

Taphonomy of freshwater molluscs in carbonate-poor deposits: a case study of the river pearl mussel in northeastern Finnish Lapland

Jan Kresten Nielsen, Samuli Helama & Jesper Kresten Nielsen

Nielsen, J.K., Helama, S. & Nielsen, J.K.: Taphonomy of freshwater molluscs in carbonate-poor deposits: a case study of the river pearl mussel in northeastern Finnish Lapland. *Norwegian Journal of Geology*, vol. 88, pp. 103-116. Trondheim 2008. ISSN 029-196X.

The river pearl mussel, *Margaritifera margaritifera*, is becoming an important tool in reconstructing past changes in climate because of its shell growth increments and longevity. Surveys of the Lutto River system and surroundings in northeastern Finland have been conducted to identify the distribution of fossil and subfossil mussel shells. By increasing the findings of mussels may enable an extension of the existing sclerochronologies, that is, temporal records based on shell growth patterns may be achieved. The distribution pattern includes the preservation characteristics of their calcareous (aragonitic) shells and periostraca, indicating which pathways these remains may have taken to survive the transition from the biosphere into the lithosphere. Principally, the distribution of the mussels depends on larval spreading by salmon fish which act as hosts. However, the post-mortem natural preservation of the shells occurs mainly as periostraca in ancient river bank and bar deposits. This is related to acidic river and percolation water. Post-mortem preservation of calcareous shells has probably been ameliorated due to anthropogenic activity. During the past centuries, the river pearl mussel has been sought after by pearl fishers who left shell remains typically around camp-fire sites. As the sites are located on topographically higher levels, the shells became less affected by acidic water. If the shells were hidden in the soil by the hunters, this may have improved their preservation potential due to higher pH values deeper in the podzol soil. Although the outer shell layer tends to be partly dissolved, these shells can be suitable for sclerochronologists. On the other hand, the limited preservation of the shells impedes reconstruction of past geographical ranges of the species, with the danger that severe spatial underestimation of their past spatial occurrence may occur.

Key words: Conservational palaeobiology, Bivalvia, *Margaritifera*, preservation, shell, periostracum, water chemistry, Finland.

Jan Kresten Nielsen, StatoilHydro ASA, TNE SST Reservoir Technology, IOR Studies, P.O. Box 273, NO-7501 Stjørdal, Norway (e-mail: bioerosion@yahoo.dk). Samuli Helama, Department of Geology, P.O. Box 64, 00014 University of Helsinki, Finland. Jesper Kresten Nielsen, SINTEF Petroleum Research, S. P. Andersens vei 15B, NO-7031 Trondheim, Norway.

Introduction

Growth increments may be found in various types of accretive tissues across a wide taxonomic range of organisms. In aquatic settings, growth increments in bivalve shells provide records of environmental variability with high accuracy (e.g., Jones 1980, 1983). Due to the great influence of environmental conditions on the growth of organisms such as bivalves, the corresponding variability in growth increment properties can be used as bio-indicators of past environmental changes. Such records could be of great importance for limnological, hydrological, climatic and ecological studies, greatly increasing our understanding of environmental variability over a range of spatial as well as temporal scales. In fact, bivalve shell growth increments, and growth rates as well as biogeochemical properties have previously been used as monitors of various aquatic variables such as temperature (Davenport 1938; Kennish & Olsson 1975; Goodwin et al. 2001), salinity (Navarro 1988; Marsden & Pilkington 1995) and food availability (Ansell 1968). In this way, the bivalve shell increments may contribute to studies of modern environmental and climatic change, on local and regional scales.

The length of these indirect environmental series (proxy records) often depends on the maximum biological age of the organisms used in the study. Thus, the temporal limit of the record could be limited by the longevity of the particular species under study. Not all, but some of the bivalves are relatively long living species. In freshwater environments, river pearl mussels (*Margaritifera margaritifera*), which are benthic filter-feeders, are able to live more than one hundred years, occasionally even more than two hundred years (Bauer 1992; Mutvei et al. 1994, 1996; Mutvei 1996; Ziuganov et al. 2000; Helama & Valovirta 2008). Even this may not, however, be the ultimate temporal limit of maximum record length. In a case when a shell specimen was found dead, either as a fossil or partially fossilized, the exact dates of its incremental layers are unknown. However, if an overlap occurs between the established growth increment chronology and growth increment series from dead specimens, the dates of the two series can be correlated using the observed synchronization of narrow and wide increments. The co-variability can be matched visually and statistically using sclerochronological cross-dating (Marchitto et al.

