# The impact of acidic precipitation and eutrophication on the freshwater pearl mussel *Margaritifera margaritifera* (L.) in Southern Norway

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In Southern Norway, there are strong indications that acidic precipitation is the main reason for the extinction of 94% of all known populations (n=47) of the vulnerable pearl mussel *Margaritifera margaritifera* (L). An example is the famous pearl mussel river, the River Audna, where the death of both young and old mussels took place in the period 1930-50. When the pH is in the range 5.0-5.5 or lower for prolonged periods of time, the mussel can no longer tolerate the acidity. The only three known localities remaining in this part of the country, with ageing populations of the pearl mussel, are all lowland streams that are only very little acidified. The main threat there is eutrophication.

*Keywords: Margaritifera margaritifera,* Southern Norway, acidification, eutrophication

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## INTRODUCTION

Acidic precipitation during the 20th century, most pronounced in Norway in the 1960s and 1970s, has greatly affected aquatic life in lakes and rivers (Rodhe et al. 1995). The most conspicuous effect has been on various fish species (Rosseland 1986, Rosseland et al. 1986). Salmon *Salmo salar* have virtually disappeared from 25 rivers (Hesthagen & Hansen 1991), and inland species, primarily the brown trout *Salmo trutta*, have been seriously affected over an area of 51 530 km$^2$ (Hesthagen et al. 1999). Southern Norway (the counties of Aust-Agder and Vest-Agder) experiences the greatest damage, due to the large amounts of acidified precipitation (Overrein et al. 1980) and low buffering capacity of the bedrock in this part of the country (Hesthagen et al. 1999, cf. Sigmond et al. 1984). Several authors (Wells et al. 1983, Valovirta 1984, Woodward 1995, Henrikson 1996) have suspected the increasing acidification of many parts of Europe to be an important factor also for the decline of the vulnerable freshwater pearl mussel *Margaritifera margaritifera* (L., 1758).

In connection with a national mapping project on the pearl mussel in Norway (Dolmen & Kleiven 1999) in 1988, we achieved a long list of localities for the mussel in Southern Norway. However, many of the populations were reported to have become extinct. To what extent could acidification be said to be the main reason for the extinction of the pearl mussel in this part of the country, and could other factors still be suspected? Since little real evidence exists for cases where acidification has exterminated the pearl mussel, it was of interest to analyse the situation in Southern Norway in more detail.

If acidic precipitation poses a serious threat to the mussel, it was expected that: 1) there exists a positive relationship between the decrease in pH of a watercourse and the decline of the pearl mussel, 2) a comparatively high number of local populations are now extinct, at least above the post-glacial marine limit (ML), and 3) any surviving populations would first of all be found below ML, where the buffering capacity of the soil is better.

## METHODS AND MATERIAL

The national mapping project was based on a questionnaire which was sent in 1988 to all 18 county governors' offices and all 454 municipal administrations in Norway. In the questionnaire we asked whether the mussel was present or not, and about its localities and status (increasing, decreasing or extinct population), local threats – and year, in case of status changes. We also had articles in Norwegian newspapers and radio broadcasting programs, with roll calls to achieve data. Nearly 200 telephone calls were made during the next few years to verify claimed observations and obtain details on status. Data on distribution were also received from the Norwegian university museums of natural history, and reports and other literature were studied for old and new information on pearl mussel sites and on the water quality of southern Norwegian rivers. Dolmen and Kleiven (1999) describe this work (1988-1994) in more detail.

In the acidified areas in Southern Norway, interviews were made during 1988-90 and 1997-99 with elderly people that had good knowledge about the pearl mussel in localities where now it is gone. Where the mussel populations were not reported for sure to have become extinct, the streams were checked for pearl mussels, using a water telescope. All the mussels recorded there were measured with vernier callipers and returned to the stream. Special attempts were made to try to find young mussels in the bottom substrate. Since questionnaires and roll-calls cannot be expected to "discover" all localities (cf. Söderberg 1995), our own fieldwork in 1990-2001 also included potential pearl mussel localities in rivers from where we got no data.

Data on water quality have been obtained from various sources (Table 1). Usually long data series exist for the watercourses, and May or June have, if possible, been chosen for the presentation (Table 2). Additional information on the river Audna has been obtained from the following sources: on history of the pearl mussels, Taranger (1890), Tryland (1977), Kleiven et al. (1989), Kleiven & Dolmen (1999), Ole Erik Larsen (pers. comm.); on water chemistry, Holtan et al. (1973), Mehli (1977); on fish catch statistics, Bjerke (1970), Tryland (1977), Haraldstad (1991). Data on fish in the three remaining pearl mussel localities, are for Vassbotnbekken from Haabesland (1972), for Hammerbekken from Matzow et al. (1990) and Johnsen & Sægrov (1995) and for Lilleelv from Matzow et al. (1990).

The definition of oligotrophy/eutrophy is according to Vennerød (1984).

