Ecology of freshwater mussels in disturbed environments

Long-lived freshwater mussels of the order Unionoida are highly threatened. Habitat degradation by turbidity and sedimentation is thought to be one major reason for their decline. The objective of this thesis was to examine recruitment patterns and identify the causes of population declines in the threatened freshwater pearl mussel (Margaritifera margaritifera). In addition, I investigated the indirect effects of turbidity on non-endangered dreissenid mussels.

Mussel population size and trout density were both positively correlated to recruitment probability of M. margaritifera. A study of the age-structure of nine populations revealed that four of these populations showed no signs of recent recruitment. Examination of different life stages revealed no differences in the gravid mussel stage or the parasitic stage on salmonid fish. Instead, differences were observed for the juvenile, benthic stage, presumably related to differences in turbidity and sedimentation. In the study of the indirect effects of turbidity, bioturbating mayflies increased turbidity and filter-feeding dreissenid mussels reduced turbidity. Mussel growth both decreased and increased with increasing turbidity, depending on sediment type.

Turbidity and sedimentation often impact entire stream systems, and a holistic, catchment-based management strategy may be needed to reduce the effects of sedimentation on freshwater pearl mussels. The effects of restoration take a long time and must start soon if recruitment of mussels is to be re-established. Restoration may also be more urgent in some streams than in others, as the maximum age of M. margaritifera populations in my study differed by as much as 60 years. As mussel and trout densities seem to be important for recruitment success, one conservation method may be to concentrate mussels into sites where trout density is high.
Martin Österling

Ecology of freshwater mussels in disturbed environments
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List of papers

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


Introduction

Today, the numbers of threatened species and species extinctions increase at an alarming rate (Baillie et al. 2004). Mankind, directly or indirectly, is largely responsible for this loss of species (Wilson 1989). Numerous factors have been implicated, many of them related to habitat alterations (Wilcove et al. 1998, Primack 2002). For example, habitat destruction and fragmentation reduce the availability of habitats, leading to smaller total population sizes, altered species distributions, and reduced dispersion and colonization abilities (Sala et al. 2000, Trombulak & Frissell 2000, Primack 2002). Habitat degradation may occur even if the total habitat area and habitat structure are not substantially changed. Pollution is a common type of habitat degradation that often acts gradually over time (Primack 2002), ultimately resulting in reduced space and habitat quality for many species (Richter et al. 1997). Understanding these habitat alterations causing species declines and extinctions is a first step in developing strategies for conservation. However, threats to a species are not only related to extrinsic factors, but also to intrinsic characters such as growth and reproduction, which evolve in close relation with habitats (Stearns 1992). Consequently, habitat alterations may result in reduced growth and reproductive output of species if they are unable to match these changes. One interesting intrinsic character is that of life span. Long-lived species generally grow slowly and have delayed maturity and low fecundity. Thus, long-lived species may tolerate short-term fluctuations in the environment, but if population numbers are severely reduced, recovery may be slow, increasing the risk of extinction (Drechsler et al. 1999, Bauer 2001, Raimondo & Donaldson 2003, Wheeler et al. 2003).

Ecology of unionoid mussels

The long-lived freshwater mussels of the order Unionoida have an obligate parasitic stage on fish species (Wachtler et al. 2001). Reproductive strategies of these mussels differ greatly among species, from strictly dioecious to hermaphroditism (Bauer 2001). Their life cycle starts with fertilization of glochidia larvae on the mussel gills. When the larvae have ripened, they must infect a host fish for continued development (Wachtler et al. 2001). When the parasitic stage is completed, the juvenile mussels fall off the host fish, settle onto the bottom to initiate their benthic stage. During their first years as juveniles, many species live buried in the sediments (Strayer et al. 2004). Adult mussels live partly buried in the sediment and are mainly filter feeders.
Unionoid mussels have extraordinarily long life spans, with a maximum life of up to nearly 300 years (Dunca & Mutvei 2001) (Figure 1).

