

Ecological and evolutionary effects of predation in environmental gradients

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LIST OF PAPERS

This thesis is a summary of the following papers that are referred to in the text by their Roman numerals:

- I.** Englund G., Öhlund G., Hein C.L. and Diehl S. (2011). Temperature dependence of the functional response. *Ecology Letters*, 14: 914-921.
- II.** Öhlund G., Hedström P., Norman S., Hein C.L. and Englund G. Temperature-dependence of predation depends on relative performance of predators and prey. *Manuscript*.
- III.** Öhlund G., Bodin M., Nilsson K.A., Mobley K., Öhlund S-O., Peedu M., Hein C.L. and Englund G. Predation drives rapid and repeated sympatric divergence in European whitefish (*Coregonus lavaretus*). *Manuscript*.
- IV.** Öhlund G., Peedu M., Nilsson K.A., Fallgren B., Magnusson M., Öhlund S-O., Bartels P., Hein C.L., Bodin M. and Englund G. The chronology of incipient speciation in whitefish. *Manuscript*.

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ABSTRACT

Understanding species interactions and how they affect densities and distributions of organisms is a central theme in ecological research. Studying such interactions in an ecosystem context is challenging as they often depend on species-specific characteristics and rates that not only change during the ontogeny of an organism, but also are affected by the surrounding environment. This thesis focuses on two separate questions and study systems that highlight different aspects of how effects of predation can depend on environmental conditions. In the first part of the thesis, we studied how temperature affects attack rate and handling time, two ecological rates with profound importance for predator-prey dynamics. Using a metaanalysis, we first show that the currently dominating model for temperature dependence in predator-prey interactions, i.e. the Arrhenius equation, has weak support in available empirical literature. This suggests that we need new rules for how and when we can generalize on the temperature-dependence of intake rates. We then use a simple model and a series of experiments to demonstrate that differences in the relative physiological capacity between predator and prey can impose strong non-linear effects on temperature-response curves of attack rate. In the second part of the thesis, we study the role of predation along a benthic-pelagic habitat gradient in promoting divergence and resource polymorphism among prey. We show that presence of a large piscivorous predator, the northern pike (*Esox lucius*), induces dwarfs, giants or divergence into both ecotypes in populations of European whitefish (*Coregonus lavaretus*) depending on lake characteristics. Using dated introductions of whitefish as controlled natural experiments, we show that pike presence induces rapid life history divergence between pelagic and littoral habitat use strategies, and that this divergence can translate into partial reproductive isolation in a matter of decades. Our results demonstrate the potential for thresholds in a crucial ecological rate, setting the stage for tipping points with potentially far reaching implications for effects of warming on predator prey dynamics and ecosystem stability. Moreover, they illustrate the potentially drastic consequences of such tipping points by demonstrating the importance of a single predator species as a driving force behind the creation and maintenance of biodiversity in a natural system.

INTRODUCTION

Understanding species interactions and how they affect densities and distributions of organisms is a central theme in ecological research. Studying such interactions in an ecosystem context is challenging as they often depend on species-specific characteristics and rates that not only change during the ontogeny of an organism, but also are affected by the surrounding environment. It has commonly been observed that interspecific interactions are condition-specific and that the outcome thereby can vary in environmental gradients (Sanford 1999, Malenke et al 2011).

Alongside competition for resources, predation is a crucial factor for structuring most ecosystems and it is known to affect everything from behaviour and phenotypic expression of individual organisms to large-scale patterns of species distributions, ecosystem functioning and macroevolution. It has been suggested that strong community-wide effects of predation such as trophic cascades might be especially frequent in aquatic ecosystems (Carpenter et al. 1985, Strong 1992, Shurin et al. 2002). At the same time, aquatic systems suffer heavily from man-made disturbances such as over-fishing and river regulation. Hence, it is important both from a theoretical and an applied perspective to understand how effects of predation in aquatic communities and ecosystems can vary and change with environmental conditions.