2000; Helama et al. 2006). This process will evidently strengthen and lengthen the chronological record. This, in turn, results in greatly elongated proxy records for palaeoenvironmental and palaeoclimatic studies.

The maximum length of the proxy record may thus depend not only on the longevity, but also the taphonomic processes affecting the species in specific environmental settings. Clearly, the understanding of the taphonomic processes may be critically important in attempting to elongate the proxy series backwards in time. In this article we study the preservation of *Margaritifera mar-*

garitifera shells in the geological context of northeastern Finnish Lapland (Fig. 1). The specific interest this area offers for such a study is due to the relative abundance of the modern populations of the same species in the region, longevity of the species and supposedly strong climatic signals of the growth increment of the species in these climatically harsh environments. The occurrence of *M. margaritifera* shells is related to the presence of salmon as temporary hosts for larvae. We show that the preservation of the different shell portions is tissue type-specific with obvious links to the geochemical properties of the Quaternary deposits and water reservoirs. Various dete-

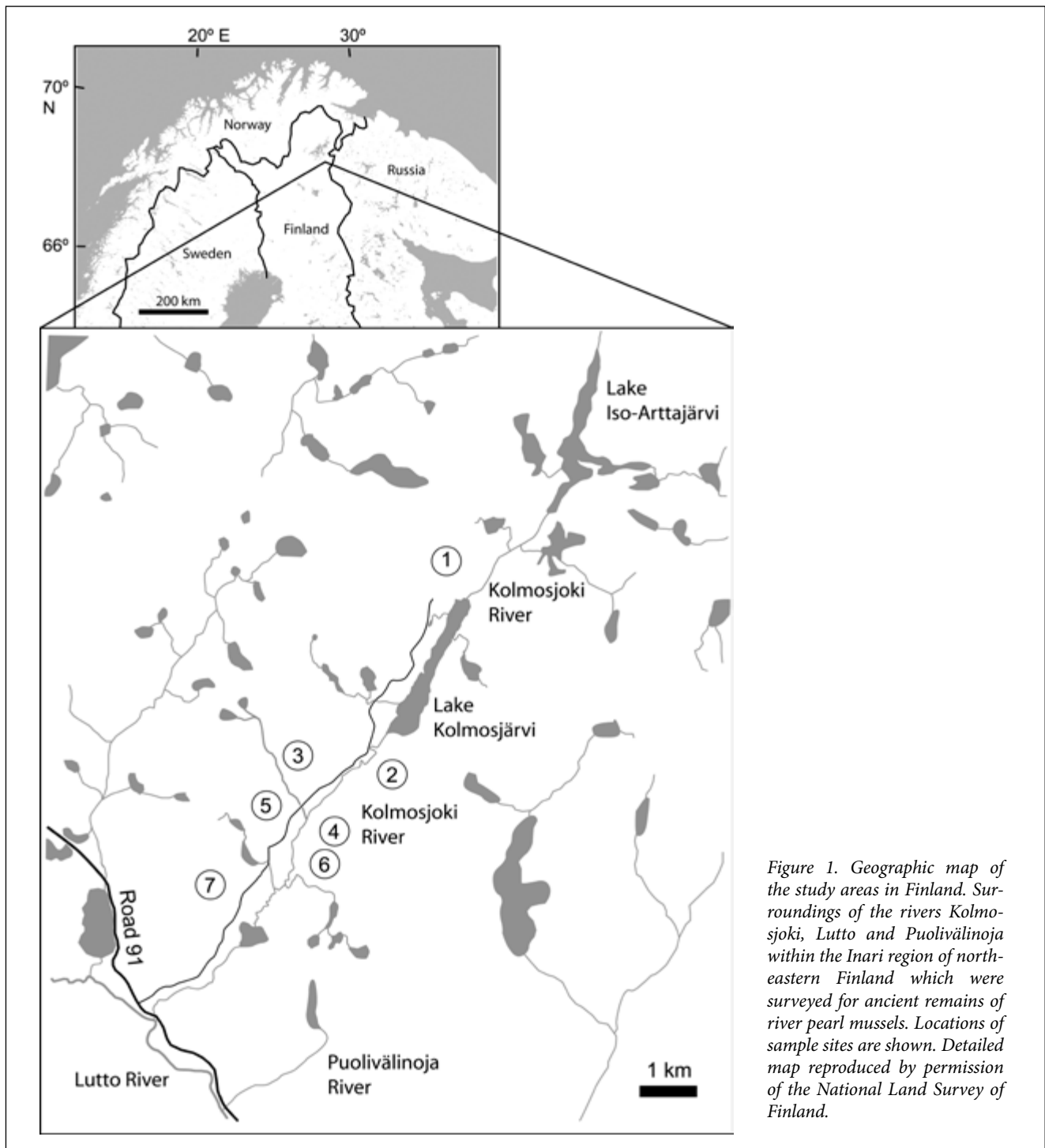


Figure 1. Geographic map of the study areas in Finland. Surroundings of the rivers Kolmosjoki, Lutto and Puolivälinoja within the Inari region of northeastern Finland which were surveyed for ancient remains of river pearl mussels. Locations of sample sites are shown. Detailed map reproduced by permission of the National Land Survey of Finland.

riorative processes affect the biogenic remains during the transition from biosphere to lithosphere, and we provide an overview showing the taphonomic pathways followed by natural and anthropogenic shell deposits.

Geological setting of the study region

The region is characteristically divided into two geological units. Precambrian bedrock consists mainly of crystalline rocks. The area belongs to the granulite zone of Lapland. These rocks originate as volcanic ashes and lavas deposited as marine sediments which later underwent a high degree of metamorphism during the Sveco-karelidic orogeny, occurring approximately 1.9 billion years ago (Meriläinen 1976). The area was glaciated during the Weichselian by the Scandinavian Ice Sheet and the Precambrian bedrock