Table 1. The data sets used for evaluating the water quality of former and present-day pearl mussel localities in Southern Norway.

| Reference | Borough | Watercourse | No. of data sets | Years |
|---|---|---|---|---|
| Boman (1982) | Tvedestrand | Strengselva=Jorstadvassdr. | 37 | 1978-81 |
| Skov et al. (1990) | Tvedestrand | Skjerkholtvassdraget | 10 | 1983-89 |
| Skov et al. (1990) | Åmli | Ufselva | 1 | 1988 |
| Skov et al. (1990) | Vegårshei etc. | Niksjåvassdraget | 12 | 1983-87 |
| Selåsdal (1950) | Vegårshei etc. | Vegårvassdraget | 9 | 1949-50 |
| Holtan (1965b) | Vegårshei etc. | Vegårvassdraget | 3 | 1964-65 |
| Holtan (1965a) | Arendal | Nidelva | 24 | 1964-65 |
| Damhaug & Holtan (1980) | Arendal | Nidelva (Rykene dam) | mean value | 1976-79 |
| Damhaug & Holtan (1980) | Arendal | Lilleelv, Øyestad | 1 | 1979 |
| Lande & Maroni (1987) | Arendal | Lilleelv, Øyestad | 6 | 1986 |
| Kaste & Håvardstun (2000) | Arendal | Lilleelv, Øyestad | 10 | 1998-99 |
| Larsen & Simonsen (2001) | Arendal | Lilleelv, Øyestad | 3 | 2000 |
| Hindar (1990) | Arendal | Lilleelv, Øyestad | 5 | 1988 |
| Hindar (1990) | Arendal | Biebekken=Ålkarbekk, Øyestad | 1 | 1988 |
| Hindar (1990) | Lillesand | Fjelldalselva | 1 | 1988 |
| Hindar (1990) | Risør | Hammerbekken | 4 | 1988 |
| Kaste & Håvardstun (1998) | Risør | Hammerbekken | 6 | 1997 |
| Larsen (2001) | Risør | Hammerbekken | 12 | 2000-01 |
| Hindar (1997) | Froland | Kvervebekken/Åselva | 2 | 1983-93 |
| Hindar et al. (1984) | Gjerstad | Gjerstadvassdraget | 5 | 1980 |
| Dolmen & Kleiven (upubl.) | Birkenes | Vassbotnbekken | 1 | 1994 |
| Holtan & Vinje (1981) | Lindesnes etc. | Audna | 36 | 1972-80 |
| Lande (1987) | Lyngdal | Lygna | 75 | 1981-86 |

Table 2. Selected water chemistry parameters (preliming values) in former and present-day pearl mussel localities in Southern Norway. Present-day localities are in bold type.

| Borough | Watercourse | Locality | Month/Year | pH | Ca2+ mg/L | K25 µS/cm | Colour mg Pt/L | Tot-Al µg/L | Tot-P µg/L | Tot-N µg/L | References |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Åmli | Ufselva, Nelaug | the river | April 1988 | 4.8 | | 23 | 20 | | | | Skov et al. (1990) |
| Arendal | Nidelva | Lindtveit | May-June 1964 (n=2) | 5.3-5.9 | 1.6 | 18 | 24-21 | | | | Holtan (1965a) |
| | - | Rykene dam | 1976-79 (mean) | 5.4 | | 25 | 10 | | 13.5 | 345 | Damhaug & Holtan (1980) |
| | Lilleelv, Øyestad | upper part (lake, 10 m) | Nov 1979 | 5.7 | | 46 | 35 | | 12 | 450 | Damhaug & Holtan (1980) |
| | - | lower part | April-Oct 1986 (n=2) | 6.2 | 3.4 | 47-132 | 41 | 160 | 58 | 2110 | Lande & Maroni (1987) |
| | | | July 1988 | 7.1 | 14.9 | 165 | 46 | | 54 | 3070 | Hindar (1990) |
| | | | June 1998-Nov 1999 (n=10) | 6.3-6.7 | | 39-45 | 38-60 | | 8-20 | 450-660 | Kaste & Håvardstun (2000) |
| | | | May-Sept 2000 (n=3) | 6.6-6.4 | 2.7-2.9 | 46-44 | 35-33 | 119-65 | 2-5 | | Larsen & Simonsen (2001) |
| | Biebekken=Ålkarbekk, Øyestad | the brook | May 1988 | 6.8 | 12 | 124 | 59 | | 91 | 2200 | Hindar (1990) |
| Birkenes | Vassbotnbekken, Berse | the brook | July 1994 | 6.6 | 3.6 | 65 | 25 | | | | Dolmen & Kleiven (unpubl.) |
| Froland | Kvervebekken/Åselva | Brattelandsvatn | Oct. 1983 | 5.0 | 1.6 | | | 222 | | | Hindar (1997) |
| | - | Gjuvvatn | Oct. 1993 | 4.7 | | | | | | | Hindar (1997) |
| Gjerstad | Gjerstadvassdraget | Storelva above Gjerstadvt. | April-July 1980 (n=5) | 4.7-5.8 | 1.2 | 22-47 | 7-15 | 140-250 | | 350-370 | Hindar et al. (1984) |
| Lillesand | Fjelldalselva/bekken | the brook | July 1988 | 4.9 | 1.7 | 47 | 17 | | 4 | 350 | Hindar (1990) |
| Lindesnes | Audna | Konsmo | July 1980 | 4.8 | 1.4 | 28 | | | 4 | 275 | Holtan & Vinje (1981) |
| Lyngdal | Lygna/Lyngdalselva | Litlåna near road to Rom | Aug 1981 | 4.5 | 1.1 | 47 | | | 7 | 242 | Lande (1987) |
| | - | Lygna at Moi/Væmestad | Aug 1982 | 6.3 | | 43 | 10 | | 8 | 400 | Lande (1987) |
| | | | June 1983 | 5.4 | 0.7 | 23 | 40 | | 6 | | Lande (1987) |
| | | | June-Oct 1986 (n=2) | 5.1-4.9 | | 28-29 | | | 2-5 | 394-425 | Lande (1987) |
| Risør | Hammerbekken | (above Hammertjenn) | June 1988 | 6.2 | 2.3 | 43 | 20 | | 6 | 340 | Hindar (1990) |
| | | | May-Oct 1997 (n=6) | 6.5-7.0 | | 66-70 | 27-34 | | 5-8 | 320-535 | Kaste & Håvardstun (1998) |
| | | | May-Nov 2000 (n=7) | 6.5-5.6 | 2.2-1.5 | 50-32 | 38-59 | 174-281 | 2-5 | | Larsen (2001) |
| Tvedestrand | Lilleelv/Vegårvassdr. | at Øynesvatn (1 m) | Aug-Nov 1964 (n=2) | 6.1 | | 31-34 | 19-24 | | | | Holtan (1965b) |
| | | | March 1965 | 5.7 | | 44 | 23 | | | | Holtan (1965b) |
| Tvedestrand | Skjerkholtvassdr. | at Åsvatn | 1986 | 5.2 | 1.4 | | | 146 | | | Skov et al. (1990) |
| Tvedestrand | Strengselva/Jorstadvassdr. | 140 m below Jorstadvt. | <1982? | 6.1 | | 46 | 19 | | 6 | 565 | Boman (1982) |
| | | | May 1978 | 6.0 | | 41 | 15 | | 9 | 570 | Boman (1982) |
| | | | May-June 1979 (n=2) | 6.1-6.3 | | 44 | 15 | | <5-20 | 560-1330 | Boman (1982) |
| | | | Jan-June 1980 (n=2) | 5.6-5.8 | | 53-48 | 30-10 | | 4 | 520-900 | Boman (1982) |
| | - | 3140 m below Jorstadvt. | May-June 1979 (n=2) | 6.3-6.2 | | 49-56 | 15-25 | | 20-100 | 910-2060 | Boman (1982) |
| Tvedestrand | lower Storelva/Vegårvassdr. | at Ubergsvatn ( 0 m) | July-Aug 1950 (n=2) | 5.9-5.7 | | 22-25 | | | | | Selåsdal (1950) |
| Vegårshei | upper Storelva/Vegårvassdr. | at Vegår | June 1949 | 6.0 | | 21 | | | | | Selåsdal (1950) |
| | | | June-July 1950 (n=2) | 5.8-5.4 | | 21-22 | | | | | Selåsdal (1950) |
| Vegårshei | Niksjåvassdraget | at Krossvatn | 1980-85 | 4.9 | 1.7 | | 27 | 150 | | | Skov et al. (1990) |