This thesis focuses on two separate questions and study systems that highlight different aspects of how effects of predation can depend on environmental conditions. The first part deals with how environmental temperature affects ecological and physiological rates that ultimately determine the outcome of predator-prey interactions. In the second part of the thesis, I study the role of interspecific predation along a benthic-pelagic habitat gradient in promoting divergence and resource polymorphism among prey.

Predation and temperature

During the last decade, predicted climate warming has inspired a renewed scientific interest in how temperature affects organisms, food webs and ecosystems (e.g. Gillooly et al. 2001, Brown et al. 2004, Vasseur and McCann 2005, Clarke 2006, van de Wolfshaar et al. 2008, Irlich et al. 2009, Petchey *et al.* 2010, Rall *et al.* 2010). While direct effects of temperature on the performance of organisms are reasonably well known (Peters 1983, Angilletta 2009), predicting changes in the strength and direction of species interactions remains a challenging task. Above all, this requires knowledge of

how temperature affects the physiological and ecological rates that determine the outcome of interactions.

In predator-prey interactions, the intake rate of an individual predator is determined by the two main components of the functional response, i.e. attack rate and handling time (e.g. Holling 1959a, b). At low prey densities, intake rate is mostly limited by attack rate whereas high prey densities lead to predator saturation and a consumption rate limited by handling or digestion rates. The temperature dependence of functional response parameters is therefore an important research area that forms the basis for quantitative system-specific modelling as well as for development of theory on temperature dependence in population and community ecology. In essence, we need to know how and why these parameters depend on temperature and if this temperature dependence can be subject to widely applicable generalizations.

For the last decade, the Metabolic Theory of Ecology (MTE) has claimed the position as a general framework for studying the role of temperature in ecological systems (e.g. Brown et al. 2004). Proponents of the MTE have suggested that the well-known Arrhenius equation, which was originally derived for chemical reaction rates, can serve as a mechanistic model for the temperature dependence of basal metabolism. Reaction rate (R) is given by:

$$R = R_0 e^{-E/kT} \quad [1]$$

where T is the absolute temperature, k is Boltzmann's constant, and E is the activation energy of the reaction (Cornish-Bowden 2004). The activation energy determines the strength of the temperature dependence and the MTE predicts values to be constrained between 0.6 and 0.7 (Gillooly et al. 2006; Allen & Gillooly 2007).

As the metabolism of all aerobic organisms share the same biochemistry, the theory states that this temperature dependence is universal, applying to all ectothermic animals as well as to a range of other biological rates that are linked to metabolism, including growth, development and maximal consumption rate (Gillooly et al. 2001; Brown et al. 2004; Savage et al. 2004). While use of the Arrhenius equation as a mechanistic representation for the temperature dependence of physiological rates has been criticised (Marquet et al. 2004; Clarke 2006; van der Meer 2006; Irlich et al. 2009), it has nevertheless become the standard method for modeling the temperature dependence of predation and consumption rates in population and community ecology (Vasseur & McCann 2005; van de

Wolfshaar et al. 2008, Savage et al 2004, Petchey *et al.* 2010; Rall *et al.* 2010).

Accumulating evidence suggest that the role of the Arrhenius equation as a cornerstone in current development of theory on temperature-dependent predator-prey interactions is potentially problematic. In the first part of this thesis, we therefore examine the relevance of the Arrhenius equation as a representation of the temperature-dependence of handling time and attack rate. Further, we use a simple model and experiments to investigate if differences in the relative performance of predators and prey can affect the temperature-dependence of attack rate.

Predation in the benthic/pelagic habitat- and resource gradient

Effects of predation and predator-prey dynamics are also known to be strongly affected by the spatial characteristics of the environment in which interactions occur (e.g. Gause 1934, Dieckmann et al. 2000, Bergström et al. 2006, Eklöv and Svanbäck 2006). In study **III** and **IV**, we focus on ecological and evolutionary effects of predation in the benthic-limnetic habitat gradient of high latitude lakes.

