Distribution, status and threats of the freshwater pearl mussel *Margaritifera margaritifera* (Linnaeus) (Bivalvia, Margaritiferidae) in Norway

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The distribution of *Margaritifera margaritifera* (Linnaeus) in Norway is mainly along the coast and in the lowland. Based on a questionnaire sent to county governors' offices and municipal administrations in Norway, about 430 former and existing localities have been recorded, of which about 300 are still-existing. However, the real number is probably more than twice as large. Central Norway has the highest number of documented sites. The northernmost locality is at Berlevåg (Finnmark) at 70°50'N lat., and the highest verified record is near Snåsa (Central Norway) at 472 m a.s.l. The great majority of localities are associated with Cambro-Silurian volcano-sedimentary rocks or situated below the postglacial marine limit, i.e. in areas not too poor in calcium. The species is an early immigrant, and a landlocked population in Central Norway has probably existed since 8900 ^{14}C-yr B.P. The pearl mussel has become extinct during the past few decades at as many as 30% of its localities, mostly due to urbanisation and pollution. There is a high correlation between the density of people in a county (or the proportion of cultivated land) and the "density" of extinct pearl mussel populations (r=0.91). Other threats considered were hydropower regulations, excavations and constructional work in the watercourse, fishing for pearls, acidification and natural droughts or floods. In spite of the negative trend, some large populations still exist, with local densities >100 ind. m^{-2} and numbers of up to 1 mill. ind. km^{-1} river stretch. The Norwegian stock probably consists of >300 mill. ind.

Keywords: *Margaritifera margaritifera*, distribution, zoogeography, conservation, threats, Norway

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INTRODUCTION

One of the most vulnerable animals in Holarctic running waters is the freshwater pearl mussel *Margaritifera margaritifera* (Linnaeus, 1758). Although distributed over large parts of Europe and North America, with good populations still existing in Scotland, Scandinavia and Russia, the species has shown a serious decline in most of its range. At the moment, the pearl mussel is threatened in at least 15 European countries (Hendelberg 1960, Willmann & Pieper 1978, Wächtler 1986, Wells & Chatfield 1992, Ziuganov et al. 1994, Starobogatov 1995, Young et al. 2001). It is therefore included in IUCN's Red Data Book (Wells et al. 1983, United Nations 1991) and since 1987 in Appendix III of the Bern Convention (Council of Europe 1992, Nordisk Ministerråd 1995). A European action plan for the species has been made by Araujo & Ramos (2000). In Scandinavia, decline has been reported from Sweden (e.g. Grundelius 1987, Henrikson 1991, 1996, Eriksson & Henrikson 1997) and from Southern Norway (e.g. Dolmen & Kleiven 2004). Action plans have also been made

for Sweden and Norway, by Schreiber & Tranvik (2005) and Direktoratet for naturforvaltning (2006) respectively (see also Larsen 2005b). However, there has still been a demand for more data on distribution and threats.

More than one hundred years ago, Esmark (1886) reported that the freshwater pearl mussel was very common over large parts of Norway. An early history of pearl mussel "fisheries" in Norway was published by Taranger (1890), who also included a list of known localities. The distribution of the mussel was studied more thoroughly in the early 1970s (Økland 1975). We now know that in Norway, too, a large number of pearl mussel populations have become extinct during the last 50 yr (Kleiven et al. 1989, Dolmen & Kleiven 1999). Other populations show an unhealthy age composition, i.e. young mussels are lacking (e.g. Larsen 1999, Dolmen & Kleiven 2004). Even though the pearl mussel is still widely distributed in Norway, the species became protected in 1993 under the terms of the Law on Salmon and Inland Fish 1992 and is evaluated as vulnerable on the Norwegian Red List (Størkersen 1992, 1999, Kålås et al. 2006).

On this basis, we wanted to gain a greater understanding of the pearl mussel's distribution and biology. And in order to promote its future conservation, it was of interest to get a realistic picture of the destructive episodes that had taken place in rivers where pearl mussels lived and the potential threats that still had to be considered. Already, in 1988, we therefore started a roll call to obtain new, improved understanding of the distribution and present status of the freshwater pearl mussel in Norway. We also asked correspondents for the reasons for possible changes in population structure.

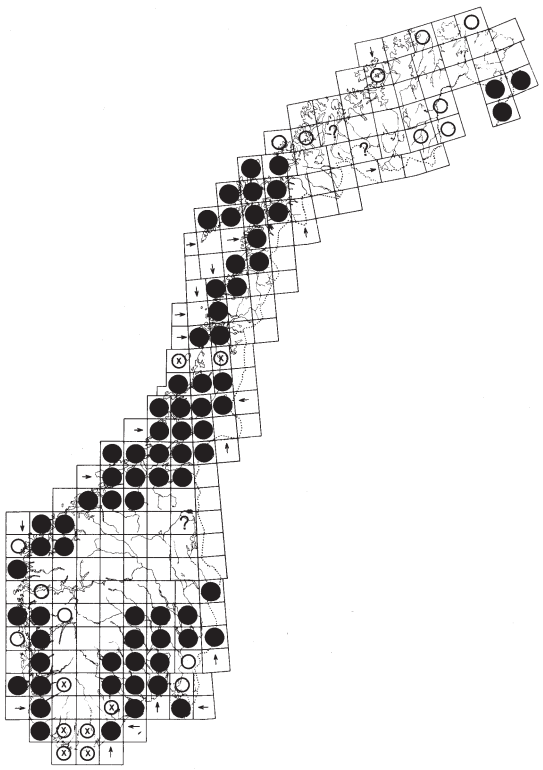

Figure 1. The known distribution of the freshwater pearl mussel *Margaritifera margaritifera* in Norway. White dots show records before 1975, black dots from 1975 onwards; "x" means known to be extinct, "?" means doubtful/not confirmed. (The EIS map is based on modified 50x50 km UTM squares. Arrows mean that possible data in a specific square are to be transferred to the neighbouring square.)

