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The Invasion of the Zebra Mussel - Effects on Phytoplankton Community Structure and Ecosystem Function

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Abstract

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Biological invasion has become a major threat to economy, ecology, global biodiversity and ecosystem function of aquatic ecosystems. The main aim of the thesis was to study the effects of the zebra mussel (*Dreissena polymorpha*), a versatile invasive species, on phytoplankton dynamics and ecosystem function of lakes.

In a first attempt, I compared the density of *Dreissena* and the physicochemical data of ecosystems that it invaded among North American and European lakes to identify important factors in its invasion success. Secondly, I investigated the impact of zebra mussels on phytoplankton community composition in a natural lake. Thirdly, I evaluated whether zebra mussel feeding behavior were affected by the presence of predatory waterborne cues. Finally, I examined the effect of *Dreissena* on seston stoichiometry.

A Generalized Additive Model revealed that a joint effect of surface area, mean depth, total phosphorus and calcium concentrations can explain the variability in *Dreissena* density. Selective grazing by zebra mussels varied in relation to seasonal phytoplankton dynamics. Risk cues released by predators affected both feeding rate and prey selection of the mussels and had cascading indirect effects on phytoplankton biomass and community structure. I found that the flux in nutrients caused by differences in zebra mussel consumption lead to a variation in phytoplankton nutrient limitation.

The flexibility of zebra mussel feeding behavior and variation in susceptibility among phytoplankton groups to mussel ingestion indicate that invading zebra mussels could alter phytoplankton community composition of lakes and have important ecosystem consequences. The results of this thesis contribute to the growing evidence that predators indirectly affect resource dynamics and food web structure through their non-lethal effects on consumers. The results suggested that zebra mussel can indirectly both reduce and increase the energy transfer efficiency from primary producers to upper trophic levels in the pelagic and benthic food webs, respectively.

Keywords: Invasive species, Zebra mussel, Invasion success, Selective feeding, Non-lethal effects of predator, Seston stoichiometry, Delayed fluorescence excitation spectroscopy, Phytoplankton dynamics, Trait-mediated indirect interaction, Ecosystem function

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To my wife

List of papers

- I. Naddafi R., Blenckner T., Eklöv P., Pettersson K. Why is an invasive species more successful in some areas than others? A comparison of zebra mussel density in North American and European lakes. (*submitted*)
- II. Naddafi R., Pettersson K., Eklöv P. 2007. The effect of seasonal variation in selective feeding by zebra mussels (*Dreissena polymorpha*) on phytoplankton community composition. *Freshwater Biology*, **52**: 823–842
- III. Naddafi R., Eklöv P., Pettersson K. Non-lethal predator effects on the feeding rate and prey selection of the exotic zebra mussel (*Dreissena polymorpha*). *Oikos*, **116**: 1289–1298
- IV. Naddafi R., Pettersson K., Eklöv P. Effect of zebra mussel, an exotic freshwater species, on seston stoichiometry. (*submitted*)

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Abbreviations

PUFA	Polyunsaturated fatty acid
C	Carbon
N	Nitrogen
P	Phosphorous
TP	Total phosphorous
TN	Total nitrogen
PP	Particulate phosphorous
PN	Particulate nitrogen
PC	Particulate carbon
SCUBA	Self-Contained Underwater Breathing Apparatus
SE	Standard error
GAMs	General additive models
DF	Delayed fluorescence
GLD	Greatest linear dimension
FIA	Flow Injection Analyzer
DIP	Dissolved inorganic phosphorus
DIN	Dissolved inorganic nitrogen
EPA	Eicosapentaenoic acid
DHA	Docosahexaenoic acid

Introduction

Biological invasion

Biological invasion has been recognized as a major threat to global biodiversity and ecosystem function (Mack et al. 2000; Kolar & Lodge 2001) and human activity have greatly participated in the invasion success through intentional or incidental spread of species beyond their natural range (Kolar & Lodge 2001; Jeschke & Strayer 2006). However a small proportion of introduced species can establish and only a small subset of established species can proliferate and/or spread in the introduced range (Lodge 1993; Kolar & Lodge 2001). The ability of invaders to become successful and dominant in a new environment depends not only on propagule pressure (Colautti et al. 2006) and species life-history traits (Williamson & Fitter 1996) but also on the characteristics of the recipient environment such as physico-chemical properties (Havel et al. 2005), diversity of the native community and the degree of disturbance (e.g., Elton 1958; Jeschke & Strayer 2006). However, the role of the physical environment in the invasion success of species is not well understood (Havel et al. 2005).

The imperceptible progression of invasion biology as well as irreversible ecological effects and substantial economic losses driven by alien species are major and ongoing worldwide dilemma. Invasive species inflict an enormous economic cost, estimated at \$137 billion per year to the United States economy alone (Pimentel et al. 2000). Thus a major challenge in invasion ecology is to unravel fundamental questions such as which factors regulate invasion success and why some invaders become widespread and abundant in a novel environment. Still, broad-scale statistical patterns of invader success are poorly understood. The rate of exotic species introduction is increasing, endangering the biodiversity of many ecological systems (Lodge 1993; Byers et al. 2002). Indirect effects involving exotic and native species can affect the invasion process (White et al. 2006); however, these effects can be difficult to predict, detect, and quantify. Dispersal and survival of an exotic species within a novel environment may be affected by its ability to recognize and respond to native predators (Carlsson et al. 2004). Predators may induce changes in life history, phenotypic traits, habitat use, feeding rate,

and morphology and behavior of their prey, thereby influencing the interactions between prey and their resources.

Trait-mediated indirect interactions require a trait shift, and prey that have no evolutionary history with a predator may not be able to appropriately recognize or respond to the risk posed by that predator (e.g., Carlsson et al. 2004). In addition, prey may require the ability to evolve proper responses to the exotic predator (e.g., Korpi & Wisenden 2001). Thus, trait-mediated indirect interactions involving invasive species may be weaker than those involving native species. This may explain why many invasive species are very effective at exploiting resources, perhaps in part because the resources lack appropriate defences. Trait-mediated indirect interactions involving exotic species should be especially important because exotic species have been shown to strongly influence the structure and dynamics of invaded communities (e.g., MacIsaac 1996; Strayer et al. 1999; Idrisi et al. 2001; Kelly et al. 2006).

Zebra mussel

The zebra mussel [*Dreissena polymorpha* (Pallas)] has both a planktonic and a benthic stage during its life cycle. There are three main periods in the zebra mussel life cycle: the larval, juvenile, and adult stages. The lifespan of the zebra mussel is typically 3-5 years, but there are data showing that it can live 6-9 years and even up to 15 years (Ludyanskiy et al. 1993). Female zebra mussels can spawn more than one million eggs, and males up to nearly 10 billion sperm (Sprung 1991). Adult mussels have strong strings or byssal threads to attach each other and to both man-made and natural structures, reaching densities as high as 779000. m⁻² (Mackie & Schloesser, 1996).

Zebra mussel provide one example of a successful invader with high reproductive output (Nichols 1996), rapid growth rate (Mackie & Schloesser 1996), great tolerance to a relatively wide range of physico-chemical factors, and successful in interactions with natives (McMahon 1996). *Dreissena* mussels have been introduced repeatedly to habitats where they have exploited available niche opportunities (Shea & Chesson 2002), and become a widespread and dominant species in the community (Colautti & MacIsaac 2004). The native zebra mussel population in the Caspian and Black Seas has spread across Europe in the 1800s (Kerney & Morton 1970). The North American introduction occurred in the mid 1980s, and may have resulted from the release of larvae in freshwater ballast from an ocean-crossing commercial vessel that originated from the northern shore of the Black Sea (McMahon 1996).

The invasion of the zebra mussel has had dramatic economic and ecological effects and their effects are difficult to reverse or mitigate. The negative

effects of the invasion have been stronger in North America than in Europe but there are some reports of the *Dreissena* causing economic problems in Europe in the past (e.g., Clarke 1952) although they are not in the same magnitude as observed in the United States and Canada (Ram & McMahon 1996). For example, problems associated with electric power generation and water treatment facilities by zebra mussel invasion are estimated to cost US \$267 million through late 2004, since 1989 (Connelly et al. 2007). It is evident that higher economical problems in North America than Europe are attributed to higher densities of zebra mussels, which are often observed to attach to each other by byssal threads and clog water intake pipes.

Sestonic particles composed of phytoplankton, large bacteria, detrital material, and heterotrophic animals (protozoa and micro-zooplankton) as well as nutrients associated with these particles serve as a potential food for *Dreissena*. Thus, zebra mussels have affected both pelagic (Figure 1A) and benthic (Figure 1B) freshwater communities through feeding on these materials. Zebra mussels invasion of most freshwater ecosystems have resulted in a reduction in plankton biomass (Figure 1A), a change in phytoplankton species composition (Figure 1A), an increase in water clarity leading to a subsequent increase in macrophyte and periphyton abundance (Figure 1B), and an alteration of energy flow from the pelagic to the benthic region (Figure 1B). Zebra mussels have also been shown to eradicate native bivalves (Figure 1B) and change nutrients dynamics (Figure 1A), alter macroinvertebrate abundance and community structure (Figure 1B), and change fish population dynamics (Figure 1A, B) (MacIsaac 1996; Caraco et al., 1997; Karatayev et al. 1997; Ricciardi 1998; Strayer et al. 1999). In this context, zebra mussel population size is one of the important key factors.

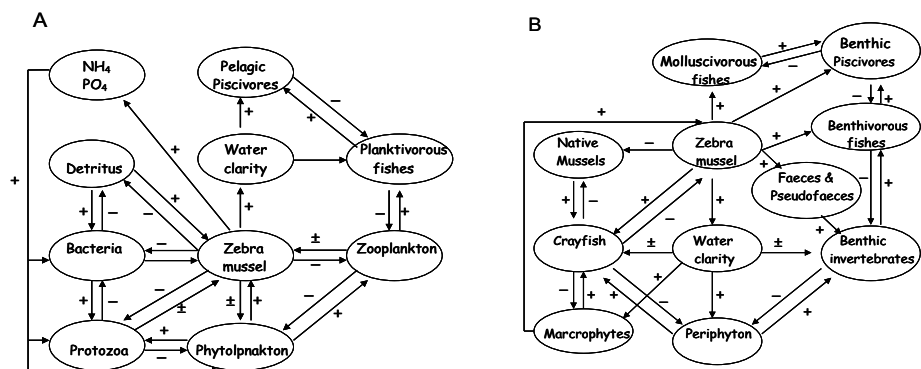


Figure 1. Impacts of zebra mussel in pelagic (A) and benthic (B) freshwater communities. Positive and negative effects are indicated by “+” and “-”, respectively. Only important interactions in which zebra mussel directly or indirectly influences other organisms are presented.