Resource polymorphism, when sympatric ecotypes formed from a single species differ in ecology and resource use, has most frequently been found among fish, where the typical pattern is coexistence of a giant or “normal” ecotype feeding on benthic macroinvertebrates, and a limnetic dwarf feeding on zooplankton (reviewed in Skúlason & Smith 1995). Although the processes underlying this pattern has been studied intensively during the last two decades (e.g. McPhail 1994, Rundle et al. 2000, Schluter 2001, Jonsson and Jonsson 2001, Snorrason and Skúlason 2004, Østbye et al. 2006, Knudsen et al. 2006, Andersson et al. 2007, Landry and Bernatchez 2010, Siwertsson et al. 2010), it seems that fundamental questions remain unanswered. For instance, we generally do not know why resource polymorphism develops in some populations and not in others, a fact that highlights the importance of improving our mechanistic understanding of where and how the presence of pelagic and littoral resources will translate into divergent ecological selection.

Although theoretical studies suggest that a range of ecological interactions can induce disruptive selection and resource polymorphism (e.g. Doebeli and Dieckman 2000), it seems that much of the empirical research on benthic limnetic species pairs have focused on the role of frequency-dependent intraspecific competition (Schluter 1994, Schluter 2000, Bolnick 2004, Bolnick and Lau 2008). A dominating idea in current literature is that resource polymorphism is promoted in species poor environments if individuals can escape intra-specific competition by adopting rare feeding strategies (e.g. Schluter 2003, Martin and Pfennig 2009, Bolnick 2011). However, this hypothesized mechanism is not necessarily compatible with observations suggesting that resource polymorphism is associated with certain species combinations (Vamosi 2003) or complex fish communities

(Siwertsson et al. 2010). Hence, as presence of pelagic and benthic resources in lakes with few fish species is not sufficient to induce polymorphism (e.g. Vamosi 2003, Andersson et al. 2007, Bolnick 2011), we need to understand how additional ecological factors can interact with density and size structure of resources to strengthen divergent selection (e.g. Landry et al. 2007).

A less studied but highly interesting candidate mechanism that have been shown to promote resource polymorphism is predation (e.g. Rundle et al. 2003, Vamosi 2003, Vamosi and Schluter 2004, Eklöv and Svanbäck 2006, Andersson et al. 2007, Marchinko 2009). Predation can stabilize resource dynamics and thereby also the incentives for consumers to specialize on a given resource (Andersson et al. 2007). Predation risk can also affect habitat choice among prey and thereby in turn affect their phenotypes (Eklöv and Svanbäck 2006). This type of habitat choice is often size-specific and can induce size-specific differences in growth rate (Werner et al. 1983, Tonn et al. 1992, L'Abée-Lund et al. 1993) Hence, a particularly interesting feature of habitat-specific predation is its potential to maintain or reinforce spatial variation in growth rates and size structure of consumer populations. In papers **III** and **IV**, we use a large empirical data set, natural experiments and an eco-evolutionary model to analyse if, how, and how fast predation can induce ecological and evolutionary divergence among prey.

AIMS

The overall objective of this thesis is to improve our understanding of how predation rate depends on environmental temperature, and if predation can drive ecological and evolutionary divergence in the benthic-pelagic habitat gradient of lakes. Specifically, I adress the following questions;

- Does the Arrhenius equation deserve its current status as a null-model for the temperature-dependence of predator-prey interactions? (**I**).
- Can the temperature dependence of attack rate be predicted based on differences in the relative physiological capacity of predator and prey? (**II**)
- Can predation drive resource polymorphism in the benthic-limnetic habitat gradient? (**III**)
- In what order do crucial ecological traits diverge during the first phase of a predation-driven speciation process? (**IV**)