As a result we have achieved a long, detailed list of pearl mussel localities in Norway, from which we here present an updated map. In the article we try to explain the reasons for the species' former and present distribution. We also address the questions: How many local populations occur in Norway, and what is the total stock? Where have the declines occurred, and what are the most important threats?

METHODS

The national mapping project was based on a questionnaire which was sent 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 – before and after 1975 – 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. Some additional data were obtained from the Ole Nordgård Archive at the NTNU Gunnerus Library in Trondheim and the files of the Norwegian Institute for Nature Research in Trondheim (data collected by Jan and Karen Anna Økland). The majority of data, and some rivers, have since then been checked, by us or by other zoologists, or are verified on a basis of multiple reports. Dolmen and Kleiven (1999) describe this work (1988-1994) in more detail, and Dolmen & Kleiven (2004) the special efforts made with respect to the acidified region of Southern Norway..

Concerning the number of localities, to get an impression of the degree of reliability of the method we used to collect data, we have compared our results with those from other recent and very thorough, local investigations, see the Discussion.

The map used (Figure 1) is that of the European Invertebrate Survey, based on modified 50x50 km UTM squares. (To avoid

Table 1. The number of localities in each county from where the freshwater pearl mussel is known. Figures for the localities reported in the questionnaires, etc., those which are probably correct, those existing today, and the status of the species are given. (* = localities for *Anodonta*/*Pseudanodonta* may be included.) Reasons are given for the decline or extinction of the pearl mussel in different regions of Norway. '+' means 'in part', i.e. other reasons are also mentioned.

		No. of localities recorded, etc.			Status (no. of localities) reported					Reasons for the decline / extinction	
Region	County	reported	probable	definite	extinct	% ext.	decl.	st.quo	incr.	(no. of localities within each region)	
South-eastern	Østfold	6*	2-3	1	1-2	-	3	-	-		
Norway	Oslo/Akershus	29*	24	7	17	71	-	-	-		
	Hedmark	9*	8	7	1	(13)	-	-	-	Pollut/eutroph. (6+10)	Pearl fishing (1)
	Oppland	11*	10	6	4	(40)	2	-	-	Regulation (2+4)	Acidification (+1)
	Buskerud	30*	29	19	10	34	2	-	-	Excavation (+5)	Nat. drought + flood (1)
	Vestfold	15*	15	8	7	47	4	-	-		
	Telemark	17*	17	13	4	24	1	-	-		
Southern	Aust-Agder	24		3	21	88	-	-	-	Pollut/eutroph. (+1)	Acidification (3+2)
Norway									-	Regulation (+1)	Nat. drought + flood (2)
	Vest-Agder	23		0	23	100	-	-	-	Excavation (1)	
Western	Rogaland	44-45		24-25	20	45+/-	7	4	1	Pollut/eutroph. (7+1)	Pearl fishing (2+1)
Norway										Excavation (1)	Acidification (1)
	Hordaland	14-15		8-9	5-7	(41+/-)	-	-	-		
	Sogn & Fjordane	4		3-4	0-1	(13+/-)	-	-	-		
	Møre & Romsdal	31		28	3	10	6	3	-	Pollut/eutroph. (16+7)	Pearl fishing (1+5)
Central	Sør-Trøndelag	45		42-43	2-3	6+/-	3	-	-	Regulation (5+2)	Nat. drought + flood (+1)
Norway	Nord-Trøndelag	65-67		62-65	2-3	4+/-	3	-	1	Excavation (3+1)	
Northern	Nordland	48		38-42	6-10	17+/-	4	5	2		
Norway	Troms	9-10	7-8	5-7	0-3	(20+/-)	-	-	-		
	Finnmark	14-15		11-13	2-3	(17+/-)	-	-	-		
Norway (total)		438-444	424-431	287-300	128-142	30+/-				Pollut/eutroph. (29+19)	Pearl fishing (4+6)
										Regulation (7+7)	Acidification (4+3)
										Excavation (5+6)	Nat. drought + flood (3+1)

