten ute på öppet vatten.

Vi har även studerat skillnaderna i skalform inom en population av vandringsmusslor. Inom varje ekosystem möter vandringsmusslorna ett antal predatorer som har olika födosöksstrategier. Musslornas främsta försvar är skalets styrka och form, som kan förändras medan de växer. Att undersöka hur vandringsmusslorna förändrar skalformen som respons på olika predatorer gav oss möjlighet att studera hur musslornas försvarsmekanismer bidrar till variationen av kroppsformer inom musselpopulationen.

En jämförelse av mörtar och abborrars kroppsformer i flera sjöar visade att skillnaderna i kroppsform mellan fisk som lever på öppet vatten och fisk som lever nära stranden var större i sjöar där det fanns vandringsmusslor.

Vi upptäckte även en ökning i båda habitatens resurstillgänglighet, något som med stor sannolikhet beror på vandringsmusslornas positiva effekter på bottenlevande djurs biomassa och biodiversitet. I öppet vatten hittade vi ett högre antal stora plankton i sjöar med vandringsmusslor. Musslan livnär sig helst på små plankton och lämnar därmed kvar stora plankton, som sedan

kan bli föda åt fiskarna. Därför antar vi att fiskar som lever strandnära såväl som de fiskar som lever på öppet vatten är specialiserade till en högre grad på de olika habitatens resurser.

Sjöar med vandringsmusslor visade sig ha ett klarare vatten. Detta kunde bidra till den ökade divergensen i fiskarnas kroppsform. För att testa detta jämförde vi skillnaderna i kroppsform hos abborre med vattenklarheten i ett antal sjöar. Vi upptäckte att abborr-populationer i klarare sjöar hade större skillnader i kroppsform. Abborren är en fisk som söker föda visuellt. En ökande grumlighet kan därför innebära minskad förmåga att specialisera sig på antingen strandnära resurser eller bytesdjur ute på öppet vatten. När vi analyserade fiskarnas maginnehåll kunde vi bekräfta att dietöverlappet mellan fiskar från olika habitat var större i grumligare sjöar. Detta tyder på att abborren inte längre specialiserade sig på ett habitats resurser, snarare livnärde sig alla abborrar (oberoende av habitat) på samma resurser. Undersökningar av hur diet och kroppsform hänger samman hos abborren visade att ju mer två fiskar skiljer sig åt i vad de äter desto mer skiljer de sig åt i sin kroppsform. Detta leder i sin tur till en ökad skillnad i den habitatkaraktäristiska kroppsformen.

Till skillnad från tidigare studier som fokuserade på interaktioner mellan exempelvis konkurrenter, kunde vi visa att även resurstillgänglighet och abiotiska faktorer kan leda till stor fysisk variation emellan individerna inom en population.

För att komplettera vår studie av vilka faktorer som styr den fysiska individvariationen i en population testade vi hur vandringsmusslor förändrar sin skalform när de utsätts för predatorer med olika födosöksstrategier. Musslorna fick ett rundare och tjockare skal när de utsattes för predatortryck av kräftor, som vanligtvis krossa musslorna. När musslorna utsattes för predatorhot av fisk som gärna sväljer musslan hel så fick musslorna ett längre och svagare skal. De olika skalformerna lär skydda musslorna mot olika predatorers födosöksstrategier. Alla musslorna som utsattes för predatorerna kom från samma ställe i samma sjö. De olika skalförändringarna är därför med stor sannolikhet en musselindivids spontana, plastiska reaktioner på ett predatorhot. Utifrån detta drar vi slutsatsen att plastiska försvar är en viktig process för inomartsvariationen i en population. Ett plastiskt försvar kan också bidra till vandringsmusslornas goda förmåga att etablera sig i nya miljöer då plasticitet kan underlätta överlevnad i nykoloniserade ekosystem där predationstrycket är oförutsägbart.

Vi kunde visa att en källa till variation inom en art är specialiseringen på olika resurser, men även att resurstillgängligheten kan påverka hur stor

inomartsvariationen är. Som en annan källa till diversitet identifierade vi plastiska försvar mot predatorer. Med tanke på att predatorer i naturen brukar ha många födosöksstrategier är plastiska försvar en viktigt anledning till varför individer inom en bytespopulation kan se så olika ut.

Den stora diversiteten i olika fenotypiska karaktärer såsom exempelvis kroppsform tyder på att det finns råmaterial ifrån vilket den naturliga selektionen kan välja ut individer som är bättre anpassade än andra. Denna selektion kan med tiden leda till att nya arter utformas, genom en process som redan Charles Darwin beskrev i sin berömda bok "arternas ursprung". Även förmågan till plastiska förändringarna som exempelvis olika skalformer kan vara ett mål för naturligt selektion. De individer som har denna förmåga har en bättre överlevnadschans än de som inte har det. Denna avhandling är ett bidrag till en bättre förståelse av de fysiska skillnadernas ursprung inom en population.

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