METHODS AND STUDY SYSTEMS

In papers **I** and **II**, we analyzed how temperature affects the two main components of the functional response, i.e. attack rate and handling time (e.g. Holling 1959a, b). In paper **I**, we conducted a meta-analysis of 48 studies on temperature dependence of the functional response published up to 2010. In paper **II**, we used a simple conceptual model and experiments to understand the effects of a potentially important mechanism underlying variation in the temperature response of attack rates, i.e. the relative physiological capacity of predator and prey. We compared the temperature-dependence of attack rates when the predator northern pike (*Esox lucius*) were fed freshwater amphipods (*Gammarus lacustris*) and brown trout (*Salmo trutta*), two prey types that differ substantially in their ability to escape predation. Gammarids are relatively slow and rely on hiding in physical refugia whereas brown trout are fast swimmers and have lower temperature optima for growth compared to pike (Casselman 1978; Elliott 1982). Attack rates of pike feeding on the amphipod *Gammarus lacustris*, were measured in ten 720 litre aquaria (2m x 0.6m x 0.6m) at five temperatures (1.5, 5, 10, 15 and 20°C). Attack rates of pike feeding on brown trout were measured in outdoor pools (area 24 m², water depth 1 m) at approximately 6, 10, 14, 18 and 22 °C. To better understand the mechanisms that determine the temperature dependence of attack rate, we also investigated the maximum swimming speed of pike chasing brown trout, and of pike and brown trout fleeing a human predator. These experiments were performed using the same type of pools as the attack rate experiments, a video camera and the software Tracker 3.10 (<http://www.cabrillo.edu/~dbrown/tracker/>).

In paper **III**, we used data from interviews, gillnet sample fishing and an eco-evolutionary model to understand if and how predation can induce life history divergence among prey. The mainly interview-based data set contained information about the number of ecotypes (one or more than one), the maximum weight of each ecotype, and if whitefish in a given lake was indigenous or introduced. We defined polymorphism as existence of two or more coexisting populations with different maximum size, and used maximum weight as a crude life history metric for two reasons: i) fishermen tend to remember the largest fish caught in their waters with a much higher precision than for instance size at maturation, and ii) maximum weight effectively captures the divergence between dwarfs and giants. The final data set contained information from 351 Scandinavian lakes distributed from 58.99 N, 8.29 E in southern Norway to 68.17 N, 21.97 E in northern Sweden. To estimate the rate of divergence, we used a set of 76 large lakes with dated introductions of whitefish populations, many of which have diverged into different ecotypes. In paper **IV**, we used the same set of introduced

whitefish populations as natural experiments to test in which order important traits like size, growth, habitat use, feeding morphology and use of spawning sites diverge during the initial stages of divergence.

RESULTS AND DISCUSSION

Predation and temperature

In paper **I**, we show that when plotted in lin-log space, temperature dependence of both attack rate and maximal ingestion rate exhibits a hump-shaped relationship and not a linear one as predicted by the Arrhenius equation. The relationship remains significantly downward concave also at temperatures below the peak of the hump. These findings add to accumulating evidence suggesting that we need to categorize between organisms and systems to establish new rules for how and when we can generalize on the temperature-dependence of intake rates.

This need seems especially urgent for attack rates (e.g. Vucic–Pestic et al. (2011)). In the metaanalysis, we found substantial variation between studies in the strength of attack rate responses, and several published studies have reported responses with strongly deviating shapes (Chow et al. 1983; Nagai and Yano 2000). The underlying mechanisms that cause this variation are not well understood. One potentially important mechanism was demonstrated by Vucic–Pestic et al. (2011), who found that attack rates of three predatory beetles had different temperature responses for mobile and immobile prey. Moreover, recent work suggests that temperature affects predators and prey in different ways. Dell et al. (2011) found that organisms have a stronger thermal response when searching for food than when escaping predators, and suggested that this might reflect a thermal version of the life-dinner principle, i.e., that selection on prey for avoiding being eaten is stronger than the selection on predators for catching prey (Dawkins and Krebs 1979; Scales et al. 2009). These observations highlight one important reason why the Arrhenius model may not hold for attack rates, i.e. that the outcome of predator-prey encounters are likely to be the result of a potentially complex interaction between the behaviors and physiological capacities of both predators and prey. This also implies that different biological factors might limit predation success in different parts of the response curve. For instance, if crucial performance curves of predator and prey intersect, threshold-effects, where attack rates drop substantially at some threshold temperature, are conceivable.