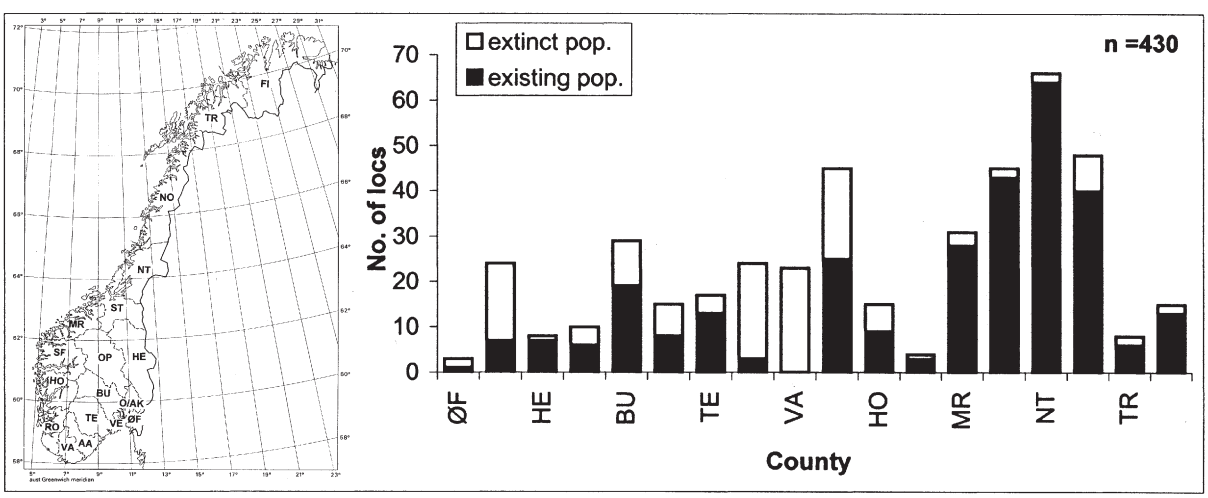

Figure 2. The number of localities of the freshwater pearl mussel per county in Norway. (Positions of counties are given to the left, see Methods.)

Table 2. Records of lentic freshwater pearl mussels.

Locality	District	Case	References
Ervikvatnet	Selje, Sogn & Fjordane	1975-81: Several reported from the lake, as well as from the inflowing stream.	e.g. Anonby (1984)
Søvatnet	Orkdal, Sør-Trøndelag	1960: Freshwater mussel recorded.	Ole Øyen (pers. comm.)
Storvatnet	Agdenes, Sør-Trøndelag	Ca. 1962-63: A number seen midway between, and as far as 500 m from, the nearest streams (inflow and outflow).	John O. Solem (pers. comm.)
Leksdalsvatnet (SW part)	Verdal, Nord-Trøndelag	2000: A dozen found on 1-3 m depth, on a stretch of 1+ km and far away from any mussel-bearing stream.	Knut Åge Storstad (pers. comm.)
Lilands/Rystadvatnet	Vestvågøy, Nordland	Ref. 1988+: Several observed on an underwater gravel bank 200-300 m from an inflow.	Kjell Rystad (pers. comm.)

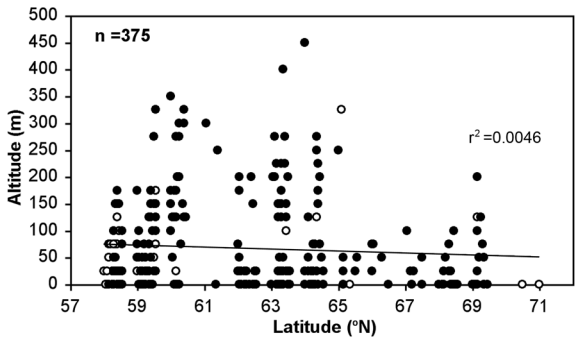

Figure 3. The relationship between latitude and altitude distribution of the freshwater pearl mussel in Norway. Black dots show existing populations, white dots extinct populations. (It has not been possible to give a specific altitude to all the localities; hence they are not included in the figure.)

Table 3. The relationship between the occurrence (total number of former and still-existing populations) of the freshwater pearl mussel and the bedrock below or above the postglacial marine limit (ML). (CS = Cambro-Silurian volcano-sedimentary bedrock, GG = granite or gneiss, > and < means higher or lower altitude, respectively) Only the GG > ML area is especially poor in Ca^{2+}.

Region \ Biotope	CS > ML	CS < ML	GG < ML	GG > ML	Total
SE Norway	5	8	62	10	85
S Norway	0	0	20	16	36
W Norway	11	25	34	11	81
C Norway	29	35	35	2	101
N Norway	4	23	27	5	59
Total	49	91	178	44	362

jeopardising the protection of the mussels, a more detailed map than this is undesirable.) In the county overview of the number of localities (or populations) (Figure 2), a watercourse is counted as more than one if mussel-bearing tributaries to the main river have their own name.

The altitude and latitude of the localities were determined on topographical maps (M-711, 1:50 000). Attempts have been made to give the altitude of the central part of mussel populations in intervals of 25 m, where 50+ means from 50 to 75 m a.s.l. The latitude is given in intervals of 5', where 60°10'N means from 60°10' to 60°15'N.

In the text, the following geographical definitions have been used: **South-eastern Norway**: the counties of Østfold (ØF), Oslo/Akershus (O/AK), Hedmark (HE), Oppland (OP), Buskerud (BU), Vestfold (VE) and Telemark (TE); **Southern Norway**: the counties of Aust-Agder (AA) and Vest-Agder (VA); **Western Norway**: the counties of Rogaland (RO), Hordaland (HO), Sogn & Fjordane (SF) and Møre & Romsdal (MR); **Central Norway**: the counties of Sør-Trøndelag (ST) and Nord-Trøndelag (NT); **Northern Norway**: the counties of Nordland (NO), Troms (TR) and Finnmark (FI).