is overlain by glacial sediments from this phase. These sediments have to some extent been reworked during the Holocene by post-glacial aeolian and fluvial processes. The late to post-glacial evolution of the study region and adjacent areas by the deglacial processes has been described by Tanner (1936), Penttilä (1963), Sorsa (1965), Synge (1969), Saarnisto (1973) and Johansson (1988, 1995). The deglaciation occurred in the early Flandrian, and the region emerged from the ice approximately between 9500 and 9000 BP (Saarnisto 1973; Johansson 1988).

Investigated sites

Stretches along the Lutto River and its tributaries, the Kolmosjoki River and the Puolivälinoja River, were investigated during fieldwork (Fig. 1). Along these stretches, areas of ancient river deposits, aerially exposed river bars and anthropogenic activity were searched for the remains of mollusc shells and periostraca (Figs. 1 and 2; Table 1). The activity of human beings was evident from sites (Kolmosjoki River, KOL1, 3, 5, 7) of former camp-

Locality	Anthropogenic remains	Sediment
KOL1	Old camp-fire	Sandy gravel
KOL2	No sign of human activity	Plant debris
KOL3	Old camp-fire	Sandy gravel
KOL4	No sign of human activity	Depression with spring water and plant debris
KOL5	Old camp-fire	Soil rich in decaying plant remains
KOL5	Old camp-fire	Sandy gravel
KOL6	No sign of human activity	River bank of gravel and soil
KOL7	Ruins of a house	Sandy gravel

Table 1. Overview of studied samples of *Margaritifera margaritifera* collected along the Kolmosjoki River, with site descriptions of individual samples.



Figure 2. Examples of sample sites (A) Well-preserved disarticulated valve almost covered by soil. Sample site KOL5, scale bar 1 cm. (B) Subaerially exposed river bar with a depression containing decaying plants and periostraca. KOL4, shovel for scale.

fires and ruins of old cottages. The campfires were commonly located upon a layer of glaciofluvial gravel from nearby eskers. Therefore, river sections through esker deposits were also scoured for shell remains. In addition, excavations were made into the ancient river bank to locate horizons with mollusc remains. Similar shovel-dug excavations were also made into recent river bars of which some were covered by vegetation (KOL2, 6). The size of the river bars was up to tens of square metres in area. One of these river bars (KOL4) contained a depression filled with plant debris and spring water.