# RESULTS

## Extinctions and hydrographical data sets

The mapping and our fieldwork showed that, in large parts of Norway, the mussel have had a dramatic decline (Figure 1). In the counties of Aust-Agder and Vest-Agder, as many as 88% and 100%, respectively, of the 24 and 23 formerly known populations have become extinct; only three small populations are now known. Most of the extinctions occurred during the 1960s and 1970s, and some even as late as the 1980s.

The extinction rate is formidable, and significantly much higher than in parts of the country where the precipitation is not anthropogenically acidified, for instance in Central Norway (the counties of Sør-Trøndelag and Nord-Trøndelag) where only 5 of 111 known localities are extinct) (P<<0.001; Chi-square test for two variables without expected values).

The only three known surviving populations in Southern Norway lay well below ML. The only other five localities below ML where the watercourses do not also drain the highland, had all extinct populations. The survival below ML (three of eight populations) was, nevertheless, significantly higher than above ML (none of 39 populations) (P<0.001).

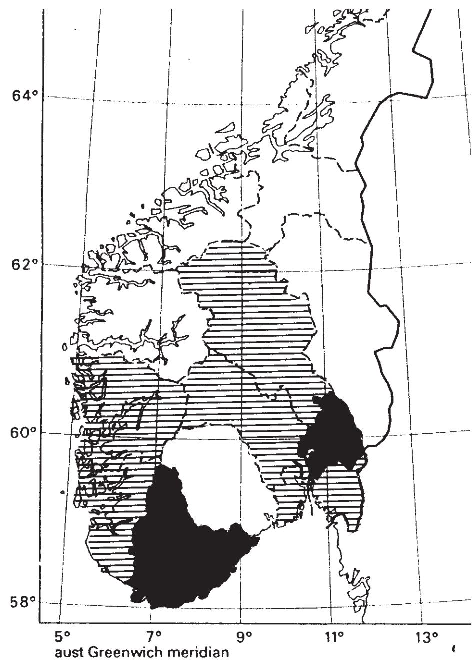


Figure 1
Counties of South Norway and the population extinctions in percentages for the pearl mussel (black: >50% extinction; grey: 25-50% extinction; white: <25% extinction). The decline has been most severe in Southern Norway (acidification and locally eutrophication) and Southeastern Norway (eutrophication and other pollution). (Data from Dolmen & Kleiven in manus.)

Data sets are available on the chemistry of 22 existing or former pearl mussel localities in Southern Norway prior to any liming. Eight of them, at least for some periods of the year, have minimum pH values <5.0, five have minimum pH values in the range 5.0-5.5 and nine have pH values >5.5 (Table 2). The table also gives some data on other hydrochemical parameters. With some notable exceptions, the calcium content and conductivity values are relatively low, the colour is low to medium and aluminium is medium. Most phosphorus and nitrogen values indicate oligotrophy, but a few show eutrophic conditions.