Perhaps the greatest concern about the ecological impact of zebra mussels on native species to date is their risk of causing an exclusion of freshwater unionid mussels in North America (Ricciard et al. 1998). Such extirpations have rarely been reported from invaded European lakes and rivers partly due to lower density of zebra mussels (Ricciard et al. 1998). Although, North American lakes apparently contain higher population densities than European lakes, much less attention has been devoted to elucidate why the zebra mussel is more successful in North American lakes. Furthermore, an identification of the important factors that influence zebra mussel density can provide a basis for understanding the capacity for populations to expand and affect the ecology and economy of invaded aquatic ecosystems.

Filtering activity

Most of the ecological impact of zebra mussels in aquatic ecosystems depends on their clearance rate on phytoplankton at the base of the food web. In fact, the mussels are capable of altering community structure and ecosystem function of lakes through a large grazing capacity and selective feeding on natural seston (MacIsaac 1996; Karatayev et al. 1997).

Dreissena filters a large but variable size range (0.7 μm -1.2 μm) of particles (Sprung & Rose 1988; Horgan & Mills 1997). Filtered phytoplankton may be either ingested or rejected as pseudofaeces, which may be resuspended into the water column and continue to grow (Baker et al. 1998; Vanderploeg et al. 2001). However, some algae can safely pass through a zebra mussel's digestive tract and survive grazer ingestion, digestion, and faecal excretion (Kotta & Møhlenberg 2002). Particle selection is performed by the cilia on the ctenidium and the labial palps in the mantle cavity of the mussels. Large, low food quality and unpalatable particles are bound in mucus and expelled as pseudofaeces through the inhalant siphon (see Figure 1B) (Ten Winkel & Davids, 1982).

Although some studies suggest non-selectivity of zebra mussel (e.g. Nicholls & Hopkins 1993; Horgan & Mills 1997) a rich literature indicates that they can be selective feeders (e.g. Baker et al. 1998; Bastviken et al. 1998; Dionisio Pires et al. 2004). However, it is less clear how the selective feeding of zebra mussels vary with the variation of phytoplankton groups over time in the natural environment. In addition, food quality, defined by concentrations of long-chain polyunsaturated fatty acid (PUFA), varies seasonally in a lake and zebra mussels experience low food quality (cyanobacteria and chlorophytes) in summer and high food quality (flagellates and diatoms) in spring and autumn (Goedkoop et al. 2000). Since the spread and abundance of this invasive species is increasing in different aquatic ecosys-

tems, an important question to investigate is how zebra mussel populations respond to variation in different phytoplankton groups.

Further, factors controlling either mussel clearance rate or the amount of excreted products are expected to have indirect effects on phytoplankton biomass. One of the factors is non-lethal effects of predators that can drive trophic interactions (Werner & Peacor 2003). Non-lethal effects of predators (i.e. trait-mediated effects) are immediate and rapid, and can affect an entire local community (Peacor & Werner 2001, Trussell et al. 2004). Thus, the strength of trait-mediated indirect interactions may rival or exceed that of density-mediated indirect interactions in shaping the structure and dynamics of food webs (Peacor & Werner 1997, 2001, Trussell et al. 2003, 2004, Wojdak & Luttbeg 2005). However, there is still little empirical evidence documenting the existence of trait-mediated indirect interactions, especially in food webs including exotic species (Werner & Peacor 2003). Although, it is likely that crayfish and roach have the potential to reduce zebra mussel populations via direct consumption (Karatayev et al. 1997, Molloy et al. 1997), it is less clear whether the risk cues released by these predators affect zebra mussel feeding behavior and subsequently the mussel-phytoplankton interaction.

Effects on seston stoichiometry

Ecological stoichiometry is defined as the mass balance of multiple key elements such as carbon (C), nitrogen (N), and phosphorus (P) in ecological interactions. The elemental imbalance stoichiometry has been inferred to cause the low quality of the food (Sterner & Hessen 1994; Sterner & Elser 2002). Especially, phosphorus is an essential element for animal growth. According to growth rate hypothesis, the fast-growing organisms have a relatively high P-content and then high ribosomal nucleic acid content which is needed for protein synthesis (Elser et al. 1996). In addition, because zooplankton maintain a rather constant C:N:P ratio, the mismatch between consumer nutrient demands and primary producer nutrient composition can place constraints on zooplankton growth (e.g., Sterner & Hessen 1994)

Stoichiometric imbalances between resources and consumers have been found to have implications both for consumer growth and for nutrient recycling in food webs, and may constrain or change key ecosystem processes (Sterner & Hessen 1994; Elser & Urabe 1999; Sterner & Elser 2002).

Consumers can indirectly change the balance of multiple chemical elements in trophic interactions, thereby affecting nutrient limitation and quality of food available to the primary producers. Measuring ecological stoichiometry has emerged as a powerful tool for understanding mechanisms and processes important for the structure, biodiversity and function of

aquatic communities. *Dreissena* may have large ecosystem-level outcomes by cycling phosphorous and/or nitrogen (Mellina et al. 1995, Arnott & Vanni 1996, Conroy et al. 2005) or by nutrient consumption (Heath et al. 1995; James et al. 1997). Phosphorous, nitrogen, and carbon associated with seston are entered into mussels' inhalant siphon and ingested. The ingested nutrients are either assimilated or egested, in which zebra mussels function as either nutrient sinks or nutrient sources. Egested nutrients deposited as faeces may become available to primary producers through mixing or microbial decomposition. Assimilated nutrients are either sequestered at relatively constant concentrations in mussels' tissues and used for growth and reproduction (mussels as a nutrient sink) or excreted in dissolved inorganic form (mussels as a nutrient source; Figure 1A) which can provide a substantial proportion of the nutrient demands of primary producers. Still, it is unclear how *Dreissena* affect seston stoichiometry by nutrients consumption and less clear how *Dreissena* affect it by nutrient excretion depending on the prevailing nutrient limitation in the environment.

Aims of this thesis

The main objective of this thesis is to study the effects of the zebra mussel, an invasive species, on phytoplankton community structure and ecosystem function of lakes. The focus of paper “I” is on identification of the important factors that influence zebra mussel density in lakes, whereas papers II and III deal with the mussel effects on primary producers through selective feeding and response to predators. Paper IV determines how zebra mussels affect seston stoichiometry through nutrient consumption and excretion, and accordingly nutrient limitation and trophic interactions.

This thesis addresses the following specific questions:

Why is an invasive species more successful in some areas than others (paper I)?

How do zebra mussels affect phytoplankton community structure in lakes? Specifically, how is zebra mussel feeding preference affected by a variation in the abundance of different phytoplankton groups? (paper II)

Can the presence of waterborne cues from predators influence *Dreissena* feeding behaviour? (paper III)

How do zebra mussels affect seston stoichiometry and energy transfer in freshwater food webs? (paper IV)

Material and methods

Paper I is a literature review, and papers II, III, and IV are a combination of field surveys and laboratory experiments.

Study area and organism (field study)

All field and laboratory studies (Paper II-IV) were conducted in Lake Erken, a moderately deep meso-eutrophic (Tot-P 26.1-51.4 $\mu\text{g L}^{-1}$) and dimictic lake situated in southeastern Sweden (59° 85' 18'' N, 18° 83' 59'' E). The lake has a surface area of approximately 24 km², a mean depth of 9 m, and a maximum depth of 21 m. Most of shoreline is stony and rocky and littoral substrate is composed of bedrock, stone, cobble, gravel, sand, mud and other sediments along with vegetation zones mostly consisted of *Phragmites australis*. Zebra mussels first appeared in Sweden in 1920s when they were introduced to Lake Mälaren, and have spread to infest to Lake Hjälmaren, Lake Erken and Lake Björklinge-Långsjön so far. They invaded Lake Erken in mid-1975, spread rapidly and have now been a dominant part of the biota since 1976 (Pettersson, *unpublished data*).

The zebra mussel consists one of the best studied invasive species and provides researchers with a unique opportunity to address questions about ecosystem structure and function. There are a large number of publications of field studies and experimental results available of the zebra mussel allowing me to use *Dreissena* as a model organism to answer the question of why an invasive species is more successful in some areas than others (Paper I). Further, the adults are usually abundant and widespread in the invaded area and are even able to survive for a week or more in a cool, moist and shaded area. This helps researchers such as me to sample and transport easily this organism from the field to the laboratory and use it extensively in laboratory experiments (paper II-IV). In papers II-IV, I collected mussels for the experiments by SCUBA (Self-Contained Underwater Breathing Apparatus) diving at one site in the eastern basin of Lake Erken (3m depth). The mussels were placed in buckets filled with lake water and were transported to the laboratory. In the laboratory, I detached the mussels from their natural substrate by severing their byssal threads with a scalpel and brushed them clean to remove silt and algae adhering to the shells.

Signal crayfish, *Pasifastacus leniusculus* is an exotic species that was imported to Sweden in 1960 as a replacement for the susceptible native noble crayfish (*Astacus astacus*). It was introduced into Lake Erken in 1966-1969 to fill the ecological and commercial gap caused by eradication of *Astacus astacus* due to crayfish plague (Schreiber et al. 1998). The crayfish prefer rocky habitats where zebra mussels are generally found, and are important predators of *Dreissena* in Lake Erken (Schreiber et al. 1998). Signal crayfish have broad diets and are efficient predators of zebra mussels (Pettersson, *unpublished data*), using pereopods and maxillipeds for pulling the flesh out of shells and mandibles to damage shells by applying pressure (Schreiber et al. 1998). I used Signal crayfish as a one of the predators in my laboratory experiment (paper III). I caught crayfish (45-55 mm carapace length) with baited traps (paper III).