Methods

The taphonomy of the shells and periostraca was studied in the field and under the binocular microscope (up to x40) by recording taphonomic features formed by abrasion, bioerosion, disarticulation, dissolution and fragmentation. A three-level scheme of taphonomic grades was applied to each of the shells to indicate the degree of taphonomic alteration (Kowalewski et al. 1995; Hallman et al. 1996). Grades 0, 1 and 2 refer to none, moderate and

high alteration, respectively. Grade 2 indicates alteration of greater than 20 percent of the shell surface. The boundary between grades 1 and 2 was chosen as the 20 percent level for all taphonomic features, with the exception of 50 percent where fragmentation has occurred. 'Flash cards' of shells displaying the three grades were applied to ease the assessment of taphonomic alteration (Hallman et al. 1996; Nielsen & Funder 2003). The scheme of taphonomic grades was applied to the remains of both shells, periostraca, ligaments and organic shell sheets of *Margaritifera margaritifera* (Table 2). The grades of taphonomic features were recorded for individual shells and periostraca. Subsequently, the grades were averaged for individual taphonomic features over the entire sample. The averaged values, which present a generalized estimate of taphonomic alteration, have proven useful in earlier studies (e.g., Flessa et al. 1993; Nebelsick & Kowalewski 1999; Nebelsick 1999; Nielsen & Funder 2003).

Samples of stream bottom water were taken from the upper and lower stretches of the Kolmosjoki River, where mollusc remains were found. Water was also sampled from groundwater and spring water flooding the bottoms of excavations. The water samples were analyzed for acidity by measuring the pH with indicator sticks. In addition, the Finnish Environment Institute provided hydrochemical data from the Kolmosjoki River system, including measurements of water temperature (°C), organic carbon (total, IR mg/l) and pH. The latter was measured electrometrically.

Results

Remains of *Margaritifera margaritifera* were only found along the Kolmosjoki River. Surveys along the Puolivälinoja River and stretches of the Lutto River (Fig. 1) yielded no additional remains.

Ancient river banks

A number of excavations were dug into ancient river banks now covered by vegetation. Remains of *Margaritifera margaritifera* were recovered in one of the excavations (KOL6) (Table 1). They included generally well-preserved periostraca of at least five valves (Fig. 3; Table 2). Eighteen fragments were present. Neither borings nor encrustations were found on any of the remains. All the remains were found in the uppermost part of a layer, at least 30 cm thick, consisting of coarse-grained, yellow sand and gravel. The remains were horizontally oriented. This sediment was overlain by 40 cm of dark gray soil with plant roots and decaying leaves.

Aerially exposed river bars

Excavations were also dug into aerially exposed river bars. Some of the bars were partly covered by vegetation. None of these excavations revealed the remains of bivalves. However, a depression filled with plant debris and spring water was found on a river bar overgrown by

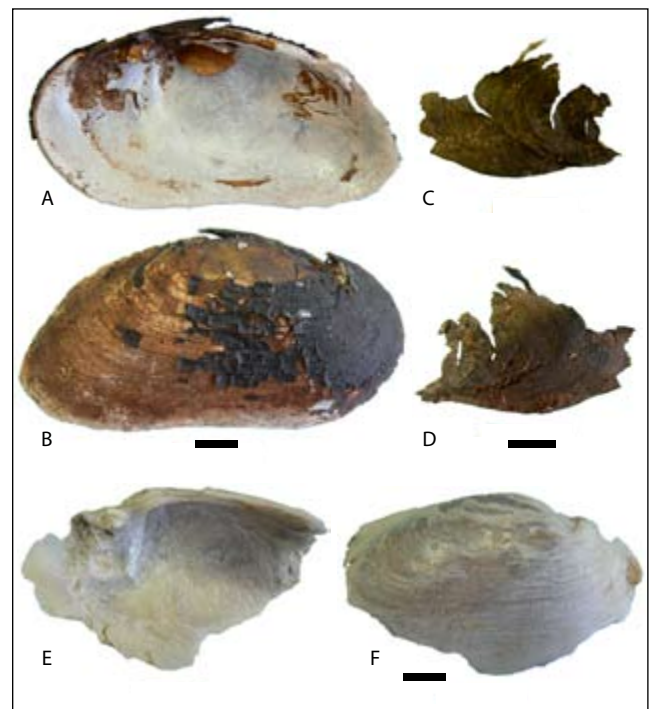


Figure 3. Preservation states of *Margaritifera margaritifera*. (A, B) Inner and outer surfaces of right valve. Ref. no. 259, sample site KOL5. (C, D) Periostracal fragment. Ref. no. 461, sample site KOL6. (E, F) Inner and outer surfaces of fragmented right valve. Outer shell layer has suffered severe dissolution and detachment. Ref. no. 394, sample site KOL3. Scale bars 1 cm.

vegetation (KOL4). Periostraca from at least eight valves of *M. margaritifera* occurred among the plant debris (Table 2). Six of these periostraca were articulated. Nine fragments of periostracum were also found. The periostraca were generally fragmented to a moderate to high degree. Seven of them were still attached to calcareous shells, which were greatly affected by dissolution. None of the remains showed evidence of bioerosion or encrustation.