![Figure 1. Life cycle of a unionoid mussel, the freshwater pearl mussel (*Margaritifera margaritifera*). A) Fertilization occurs during early summer. B) The larvae are released in late summer, and infect gills of trout (*Salmo trutta*). C) The juvenile mussels fall off the fish in late spring the next year and become benthic. D) After some years buried in the sediment, the mussels become adults. Drawing by Gunnar Lagerkvist.](image)

The large-scale distribution of unionoid mussels is to a large extent determined by the distribution of their host fish (Watters 1992, Haag & Warren 1998, Vaughn & Taylor 2000), although historical patterns of dispersal and climate may also be important determinants of their distribution (Strayer et al. 2004). The general within-stream distribution of freshwater mussels is patchy. Interactions with the host fish (Haag & Warren 1998, Hastie & Young 2001, Hastie & Young 2003) and with physical factors such as substrate structure, water flow, water depth (Hamilton et al. 1997, Hastie et al. 2000a, Brown & Banks 2001, Box et al. 2002), sedimentation (Box & Mossa 1999) and water chemistry (Bauer 1988, Buddensiek et al. 1993) are believed to contribute to the distribution of mussels. Stability of sediments during flooding and low shear stress are also factors which have been shown to be associated with mussel assemblages (Strayer 1999, Hastie et al. 2001). However, these multiple...
controlling factors interact with all mussel life stages, and the processes behind mussel distributions are therefore complex (Strayer et al. 2004).

The patchy distribution of unionoid mussels may have repercussions for population regulation. A high mussel density may increase the chance of fertilization (Downing et al. 1993, McLain & Ross 2005), and result in the production of high numbers of larvae (Hastie & Young 2003). Mussel population size should also be positively related to larval production, which in turn should be positively related to the numbers of infections (Bauer 1988). Furthermore, the numbers of infections may also depend on susceptibility (Bauer 1987a) and distribution of host fish. The total larval production and the number of juvenile mussels entering the benthic stage may therefore be a function of both mussel and host fish distributions.

**Habitat degradation – impacts on unionoid mussels**

Mollusks is one of the most threatened major taxonomic groups worldwide, comprising 42% of all species extinctions (Lydeard et al. 2004). Within this group, the freshwater mussels of the order Unionoida are highly threatened throughout their distribution (Bogan 1993). The threats responsible for the decline have been difficult to identify, as many anthropogenic activities probably contribute. Many of the major threats seem to act together (Strayer et al. 2004), although habitat alterations and destructions are among the most common threats. In freshwaters, such anthropogenic activities lead to an increased input of material to the water, which contributes to large scale habitat degradation (Box & Mossa 1999).

The cause of the decline of a species may be difficult to identify if this species has distinctly different life stages. Thus, it is not simply a question of which factor is threatening the species’ existence, but also which life stage is being affected. This may be particularly problematic for a species with a life cycle that includes a parasitic stage on a host. Therefore, one may also need to examine the ecology of the host population (Bogan 1993, Vaughn & Taylor 2000, Haag & Warren 2003). Thus, any decline in the species with a complex life history may not only be related to direct threats to its own population, but also to threats to the host population (Hastie & Young 2001, Malcolm et al. 2003).
Habitat degradation by increased fine particulate material may act on all the stages in the complex life cycle of unionoid mussels. As the mussels are filter feeders, the cost of filtering may increase with decreasing quality of suspended material and result in reduced clearance rates and growth rates (Aldridge et al. 1987, Alexander et al. 1994, Baldwin et al. 2002). Clearance rates also decrease during brooding, as the mussels brood the larvae on their gills (Tankersley & Dimock 1993). Thus, environmental factors that interfere with filtering may potentially restrict larval production. If there is a low production of larvae, this may also be expressed in the parasitic life stage as a lower infection load on host fish. Furthermore, survival of host fish may be reduced by fine particulate matter (Chapman 1990, Wood & Armitage 1997, Malcolm et al. 2003), and reduced numbers of host fish can result in lower numbers of larvae infections and consequently reduced recruitment of mussels to the benthic population.