The roach is the most prominent predator of *Dreissena* in European freshwaters (Stańczykowska 1977; Karatayev et al. 1997). Zebra mussel comprise from 95 to 100% of the diet of roach larger than 18 cm in a number of Polish lakes (Stańczykowska 1977). Roach use a rapid suction movement to dislodge and swallow zebra mussels and move the shell to the chewing cavity, where it is crushed by large static forces exerted by upper pharyngeal teeth (Nagelkerke & Sibbing 1996). I caught roach (180-190 mm total length) with flexible umbrella-shape nets (Ellafishing AB) to use in my laboratory experiment (paper III). Roach and signal crayfish are size-selective predators with a preference for zebra mussels ≤ 15 mm (Karatayev et al. 1997, Schreiber et al. 1998).

In two studies (paper II, paper IV), the mussels were kept in the aerated containers with natural lake water and placed in a climate-controlled room at ambient lake temperature for almost one day prior to running the experiment. In one study (paper III) the mussels were placed in aerated containers with natural lake water at ambient temperature in the laboratory for two weeks. The water in the containers was exchanged with new lake water once a day and also 2 h before the experiment began (papers II-IV). After the acclimation period, all mussels chosen for the experiments were visibly healthy and active (as indicated by comparing their filtration activity to recently collected mussels).

Roach and crayfish were held in separate cylindrical cages that hung freely in the water column at 2m depth (paper III). After about two weeks, the selected roach and crayfish were brought to the laboratory and put in aerated aquaria with natural lake water for 2 days prior to start of the experiment. We fed the roach and crayfish once a day with small zebra mussels (10-15 mm) while they were in cages and aquaria during the acclimation period and the day of the study (paper III). Visual observations of animals in the aquaria and broken shells in the cages showed that predators fed on mussels during the acclimation period. The mussels and water sampling were

performed twice per month from April to November 2005 in paper I and once per month from June to November 2005 in paper IV.

Literature review (paper I)

We analyzed data on zebra mussel density and standard error (SE) of density (22 lakes) and limnological parameters for 69 lakes from North America and Europe. The parameters that we were able to find for most of the lakes were surface area, volume, mean depth, maximum depth, total phosphorus, phosphate, Secchi depth, dissolved oxygen, calcium, pH, chloride, potassium, sodium, iron, annual temperature, dissolved oxygen, chlorophyll *a*, and time since initial colonization. After using a non-parametric Spearman rank correlation and removing variables with high collinearity as well as eliminating variables with low number of observations, five predictors were chosen for our model: lake surface area, mean depth, calcium concentration, total phosphorus, and time since invasion.

We used General additive models (GAMs), i.e. non-parametric modifications of Generalized Linear Models to test the effect of limnological parameters on the zebra mussel density and SE of density (Hastie & Tibshirani 1990; Quinn & Keough 2002). This regression technique is flexible, is able to accommodate non-linear functions (Quinn & Keough 2002) and can provide a clearer comprehension of the relationships between components of environmental variables. In principle, GAM has been utilized in ecology and biogeography surveys related to the prediction and interpretation of biodiversity features such as species occurrence (presence/ absence) or species richness (Yee and Mitchell 1991; Lehmann et al. 2002). We used a non-parametric Kruskal-Wallis to test for differences in density of zebra mussels between North American and European lakes.

Delayed fluorescence (DF) excitation spectroscopy

I used Delayed fluorescence (DF) excitation spectroscopy technique to determine biomass of each phytoplankton group and total phytoplankton biomass (measured by chlorophyll-*a* content) in all experiments (paper II-IV). DF is a measurement of the photosynthetic activity that occurs in living cells and originates from a recombination of electrons at the oxidized reaction centre P680 of photosystem II (Yacobi et al. 1998; Gerhardt & Bodemer, 2000). Phytoplankton assemblages can be distinguished by the DF technique because the algal classes contain different photosynthetically active chlorophylls and accessory pigments that have different excitation spectra when

excited by monochromatic light (400-730 nm) (Gerhardt & Bodemer 2000). The DF excitation spectra are analysed by a deconvolution program to determine total chlorophyll *a* (paper III-IV) and six phytoplankton functional groups: cyanobacteria (blue-green algae), chlorophytes (green algae), diatoms, cryptophytes, chrysophytes and dinoflagellates (paper II). However, the water samples used in one study did not contain chlorophytes and dinoflagellates (paper III). DF excitation spectroscopy has been previously applied to studies of chlorophyll concentration and phytoplankton composition in many aquatic systems, including: the River Danube, Germany; River Rhine, Germany; and Lake Kinneret, Israel (Bodemer, 1998; Yacobi et al. 1998; Bodemer et al. 2000).

Experiments

To investigate how zebra mussel feeding preference was affected by a variation in the abundance of different phytoplankton groups, I transferred 48-L of lake water containing natural seston to a container on each sampling date (paper II). After homogenization the water was poured into six 8-L vessels. Grazing (clearance) experiments were performed in triplicates with 12 mussels in each vessel. Three vessels with lake water and no mussels served as controls to correct for changes in phytoplankton biomass due to zooplankton grazing and/or pigment degradation (Fanslow et al. 1995). Water samples of 800 mL were taken from the vessels at the start and end (after 2 h) of the experiment and immediately analysed by DF excitation spectroscopy (papers II-IV). Initial and final seston samples (well-mixed 100-mL aliquots) were preserved in Lugol's solution for later analysis. Phytoplankton were identified to genus and species when possible by light microscopy. Phytoplankton sizes were measured with a micrometer as the greatest linear dimension (GLD) for 15 randomly selected individuals of each common species.

After the grazing experiment, the mussels from each vessel were cleaned under running de-ionised water and placed in three separate vessels containing 800 mL 0.45 µm filtered lake water for 30 min to allow for excretion of phytoplankton as pseudofaeces and for the identification of phytoplankton groups and species rejected by the mussels (papers II-III; Dionisio Pires & Van Donk, 2002; Dionisio Pires et al. 2005). At the end of the experiments, the mussels were measured (shell length) with a vernier calliper (0.05mm), dried at 105°C for 24 h, and weighted to determine weight-specific clearance rates and pseudofaeces production (paper II). In paper II, the period from the end of ice cover to the start of temperature stratification was defined as spring (mid April-late June), whereas summer was defined as the stratified period (late June-early September). The mixing period from the end of strati-

fication to the commencement of ice cover was considered as autumn (early September–November).

To evaluate the non-lethal effects of roach and signal crayfish (water-borne risk cues) on zebra mussel feeding behavior and subsequent effects on phytoplankton biomass, I conducted a 2×3 factorial designed experiment (replicated three times) using two levels of grazers (mussels absent, mussels present) and three levels of risk (no predator, roach only, and crayfish only) (paper III). For the grazer present treatment, each aquarium received 24 litres of lake water and 36 mussels (10–15 mm shell length). Because I wanted to be certain that our observed results were not day specific, the whole experiment was replicated 6 times on six different days with new lake water, mussels, roach, and crayfish during three weeks, yielding a total replication of $n = 18$ per risk cue level. The no mussel treatment in the presence or absence of predators was included to assess whether the presence of predators (roach or crayfish) had any effect on the phytoplankton biomass and composition. On the first day of the experiment, 432 litres of lake water were filtered through a 100 μm mesh net to remove most of the zooplankton, and then transferred to a separate container. After homogenization the water was poured into eighteen 32-L aquaria (24 L per each) and each predator treatment received either one roach, or two crayfish.

To prevent tactile effects of predators and direct consumption, a fine-meshed screen separated the predators and mussels into two compartments of each aquarium, in which the mussel compartment composed of 1/3 of the aquaria. All aquaria had this partitioning, as well as a plastic screen on top to permit light penetration and keep the predators within the aquaria. All experimental aquaria were placed in the laboratory at ambient temperature. Water samples of 800 mL were taken from the centre of the aquaria at the start and end (after 2 h) of the experiment and were immediately analysed using DF excitation spectroscopy (paper III). After the grazing experiment, I measured excreted product (faeces and pseudofaeces) of zebra mussels using DF technique to determine whether mussels induced by risk cues of predators differed in excreted products from those in the absence of risk cues (paper III). At the end of the experiments, the mussels were measured (shell length) with a vernier calliper (0.05mm) to calculate dry tissue weight (mg) using a length-weight regression from Mackie (1993) ($W = 0.007L^{2.982}$) and to determine weight-specific clearance rates and excretion products.

To address the effect of zebra mussels on seston stoichiometry, I conducted monthly (June–November 2005) laboratory experiments in which I measured nutrient composition of seston and mussels as well as nutrient consumption and excretion rates by zebra mussels using three size-classes: small (<14 mm shell length), medium (14–20 mm shell length), and large (>20 mm shell length) mussels (paper IV). On day of the experiment, 96 litres of lake water were filtered through a 100 μm mesh net to remove most of the zooplankton, and then transferred to a separate container. After ho-

mogenization the water was poured into twelve 10-L vessels (8 L per vessel). The 9 vessels were randomly assigned to three treatments each containing 20 individuals of small, medium and large size-classes of zebra mussels and each treatment was replicated three times. In addition, one treatment with 3 vessels containing lake water and no mussels served as controls. Immediately before the experiment started the water was sampled in the vessels to measure total phytoplankton biomass (measured by chlorophyll-*a* content), and concentrations of total phosphorus (TP), total nitrogen (TN), particulate phosphorus (PP), particulate nitrogen (PN), particulate carbon (PC), ammonia-nitrogen (NH_4^+ -N), nitrate plus nitrite nitrogen ($\text{NO}_3^- \text{NO}_2^-$ -N), and phosphate-phosphorus (PO_4^{3-} -P) (paper IV).