## The River Audna story

On the basis of the literature and personal communications (see Methods), the acidification of the river Audna and the extinction of the pearl mussel can be summarized as follows:

1) Audna used to be one of the most famous pearl mussel rivers in Southern Norway. "The bottom on many stretches of the Audna was completely 'paved' with mussels before 1900, and some landowners earned substantial sums of money fishing pearls."
2) "Mussels still existed in the river shortly before 1920, but the number had decreased considerably. In 1921, hydroelectricity began to be produced at the Tryland Power Station, sited at the confluence of the main river and its tributary, Trylandselva, midway along the stretch of the Audna where salmon run. The number of mussels then decreased dramatically, and after 10 years the population was extinct downstream from the power plant. The tributary was significantly more acidic (approx. 1 pH unit lower) than the main river. The mussel population also decreased upstream from the confluence and the power plant, but more slowly, and it disappeared around 1950."
3) 1966 was the last year when the measured pH value was higher than 5.0 for all the individual months (the average for the year was 5.39).
4) From 1970, the average pH was 5.0 or lower, in 1970: 5.00 (4.78-5.50, n=24), in 1971: 4.99 (4.47-5.36, n=11), and in 1972: 4.97 (4.66-5.12, n=12).
5) The official river catch statistics for salmon and sea trout in the Audna showed a steady decline from the turn of the 20th century to the late 1970s, when the salmon disappeared (Figure 2). The sea trout and inland trout survived the acidification, but their catches were significantly reduced.
6) Audna has been restocked with salmon and sea trout, especially since 1985 when liming started.
7) Old periostracum fragments still turn up after 50 years or more in the river. On land, stranded shells may be more or less intact, but in the water the calcium is rapidly dissolved.

## The three remaining populations in Southern Norway

The three known pearl mussel localities still existing in Southern Norway are in small, lowland watercourses situated only 20-30 m above sea level (i.e. well below the postglacial marine limit, which is approx. 40-75 m a.s.l.). They therefore still have relatively good pH values (Table 2). Table 3 shows the number of mussels that we found, and biotope data.

Vassbotnbekken, Birkenes, is a small brook running through a grazing pasture, close to woodland and a farm. Mussels were found in 1994 and 1998 on a 100 m long stretch, where the substrate is sand and gravel, locally covered by mud and largely overgrown with aquatic vegetation. The fish species in the nearby (downstream) lake are brown trout, whitefish *Coregonus lavaretus*, vendace *C. albula* and perch *Perca fluviatilis*. We observed lamprey *Lampetra fluviatilis* in the brook, and a few brown trout probably ascend it.

Hammerbekken, Risør, is a medium-sized stream with small rapids and deep pools, situated in deciduous woodland and also draining cultivated fields. The mussels were distributed on a stretch of approx. 600 m (upstream from a small lake at 5 m a.s.l. and up to a high waterfall) in 1998 and 2000, on a gravely bottom with stones, sandy patches and some scattered patches of clayey substrate. The fish species that ascend the stream, are brown trout and some salmon, and occasionally brook trout *Salvelinus fontinalis*. It is a good sea trout stream with a high density of brown trout fingerlings of good condition, i.e. 10 ind./100 $m^2$ of 0+ and 5 ind./100 $m^2$ of >0+ in 1995.

Lilleelv, Arendal, is the largest. The surroundings are chiefly deciduous woodland, but the stream also drains agricultural land. The substrate is mostly stones and gravel and stretches of sand. On a stretch of approx. 600 m, with at least two large, deep pools and a few rapids, and with large waterfalls both downstream and upstream, we found some mussels in 1998. The next 500 m upstream (up to a lake) had no mussels in 2000. The only salmonid fish on the pearl mussel stretch is stationary brown trout. Earlier, sea trout could ascend the stretch in question, but a dam has now prevented their ascent for many decades. The spawning possibilities and growth conditions for fish upstream from the dam are characterised as "good to very good".

The size frequencies of the mussels at the three remaining localities are shown in Figure 3. For two of the three populations, the highest number of individuals lay in the 105-110 mm category,

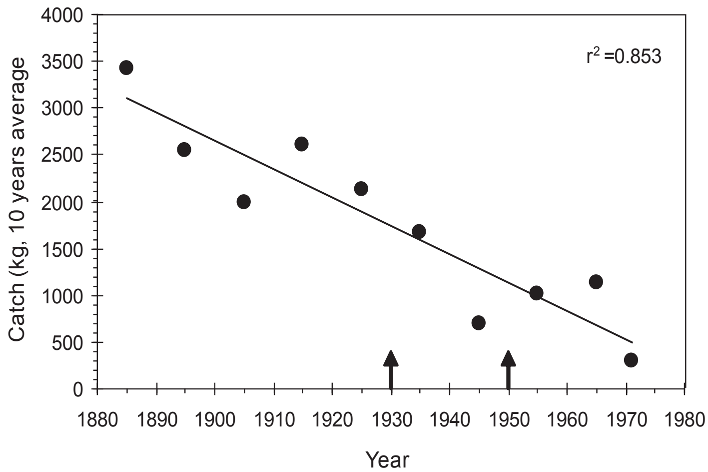


Figure 2
Official catch statistics (ten-year averages) for salmon and sea trout in the River Audna for the period 1876-1973 (data from Bjerke 1970 and Mehli 1977). The 1930 arrow shows when the pearl mussel became extinct in the Audna downstream from the Tryland Power Station; the 1950 arrow shows when it became extinct upstream from the power station outflow (data from Tryland 1977).