RESULTS

The distribution and number of localities

Our mapping project has revealed about 430 (possibly up to 444) existing and former localities (rivers and main tributaries) for the pearl mussel in Norway (Table 1). The species has been recorded in 94 of the 189 EIS squares on the map (Figure

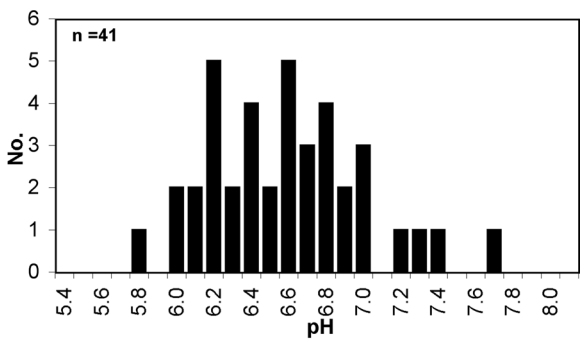

Figure 4. Reported pH at existing freshwater pearl mussel localities. (Some values are averages.)

1), although 22 of these represent extinct populations and old records (before 1975). In addition are three localities/squares which are doubtful/not confirmed.

The pearl mussel is present in all 18 counties, but seems to be rare in the north in recent times (Figure 1). The region containing the largest quantity and density of pearl mussel localities is Central Norway, Sør-Trøndelag having 45 and Nord-Trøndelag 65-67 known localities (Figure 2).

The altitudinal and latitudinal distributions (Figure 3) show that the pearl mussel is first and foremost a lowland species, mainly distributed in coastal areas. It is very rare above 300 m a.s.l., and there is no clear difference in the altitudinal distribution between southern and northern parts of the country (r=0.068).

The record at the highest verified altitude is in Snåsa, in a tributary to Verdalsvassdraget in Central Norway, situated 472 m a.s.l.

The two northernmost localities are situated at about 71°N lat. However, the population at one of these localities, at Berlevåg in Finnmark (70°50'N lat.), is reported to have become extinct after 1950 (Berlevåg means "Pearl Harbour").

Ecological observations

Pearl mussels are sometimes reported from large rivers, but more often from medium or small ones, or streams down to a water flow of 0.05 $m^3 s^{-1}$ or less. The bottom substrate is quite stable: usually gravel and sand intermingled with stones and boulders, but in a few cases finer sediments, even (for adults) silt or clay. The substrate usually lacks vegetation. The density of mussels is often low, but may in favourable streams locally exceed 100 mussels per m^2. However, the pearl mussel is also in a few cases reported from lentic waters, and in at least three of these cases, the mussels were recorded far away from an inflowing stream (Table 2).

Of the 362 former and present-day pearl mussel localities that we have been able to relate to the bedrock or the postglacial marine limit (ML), approx. 39% are situated on Cambro-Silurian volcano-sedimentary rocks and as many as approx. 74% are below ML (including many of the Cambro-Silurian sites) (Table 3). Only about 12% of the localities are situated above ML on bedrock poor in calcium, for example Precambrian granites, gneisses, etc. In Southern Norway, where the pearl mussel is now almost extinct, all the localities are on granite or gneiss; more than half of them, however, are below ML. In Central Norway, where pearl mussel localities are most abundant, a high proportion of the localities are on Cambro-Silurian rocks, and all but two of the others are below

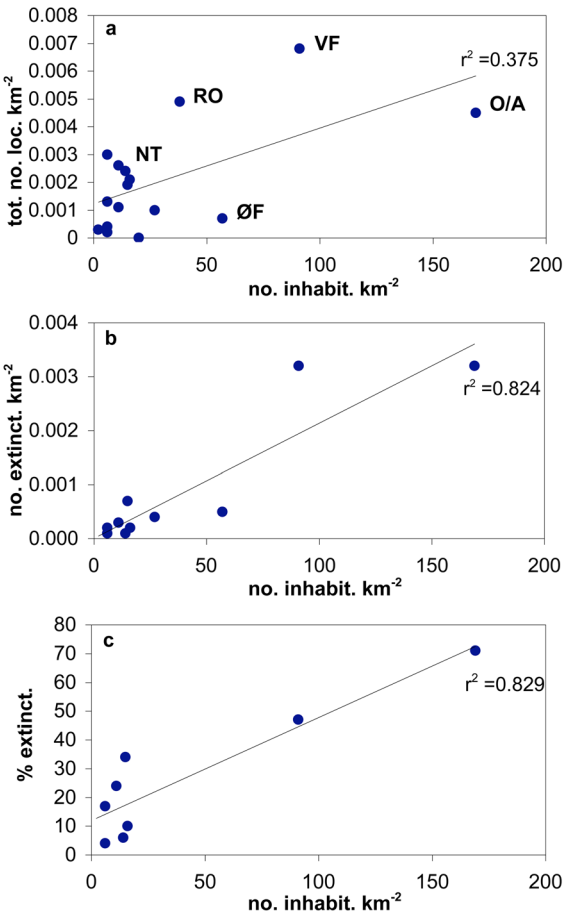

Figure 5. The relationship between the density of human populations and a) the total number of known (former and present) pearl mussel localities, b) the "density" of extinct mussel populations, and c) the percentage of extinctions. (Counties: NT = Nord-Trøndelag, O/AK = Oslo/Akershus, ØF = Østfold, RO = Rogaland, VF = Vestfold.)