The mussels were placed in the vessels and the experiment started when the inhalant and exhalant siphons were fully extended, which was generally within 3-5 min after the introduction of the mussels (papers II-IV). Subsequent water samples were taken at 2 and 6 h after the mussels were added to the vessels. The first water sample (after 2 h) was immediately analysed by Delayed Fluorescence (DF) excitation spectroscopy to determine total phytoplankton biomass and the second water sample (after 6 h) was used to measure all nutrient concentrations. In addition, molar ratios of C:N, C:P, and C:N for seston stoichiometry were defined initially and at the end of experiment (after 6 h) (paper IV). Particulate C and particulate N of seston were measured simultaneously with a CHN analyzer (LECO CHN-932, Carlo-Erba Strumentazione), and particulate P of seston was measured as phosphate after hot hydrolysis with potassium persulfate (Grasshoff et al. 1983) (paper IV).

Dissolved inorganic nutrients (ammonia-nitrogen, nitrate plus nitrite nitrogen, and phosphate-phosphorus) were analyzed, immediately after sampling, with standard methods (Grasshoff et al. 1983) in an auto-analyzer (FIA Flow Injection Analyzer). Total P and total N were also measured with FIA. At the end of the experiments, the mussels were measured (shell length) with a vernier calliper (0.05mm) to calculate dry tissue weight (mg) using a length-weight regression from Conroy et al. (2005) ($W = 0.01213L^{2.537}$) and to determine weight-specific clearance rates, changing rate of C:N:P stoichiometry of seston, and excretion rates (paper IV). I determined tissue nutrient content of mussels separately for small, medium and large size groups. Similar tissue parts were sampled for all specimens and analyzed for C, N, and P tissue content using the same methods as for seston nutrient analyses. The same individual was used for the P analysis as for the CHN analysis. C:N, C:P, and N:P ratios were calculated in molar units (paper IV). I determined P and N turnover, as the time required to excrete nutrients in relation to content in tissue (Hatcher 1994), and calculated it as tissue content divided by excretion per day.

Data analysis

Clearance rate, an indicator of mussel grazing activity, is calculated as the volume of water from which a mussel has removed all of the suspended particles per unit time. Specific clearance rates of zebra mussels were calculated from the depletion of total chlorophyll *a* (paper **III-IV**) and reduction of chlorophyll content of each phytoplankton group in an 8-L suspension for a 2-h period (paper **II-III**) as well as from the reduction of particulate P, particulate N, and particulate C in an 8-L suspension for a 6-h period (paper **IV**) according to Coughlan (1969):

$$CR = [V / (N \times T)] \times [\ln (C_0 / C_t) - \ln (C'_0 / C'_t)]$$

where: V = the volume of lake water in the containers; N = the weight of the experimental mussels (mg DW); T = the duration of the experiment (in hours); C_0 = initial concentration ($\mu\text{g L}^{-1}$) of each particles in the containers with mussels; C_t = final concentration ($\mu\text{g L}^{-1}$) of each particles in the containers with mussels; C'_0 = mean initial concentration of each particle in all control containers; and C'_t = mean final concentration of each particle in all control containers.

Results

Zebra mussel invasion success (paper I)

We found that lake morphometry and water chemistry affected zebra mussel invasion success (paper I). Zebra mussel density increased with increasing lake surface area and mean depth and decreased with lake TP. But there was no relationship between the mussel density and calcium concentrations. Zebra mussel density was higher in North America lakes than European lakes. Lake surface area was the only variable that was selected based on the backward selection method in the GAM to predict standard error of density of zebra mussels.

Zebra mussel a selective filter feeder (paper II)

The results revealed a significantly higher clearance rate of flagellates (cryptophytes, chrysophytes and dinoflagellates) than other phytoplankton groups, indicating selective feeding of mussels (Figure 2). Zebra mussels cleared dinoflagellates, consisting almost exclusively of *Ceratium hirundinella* (250 μm), and chrysophytes, dominated by *Dinobryon sociale* (60 μm) and small chrysophytes ($\leq 7 \mu\text{m}$), with lower efficiency in July and September, respectively (Figure 2). The clearance rate of cyanobacteria (mainly *Gloeotrichia echinulata*; 900 μm) was lower than of any other phytoplankton group during July-August. However, in September and October, zebra mussels cleared *Microcystis aeruginosa* (100 μm) with efficiency equal to other phytoplankton groups (Figure 2). Relatively lower clearance rates were consistently observed for chlorophytes (gelatinous chlorococcales, *Oocystis lacustris*, *Chlamydomonas debaryana*, *Elakatothrix gelatinosa* and *Scenedesmus acuminatus*) during spring and for large-colony forms of chlorophytes during summer and autumn (Figure 2). Diatoms responded differentially to zebra mussel grazing. The clearance rate was lower for diatoms, dominated by *Stephanodiscus hantzschii* v. *pusillus* (6 μm) as well as *Fragilaria crotonensis* (110 μm) and *Aulacoseira* sp. (240 μm) than for flagellates in April, and for cryptophytes and dinoflagellates in September (Figure 2). Zebra mussels cleared diatoms, dominated by medium (20-30 μm) and large centric (40-50 μm) diatoms and *Stephanodiscus rotula* (40 μm) at equal rates to flagellates.

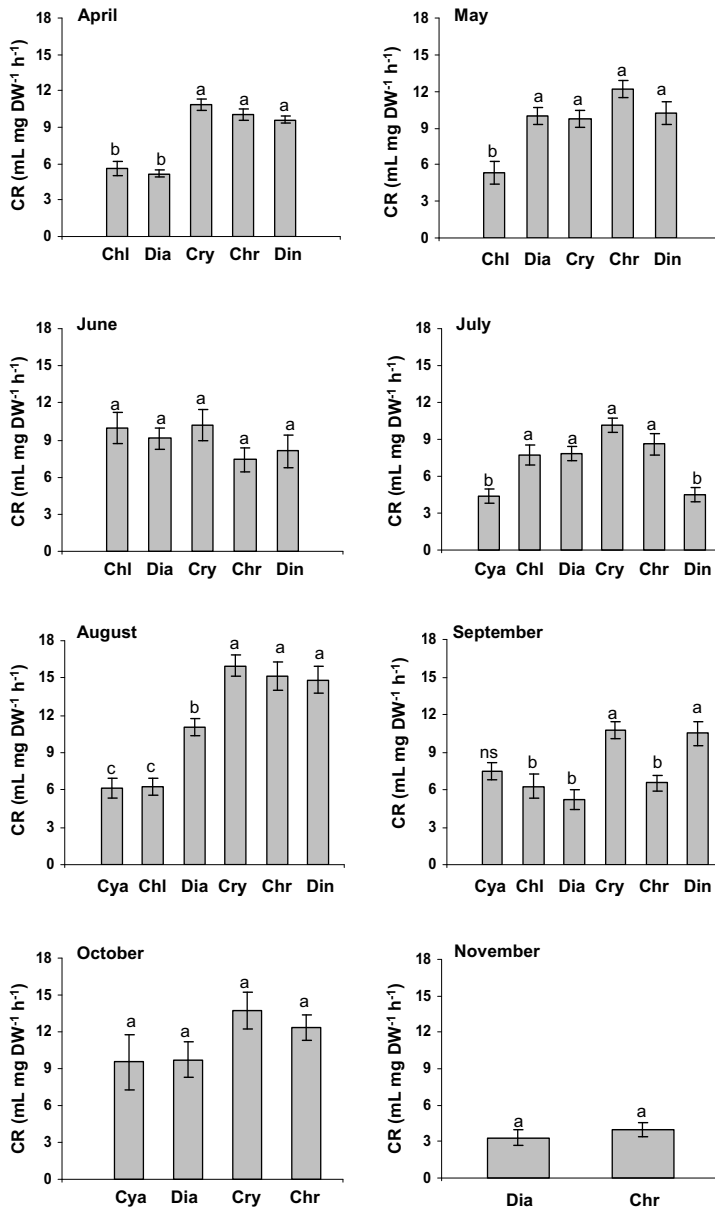


Figure 2. Clearance rate (CR) (mL mg DW⁻¹ h⁻¹) of zebra mussel classified by phytoplankton functional groups. Similar single labels (a, b, and c) indicates groups that are not significantly different ($P > 0.05$, Bonferroni's test). The group with symbol of 'ns' is not statistically different compared to other groups. For abbreviations refer to Fig 1. Values represent adjusted means (\pm SE) (Fig. 4 in paper II).

The high concentration of expelled diatoms (spring and autumn), chlorophytes (summer and autumn), dinoflagellates (summer), and cyanobacteria (summer and autumn) by the gills and labial palps of zebra mussels revealed a high tendency for preferential size-dependent rejection of larger particles ($> 50 \mu\text{m}$). Nevertheless, excreted products of mussels consisted primarily of phytoplankton, including chlorophytes during spring and cyanobacteria [*Limnothrix* sp. ($9 \mu\text{m}$) and *Aphanocapsa elachista* ($50\mu\text{m}$)], indicating that some factors other than size were important. Zebra mussels expelled fewer cryptophytes, chrysophytes and dinoflagellates throughout the year, with the exception of *Dinobryon sociale*, *Mallomonas* sp. ($80 \mu\text{m}$), *Ceratium hirundinella* and *Peridinium cinctum* ($60 \mu\text{m}$), and fewer diatoms during summer stratification than other phytoplankton groups (paper II). Small species ($\leq 7 \mu\text{m}$) were also observed in pseudofaeces of mussels along with small chrysophytes, some small cryptophytes, and *Stephanodiscus hantzschii* v. *pusillus*. Phytoplankton rejected in pseudofaeces were viable.