Studies that specifically address the underlying mechanisms that cause variation in the temperature dependence of attack rate can potentially help us discriminate between interactions, systems and questions where coarse generalizations are sufficient and situations where response curves need to be more rigorously parameterized. In paper **II**, we therefore used a simple model to investigate the temperature dependence of attack rate under the assumption that it is the relative performance of predators and prey that determines attack success. The model predicted that differences in the

relative performance of predator and prey can cause large variation in the temperature dependence of attack rates including strong threshold effects. Testing these model predictions, we found that attack success of northern pike (*Esox lucius*) feeding on highly mobile and cold water-adapted brown trout (*Salmo trutta*) fell sharply below a threshold temperature of +10 °C. When pike were fed the slower amphipod (*Gammarus lacustris*) on the other hand, the temperature response of attack rate was substantially weaker. Measurements of maximal attack and escape speeds of pike suggested that the threshold is caused by a behavioural switch rather than by direct effects of temperature on the maximal physiological capacity. Thresholds in the temperature dependence of crucial ecological rates can create tipping points in the responses of ecosystems to increasing temperatures. Thus, identifying such thresholds is crucial when predicting future effects of climate warming.

Predation in the benthic/pelagic habitat- and resource gradient

In paper **III**, we demonstrate that predation can induce divergent life history strategies on an extremely short timescale. Data from 351 Scandinavian lakes show that presence of a large piscivore, the northern pike (*Esox lucius*), induces dwarfs, giants or divergence into both ecotypes in populations of European whitefish (*Coregonus lavaretus*) depending on lake characteristics. Using 76 whitefish introductions made between year 1784 and 2009 as natural experiments, we found that 50% of populations exposed to predation from pike had formed distinct ecotypes in 72 years. This demonstrates that divergence into the frequently observed “species pairs” of dwarfs and giants can be much faster than what is currently recognized.

In our eco-evolutionary model, we analyse how habitat-specific predation in the littoral habitat affects whitefish prey that can utilize a zooplankton resource in a pelagic “refuge” habitat, but need to switch to more profitable littoral resources as they grow larger (see paper **III** for details). Our model analysis suggests that it is the large gape size and the ability to consume large prey that separates pike from other predators in our study system, and allows it to drive life history divergence in whitefish. If predation risk is confined to a size when prey are equally well or better off in the refuge habitat, presence of the predator has limited effect on resource dynamics and mortality. However, if the predator can consume larger prey that need to switch from the refuge to utilize more profitable resources, the model illustrates how habitat-specific predation can give rise to two different strategies; individual prey can avoid predation risk either in space or by growing large. The first strategy comes at a cost of intense resource competition for a resource that provides little scope for growth of large individuals, and will therefore induce maturation at a small size. The latter strategy on the other hand is subject to higher predation risk and benefits

from a delayed maturation so that a large fraction of available energy can be allocated to growth.

Our findings question the prevailing idea that intraspecific competition and ecological opportunity are the main drivers of resource polymorphism in post-glacial fish populations. With very few exceptions, whitefish in lakes without pike grow to intermediate sizes and display low variation in size among mature individuals. While pike presence can lead to improved growth and induce giants, perhaps the most striking feature of whitefish in large pike lakes is the presence of dwarf ecotypes that either exist on their own or coexist with giants. It has been suggested that strong directional selection acting on dwarf whitefish may be more important than divergent selection acting on both sympatric forms in driving phenotypic divergence in whitefish (e.g. Landry and Bernatchez 2010). Although our findings may not support this hypothesis in a strict mechanistic sense, they demonstrate that when there is limited scope for prey to outgrow their predator in refuge habitats, predation risk can be the key selective agent that explains why dwarf ecotypes “get stuck” in suboptimal growth conditions. The presence of dwarf ecotypes is a characteristic of benthic-limnetic species pairs also in other important model species like lake whitefish (*Coregonus clupeaformis*, Bernatchez 2004), threespine stickleback (*Gasterosteus aculeatus*, Rundle et al. 2000) and arctic char (*Salvelinus alpinus*, Knudsen et al. 2006). Our results may provide a new and possibly general explanation as to why resource polymorphism develops in these systems; prey avoid predation risk either in space or by growing large.