Increased sediment load into streams may also reduce survival of the juvenile life stage. Sedimentation can clog the interstitial spaces within the sediment, and may lead to reduced water circulation in the sediment. This affects the chemical conditions in the sediment, and oxygen levels may become reduced at low water flow, too low for juvenile mussel survival (Buddensiek et al. 1993, Wood & Armitage 1997, Box & Mossa 1999). Sedimentation may also be associated with increased nutrient levels which has been related to reduced survival (Bauer 1988).
Objectives

*Margaritifera margaritifera*, which parasitizes salmonid fish, is one of the most long-lived unionoid mussels, and is decreasing in abundance throughout its range (Bauer 1986, Beasley & Roberts 1996, Dunca & Mutvei 2001, Young et al. 2001b) (Figure 1). The major objective of this thesis was to investigate recruitment patterns of *M. margaritifera*. Large-scale recruitment patterns of *M. margaritifera* in relation to mussel population size and host fish density were studied in streams located throughout Sweden (Paper I). A more detailed study of age distribution, recruitment and growth was then conducted (Paper II). As it was found that recruitment was low in some streams, I examined the different life stages of the mussels to identify why recruitment was largely failing (Paper III). The next step was to determine which environmental factor was disrupting recruitment. Thus, I examined the influence of turbidity and sedimentation on recruitment patterns (Paper IV). Furthermore, I looked for relationships between adult mussel density, juvenile mussel density, gravid mussels, infection load on trout and trout density in an attempt to identify how recruitment is regulated (Papers I – IV). As turbidity may affect mussel feeding efficiency, I examined the effects of turbidity on non-threatened mussel species (*Dreissena* spp.). Turbidity was manipulated through use of bioturbating mayflies. Sediment type was of particular interest, as mussels may respond differently, dependent upon the sediment composition. Consequently, I studied the indirect environmental interactions between filter-feeding dreissenid mussels and bioturbating mayflies at different densities, using two different sediment types (Paper V).
Summary of methods

Study Areas

The studies of *M. margaritifera* populations (Papers I-IV) were performed in 12 Swedish counties (Figure 2). The study of filter-feeding mussels and bioturbating mayflies (Paper V) was conducted at Cornell Biological Field Station at Oneida Lake, NY, USA.

Figure 2. Map showing the Swedish counties where the investigations of *Margaritifera margaritifera* were performed. Paper I (107 populations), paper II (9 populations), paper III (10 populations) and paper IV (24 populations).
Paper I

Mussel population size was estimated using a standardized method developed by the Swedish national survey programme. The aim of this survey is to estimate mussel population size, look for signs of recent recruitment, and how recruitment has changed over time (Eriksson et al. 1998). Recruitment is defined to occur if at least one mussel with a length of 50 mm or less is found in the survey. Mussels up to this length are approximately 10 years or younger.

Trout density was obtained from local authorities and from the electrofishing database compiled by the Swedish Board of Fisheries. The trout data were collected in areas downstream of the mussel inventory sites, on average 2.4 years prior to the mussel inventory work, as this was thought to coincide with when and where recruitment occurred.

Paper II

A survey by local authorities indicated that seven out of fourteen of the streams with the largest population sizes in this area in Sweden lack recruitment, and nine of these streams were surveyed in this study.

The study reaches were 0.5 to 3 km long, and each stream was divided into two to four sub-reaches, to ensure that the entire study reach would be evenly sampled. One or more sites with a stream length of 3 or 5 m were randomly assigned for mussel sampling. Each site was searched for an hour, digging to a depth of ten cm in the sediment. The length of the mussels’ ligament was measured with calipers to the nearest 0.1 mm and could thereby be related to age.

Two methods of age determination were performed, one using the relationship between length of the ligament and annual growth lines of the ligament (Hendelberg 1961), and the other using annual growth lines on the shell (Dunca et al. 2005). Growth curves were then constructed for each stream and the age of the mussels was estimated based on the ligament lengths of the mussels sampled in the field. Growth of adult mussels (40 to 80 yrs) was estimated over the last ten years (1993-2003), based on ligament measurements. This was done to compare growth conditions between streams with and without recent recruitment.
Streams with mussels ≤ 10 years of age were classified as streams with recent recruitment, whereas streams lacking mussels ≤ 10 years were classified as streams without recent recruitment. Mussels ≤ 20 years were classified as juveniles, as they do not usually start to reproduce before this age (Bauer 1987b), and consequently mussels > 20 years were classified as adult mussels.

**Paper III**

In this study, ten streams, six of which were known to have recent recruitment, and four, which lacked recent recruitment, were studied. Trout were present in all streams (analysis in electrofishing database compiled by the Swedish Board of Fisheries).