ML.

The great majority of pH (summer) values for Norwegian pearl mussel localities as reported in the questionnaires and in the literature, lie between 6 and 7; only a very few values are below or above this interval (Figure 4).

The declines

About 128-142 local populations (approx. 30%) of the known pearl mussel population have been reported to have become extinct during the last 50 yr or so. In addition to our own investigations, personal communications and numerous printed reports, approximately 20% of the municipal addressees who responded to our questionnaires, also answered questions about the status and changes in the status of the pearl mussel. And

there are clear regional similarities in population trends, i.e. the decline has been most dramatic in the south-east, south and south-west of Norway (Figure 2, Table 1). The reasons suggested for the declines and extinctions can be grouped into six categories: pollution and/or eutrophication, hydropower regulation, excavation work in the watercourse, pearl fishing, acidification and natural (not man-made) drought and flood (Table 1). More than one of these factors have often acted in combination. To summarise, it can be said that in all parts of the country, except Southern Norway, pollution/eutrophication of the streams is thought to be by far the most important reason for negative trends. Although serious enough, excavation and regulation are much less important than pollution. In Southern Norway, however, acidification is reported to rank highest among the negative factors.

Pollution/eutrophication is first of all related to sewage and to intensive farming practice. Norwegian counties display a high correlation between the density of people and the percentage of cultivated land (r=0.81), although Oslo and Akershus deviate slightly, having relatively more people (r=0.94 if O/AK is excluded). The relationship between the density of people and the density of former and present-day mussel localities (r=0.61) (r=0.65 if O/AK is excluded) is shown in Figure 5a. The two counties that have no shoreline, Hedmark and Oppland, have been omitted from the calculations, since they have no salmon and sea-going trout, and hence the mussels are less easily spread. The relationship between the density of people and the "density" of extinctions is shown in Figure 5b. Since we want to focus on the direct human influence like local polluting effluents and eutrophication, we have tried to eliminate extremely harsh climate (the two northernmost counties) and acidic precipitation (Southern Norway and Rogaland) – in addition to Hedmark and Oppland. Most extinctions have taken place in the counties that have the highest population density (r=0.91) (r=0.88 if O/AK is excluded). A similar picture (r=0.91) (r=0.76 if O/AK is excluded) appears when the percentage extinction of pearl mussel populations is considered (Figure 5c). For the sake of accuracy, counties with only a few localities (Østfold, Hordaland, Sogn & Fjordane, Troms, Finnmark) have been omitted from the calculation.

Reported increases

"No change" or "increase" in population size were only reported from 16 localities. In four or five instances, mussel populations are said to have been increasing in the last few years. The reasons are improved water quality (after many years of pollution), protection of the species and a complete stop in pearl fishing. Details on these claimed increases are lacking, however.

DISCUSSION

Doubtful and incorrect earlier reports

Some old reports of the pearl mussel are doubtful, some others have been shown to be incorrect. In South-eastern Norway, other large freshwater mussels than the pearl mussel are also found, i.e. *Anodonta anatina* (Linnaeus, 1758), *A. cygnea* (Linnaeus, 1758) and *Pseudanodonta complanata* (Rossmässler, 1835) (Larsen et al. 1999) and may possibly in old reports in a very few cases have been mistaken for the pearl mussel (see Dolmen 2003a, see also Table 1).

The earlier highest reported locality, at Oppdal in Central Norway, situated about 525+ m a.s.l. (see Dolmen & Kleiven 1997a,b) has turned out to be incorrect (or a fake) (Dolmen 2003a). Another doubtful or very unprecise "record" was reported by Helland (1903) from the Røros district, also in Central Norway, about 600-700 m a.s.l.

A rough estimate of the total number of populations

Our picture of the distribution of *M. margarita* in Norway is roughly the same as that achieved by Økland (1975), only more complete.

Concerning the number of localities, to get an impression of the degree of reliability of the method we used to collect data, we have compared our results with those from other recent and very thorough, local investigations.

In the Oslo/Akershus area, we were informed of nine former and still-existing pearl mussel localities, whereas Kjell Sandaas and Jørn Enerud (pers. comm.), in search for pearl mussels during the 1990s, have come across as many as 15 additional (former and still-existing) localities. Hence, the real number is at least 2.7 times higher than we recorded. Rogaland is another area that has been extensively surveyed. Whereas we received information about 12 localities, Ledje (1996a,b) reported as many as 33 former and still-existing localities in 26 watercourses, i.e. 2.8 times more. In Sweden, Söderberg (1995) found twice as many localities as from where he got information.

These three examples give an indication that our number of pearl mussel localities in Norway should probably be more than doubled. A total of up to 444 former and present pearl mussel localities were reported in the questionnaire (Table 1), but only up to about 430 are by us considered to be highly probable. A guarded estimate of the total number of existing pearl mussel localities in Norway can be made along the following lines: Of the total of approximately 430 (probable) pearl mussel localities in the questionnaire, around 300 are still-existing (Table 1).