**Table 3.** Characteristica of the three present-day pearl mussel localities in Southern Norway. (Data from own measurements and from Matzow et al. (1990); see also Table 2.)

| Locality | Borough | Width of stream (m) | Depth of stream (m) | Water flow (m3/s) | Stretch (m) | No. of mussels | Smallest ind. (mm) | Year of investigation |
|---|---|---|---|---|---|---|---|---|
| Vassbotnbekken | Birkenes | 1 | 0,5 | 0.05 (normal) | 100 | 57 | 65.8 | 1994, 1998 |
| Lilleelv | Arendal | 4-5 | - | 1 (0.08-8.2) | 600 | 10 | 76.8 | 1998, 2000 |
| Hammerbekken | Risør | 3-4 | - | 0.4 (0.04-2.8) | 600 | 285 | 83.3 | 1998, 2000 |

and there is a lack of rejuvenation. For the third population, only a few individuals were found. No young mussels were recorded. For minimum sizes, see Table 3.

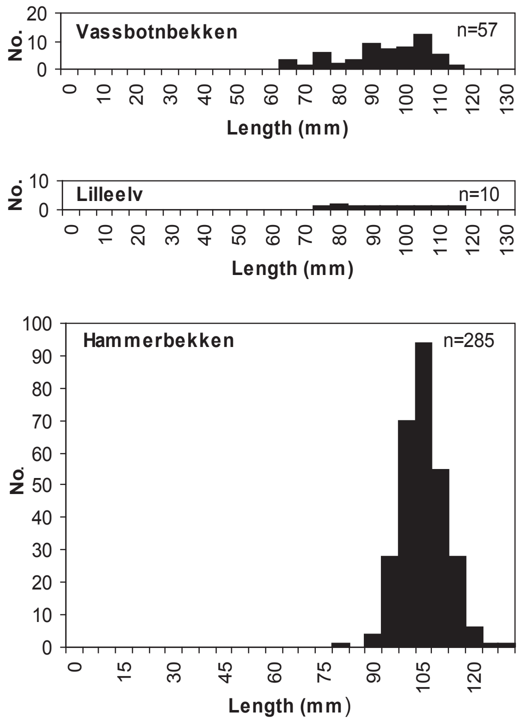


Figure 3
Size frequencies of pearl mussels from the three existing populations in Southern Norway.

# DISCUSSION

## The declines and extinctions

Most of the extinctions in Southern Norway occurred during the 1960s and 1970s, and some even as late as the 1980s, presumably due to acidic precipitation. (Exact time for the extinction is usually not known.) The pH situation for this period, of many of the former and present-day pearl mussel localities is shown in Table 2. Since there are few data sets from the snow melt season, the minimum pH values of the watercourses are probably lower than shown in the table. However, the two most recent extinctions in Southern Norway have been ascribed to drought during an extremely dry summer (1977) and to excavation in the river bed (1986) (Dolmen & Kleiven 1999). The size frequencies of the mussels at the three remaining localities (Figure 3) are typical for ageing or decreasing populations.

## The pH tolerance of the pearl mussel

The mollusc fauna generally decreases as the pH value drops, as shown by Økland & Økland (1986) for 593 lakes in Norway. Only a few mollusc species were present at values below pH 6.0. No gastropods were recorded below pH 5.2 and no small mussels (Sphaeriidae) below 4.7. Thus, due to acidosis, molluscs are generally not present in acidic waters (cf. Heming et al. 1988).

Both empirically and experimentally, acidic water has been shown to negatively influence the growth and survival of the pearl mussel (Carell et al. 1995, Henrikson 1996). When the pH is in the range 5.0-5.5 or lower for prolonged periods of time, like in the River Audna (see above), the mussel can no longer tolerate the acidity. In Jungbluth & Lehmann's (1976) study in Sachsen, Germany, the lowest pH value at which pearl mussels were recorded was 5.1. Heming et al. (1988) suspected that the critical pH level was approx. 5.25, or even higher (cf. Moog et al. 1993). Other factors, like calsium can positively modify the effect of acidic water, and increasing inorganic aluminium can make the water even more toxic (cf. Henrikson 1996).

## The pH - Ca connection

According to Henriksen (1979), acidification can be defined as the difference between pre-acidification alkalinity and present-day alkalinity, and the degree of acidification at a locality can be seen from the relationship between $Ca^{2+}$ ions and pH. In Figure 4 it can be seen that the pearl mussel populations are extinct at all the localities which have pH<5.5 and that the three surviving localities all have pH>6.0. However, three of the localities with pH>6.0 (Hammerbekken, Lilleelv, Biebekken) are nonetheless acidified, i.e. they lie on the upper side of Henriksen's line, and the fourth (Vassbotnbekken) is only slightly below the line. Biebekken has lost its pearl mussel population, and we found only 10 old mussels at Lilleelv. The least acidified localities (Hammerbekken and Vassbotnbekken) are the only two that have reasonably large (although ageing) populations of the pearl mussel.

It is reasonable to believe that all the populations of the pearl mussel that can be seen above the acidification line, except those at localities where the pH>5.5, became extinct as a result of acidification. This happened in the 1950s and up to 1975, or later.

## The extinction of the pearl mussel in the Audna

The history of the River Audna at Mandal, Vest-Agder, during 1885-1985 is a typical example of the fate of pearl mussel rivers in Southern Norway.

Prior to the liming of the river in 1985, the pH had already long ago reached values as low as about 5.0±±0.2 and had probably already in 1966 exceeded the tolerance limit for anadromous salmonid species (Blakar et al. 1989).