Non-lethal predator effects mediate zebra mussel feeding behaviour (paper III)

Risk cues released by both predators had similar negative effects on clearance rate of zebra mussels (Figure 3A) and then cascading positive indirect effects on phytoplankton resources. The clearance rate and amount of excreted mussels' products differed among phytoplankton groups, suggesting selective grazing by the mussels. In the presence of predator risk cues; clearance rate was significantly reduced for cyanobacteria and diatoms, but not for cryptophytes or chrysophytes (Figure 3B-E). Nutrient addition by predator excretion alone did not affect the final phytoplankton biomass. The presence of predators did not affect the rate at which zebra mussels expelled and excreted phytoplankton, although there was a tendency for more phytoplankton to be expelled and excreted in the presence of predators

Nutrient consumption and excretion by zebra mussel alter seston stoichiometry (paper IV)

Zebra mussels altered the stoichiometry of seston through removal of particulate organic nutrients and changed the stoichiometry of the dissolved nutrient pool through nutrient excretion. In Lake Erken, dissolved inorganic phosphorus (DIP), i.e. $\text{PO}_4^{3-}\text{-P}$, concentration was lower during June-August than during September-November (paper IV). In addition, dissolved inor-

ganic nitrogen (DIN) concentrations in both forms of $\text{NH}_4^+\text{-N}$ and $\text{NO}_3\text{-NO}_2^-\text{-N}$ were low during June-August and high during September-November. Both DIN and DIP were at the minimum value in June. The mussels consis

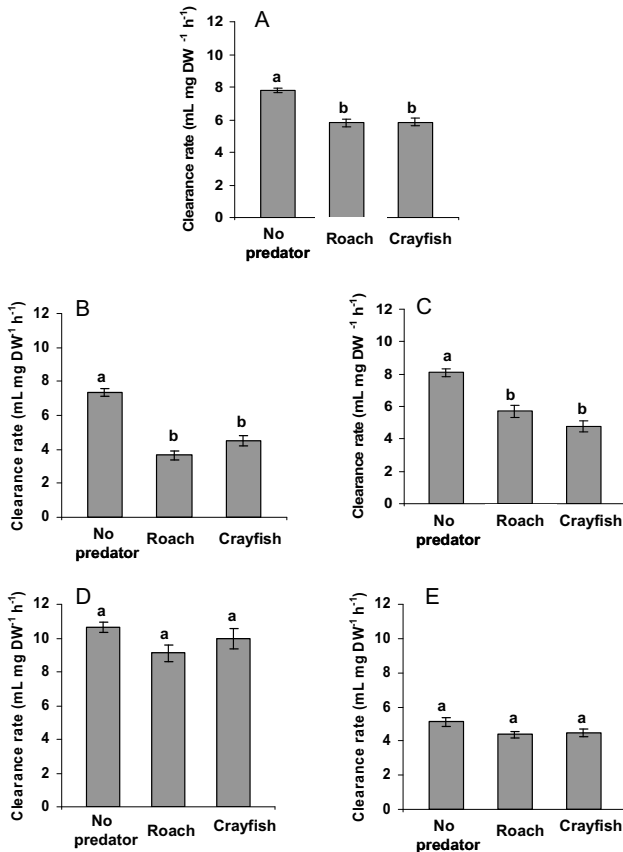


Figure 3. Zebra mussel clearance rates of total phytoplankton biomass (A), cyanobacteria (B), diatoms (C), cryptophytes (D) and chrysophytes (E) in relation to predation risk. Similar single labels (a and b) indicates groups that are not significantly different ($P > 0.05$, Tukey's test). Mean values ± 1 SE ($n = 18$ per bar) are given (Fig. 2 in paper III).

tently cleared chlorophyll *a* with the highest efficiency and the clearance rate was higher for particulate P than for particulate N and particulate C. *Dreissena* increased the molar ratios of C:P and N:P during June-August and caused them to decline in October and November (Figure 4A, B). They increased the molar C:N ratio of seston only in June (Figure 4C). The mussels did not excrete nitrate. Ammonium and soluble reactive phosphorus increased significantly at the end of experiment among treatments revealing excretion of some of the ingested seston in the form of soluble nutrients. The

value of inorganic N:P ratio of seston was increased across the months, except in August when the N:P ratio of seston declined. When experiments from all months were combined, the estimated nutrient budget showed higher uptake rate of particle nutrients than regeneration of soluble nutrients by zebra mussels. Small mussels excreted more nutrients per milligram dry weight and lower N:P ratio than medium and large mussels. The turnover time of N and P in small mussels, was shorter than that in medium and large size-classes of mussels. There was a longer turnover of N during June-August than that during September-November as well as highest turnover of P in June. On average P turnover was shorter than N turnover.

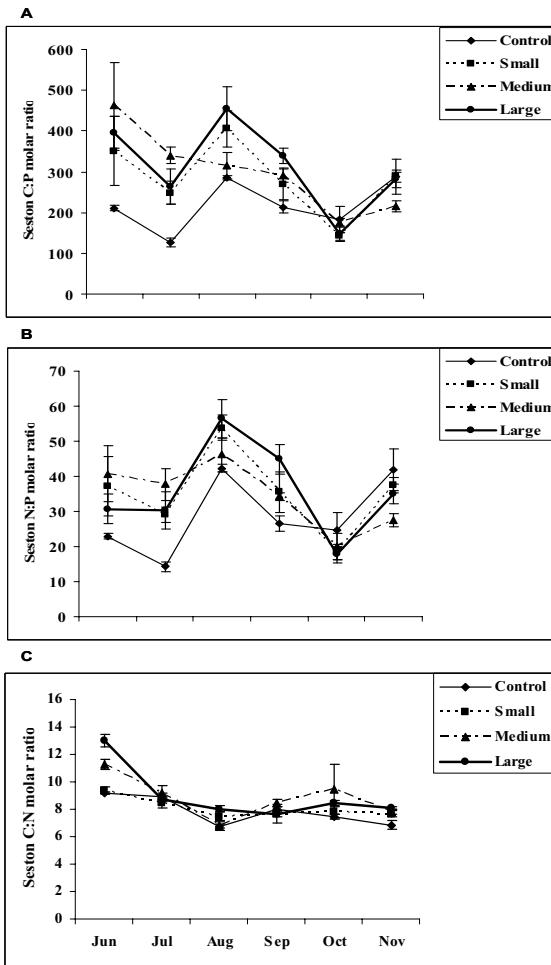


Figure 4. Molar ratios of C:P, N:P, and C:N of seston stoichiometry in treatment vessels that were measured at the end of each experiment from June to November. Mean values \pm 1 SE ($n = 3$ per error bar) are given (Fig. 2. in paper IV).

Discussion

Why is an invasive species more successful in some areas than others?

I addressed this question by comparing zebra mussel densities in North American and European lakes (paper I). *Dreissena* density is considerably greater in North American lakes than European lakes (paper I). The results indicated that zebra mussel density tended to be higher in larger and deeper lakes (paper I). Such lakes would provide more habitat and substrate for the mussel, because space and substrate limitation are the factors that may affect densities and population dynamics of the zebra mussel in lakes (Burlakova 2006; Strayer & Malcom 2006). In addition, higher surface area and depth (paper I) may supply more refuge to protect the settling of juvenile mussels from wave action. Further, the Great Lakes, although on average quite deep, have many relatively shallow habitats to which the water column can be disturbed regularly by windy conditions. Habitat disturbance can increase resource availability and opportunity for invasion and, thus, frequently disturbed ecosystems are more vulnerable to invasion than less disturbed ecosystems (Elton 1958).

An increased frequency of cumulative number of attempted and successful introductions may cause an ecosystem to be more vulnerable to invasion, leading to an “invasional meltdown” (Simberloff & Von Holle 1999; Ricciardi 2001), and could possibly explain the high susceptibility of the Great Lake communities to invasion (paper I). In addition, positive interactions among introduced species can enhance the probability of invasion success by producing new trophic or habitat opportunities, thereby facilitating population growth and abundance of invaders (Simberloff & Von Holle 1999; see also Ricciardi 2001). It is likely that North American zebra mussels’ abundance can increase by facilitative interactions with other invaders and result in a synergistic impact. Furthermore, large lakes may be stocked more by alien species due to higher propagule pressure through high recreational boating activity and shipping traffic (Johnson et al. 2001). Large sizes of new established populations would decline or eliminate the probability of stochastic extinctions (e.g., Colautti & MacIsaac 2004) resulting in successful population growth.

It appears that less productive lakes contain higher densities of mussels than productive lakes (paper I). It is possible that a higher TP in European lakes would negatively affect the oxygen saturation in deep zones and, therefore, limit zebra mussel distribution (Stańczykowska 1984; Strayer 1991). In addition, high concentration of algae may clog the mussels gills (Ramcharan et al. 1992). Dense North American zebra mussel populations could increase water clarity through extremely high filtration rate, thus enhance light penetration and allow macrophytes to distribute into deeper zones (e.g., MacIsaac 1996; Berkman et al. 1998). Macrophytes, in turn, can act as an autogenic ecosystem engineer by providing suitable substrate (Stańczykowska 1977; Vanderploeg et al. 2002) and as an allogenic ecosystem engineer by reducing turbidity through their stabilizing effect on the sediments (Vanderploeg et al. 2002). They can also contribute to oxygen supply in the mussel habitats, as *Dreissena* have been indicated to be relatively intolerant to anoxia compared to most bivalve species (MacMahon 1996). In addition, the microbial activity may be larger in lakes with high primary productivity such as European lakes, thereby consuming a large amount of oxygen. On the other hand, TP *per se* has an adverse effect on *Dreissena* invasion success, but when it is combined with other environmental properties such as surface area that increases invasion success, it could possibly have a positive effect on *Dreissena* density.

However we observed no relationship between calcium level and zebra mussel density among our studied lakes, but our model indicated that calcium in combination with other factors could be important also for the density of zebra mussels (paper I). Larger lakes such as the Great Lakes with a large volume of water contain a considerable amount of calcium which can be utilized by *Dreissena* for shell production and growth, thereby providing excellent environment for mussel survival and growth. In addition, both Appleton and Hawkins bays (Lake Champlain) in our study had a calcium concentration below a threshold of 28.3 mg.L⁻¹ reported in European lakes for shell production of zebra mussels (paper I). Hence, North American zebra mussels seem to need lower limits of Ca²⁺ for beginning of shell growth than European populations (Mackie & Schloesser, 1996), thereby being able to colonize a broader range of habitats. Time since initial colonization is a poor predictor for zebra mussel abundance in our study (paper I). In general, invaders can evolve rapidly in a new environment (Freeman & Byers, 2006), are able to recognize predators' presence (paper III) and adjust their life history traits in relation to local environmental conditions (Strayer et al. 2006). Thus, we would not expect North American zebra mussel populations to decrease in the future, i.e., after long time after invasion, like European communities.