Gravid mussels were investigated in nine of the streams, and were visited every 10-14 days over the gravid period until no mussels were no longer gravid. Mussels were considered gravid when the gills were swollen and filled with glochidia larvae. Turbidity was measured in all streams with a turbidimeter five to six times during the same period and at the same place as the gravid mussels were measured.

Electrofishing of trout was performed approximately one and a half months after the mussels released their glochidia larvae, and trout density was estimated based on three successive removals of fish (Bohlin et al. 1989). The numbers of glochidia per trout was counted in the laboratory. Only 0+ fish were sampled, as local authorities wanted the older fish to be available for future reproduction of the trout and *M. margaritifera*. This should probably not affect our interpretation of the data as older trout have been shown to excyst glochidia larvae before the larvae have metamorphosed and are therefore less likely to be important as hosts for *M. margaritifera* (Young & Williams 1984, Bauer 1987b, Bauer 1987c, Hastie & Young 2001). Mussel density was estimated in one meter wide transects, which extended from one stream bank to the other.

**Paper IV**

Turbidity and sedimentation were measured at one site (9.5 to 22.5 m long) in 24 streams. Modified Whitloch-Vibert boxes filled with small pebbles were buried into the sediments to measure sedimentation over three months during
summer – autumn. At the end of this period, the sediments were divided up into three particle size fractions (1.2 – 63, 63 – 250 and 250 – 1000 µm) for organic and inorganic material. Turbidity was measured in all streams with a turbidimeter five to six times over the study period. Mussel density was measured in 0.64m² quadrates within each site. Ligament length of the mussels was measured and converted to age.

**Paper V**

Investigation of indirect environmental interactions between filter feeding dreissenid mussels (zebra: *Dreissena polymorpha* and quagga mussels: *D. bugensis*) and bioturbating hexagenid mayflies (*Hexagenia* sp.) was performed in a 3 × 3 orthogonally crossed design, with mussel density as one factor and *Hexagenia* sp. density as the other. The mussel densities were 0, 100 (4 zebra and 4 quagga mussels per aquarium) and 1000 (38 zebra and 38 quagga mussels per aquarium) mussels m⁻², and the *Hexagenia* sp. densities were 0, 50 (4 per aquarium) and 300 (23 per aquarium) mayflies m⁻². Separate experiments were run for artificial and natural lake sediments. Three replicates of each treatment were run for the artificial sediment and two replicates were run for the lake sediment. Zebra and quagga mussels were collected in Oneida Lake and St. Lawrence River, respectively. Nymphs of *Hexagenia* sp. were collected in western Lake Erie.
Summary of results

Recruitment in relation to mussel population size and trout density (Paper I)

There were signs of recent recruitment in 58.9% of the 107 Swedish M. margaritifera populations that were investigated. Populations in streams with recent recruitment were significantly larger (48263 ± 10524 mussels stream⁻¹) than populations in streams without recent recruitment (12628 ± 4699 mussels stream⁻¹). Recruitment probability increased with population size, and there was a 50% recruitment probability at a population size of about 10 000 individuals.

There was a higher total density of trout, both 0+ and >0 trout, in streams with (26 ± 4 trout 100⁻²) than without recent recruitment (14 ± 2 trout 100⁻²). There was also a positive correlation between total trout density and recruitment probability, with a 50% recruitment probability at about a density of 10 trout 100⁻².

We also tested the relative importance of mussel population size and trout density. The first model, with mussel population size and overall density of trout as independent variables, indicated that only mussel population size significantly influenced recruitment probability. The second model, with population size and density of 0+ and >0+ trout, indicated a significant influence of mussel population size and density of >0+ trout but not of 0+ trout.

Age, density and growth relationships (Paper II)

All nine populations had a relatively high proportion of middle-aged mussels and mussels ≤ 10 yrs of age were found in four streams, and were absent from five streams. Maximum age varied between populations, and was between 89 and 150 years (Figure 3).

The distribution of age classes differed between streams, and mean age varied from 36 ± 3 to 76 ± 12 years between streams. A lower frequency than expected was found for the 11 – 20 age class in the streams without recent recruitment (Figure 3, A - E), whereas higher frequency than expected were found for the 11 – 20 age class in the streams with recent recruitment (Figure 3,
For older age classes the difference between these two stream types was lower. There was also large variation in the distribution of age classes and mean age (18 to 66 years) within streams.