The contribution of large amounts of highly acidic water from Trylandselva seems to be the main and direct reason for the extinction of the pearl mussel in the lower parts of the river. Two decades later, the water in the main, upper part of the Audna had become just as acidic, leading to the extinction of the remaining population of pearl mussels there.

Salmon *Salmo salar* and brown trout *S.trutta* are obligatory vectors for the pearl mussel's glochidia larvae (Young & Williams 1984a,b). Since the density of salmon and trout in the river decreased radically, it could be argued that the disappearance of the pearl mussel in the Audna could be due to the lack of hosts for their glochidia. According to Ziuganov et al. (1994), the density of a population of the freshwater pearl mussel cannot be maintained in the long run unless the density of 1+ fish hosts (salmon) is more than 5 ind. per 100 $m^2$ in May/June (when the glochidia drop from the fish).

However, as explained below, we do not believe that the pearl mussel in the Audna disappeared as a result of the density of host fish becoming too low. Firstly, not only did reproduction fail and young mussels die, but older mussels also died. Such a long-lived creature as the pearl mussel, living up to 150-200 years in Scandinavia (Mutvei & Dunca 1995), would not otherwise be expected to disappear so fast.

Secondly, a rough estimate of the probable density of salmonid fry in the 1950s, i.e. when the pearl mussel disappeared, suggests that the fish density was not particularly low. (The estimate – see below – is based on the assumption that the same relationship between the density of fry and subsequent yearly catches of salmon and trout in the 1990s was also valid for the 1950s.)

The reasoning below is based on the assumption that salmon- and trout fry are used approximately equally (intensity and prevalence) as hosts for the glochidia, which may not always be the case (cf. Larsen et al. 2002). According to official statistics (Johannessen 1970), the annual catch of salmon and trout in the Audna between 1920 and 1950 was around 2000-1000 kg (cf. Figure 2). We lack data on fish fry densities prior to 1991, but after the liming of the river started in 1991, electrofishing in October/November has revealed increasing densities of young salmon (0+ and $\geq^{3}$1+) and more variable ones of brown trout (Barlaup et al. 1998). The relationship between the yearly catches of salmon and trout and the densities of (0+ and ≥1+) fry in the Audna during 1991-1998 is shown in Figure 5. (Some of the fry may derive from stocking, but this does not affect our reasoning below.)

Most of the salmon and trout fry (92% of the salmon) in the River Audna reach smoltification in the spring following only two growth seasons in the river (2+); the rest one year later. After one year in the sea, most individuals (79% of the salmon) mature and return to the river to spawn, whereas some return after two or three years (Barlaup et al. 1997). In our estimate, we have used three years as an average time span from 1+ fry (host for glochidia) to mature salmon and trout being caught in the river.

When the density of ≥1+ fry in (October/November) 1991-1995 is compared with the catch of salmon and trout in 1994-1998, a low density of fish fry is seen to give a low catch three years later, and a high density a high catch (Figure 5, upper part). A similar picture (Figure 5, lower part) can be seen for 0+ fry in

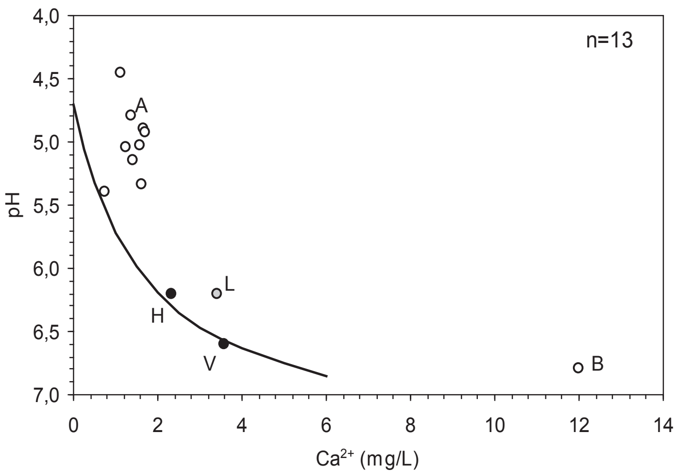


Figure 4
The relationship between $Ca^{2+}$ and pH in former and present-day localities for the pearl mussel in Southern Norway. The diagram also shows Henriksen's (1979) acidification indicator line; localities above/to the right of the line are acidified. White dots: localities where the population is extinct; grey dot: locality with a few remaining mussels; black dots: localities with a surviving (though not rejuvenating) population. Letters indicate locality names (A=Audna, B=Biebekken, H=Hammerbekken, L=Lilleelv, V=Vassbotnbekken).

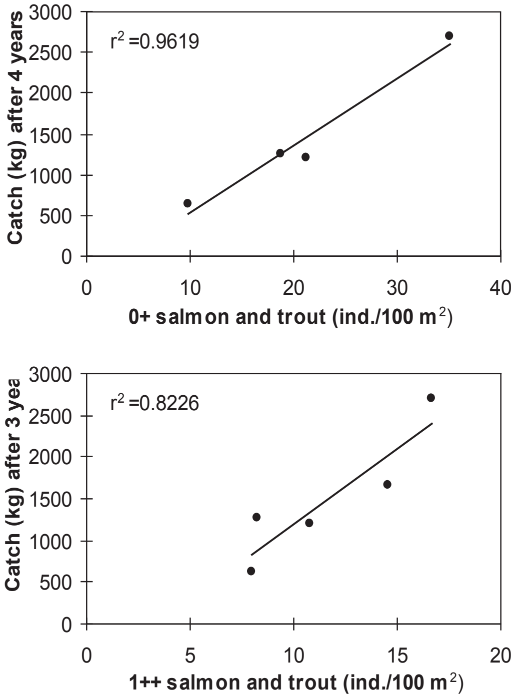


Figure 5
The relationship between densities of 0+ and 1++ salmon and trout fry and the subsequent yearly catches in the River Audna during 1991-1998.