In paper **IV**, we use dated introductions of whitefish as controlled experiments, and show that presence of pike induces rapid life history divergence between pelagic and littoral habitat use strategies, and that this divergence can translate into partial reproductive isolation in a matter of decades. Variation in gill raker numbers start to diverge substantially later, suggesting that divergence in feeding morphology depends on, rather than drives the initial divergence. Based on results from this and the previous study, we suggest that predator-induced differences in the intensity of competition between habitats are important for “capturing” small or slow-growing individuals in the pelagic habitat, promoting growth among giants in the littoral zone, and hence, for driving life history divergence. These effects of competition are fundamentally different from the traditional view offered by the theory of character displacement, in which frequency-dependent competition between incipient morphs and their hybrids are the essential mechanism that drives divergence. Our results from paper **III** and **IV** demonstrate that habitat-specific predation can cause prey to mature in a safe place or at a safe size, a simple mechanism for divergence in life history-strategies and habitat use that has potentially far reaching importance beyond the realms of our study system.

CONCLUDING REMARKS

This thesis adds to previous work in demonstrating that we will never be able find one single general model that can be used to represent temperature-dependence in predator-prey theory. Instead, we need to find new ways to generalize between systems, organisms and physiological characteristics of organisms in order to find new rules for when it is reasonable to use general models and when we need to use rigorously parameterized response curves. Our results suggest that the relative capacity of predator and prey is a characteristic of predator-prey interactions that could form the basis for establishing such rules.

Our results question some of the cornerstones in current theory on resource polymorphism and ecological speciation. Presence of a keystone predator is the main selective agent behind divergence, and competition seem to be more important within ecotypes rather than between them and their hybrids. These observations, the very large number of species pairs and a large number of available natural experiments sets our study system apart from most other model systems for speciation research. We therefore argue that the Scandinavian whitefish study system will provide ideal opportunities for future research to test crucial assumptions and predictions of speciation theory.

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AUTHOR CONTRIBUTIONS

Paper I

Gunnar Öhlund and Göran Englund conceived the study. GE, GÖ and Catherine Hein extracted data. GE performed meta-analyses and wrote the first draft of the parts other than introduction. GÖ wrote the first draft of the introduction. Sebastian Diehl rewrote part of the first draft and suggested additional analyses. All authors contributed substantially to the revision of the manuscript.

Paper II

Gunnar Öhlund and Göran Englund conceived, planned and coordinated the study. GÖ and Per Hedström organized and executed attack rate experiments. PH also constructed the temperature controlled aquarium system. Sven Norman performed and analyzed swimming speed experiments as a part of his candidate thesis. GÖ analyzed data and wrote a first draft of the text. All authors contributed to the revision of the manuscript.

Paper III

Gunnar Öhlund and Göran Englund conceived, planned and coordinated the study. Mats Bodin developed the eco-evolutionary model with ecological input from GE, GÖ and Karin Nilsson. The model was analyzed by MB and KN. Kenyon Mobley performed genetic analyses. GÖ and Sven-Ola Öhlund performed interviews and collected information from different archives. Mikael Peeduu organized and performed net fishing surveys and performed analyses of fish in the lab as a part of his candidate and master theses. GÖ, SOÖ and GE also participated in fishing surveys. GÖ analyzed data and wrote the text, except Appendix 1 (MB, KN) and the methods section for genetic analyses (KM). All authors contributed substantially to the revision of the manuscript.

Paper IV

Gunnar Öhlund and Göran Englund conceived, planned and coordinated the study. GÖ analyzed data and wrote a first draft of the text. Gunnar Öhlund and Sven-Ola Öhlund performed interviews and collected information from different archives. Mikael Peeduu organized and performed net fishing surveys and analyzed gill rakers as a part of his candidate and master theses. Björn Fallgren and Martina Magnusson performed age determination as a part of their candidate theses. GE, GÖ, SOÖ, BF and Pia Bartels participated in the fieldwork. GE, GÖ, KN, MB, and CLH contributed substantially to the revision of the first draft.

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