However, from what we have seen above, the real number is probably about 2½ times higher, i.e. around 750 localities.

Densities and population sizes

In Norway, the densities of mussels have so far only been estimated at a relatively small number of localities. The known local densities of pearl mussels in Norwegian rivers are "usually" fewer than 10 mussels per m^2, often far fewer (Larsen 1999). However, there are many exceptions. A stream in Oslo had 450-500 individuals m^{-2} on a short stretch of the bottom, and a total transect count for the whole watercourse (4.8 km) was 150 000 mussels (Kjell Sandaas pers. comm., Sandaas & Enerud 1998b). Up to 600 mussels m^{-2} were counted locally in a river in North-western Norway, and 1.6 million were the estimate for the whole river (4.5-5 km). This is approximately the same as the entire Finnish pearl mussel population (Valovirta 1990). Another small river in North-western Norway had an estimated population of 2 million mussels on a 5 km stretch (references in Dolmen & Kleiven 1999). However, these numbers will probably prove to be comparatively small when the really large populations in Central Norway and further north are estimated in the future. So far, Larsen et al. (2000) have estimated that there are 6.4 million mussels in a 20 km long river near Steinkjer, Nord-Trøndelag (Central Norway), and an additional 1.7 million in the neighbouring river. Dolmen (2003b) roughly estimated close to 24 million mussels on a 19 km stretch of a river at Grong, also Nord-Trøndelag.

Recent systematical monitoring of the pearl mussel has given additional data, and according to Larsen (2005b) the population sizes in 40 representative watercourses for Norway have now been estimated at a total of 16 million visible (on the surface) mussles. (The Grong locality has not been included). This makes an average of 400 000 individuals per river, which is a very minimum since additional mussels (on the average 20%, but varying from 10 to 60% of the population) may be hidden in the substrate (Larsen 2005b).

On a different set of criteria than ours, and suggesting only 350 present localities, Larsen (2005b) estimated the total Norwegian stock at a minimum of 140 million specimens. If he did not include Russia, this would make up more than 80% of the European stock of pearl mussels. On the basis of "our" probable 750 localities (see above), we estimate a total of at least 300 million individuals of the freshwater pearl mussel in Norway. And considering large, so far unknown populations in Central Norway and further north, like the one at Grong (see above), the total number of mussels may even be higher.

Dispersal

Our survey shows that the majority of the freshwater pearl mussel localities are on the coast or along the fjords, especially in Central Norway and in areas just north and south of this region. The two old localities at about 71°N lat. probably represent the northernmost freshwater pearl mussel populations in the world.

In order to explain the distribution of the pearl mussel and its stronghold in the coastal lowland, we must consider the following: The distribution of the pearl mussel in Norway is mostly a result of the dispersal of (glochidia on the gills of) anadromous salmon *Salmo salar* and brown trout *Salmo trutta* (see Young & Williams 1984a,b). The post-metamorphic pearl mussel is a typical freshwater creature and has only been recorded in salinities below 0.5 (Koli 1961). The glochidia, however, are probably able to perform osmotic regulation well. On the gills of the female mussel they experience an osmotic pressure of 1.4, in free water 0.05-0.2, and encysted on the fish gills 11-14 (Khlebovich 1965, cited in Ziuganov et al. 1994). Moreover, Bruno et al. (1988) found that the encysted (and thereby protected) glochidia on the gills of salmon parr survived a salinity of 33.3 for at least 24 hrs. These facts support the theory that sea-going salmon and (especially) trout have dispersed the pearl mussel along the Norwegian coast from one watercourse to the next through salty (or brackish) water (see Ekman 1922, Rost 1952). A similar means of dispersal has been indicated for the (freshwater) salmon parasite *Gyrodactylus salaris* Malmberg. During the two decades following its introduction to Norway in the 1970s, it quickly dispersed from infested watercourses to new ones within certain fjord systems (Johnsen & Jensen 1986, Lund & Heggberget 1992, Soleng et al. 1998, Johnsen et al. 1999).

The young, see-going anadromous brown trout, and to some extent the salmon, mostly move along the littoral zone, close to the surface, and are likely to regularly visit nearby river mouths (Cunjac 1992, Lyse et al. 1998). Re-migration of salmon presmolt from brackish or salt water back into fresh water is also well documented (Lund & Heggberget 1992). The salmon smolt run to salt water takes place in April – June/July, partly depending on the latitude (Hvidsten et al. 1995). Brown trout may leave the river about the same time (Hembre et al. 2001). Moreover, the tiny, young mussels also drop from the fish gills during this period (Young & Williams 1984a, Hruska 1992, Sandaas & Enerud 1998a,b). From what is said above, this means that the mussel is relatively easily dispersed to other watercourses.

In Norway, the natural distribution of salmon and brown trout, and therefore also of the pearl mussel, is to a great extent restricted by the abrupt, mountainous topography, especially along the western coast. However, in South-eastern and Central

Norway, which are more gently inclined, fish can penetrate much further inland. Hence, the pearl mussel also reaches higher altitudes here (Figure 3). The highest verified locality for the pearl mussel in Norway is 450+ m a.s.l. (highest record 472 m a.s.l.; Berger & Lehn 2007). In other parts of Europe, maximum altitudes for pearl mussels include 360-520 m a.s.l. in North and North-central Sweden (Hendelberg 1960, Fängstam 1986) and 800-900 m a.s.l in Czechia and Austria (Hruska 1992, Frank 1983).