1991-1994 compared with catches in 1995-1998. The final step in our reasoning is thus that a yearly catch of 1000 kg of salmon and trout, as in the years following 1950 (Figure 2), is based on a density in October/November of approx. 16 0+ or 9 ≥1+ fish fry per 100 $m^2$. The corresponding number for May/June would be even higher, probably around 10-15 1+, i.e. 2-3 times the critical density (5 ind. per 100 $m^2$ in May/June) which Ziuganov et al. (1994) suggested was necessary for the maintenance of a pearl mussel population.

One uncertainty remains, however: Since the salmon is more vulnerable to acidic water than the trout (Poléo et al. 1997), and since salmon fry may have been a preferred host for the glochidia in the Audna (cf. Larsen et al. 2002), it still leaves a possibility of reproduction failure in the pearl mussel due to the lack of an appropriate host. Our catch statistics do not enable us to discriminate between the salmonids. However, not only failed the reproduction, but big, usually long-lived mussels also died in the river.

Although the estimation above contains many assumptions and approximations, the reasoning indicates that the extinction of the pearl mussel was not primarily due to the disappearance of its host fish, but rather to the direct effect of the acidification itself on the pearl mussel.

With respect to other environmental parameters, chemical analyses of water from the Audna show low values for phosphorus in 1980-86, varying in the range 1-9 µg Tot-P/L throughout the year in central stretches of the river (cf. Table 2, Figure 6). Nitrogen values, much of which derives from acidic precipitation, are not ominously high, i.e. 150-478 µg Tot-N/L in 1980-1986 (Holtan & Vinje 1981, Lande et al. 1987). The values for both phosphorus and nitrogen were probably even lower in the 1930s to 1950s, when the pearl mussel became extinct. No construction work or excavations in the river, or other impacts except acidification, can explain the relatively rapid extinction of the pearl mussel population in the Audna.

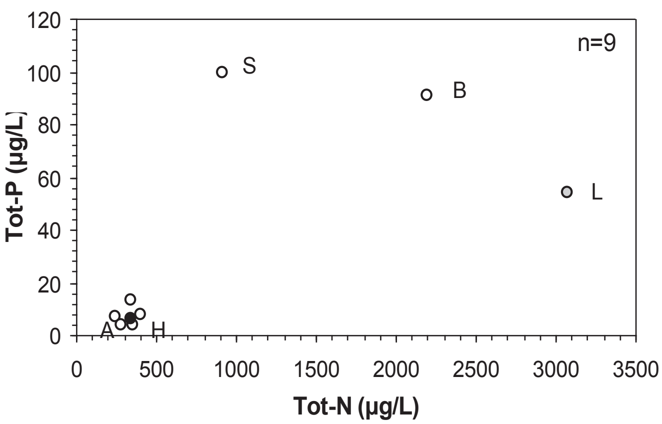


Figure 6
The relationship between nitrogen (Tot-N) and phosphorus (Tot-P) in former and present-day localities for the pearl mussel in Southern Norway. The area next to the origo represents oligotrophy. White dots: localities where the population is extinct; grey dot: locality with a few remaining mussels; black dot: locality with a surviving (though not rejuvenating) population. Letters indicate locality names (see Figure 4; S=Strengselva).

## Further problems for the pearl mussel in Southern Norway

Whereas larger streams and rivers are often influenced by acidic water from the highlands, small lowland brooks have a better buffering capacity and a better pH (cf. Overrein et al. 1980). The water at most former mussel localities in Figure 4 is thus very acidic, and only two present-day localities (Hammerbekken and Vassbotnbekken) are not, or are only very slightly, acidified. The other two localities that also have relatively high pH and $Ca^{2+}$ values, still clearly above the acidification line, have only a very small mussel population (Lilleelv), or it has already become extinct (Biebekken).

Nevertheless, no really young mussels were found in Vassbotnbekken, Hammerbekken and Lilleelv; i.e. rejuvenation is failing. The size of the smallest individual in Vassbotnbekken corresponds to a minimum of 10 years of age, probably more, and perhaps twice as much (cf. Buddensiek 1995, Sandaas 1995, Larsen 1999). Ages of 20-40 years seem realistic for the smallest individuals from the other two streams. The problem that these mussels face, or have faced, however, is not primarily acidification (see below). And only in Vassbotnbekken, low density of salmonid fish is a probable limiting factor.

## Water hardness, conductivity or humus problems?

The freshwater pearl mussel is usually found in localities with soft water (i.e. $\leq$10 mg $Ca^{2+}$/L (def. Ohle 1937)), a water quality that is very common in Norway. Only one of the former pearl mussel localities in Southern Norway, on one occasion, had a slightly higher value than this (Table 2). In Central Europe, the pearl mussel has been recorded at 5.7-18.8 mg $Ca^{2+}$/L (Bauer et al. 1991, Moog et al. 1993, Silkenat et al. 1991). Its strongest growth, as recorded by Alimov (1974), was at values as low as 6-7 mg/L. Occasionally, however, the species has been found at much higher values, even up to 79 mg/L, and experimentally they survived for several months at 100-130 mg/L (Boycott 1936).