Figure 3. Age distribution of mussels (proportions) in nine streams in south-central Sweden, given for ten year increment ranges. Streams without recent recruitment, A – E: Trösälven, Kolarebäcken, Lekhytteån, Rällsälven, Bratteforsån. Streams with recent recruitment, F – I: Teåkersälven, Lerkesån, Lindåsabäcken, Stommebäcken.
Mean mussel density in the streams varied between 2.1 ± 0.6 and 5.9 ± 2.5 mussels m⁻² and this difference was not significant. There was no relationship between adult and juvenile mussel density between streams.

Within stream variation in density was large (0.3 to 12.3 mussels m⁻²) and heterogeneous in all streams except one. Furthermore, within-stream adult mussel density was nearly twice as high at sites containing juvenile mussels than at sites lacking juvenile mussels (Figure 4). There was also a positive relationship between juvenile mussel density and adult mussel density for Stommebäcken (r² = 0.56, p < 0.05), Teåkersälven (r² = 0.62, p < 0.05) and Bratteforsán (r² = 0.79, p < 0.05), but not for other streams.

Comparisons of mussel density were also performed between streams with and without recent recruitment. There was no significant difference in mean mussel density between these stream types. However, mussel density of the 11-20 age class was significantly higher in the streams with recent recruitment, but there were no differences for the older age classes.

The mean annual growth of adult mussels was significantly higher in streams with than without recent recruitment (Figure 5). There was also a significant positive relationship between growth rate of adult mussels and juvenile mussel density (r² = 0.74, p < 0.05).
Gravid mussels (Paper III)

Gravid mussels were found between 6 July and 26 August 2005 in all streams and were present 13 to 32 days within a given stream. There was a significant negative relationship between date of maximum proportion of gravid mussels and mean water temperature ($r^2 = 0.58$, $p = 0.05$). However, there was no difference in the maximum proportion of gravid mussels between streams with and without recent recruitment.

Turbidity was higher in streams without (3.6 ± 1.0 NTU) than in streams with recent recruitment (0.94 ± 0.17 NTU), but was not related to the maximum proportion of gravid mussels between these stream types. Furthermore, mussel density did not have any influence on the maximum proportion of gravid mussels between streams with and without recent recruitment.

Parasitic life stage (Paper III)

There was no difference in mean glochidial load on trout gills in streams with and without recent recruitment. However, glochidial load on trout gills was positively related to mean mussel density in both stream types, but there was no effect of trout density on mean glochidial load on trout gills (Figure 6).
Figure 6. Glochidia load (filled squares: $r^2 = 0.66, p < 0.05$) and trout density (open squares) as a function of mussel density.

**Juvenile mussels (Paper IV)**

There were positive relationships between turbidity and sedimentation for each inorganic fraction and a positive relationship between turbidity and sedimentation of organic material for the 1.2 – 63µm size class, but not for the other size classes. Mean turbidity was lower in the streams with (0.96 ± 0.14 NTU) than without recent recruitment (4.1 ± 1.4 NTU). There was also a significant positive regression between turbidity and age of the youngest mussel in the sediment ($r^2 = 0.27, p = 0.03$).

Sedimentation of the three inorganic size classes was three to four times lower in the streams with than without recent recruitment. In contrast, sedimentation of organic material was lower in the streams with recent recruitment than in the streams without recent recruitment for the 1.2 – 63µm size class, but not for the other two size classes.

Age of the youngest mussel generally increased with increased sedimentation of inorganic material. For the organic material, age of the youngest mussel increased with increased sedimentation for the 1.2 – 63µm size class, but not for the other two size classes (Figure 7).
A discriminant function analysis showed that the streams with recent recruitment were associated with low levels of turbidity and sedimentation, whereas the streams without recent recruitment were associated with high turbidity and sedimentation.

**Adult mussels (Paper IV)**

The mean mussel density was not significantly different between streams with \(6.9 \pm 2.1 \text{ mussels m}^{-2}\) and without \(5.0 \pm 1.8 \text{ mussels m}^{-2}\) recent recruitment. There were no relationships between mussel density and recruitment, mussel density and turbidity or mussel density and the different sediment size classes.