The results suggested that the local mussel density is more variable among sampling sites in large lakes (paper I) such as the Great lakes apparently owing to great habitat heterogeneity and different local predator densi-

ties (Naddafi et al. unpublished manuscript). Greater local habitat heterogeneity may increase colonization success of alien species, supporting larger local populations (Havel et al. 2005).

How is zebra mussel feeding preference affected by a variation in the abundance of different phytoplankton groups?

Zebra mussel selectivity varies in relation to seasonal phytoplankton dynamics depending on phytoplankton morphology (size and structure) and quality (Paper II). Dionisio Pires *et al.* (2004), proposed that zebra mussels have the highest clearance rates on natural seston in the size ranges of 0–1 and 30–100 μm , which could explain why mussels cleared chlorophytes in July, dominated by *Staurastrum* sp. (71 μm), and cyanobacteria in September, dominated by *Microcystis aeruginosa* (95 μm), at a rate equal to cryptophytes (paper II). However, most cyanobacteria and chlorophytes were larger than 50 μm and were rejected by mussels as pseudofaeces, which lend support to the conclusions of Ten Winkel & Davids (1982). Nonetheless, selecting for small phytoplankton may not always be advantageous for the mussels, because this kind of phytoplankton may have lower digestible ingredients due to a scaling of food value with volume in many cases. Moreover, small phytoplankton species (such as *Stephanodiscus hantzschii* v. *pusillus* and probably small chrysophytes and small cryptophytes) have low long-chain PUFA concentrations and could not support mussel growth (Vanderploeg et al. 1996). Thus, phytoplankton $\leq 7 \mu\text{m}$ were not preferred by the mussels and were rejected as pseudofaeces in our study. Zebra mussels appeared to use both strategies of adjusting clearance rate and rejection of unfavourable particles as pseudofaeces. In addition to size, other factors might affect particle selection since similarly sized phytoplankton were affected differently.

A gelatinous layer of small chlorophytes (*Oocystis lacustris*, *Elakatothrix gelatinosa*) and gelatinous chlorococcales as well as the rigid cell walls of *Chlamydomonas debaryana* could affect zebra mussel avoidance of this phytoplankton group in spring. Similarly, diatoms have heavy silicate frustule protections that render them unpalatable to mussels, which may have lead them to be rejected through pseudofaeces. Diatoms were in general not preferred food items for the zebra mussels (paper II) which correspond to earlier findings (e.g., Baker et al., 1998). Further, toxins in diatoms that would make this group a poor food source (e.g. Miralto et al., 1999) may be expected to have an adverse effect on zebra mussel clearance rate. The interaction between the zebra mussel's feeding organ and the surfaces of phyto-

plankton cells is an important issue that should be considered in selective grazing of the mussels (paper II). For instance, the clearance rate of *Mytilus galloprovincialis* for the toxic dinoflagellate *Heterocapsa circularisquama* has been reduced by a protein-like substance (as the source of toxicity) involving the outer cell components (Matsuyama et al. 1997). It is possible that mussels such as *D. polymorpha* lack the enzymatic capability to degrade the surfaces of phytoplankton cells and possess an opportunistic feeding strategy instead, in which the mussels are able to adapt to whatever food becomes available. Zebra mussels may also recognize and select food according to its chemical nature (Ten Winkel & Davis 1982) or employ a higher clearance rate on a mixture of phytoplankton than on one species alone through higher sensory impacts and motivation of the mussels to pump at a faster rate (Dionisio Pires et al. 2004).

In general, flagellates are rich in both EPA (eicosapentaenoic acid) and DHA (docosahexaenoic acid); diatoms are rich in EPA but not DHA; and cyanobacteria and chlorophytes contain no or little EPA and DHA (Goedkoop et al. 2000). Zebra mussels appeared to graze effectively on cryptophytes and most high-quality species of chrysophytes and dinoflagellates, whereas cyanobacteria and chlorophytes were rejected (paper II). Diatoms were only preferred by zebra mussels in the summer when zebra mussels were exposed to low-quality food (cyanobacteria and chlorophytes). It appears that zebra mussels select high food-quality phytoplankton to maximize energy uptake in a similar manner to marine bivalves that alter their feeding behaviour to compensate for a reduction in food quality to maintain energy intake (Iglesias et al. 1996). In addition, flagellate algae are mixotrophic and have very low ash content (< 5%), i.e. high organic and energy content (Lampert & Sommer 1997). Because *Dreissena* is a prey for animals in upper trophic levels, it can strengthen benthic food web structure and increase the efficiency of energy transfer between trophic levels and between pelagic and benthic communities in lakes through selective grazing on high quality and mixotrophic (e.g., flagellates) phytoplankton. For example roach feeding on *Dreissena polymorpha* may grow faster than those feeding on plankton (Naddafi et al. 2005).

How do zebra mussels affect phytoplankton community structure in lakes?

The results showed that cyanobacteria, diatoms, and chlorophytes were not grazed efficiently by zebra mussels and were rejected as pseudofaeces (paper II). Cyanobacteria, dominated by large colonial *Gloeoetrichia echinulata*, were viable after rejection and could return unharmed to the water column

and migrate vertically due to their possession of gas vacuoles. Similarly, pseudofaeces that contain primarily diatoms are fragile and diffuse, and can resuspend readily under turbulent mixing during seasonal circulation and autumn turnover (Baker et al. 1998). Chlorophytes could be successful under high grazing pressure due to their relatively high growth rate (Schöl et al. 1999). Therefore, it is likely that in systems where phytoplankton biomass is regulated by zebra mussel feeding, the grazing-resistant phytoplankton groups could have a tendency to increase after zebra mussel invasion so that community structure might be shifted toward a community dominated by chlorophytes, diatoms, and cyanobacteria. This is supported by observations after zebra mussel invasion where all basins (west, central and east) of Lake Erie have experienced an increased prevalence of chlorophytes after four years and a combination of chlorophytes and diatoms are predominant 10 years after zebra mussel establishment (Munawar et al., 2005). Dramatic increases in cyanobacteria abundance have been reported after invasion by zebra mussels in some systems, including western Lake Erie and Saginaw Bay, lake Huron (MacIsaac 1996).

Another prediction from the experimental results is that flagellate phytoplankton (chrysophytes, cryptophytes and dinoflagellates) may suffer a loss from zebra mussel invasion because they were grazed effectively by zebra mussels (paper II). Corroborating results from Oneida Lake (Idrisi et al. 2001) and Lake Erken (K. Pettersson, unpublished data) have indicated that chrysophytes were rare after invasion by zebra mussels. However, we do not expect any reduction in the abundance of chrysophytes bearing silica scales (e.g. *Mallomonas* and *Synura*) as a result of zebra mussel grazing. Overall, chrysophytes characteristically require high N:P ratios for growth (Sandgren 1988) and may be limited by periods of low N:P ratio in lakes. However, cryptophytes have a fast growth rate, a trait that allows them to compensate for direct predation losses and may even be favoured under high grazing pressures (Caraco et al. 1997; Vanderploeg et al. 2001). Additionally, most dinoflagellate species except *Gymnodinium helveticum* are capable of producing cysts and could survive as resting cysts on the lake sediments during a major portion of the year (Rengefors 1998). These cysts have rigid cell walls and are resistant to grazing.

How does the presence of waterborne cues from predators influence zebra mussel feeding rate and prey selection?

Zebra mussels recognized and responded to risk cues released by predators (paper III). In fact, non-lethal effects of predators reduced the influence of

mussels on their food resources by suppressing zebra mussel feeding rate, thereby releasing phytoplankton from grazing pressure (paper III). The reduction of zebra mussel feeding rate in response to predatory risk cues may make mussels less apparent to predators, a behavior that observed in other bivalves to minimize predation risk (e.g., Irlandi and Peterson 1991, Smee and Weissburg 2006). In addition, a recent study indicated that small zebra mussels (8-14 mm long) increased the crush resistance of their shell and shifted their resources allocation from growth to reproduction in response to common predators (crayfish, fish, and diving birds) (Czarnołęski et al. 2006). On the other hand, it is more likely that the threat from predators caused the mussels to reject phytoplankton. We do not know the exact reason for the higher rejection rate of phytoplankton but it could possibly be due to the cost of being a more selective grazer in the presence of predators.

It appears that the relatively smaller reduction in zebra mussels' clearance rate of cryptophytes, chrysophytes, and to some extent, diatoms, in comparison to cyanobacteria (paper III) were due to changes in resource selection under the risk of predation. Cryptophytes and chrysophytes lack thick cell walls and have a high nutrition value. These phytoplankton groups were efficiently grazed upon by zebra mussels in another study examining seasonal selective feeding of mussels on natural seston (paper II). Therefore, it is possible that a decrease in diet breadth and maintenance of increased clearance rate of higher quality phytoplankton was a response to the overall reduction in clearance rate under the presence of predators. In the period of our experiment, the zebra mussels were limited to small sized chrysophytes ($\leq 7 \mu\text{m}$); such that size could be a limiting factor in their preference (paper II). Still, zebra mussel clearance rate for chrysophytes revealed no difference between presence and absence of predators. In addition, diatoms have heavy silicate frustules and cyanobacteria (i.e., *Microcystis*) are surrounded by a gelatinous layer, which possibly explained why zebra mussels reduced their clearance rate of diatoms and cyanobacteria in the presence of predators. In a recent study, omnivorous crayfish switched their food sources to less risky prey to reduce the negative effects of predators on growth rate when exposed to non-lethal effects of predators (Nyström 2005). Thus, it is likely that behavioral mediation of feeding rates interacts with selective mechanisms in the presence of predators, causing the mussels to select prey items lacking thick cell walls such as cryptophytes and chrysophytes to reduce the feeding cost associated with predator avoidance. Consequently, trait mediated indirect effects of predators may be important for the development of cyanobacteria and diatoms, especially in shallow systems with dense zebra mussel populations. In these systems, zebra mussels can filter large volumes of water in relatively short periods of time.