Concerning conductivity of the pearl mussel localities in Southern Norway, only 4-6 of the 22 localities from which we have data, showed values higher than 50 µS/cm (Table 2). Some of the highest conductivity values measured at pearl mussel localities on the Continent are 65-158 and 192 µS/cm (Moog et al. 1993, Silkenat et al. 1991).

The humic content is probably another potential limiting factor for the distribution of the pearl mussel (e.g. Ziuganov et al. 1994, Lundstedt & Wennberg 1995). The three remaining localities in Southern Norway (Table 2), however, are mesohumic to slightly polyhumic (as defined by Åberg & Rodhe 1942). This is far below 100 mg Pt/L, the approximate figure mentioned by Söderberg (1995) as an “upper limit” for pearl mussels in Sweden.

Consequently, we believe that neither pH, $Ca^{2+}$, conductivity nor humus content have been of any importance for the decline or extinction of the pearl mussel in the four lowland streams mentioned here. Buddensiek (1995) found that the survival and growth of young mussels were negatively correlated with the $Ca^{2+}$ content, and with conductivity in localities rich in electrolytes (175-283 µS/cm). Moreover, Bauer (1988) suggested that a pearl mussel population might have reproductive problems already at a conductivity of only 70 µS/cm. However, these parameters may only be indications of some other, more important, pollution of the streams, i.e. eutrophication.

## Eutrophication

Outside the two southernmost counties, eutrophication is the main reason for the decline of the pearl mussel in Norway (Dolmen & Kleiven 1999). The young mussels, which live buried in the river bed, are thought to be choked by mud preventing oxygen-rich water from seeping through the gravel (Bauer 1988).

A good measure of eutrophication is the content of phosphorus and nitrogen in the water. Our data series – some representative values are listed in Table 2 – show that most former and existing pearl mussel localities from which we have data, had phosphorus values below 10-15 µg Tot-P/L. Among the few exceptions were Lilleelv, Biebekken and Strengselva (up to 120 µg/L in October 1979 – not shown in the table). We unfortunately lack data for Vassbotnbekken. The highest values mentioned here by far exceed those indicated by Söderberg (1995) as healthy for the pearl mussel in Sweden. In Central Europe, a healthy environment seems to be characterised by no more than 30-35 µg Tot-P/L (Bauer 1988, Moog et al. 1993).

The corresponding values for nitrogen in the less eutrophicated localities of those in question, in accordance with our data sets, vary from 242 to 425 µg Tot-N/L (Table 2). However, the values of Lilleelv and Biebekken are as high as 450-3070 µg/L (3230 µg/L in October 1989, not in the table) and 2200 µg/L, respectively. Strengselva had 520-2060 µg/L. In Sweden, Grundelius (1987) found mussels in localities with values no higher than 50-280 µg Tot-N/L, and for Central Europe Bauer (1988) put an upper limit to healthy populations of 500 µg/L. In addition to sources deriving from the use put to the land, an important part of the total nitrogen in streams in this part of Norway comes from $NO_3^-$ in the (acidic) precipitation.

Most pearl mussel localities, such as Audna (where the mussels became extinct due to acidification), are low in plant nutrients (Figure 6), whereas Lilleelv, Biebekken and Strengselva are comparatively very high. (According to Larsen & Simonsen

(2001), the water quality of Lilleelv is better now than in the 1970-80s.) The ageing population in Hammerbekken cannot be easily explained by the above-mentioned values, however, although Larsen (2001) ascribes the decline in part to eutrophication. Unfortunately, for this locality we have data from only one water sample prior to 1990. Although acidification episodes at the time of snow melt or heavy rain cannot be ruled out completely as a reason for the decline and extinction of the pearl mussel in some of the last mentioned localities, the most probable reason is eutrophication, which is also the main problem for the species in Southeastern Norway (cf. Fig. 1).

## CONCLUSIONS

1) There exists a positive relationship between the gradual decrease in average pH of a watercourse and the decline of the freshwater pearl mussel in Southern Norway. 2) A comparatively very high number of local pearl mussel populations have become extinct during the past decades, especially above the post-glacial marine limit (ML), where the acidification is most severe. 3) The only three known surviving populations are all below ML; but even these populations have rejuvenation problems. 4) The three points above strongly indicate that acidification is the main reason for the extinction of the pearl mussel in Southern Norwegian streams; however, for the smaller number of lowland populations the current threat is eutrophication.

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## SAMMENDRAG

### Skadevirkningene av sur nedbør og eutrofiering på elvemuslingen *Margaritifera margaritifera* (L.) på Sørlandet i Norge

Med bakgrunn i et nasjonalt kartleggingsprosjekt for elvemuslingen *Margaritifera margaritifera* (L.) ble det funnet at sur nedbør må anses å være hovedårsaken bak en nedgang på 94% av de 47 kjente lokale elvemuslingpopulasjonene på Sørlandet (Aust-Agder og Vest-Agder). Et eksempel er elva Audna ved Mandal, der både unge og eldre elvemuslinger døde ut i perioden 1930-50. Når pH ligger i området 5.0-5.5 eller lavere i lengre tid, blir dette for ekstremt for muslingens tåleevne. Den største ekstinksjonen (100%) har funnet sted over marin grense. De eneste tre gjenværende kjente elvemuslinglokalitetene på Sørlandet, alle med aldrende populasjoner, er lavlandsbekker som bare i liten grad er forsuret. Hovedtrusselen for disse bestandene synes å være eutrofiering, med algevekst og akkumulasjon av organisk materiale i grusen på elvebotnen.

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