Before the main land uplift after the Ice Age, salmonid fish could reach even further inland than today, and if they have not been introduced by man, local inland populations of brown trout (and salmon) are landlocked descendants of anadromous forms (Behnke 1972, Berg 1984). The land uplift has varied considerably from one part of the country to another, ML being, for example, about 10-30 m on the extreme south-west coast and more than 220 m in South-eastern Norway (Holtedahl & Andersen 1960).

However, some populations of pearl mussels are probably of anthropogenic origin, in part because people have, from earliest times, carried fish (especially brown trout) from one watercourse to another, including inland sites out of reach of anadromous salmonids. The oldest testimony to this practice is an inscription from about A.D. 1100 on a rune stone in Gausdal (Huitfeldt-Kaas 1918).

When did the pearl mussel arrive in Norway?

Is it possible from our data to say anything about the age of the Norwegian populations of the pearl mussel? As mentioned earlier, our highest verified pearl mussel population, near Snåsa, in the Verdalsvassdraget in Central Norway, is at more than 450 m a.s.l. (highest record 472 m a.s.l.). The site lies in an undisturbed area far above the stretch of the watercourse where salmon and sea-going trout are able to reach today. It is separated from this "anadromous" stretch by a high waterfall, Skjækerfossen, at about 110-125 m a.s.l., possibly also by Oksfossan, a series of rapids and small waterfalls a couple of kilometres higher up, at about 140-190 m a.s.l. We still believe the mussel population at 450+ m can be natural, and that it is ancient in origin, for the following reasons. (Mostly based on information given by Harald Sveian (pers. comm.) at the Geological Survey of Norway – see also Sveian & Olsen (1984), Sørensen et al. (1987) and Dahl et al. (1997)):

The upper parts of the Oksfossan area (180-190 m a.s.l) became ice free approx. 9700 ^{14}C-yr ago, when the sea also reached there. At that time, the river was depositing large delta terraces of glacifluvial gravel in this area; further down the valley (then a fjord) clay was being deposited in the sea. As the sea level sank continuously, the material deposited in the valley became eroded by the river, and about 9000 ^{14}C-yr (about 10 000 ordinary yr) ago the Skjækerfossen waterfall started to appear from the glacifluvial gravel. All supply to the watercourse of muddy meltwater from ice-dammed lakes on the Swedish side of the border had probably ceased by then, and the river had therefore probably been habitable for salmonid fish and the pearl mussel for a long time. The shoreline gradient in the region 9000 ^{14}C-yr B.P. has been calculated to be 0.80 m km^{-1}, which means that the river was 0.80 m km^{-1} less steep than today. This would probably suffice for fish ascent beyond the Oksfossan rapids. About 9000-8900 ^{14}C-yr ago, the waterfall below 125 m a.s.l. must have begun to become an obstacle for salmonid fish, and it probably became the 15 m high waterfall (Skjækerfossen) we know today approx. 8800 ^{14}C-yr ago.

Consequently, if, as we think, the pearl mussel population above the anadromous salmonid stretch has a natural distribution there, it must have existed for at least 8900 ^{14}C-yr. Moreover, in view of its origin, the implication is that many coastal and inland populations of the freshwater pearl mussel must have been established even earlier. The landlocked salmon in the river Namsen (80 km further north), was thus estimated to have become isolated about 9500 yr ago (Berg 1984).

The calcium connection

Many, especially early, authors have emphasised the connection between the distribution of the freshwater pearl mussel and bedrock poor in calcium (e.g. Boycott 1936, Thienemann 1950, Hendelberg 1960, Bauer 1986, Proschwitz et al. 2006). In Norway, most localities are situated either on metamorphosed Cambro-Silurian volcano-sedimentary rocks (see Sigmond et al. 1984), which are relatively rich in calcium (compared to Precambrian granites etc.), or in areas below the ML (see Holtedahl & Andersen 1960), which are more or less affected by calcium- and manganese-rich marine deposits (Table 3). A certain amount of calcium is necessary for building the mussel shell. Calcium also takes part in buffer systems against acidification of the watercourse and against acidosis within the animal (Dolmen & Kleiven 2004).

The freshwater pearl mussel in Norway therefore seems to prefer areas that are not too poor in calcium, as also indicated by the relatively high pH values at its localities (Figure 4). This relationship, however, does not necessarily break with the general European view on its distribution (see above), because the Norwegian standards for "high" or "low" calcium content (and also for pH) are far lower than in Central Europe. A further discussion on water hardness and the occurrence of pearl mussels was made by Dolmen & Kleiven (2004).

Pollution and eutrophication problems

The pearl mussel in Northern Europe can reach an age of more than 100 yr, even 150-200 yr or more (Ziuganov et al. 1994, Mutvei & Dunca 1995, Schreiber & Tranvik 2005). Since old mussels are relatively tolerant to a deterioration in the environment (Heming et al. 1988, Dolmen et al. 1995, Söderberg 1995, Dolmen & Kleiven 1999; see also Ornatowski 1967), the extinction of pearl mussels in a moderately polluted river may take a long time. The first sign of an unhealthy environment in an otherwise good pearl mussel stream is therefore the lack of young mussels.