**Indirect environmental interactions (Paper V)**

Turbidity increased with increasing density of bioturbators and decreased with increasing density of mussels in the artificial sediment treatment and the lake sediment treatment. Turbidity was higher in the artificial sediment than in the lake sediment. The strongest declines in turbidity were observed in the treatments with 1000 mussels m\(^{-2}\). Mean turbidity increased with increasing mayfly densities at all mussel densities and for both sediment types. Growth of zebra mussels was higher than quagga mussels at the low total mussel density but not at the high total mussel density. There was a trend towards an effect
between *Hexagenia* sp. density and mussel density, which was due to an effect of *Hexagenia* sp. density at the low mussel density but not at the high mussel density. Furthermore, mussel growth decreased with increased turbidity at the low mussel density (zebra: $r^2 = 0.44$, $p = 0.051$; quagga: $r^2 = 0.60$, $p = 0.014$), but not at the high mussel density in the AS. In contrast, there was no effect on growth at the low mussel density in LS, but an increased zebra mussel growth at the high mussel density in LS ($r^2 = 0.97$, $p = 0.00033$) (Figure 8).

**Figure 8.** Regressions between instantaneous rate of mass change ($\text{day}^{-1}$) and mean turbidity for zebra and quagga mussels in the artificial sediments (a) and in the lake sediments (b). Filled and open squares are zebra and quagga mussels, respectively, at 100 mussels m$^{-2}$, whereas filled and open triangles are zebra and quagga mussels, respectively, at 1000 mussels m$^{-2}$. 
Discussion

Recruitment failure

The freshwater mussels of the order Unionoida are threatened throughout its distribution (Lydeard et al. 2004). Recruitment was absent in 41.1% of the *M. margaritifera* streams (Paper I), which emphasizes the threatened status of this mussel species. However, these investigations only looked at the presence / absence of mussels < 50 mm and did not investigate the distribution of age classes, which can add more nuanced information about the status of *M. margaritifera* (Hastie et al. 2000c). Previous investigations of age structure have shown that many populations have low proportions of juveniles (Bauer 1983, Cosgrove et al. 2000, Hastie et al. 2000c, Morales et al. 2004). High proportions of the 11-20 year class and at least some mussels ≤ 10 years have been proposed as criteria for classifying a population as viable (Young et al. 2001a). Thus, the streams with recent recruitment should have sufficient recruitment to be considered as functional populations (Cosgrove et al. 2000). Our study of age structure (Paper II) was conducted on the largest populations in that area, and half of these populations were deemed as viable. However, it is likely that this is an overestimate as recruitment is presumably lower in streams with smaller populations, as mussel population size was positively related to recruitment probability (Paper I).

There were no differences in adult mussel density between streams with and without recent recruitment, and larval production is therefore not expected to differ between these stream types. Interestingly, however, we found that growth of adult mussels was higher in streams with than without recent recruitment, and that growth of adult mussels was positively related to juvenile density. This indicates that some factor / combination of factors is acting in the entire stream, leading to both reduced adult growth and juvenile survival. A negative impact on adult mussel growth may result in lower reproduction (Bauer 1998), which may be one explanation for low recruitment of *M. margaritifera*.

Habitat degradation – impacts on mussels

The negative effects on growth of adult *M. margaritifera* (Paper II) may be related to growth responses that were found for the dreissenid mussels (Paper V). There was a negative relationship between dreissenid mussel growth and
turbidity in the artificial sediments, whereas the situation was the opposite in the lake sediments, with a positive relationship between dreissenid mussel growth and turbidity. Therefore, the composition of suspended materials seem to differ, with a high inorganic content in the artificial sediments, resulting in reduced growth (Aldridge et al. 1987, Alexander et al. 1994, Baldwin et al. 2002), and a low inorganic content in the lake sediments resulting in increased growth. As inorganic material constituted the major part of sedimentation in the streams without recent recruitment (Paper IV), reduced growth of adult *M. margaritifera* may have been a result of high inorganic fraction.