How do zebra mussels affect seston stoichiometry and energy transfer in freshwater food webs?

Zebra mussels reduced phosphorus availability through enhancing C:P and N:P molar ratios of seston during June-August when P was limited in the lake (paper IV). This was probably a result of the relatively high clearance rate for PP and low clearance rate for PN and PC potentially leading to a P limitation for phytoplankton growth during this time period (paper IV). Conversely, the mussels increase P availability by decreasing C:P and N:P molar ratios of seston during October and November when there was no limitation of P, possibly because of relatively high clearance rate for PN and PC and low clearance rate for PP, although the mussels' changing rate of C:P molar ratio did not differ from zero in November (paper IV). Zebra mussels contributed to the N deficiency of the phytoplankton by increasing C:N molar ratio of seston only in June when DIN was at the minimum level in the lake (paper IV). Thus, the flux in nutrients caused by differences in zebra mussel consumption would lead to a variation in phytoplankton nutrient limitation.

Ammonium was the main component of the DIN congruent with most observations on benthic nitrogen regeneration (e.g., Gardner et al. 1995; Heath et al. 1995). Further, mass-specific nutrient excretion rate of zebra mussels was higher for small-size classes than for medium and large size-classes (paper IV) probably due to allometric constraints on metabolism (Peters 1983). A decline of nutrient excretion with increasing body mass has been observed in many field studies (Vanni 2002). I observed that the dissolved inorganic N:P molar ratio of seston was reduced by zebra mussel presence only in August (paper IV). There is a negative correlation between the N:P ratio released by an animal and the N:P ratio of its body tissues (Vanni 2002). Hence, it is possible that the skewed N:P ratio of seston in August reflect a similar pattern in our study although we do not know whether this is related to a higher accumulation of N in zebra mussel tissue or a homeostatic excretion by the mussels (paper IV).

Shorter turnover time of phosphorus and nitrogen in smaller mussels indicated that loss of elements through excretion was relatively high in comparison with tissue content (paper IV). Moreover, the longer turn over time of P and N when they are limiting in the lake, revealed that the consumer will store nutrients and release them at low rates, when the concentration is low in the water (paper IV). Finally, longer turnover time of N than P indicates that nitrogen was retained more efficient than P in *Dreissena* tissue (paper IV) which is similar to what Smaal & Vonck (1997) found in *Mytilus edulis* (but see Hatcher 1994).

Hence, the observed flux in nutrients due to *Dreissena* consumption and nutrient turnover time, relative to tissue content, suggested that zebra mussel

establishment may result in a reduction in soluble nutrient concentration when that nutrient is limiting and an increase when that nutrient is abundant in the recipient environment.

Zebra mussels can act either as nutrient sinks or nutrient sources in lakes, but the direction of the flux of nutrients depends mostly on zebra mussel population density and biomass (Mellina et al. 1995; Heath et al. 1995; James et al. 1997). The results showed that nutrient mass-specific uptake rate is higher than excretion rate by zebra mussels (paper IV). Thus, dense zebra mussel populations with high biomass can sequester a large amount of nutrients in their tissue over relatively short time scales and thereby acting as nutrient sinks in lakes (see also Johengen et al. 1995), a function that also have been observed in the phosphorus budget of *Daphnia* (Urabe et al. 1995). Hence, although, the relative effect of filtration and nutrient generation on phytoplankton dynamics is poorly understood (Conroy et al. 2005), it is possible that zebra mussels may function as a sink rather than a source for nutrients in lakes (see also Heath et al. 1995; James et al. 1997).

Zebra mussels are able to facilitate the benthic-pelagic coupling in lakes through increasing the rate at which particles are transported from the water column to the sediments. This can result in increased light penetration and diminishing of nutrients and energy from the water column and therefore, shift primary pelagic production to benthic production (MacIsaac 1996; Karatayev et al. 1997). Nutrients excreted by zebra mussels can be utilized mainly by grazing-resistant phytoplankton such as cyanobacteria, large diatoms and large dinoflagellates and fast-growing species (e.g., cryptophytes) (paper II), thereby affecting phytoplankton community structure in lakes.

Changes in nutrient content of the water and quality of the seston (paper IV) can largely affect the mineral content of algae. Hence, algal cells grown under N-limited and/or P-limited conditions may have a low nutritional value and a low content of polyunsaturated fatty acids (Brett & Müller-Navarra 1997), and may be difficult to digest (Van Donk & Hessen 1997). Zooplankton, feeding on such phosphorus-starved algae, may grow slowly in lakes (Sterner 1993; see also Hessen et al. 2005 and references therein). If algae and zooplankton have low nutritional value, the trophic transfer efficiency through the food web would be low. Low energy transfer can result in decreasing growth rates and standing stocks of animals at higher food chain levels in pelagic food webs. On the other hand, a reduction in zooplankton growth rate as a result of low food quality would lead to decreasing carbon transfer rate into zooplankton biomass, thereby accumulating a large carbon pool in the primary producers and then a phytoplankton bloom, which would affect lake food web structure. Moreover, zooplankton reproduction can also be affected by high C: nutrient ratios in algae, i.e. low food quality, (Sterner & Hessen 1994) thereby reducing food quantity for upper trophic levels.

The amount of N and P, and the ratio at which these nutrients are provided, can control phytoplankton growth. Ammonium-nitrogen, when served as a pool or when recycled at a rate adequate to support phytoplankton growth, favours the development of non-nitrogen-fixing cyanobacteria (e.g., *Microcystis*) (Vanderploeg et al. 2002). Moreover, the dissolved inorganic N:P molar ratio of excreted nutrients by small mussels was slightly (14:1) below the Redfield ratio of 16:1, which may lead to an N limitation. The N deficiency of seston may favor succession of cyanobacteria, which are able to fix molecular nitrogen (N₂), over other phytoplankton groups (Smith 1983). Thus, zebra mussels have the ability to increase ammonium supply (this study; Conroy et al. 2005), and skew N:P molar ratio toward an N limitation (paper **IV**; Arnott & Vanni; 1996). This together with selective rejection of cyanobacteria in pseudofaeces (Vanderploeg et al. 2002; paper **II**) as well as longer turnover time of N than P (paper **IV**), results in a dominance of low quality phytoplankton, i.e. cyanobacteria (e.g., Brett & Müller-Navarra 1997), thereby keeping the lakes in a state with low trophic transfer efficiency (Hessen et al. 2005). Consequently, I suggest that zebra mussels can indirectly reduce the energy transfer efficiency from primary producers to upper trophic levels in the pelagic food web whereas, the efficiency of energy transfer through the benthic food web can be increased by zebra mussels selective feeding on flagellates (paper **II**).

Conclusions and perspectives

In summary, the major conclusions that can be drawn from the papers presented in this thesis are:

1- The invasion success of zebra mussels with greater density in North American than European lakes is suggested to be attributed to the larger surface area and depth, which provide more suitable substrates, local habitat heterogeneity, food resources, propagules pressure, and facilitative interactions, by co-evolved invaders. In addition, a lower productivity in North American lakes, which supply great oxygen saturation and increase macrophyte distribution along with lower threshold of calcium concentration for shell production of mussels, are suggested to support larger local populations. Thus, the North American zebra mussel populations are expected to continue to increase in density relative to European populations. Moreover, proliferation on an exotic species in an area can be explained by physico-chemical properties of the recipient environment (paper **I**).

2- The zebra mussel is a selective filter-feeder that alters its feeding behaviour in relation to phytoplankton composition to capture and ingest high quality phytoplankton, especially when phytoplankton occur in preferred size ranges. Flexibility of zebra mussel feeding behaviour and variation in susceptibility among phytoplankton groups to mussel ingestion indicate that invading zebra mussels could alter phytoplankton community composition of lakes and have important ecosystem consequences (paper **II**). Further, in lakes regulated by benthic grazers, a shift in dominance of vulnerable phytoplankton groups to more grazing resistant groups such as cyanobacteria, diatoms, and chlorophytes is predicted after the invasion of zebra mussels and this shift could possibly be stronger in lakes with high nutrient enrichment (see Leibold 1996). However, some compensation might occur via selection for faster growing species (paper **II**).

3- The waterborne cues associated with predation risk reduce zebra mussel feeding rate and this predator-induced modification in prey behavior cascaded through the food web to affect the phytoplankton biomass (abundance) and structure. In general, an exotic species such as zebra mussels can show behavioural responses to both native (e.g., roach) and exotic (e.g., crayfish) predators.

4- Zebra mussel invasion may change soluble nutrient concentration depending on the prevailing nutrient limitation in the recipient environment. In addition, shorter turnover time of N and P relative to tissue

content of *Dreissena* in conjunction with high mass-specific nutrient excretion by small mussels, suggest that a community consisting of small consumers is more efficient recyclers than a community of large consumers of the same biomass. The results proposed that the increased ammonium supply and a skewed seston N:P molar ratio toward N limitation by zebra mussels as well as retaining N more than P in *Dreissena* biomass (paper IV) together with selective rejection of cyanobacteria in pseudofaeces (paper II) may facilitate dominance of cyanobacteria. Further, the results suggest that zebra mussels can indirectly reduce the energy transfer efficiency from primary producers to upper trophic levels in the pelagic food web. However, the efficiency of energy transfer through the benthic food web can be increased by zebra mussels selective feeding on flagellates (paper II). Consequently, a reduction of the abundance and growth of planktivorous fish (paper IV) and an increase in the abundance and growth of benthivorous fish (paper II) can still be expected after zebra mussel invasion.

My findings in this thesis elevate a number of topics that might be worth considering in future studies. One of the hypotheses that can explain the abundance and/or impact of a given invader is enemy release hypothesis (paper I), which implies that the alien species loose natural enemies (e.g., pathogens, parasites and predators) and are released from the effects of co-evolved enemies (e.g., Elton 1958). Because the invader has no evolutionary history with the natural enemies, it may not be properly protected against them and can be particularly vulnerable in the invaded ecosystem. There are increasing evidences that adult zebra mussels are consumed largely by crayfish, fish, and waterfowls in invaded areas in both North America and Europe (e.g., MacIsaac 1996). However, the high predation pressure can also drive zebra mussel population dynamics in lakes (Strayer & Malcon 2006), but it is not clear of how much of the difference in population density between North American and European continents that can be explained by predation. This is a fertile area of speculation about invasion success of zebra mussels.