The most important negative factors reported in the questionnaires are various kinds of pollution/eutrophication (Table 1). Eutrophication caused by runoff from agricultural land, especially a few decades ago, resulted in nutrient enrichment, increased algal growth, increased density of particles in the water and mud sedimentation on the bottom and mixed with the gravel. The mud prevents oxygen-rich water from seeping through the gravel in which the smallest, most sensitive and oxygen-demanding (approx. 1-5 yr old) mussels live (e.g. Jungbluth & Utemark 1981, Bergengren 2000). In a "normal" river they already have a very high death rate (Jungbluth & Utemark 1981, Young & Williams 1984a). The most favoured hypothesis for the lack of reproductive success in the pearl mussel in Europe is that the small mussels, under conditions like those described above, are choked (Bauer 1988, 1991, Henrikson 1991, Young 1991, Buddensiek et al. 1993). They may possibly also starve to death. Decomposition of organic material in the mud also leads to an oxygen deficit and the production of NH_4^+, which comes in addition to possible toxins originating from agriculture, households, industry, etc. In extreme cases, the host fish for the glochidia can also become scarce. Although pollution/eutrophication is important, whether or not it is the "whole truth" remains to be seen.

The different regions

Apparently, man and the pearl mussel in earlier times tended to choose to live in the same kind of area, i.e. relatively fertile lowlands, as also suggested by Sandaas & Enerud (1999). However, the extinction of the pearl mussel in South-eastern Norway, at least in the Oslo and Akershus area, has been formidable. Oslo and Akershus are also the most densely populated counties in Norway, and have the third highest percentage of intensively cultivated land, and also heavy industrial pollution of running water (see the Results) (Vogt 1983, Brunvoll et al. 1994). Other counties with a relatively dense population and large areas of agricultural land are Vestfold, Østfold and Rogaland, and the extinction of pearl mussel populations has also been severe there. In Rogaland, where almost one half of the pearl mussel populations have become extinct, agriculture has been especially intensive; the county has had by far the highest runoff of phosphorus (up to 400 g daa^{-1} in 1979) and nitrogen (6-7 kg daa^{-1} in 1979) (Brunvoll et al. 1994). Like the Agder counties, Rogaland, is also affected by large quantities of acidic precipitation (Vogt 1983), but more favourable types of bedrock and a significantly greater cover of superficial deposits make it locally better able to withstand the acidification (Sigmond et al. 1984). Dolmen & Kleiven (1997a,b, 1999, 2004) give more details on this topic. The mussels' problems related to the acidification in Southern Norway, where only three pearl mussel populations have survived, have been described by Dolmen & Kleiven (2004). Also large numbers of fish populations have become extinct there (Hesthagen et al. 1999).

Attitudes and conservation prospects

Pearl fishing may have been very detrimental to the species a century or two ago. The pearl fishing practice and its history in Norway is summarised by Kleiven et al. (1989) and Kleiven & Dolmen (1999). Despite the vulnerability of the pearl mussel and the fact that it is protected by law, pearl fishing was quite seriously proposed as a tourist attraction in combination with gold washing near Oppdal in Central Norway as recently as 1991 (Dolmen & Kleiven 1997a). Moreover, in Numedalslågen, a river in Vestfold, a pilot project was quite recently started to use freshwater pearl mussels to produce "cultured" pearls. The pearl production is based on implants in mussels kept in cages in the river, and the mussels are later "slaughtered", as shown on Norwegian television in 1998.

The release of non-indigenous fish has been another popular practice in many parts of Norway, and it may have had a negative influence on the pearl mussel. Larsen (2005b) refers to studies showing that at least some local pearl mussel populations are adapted to only one species of host, either salmon or brown trout (not both), or even to a specific tribe of fish. Because introduced stocks can sometimes outcompete or suppress the old, indigenous one, to which the mussels are adapted, fish stocking can easily be harmful to a population of pearl mussels.

However, the Directorate for Nature Management in Norway launched an action plan for the large freshwater mussels, of which the pearl mussel is among the most important (Larsen 1999). In this connection, a special issue of the national zoological journal "Fauna" (1999, vol. 52 (1)) was devoted entirely to the large freshwater mussels. Later, a monitoring programme for the pearl mussel commenced in 2000 (see e.g. Larsen 2005a). And as one of five selected species, the pearl mussel in Norway has got its action plan, which is now being implemented (Larsen 2005b, Direktoratet for naturforvaltning 2006).

The number of pearl mussels in Norway, roughly estimated above (probable 750 localities and more than 300 million individuals), is a high number. Investigations during the next few years will reveal whether this is a good estimate or not. However, the numbers are decreasing, since the pearl mussel has reproductive problems in so many watercourses, at least in South Norway. Some positive reports exist, though, for example from the river Ogna in Rogaland, South-western Norway. After many years of pollution and acidification, liming of the watercourse seems to have made the environment better for the species, and young mussels have again been registered (Larsen & Brørs 1998). The conservational status of the pearl mussel will again be evaluated in 2010, in connection with a new Norwegian Red List.

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