Turbidity and sedimentation were correlated to each other, and both are measures of the transport of fine sediments (Paper IV), and both may have negative effects on the early life stages of *M. margaritifera*. However, the maximum proportion of gravid mussels was not related to recruitment patterns, and it therefore seems that this stage was not affected by transport of fine sediments. Likewise, we could not find any indication that glochidial infection differed between streams with and without recent recruitment, as glochidial load was similar in both types of streams (Paper III). This suggests that recruitment is probably limited at a later stage, namely the benthic stage.

We found that turbidity and sedimentation were about three to four times lower in streams with than without recent recruitment, indicating that turbidity and sedimentation may negatively affect the juvenile stage. Several potential mechanisms of increased turbidity and sedimentation may be involved in low survival of juvenile mussels. The smallest size fraction of sediments, which were more abundant in the streams without recent recruitment, is generally responsible for clogging sediments, (Kreutzweiser & Capell 2001), although sediments of this size have also been found not to affect exchange of water in sediments (Rehg et al. 2005). Nevertheless, sedimentation may hinder water flow in the gravel, resulting in low oxygen and pH conditions, which could reduce survival (Buddensiek et al. 1993, Wood & Armitage 1997). Sedimentation and turbidity may also be positively correlated with nutrients (Dodds & Whiles 2004), which may be associated with increased oxygen consumption and/or have toxic effects on the mussels, resulting in reduced survival (Bauer 1988).

Our results revealed that the organic portion of sedimentation was about 10%, which is similar to that reported in other investigations (Wood & Armitage
Only the smallest fraction of organic material differed between streams with and without recent recruitment, and it was higher in streams without recent recruitment than in streams with recent recruitment. If this organic fraction is an important source of food (Nichols & Garling 2000), then we cannot explain differences in recruitment based on food availability. Instead, it seems more likely that the inorganic fractions, which were higher in streams without recent recruitment, are negatively affecting recruitment.

The effects of turbidity and sedimentation seemed to have occurred over a long time in some streams, as age of the youngest mussel increased with increased turbidity and sedimentation. Previous studies have shown that sedimentation in a stream is often within the same order of magnitude between years (Madej 2001). Therefore, our study does not only give an indication of what is happening today but also what has been happening in the past (Paper IV).

Trout density was higher in streams with than without recent recruitment (Paper I). The difference in trout density between these stream types may be related to sedimentation (Paper IV), which is known to negatively affect survival (Crisp 1993, Wood & Armitage 1997, Soulsby et al. 2001, Malcolm et al. 2003). Nevertheless, the results of my other studies indicate that survival of juvenile mussels is the most probable reason for the lack of recruitment (Papers II-IV) even if sediment effects of trout density cannot be ruled out.

**Filter-feeding effects**

Habitat alterations may negatively affect mussels, but mussels may also alter the environment as they influence processes in the water column and in the sediment. Dreissenid mussels had strong effects on turbidity, depending on the mussel density (Paper V). These mussels have been shown to increase water clarity and also change ecosystems, due to their filter-feeding effects (Smith et al. 1998, Idrisi et al. 2001, Mills et al. 2003, Aldridge et al. 2004). In contrast, filter-feeding effects of unionoid mussels in running water are poorly known (Vaughn & Hakenkamp 2001). Nevertheless, there was no relationship between turbidity and mussel density of *M. margaritifera* (Paper IV). However, the patchy distribution of *M. margaritifera* may affect within-stream variation of turbidity, and future studies should take into account how this affects fine material distributions and impacts on mussels in streams.
Recruitment regulation

The positive relationship between glochidial load and adult mussel density indicates that glochidia infection of trout increase as mussel density increase, which should result in more juvenile mussels entering the benthic stage. In contrast, trout density was not related to mean glochidial load. This lack of relationship between trout density and glochidial load indicates that there should be a positive relationship between the total number of glochidia infections and trout density. Thus, high trout density should result in a higher total number of glochidia infections than low trout density (Paper III). The positive relationship between trout density and recruitment also indicates a positive effect on recruitment (Paper I). Mussel recruitment may thus be positively related to both mussel and trout density.