The impact of zebra mussels on the aquatic ecosystems is not only assumed to be density-dependent (Griffiths 1993) but also depends on their size-related filtering capacity (Bunt et al. 1993; Horgan & Mills 1997). Since the aim of paper II was to investigate selective feeding by mussels under natural conditions, the dominant size-class at the study site (12-20 mm) was used in the experiments. In a reproducing population of zebra mussels the vast share of individuals could be small. These small individuals may account for a relatively large share of the total filtration capacity by zebra mussels. Further studies are required to draw any conclusions about the impacts that different sized mussels might have on food web structure.

It has been shown that after the establishment of zebra mussels there is a marked reduction of Chl *a* due to mussel grazing, but some of the grazing losses could be compensated by a shift in phytoplankton species to grazing-

resistant forms and also by increased growth rate from improved water clarity and nutrient cycling (paper II). Because there is a trade off among phytoplankton species between grazing resistance and resource-saturated population growth rate (Agrawal 1998), future research involving a large-scale, long-term and controlled field experiment is recommended to assess the role of grazing resistance versus growth rate strategies to evaluate vulnerability of phytoplankton to herbivory by zebra mussels.

In paper III, both roach and crayfish displayed similar per capita effects on the feeding rate of their prey (zebra mussels) in the closed habitat, i.e. aquaria. Whether roach and crayfish have the same effect on habitat use and other traits such as life history and phenotypic traits of zebra mussels in open systems where prey can change their habitat use in relation to predator density, is open for future research. In addition, I have evaluated non-lethal effects of predators on small zebra mussel (< 15 mm shell length) feeding behaviour, but vulnerability to predation and size-specific behavioral responses could be related to ontogenetic changes in prey (e.g., Eklöv & Werner 2000). Thus it is not clear if zebra mussel > 15 mm respond to non-lethal effects of predators in the field. Further, because physiological and behavioral adaptations to environmental infochemicals can occur quickly (e.g., Freeman & Byers 2006) and zebra mussel and signal crayfish have been in Lake Erken for a long time and perhaps have co-evolved adaptive responses in sympatry since the invasion. Hence, it is possible that they no longer can be considered as exotic species. Further studies are required to compare the importance of trait mediated indirect interactions in shaping community structure testing species interactions managed by the exotic mussels, with interactions mediated by native mussels.

Although I indicated that zebra mussels may function as a sink rather than a source for nutrients in lakes (paper IV) but the balance between nutrient consumption and nutrient excretion by *Dreissena* is still poorly understood. Moreover, non-lethal effects of predators can mediate zebra mussel clearance rate in the field, thereby cascading positive indirect effects on phytoplankton resources (paper III). Appropriate long-term and controlled field experiments are needed to determine how nutrient excretion, nutrient consumption and non-lethal effects of predators interact with each other to affect phytoplankton dynamics in the aquatic ecosystems.

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Summary in Swedish (Sammanfattning)

Invasion av främmande arter har visat sig få stora ekonomiska konsekvenser, är ett hot mot global diversitet och ekosystemens funktion i akvatiska miljöer. Enbart i USA uppgår invasionen av främmande arter till 137 miljarder US\$ per år. En viktig fråga att belysa i detta sammanhang är vilka faktorer som påverkar hur framgångsrika invaderande arter är och varför vissa arter är mera framgångsrika och snabbare på att etablera sig än andra arter.

Vandarmusslan (*Dreissena polymorpha*) är ett exempel på en framgångsrik invasionsart som har en hög reproduktionshastighet, snabb tillväxt, är tålig mot en variationsrik miljö och är framgångsrik i samspelet med inhemska arter. Honor av vandarmusslan kan lägga fler än en miljon ägg och hannarna upp till 10 miljoner spermier. Vuxna musslor har starka byssaltrådar som de kan fästa på varandra, på naturliga och andra substrat. De kan uppnå mycket stora tätheter såsom upp till 750 000 individer m⁻².

Invasionen av vandarmusslor har haft mycket stora ekonomiska och ekologiska konsekvenser och dess effekter är svåra att hantera och reversera. De negativa ekonomiska konsekvenserna av vandarmusslans invasion har varit större i Nordamerika än i Europa. Även om det finns rapporter om ekonomiska förluster av vandarmusslans invasion i Europa så är de mycket mindre än i Nordamerika och Kanada. Till exempel har kostnaderna för invasionen av vandarmusslan inom kraftverksindustrin och vattenverk visats uppgå till 267 miljoner US\$ mellan 1989-2004. De är tydligt att de större ekonomiska effekterna i Nordamerika är kopplade till en kraftigare etablering med högre tätheter av vandarmusslan vilka ofta ses sätta igen vattenledningar. Även vandarmusslan har visat sig ha mycket större tätheter i Nordamerika än i Europa har man inte ägnat någon forskning kring varför vandarmusslan är mera framgångsrik i Nordamerika än i Europa. En identifiering av de viktigaste faktorerna som påverkar vandarmusslans täthet skulle utgöra en viktig bas för att förstå vilken betydels främmande arter har på inhemska arter och deras ekologi i allmänhet.

Den största ekologiska påverkan som vandarmusslan har på akvatiska system är genom dess stora filtreringskapacitet på växtplankton. Musslornas filtrering kan förändra hela ekosystemets struktur och funktion genom en enorm filtreringskapacitet och selektivt födoval på plankton. Eftersom spridningen och förekomsten av vandarmusslan ökar i olika ekosystem blir en viktig fråga att undersöka är hur vandarmusslan svarar på en variation i förekomst av olika växtplanktongrupper. Dessutom kan faktorer som påverkar filtreringshastigheten eller mängden exkretionsprodukter från musslorna

förväntas påverka växtplanktons biomassa indirekt. En annan viktig faktor är icke-letala effekter av predatorer som kan påverka de trofiska interaktionerna. Även om det är troligt att predatorer som kräftor och mört har möjlighet att minska vandrarmusslans populationsstorlek genom direkt konsumtion så är det oklar hurvida dessa predatorer påverkar vandrarmusslans beteende och vidare interaktionen mellan växtplankton och musslor.

Ekologisk stökiometri definieras som massbalansen av flertalet betydelsefulla näringsämnen såsom kol (C), kväve (N) och fosfor (P) i ekologiska interaktioner. Konsumenter kan indirekt förändra balansen av kemiska ämnen genom trofiska interaktioner och därigenom påverka näringsbegränsning och kvalitet av tillgänglig föda för primärproducenterna. Det är emellertid oklart hur vandrarmusslan påverkar stökiometrin hos seston genom selektiv konsumtion och vidare genom exkretion av näring i förhållande till rådande näringsbegränsning i miljön.

Huvudsyftet med avhandlingen var att utvärdera effekter av vandrarmusslan på växtplanktons samhällsstruktur och ekosystemfunktion i sjöar.

Först jämförde jag tätheter av vandrarmusslan med fysikaliska och kemiska data i sjöar som den hade invaderat i Nordamerika och Europa för att identifiera faktorer som är viktiga för dess invasionsförmåga (artikel I). Sen undersökte jag vandrarmusslans påverkan på olika växtplanktongruppers sammansättning i sjöar (artikel II). I ett tredje arbete utvärderade jag hurvida filtrering och exkretion av fytoplankton hos vandrarmusslan påverkades av vattenburna kemiska signaler från mört (*Rutilus rutilus*) och signalkräfta (*Pasifastacus leniusculus*) (artikel III). Slutligen undersökte jag i ett labexperiment vandrarmusslans effekt på sestons stökiometri med avseende på näringsämnens sammansättning hos seston och vandrarmusslans vävnader och hur dessa förändrades över tiden (artikel IV).

En generaliserad additiv modell visade att sjöarea, medeldjup, totalfosfor och kalciumkoncentration tillsammans förklarade mer än 63 % av variationen av vandrarmusslans täthet (artikel I). Selektiv betning hos vandrarmusslor varierade i förhållande till fytoplanktons säsongsvariation; musslor föredrog cryptophyceae och undvek chlorophyceae och cyanophyceae (artikel II). Diatomerer, chryptophyceae och dinoflagellater svarade olika på betning av olikstora vandrarmusslor (artikel II). Kemiska signaler från predatorerna hade liknande negativa effekter på vandrarmusslans filtreringshastighet och positiva indirekta effekter på förekomst av fytoplankton (artikel III). Predationsrisk hade en större effekt på vandrarmusslornas filtreringshastighet på blågröna bakterier och diatomerer än cryptophyceae och chrysophyceae (artikel III). Jag fann att flödet av näringsämnen som orsakades av skillnader i vandrarmusslans konsumtion ledde till en variation i fytoplanktons näringsbegränsning. Små individer av vandrarmusslan var effektivare än större individer/biomassa (artikel IV).

Med dessa resultat drog jag slutsatsen att stora, djupa sjöar och mindre produktiva sjöar i Nordamerika kan hålla större lokala populationer av vandrarmusslan och att utbredningen av en invaderande art kan förklaras med

inneboende fysikaliska/kemiska variabler hos den invaderade miljön (artikel I). Dessutom kan vandrarmusslan genom sitt flexibla furageringsbeteende tillsammans med olika känslighet för betning hos växtplanktongrupper påverka växtplanktons sammansättning i sjöar och därigenom ha stor ekosystemeffekter i sjöar (artikel II).

Resultaten i denna avhandling bidrar till en växande forskning som visar att predatorer indirekt påverkar resursers dynamik och födovävsstruktur genom deras icke-letala effekt på konsumenter (artikel III). Vandarmusslan kan därigenom indirekt påverka effektiviteten av energiöverföringen från primärkonsumenter till högre trofiska nivåer i pelagiska och bentiska födovävar (artiklar II, IV). Resultaten föreslår att en invasion av vandarmusslor kan förändra näringskoncentrationer beroende på omgivningens näringsbe-gränsning (artikel IV).

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