Recruitment was positively related to mussel population size. Logically, this is supposed to be due to the fact that more mussels should produce more glochidia that can infect host fish (Bauer 1988) and thus, a higher chance for recruitment (Paper I). Furthermore, within the streams, adult mussel density was higher at sites where juvenile mussels were found than at sites lacking juvenile mussels. Also, juvenile mussel density increased as a function of adult mussel density in three streams (Paper II). However, as both mussels and trout have patchy distributions (Hastie et al. 2000c, Hastie & Young 2001), there may be a large within-stream variation in recruitment. This may be an explanation as to why a general within-stream density of adult mussels was related to recruitment, whereas a relationship between adult and juvenile mussel density was only present in some streams, but not in others.

Management implications for the freshwater pearl mussel

The long life span of freshwater pearl mussels (Bauer et al. 1991) may have implications for survival. Any large population reduction, as might be expected to occur in response to a disturbance, may result in a very slow recovery. This was not observed in the present study, as adult mussel density was similar in streams with and without recent recruitment. A long life span may buffer populations from disturbances that are of short duration, but if the disturbances continue over a long time, the risk of extinction increases (Drechsler et al. 1999, Raimondo & Donaldson 2003). However, there was a large difference in
maximum age (89 – 150 yrs) (Hastie et al. 2000b), and the buffering capacity to disturbance seems to differ by about 60 years in this area. This underscores the importance of measuring age in all streams, and that management actions may be more urgent in some streams than others.

The present investigation showed that mussel populations without recruitment face the risk of extinction, and that turbidity and sedimentation seem to be negative factors involved. Sedimentation has several sources and often impacts entire stream systems (Poff et al. 1997, Wood & Armitage 1997, Ward 1998, Jones et al. 2000). Therefore, a holistic approach at the catchment scale is needed if we are to reduce the input of fine materials to streams (Wood & Armitage 1997, Harper et al. 1999). This will involve reducing erosion and sedimentation associated with human activities such as forestry and agriculture (Kreutzweiser & Capell 2001, Nisbet 2001, Dodds & Whiles 2004). Furthermore, flushing flows are needed if fine sediments are to be washed out (Ward & Wiens 2001). Restoring a stream often takes a long time (Wood & Armitage 1997), which means that restoration must start soon if recruitment of mussels is to be re-established.

Mussel distribution was patchy, and high mussel density seems to be important for recruitment, resulting in high production of larvae, increasing the probability for host fish infection and therefore more juveniles to the benthic population. Furthermore, the trout distribution is also patchy, and high trout density may result in higher recruitment of juveniles. If, however, mussel populations are reduced, one opportunity may be to concentrate mussels into higher density patches. This may be more efficient if these mussel beds are placed in areas where trout density is also high, thereby increasing the probability for successful recruitment. However, such conservation efforts may only be worthwhile if the streams are returned to a clear water state where juvenile mussels can survive.
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References


Ecology of freshwater mussels in disturbed environments

Long-lived freshwater mussels of the order Unionoida are highly threatened. Habitat degradation by turbidity and sedimentation is thought to be one major reason for their decline. The objective of this thesis was to examine recruitment patterns and identify the causes of population declines in the threatened freshwater pearl mussel (*Margaritifera margaritifera*). In addition, I investigated the indirect effects of turbidity on non-endangered dreissenid mussels.

Mussel population size and trout density were both positively correlated to recruitment probability of *M. margaritifera*. A study of the age-structure of nine populations revealed that four of these populations showed no signs of recent recruitment. Examination of different life stages revealed no differences in the gravid mussel stage or the parasitic stage on salmonid fish. Instead, differences were observed for the juvenile, benthic stage, presumably related to differences in turbidity and sedimentation. In the study of the indirect effects of turbidity, bioturbating mayflies increased turbidity and filter-feeding dreissenid mussels reduced turbidity. Mussel growth both decreased and increased with increasing turbidity, depending on sediment type.

Turbidity and sedimentation often impact entire stream systems, and a holistic, catchment-based management strategy may be needed to reduce the effects of sedimentation on freshwater pearl mussels. The effects of restoration take a long time and must start soon if recruitment of mussels is to be re-established. Restoration may also be more urgent in some streams than in others, as the maximum age of *M. margaritifera* populations in my study differed by as much as 60 years. As mussel and trout densities seem to be important for recruitment success, one conservation method may be to concentrate mussels into sites where trout density is high.