Camp-fire sites

Calcareous shell material was most common around campfire sites. The campfires were usually placed 1 to 2 m above present river surface level. The ground was sandy to gravelly, of glaciofluvial origin and partly covered by low vegetation. Glaciofluvial sediments exposed in river sections of local eskers were without shell remains. All valves found at the camp-fire sites were disarticulated; however, many of the valves from KOL5 appeared to fit each other in left-right pairs (Fig. 3; Table 2). At this site, the valves were unfragmented or only slightly fragmented, and covered by soil rich in decaying leaves and roots. These valves were nearly entirely covered by periostraca and held remains of ligaments. Incipient detachment of the periostraca had occurred along the annual growth lines of the calcareous material. The other camp-fire sites led to the discovery of less well-preserved valves. These valves were moderately to highly fragmented, and

Table 2. List of *Margaritifera margaritifera* specimens investigated for taphonomic features, which are recorded by using taphonomic grades. Abrasion, bioerosion and encrustation features are absent. Grade 0, unaffected by the taphonomic process; 1, moderately affected; 2, highly affected; +, process occurred; -, feature absent; (-), evidence of process impossible to score as the shell portion holding that feature is absent; Frag, fragment; LV, left valve; RV, right valve; Perio, periostracum.

Ref. no.			Disarticulation	Shell dissolution				Fragmentation			Organic sheets (inner shell surface)	Shell fractures	
				Outer surface	Inner surface	Muscular scars	Umbo	Shell	Periostracum	Ligament		Dorso-posterior	Ventral
329a	Frag	KOL1	+	2	1	(-)	(-)	2	-	(-)	-	(-)	(-)
329b	Frag	KOL1	+	2	2	(-)	(-)	2	-	(-)	-	(-)	(-)
329c	Frag	KOL1	+	2	2	(-)	(-)	2	-	(-)	-	(-)	(-)
329d	Frag	KOL1	+	1	2	(-)	(-)	2	-	(-)	-	(-)	(-)
329e	Frag	KOL1	+	2	1	(-)	(-)	2	-	(-)	-	(-)	(-)
329f	Frag	KOL1	+	2	2	(-)	(-)	2	-	(-)	-	(-)	(-)
329g	Frag	KOL1	+	2	1	(-)	(-)	2	-	(-)	2	(-)	(-)
329h	Frag	KOL1	+	2	2	2	(-)	2	-	(-)	-	(-)	(-)
331	LV	KOL1	+	2	1	1	2	1	-	-	-	+	+
333	LV	KOL1	+	2	1	2	2	1	-	-	-	+	-
335	LV	KOL1	+	2	2	2	2	1	-	-	-	+	+
337	LV	KOL1	+	1	0	1	2	0	2	-	-	-	-
339	RV	KOL1	+	2	2	2	2	2	-	-	-	+	+
341	RV	KOL1	+	2	1	2	2	2	-	-	2	+	+
343	RV	KOL1	+	2	2	1	2	1	-	-	2	+	+
345	LV	KOL1	+	2	1	2	2	1	-	-	-	+	+
347	LV	KOL1	+	2	2	2	2	1	-	-	-	+	+
349	RV	KOL1	+	2	0	1	2	1	-	-	-	+	+
351	RV	KOL1	+	1	1	1	2	1	2	-	2	+	+
353	LV	KOL1	+	2	1	2	2	2	-	-	-	+	+
355	RV	KOL1	+	2	1	2	2	2	-	-	2	+	+
357	RV	KOL1	+	2	0	1	2	2	-	-	2	+	+
359	RV	KOL1	+	2	1	2	2	2	-	-	-	+	+
361	LV	KOL1	+	2	1	2	2	2	-	-	-	+	+
363	RV	KOL1	+	2	0	2	2	2	-	-	-	+	+
365	RV	KOL1	+	1	1	1	2	0	2	-	2	-	-
369	LV	KOL1	+	2	0	0	2	0	2	2	-	-	-
371	RV	KOL1	+	2	2	2	2	1	1	1	2	+	+
373	LV	KOL1	+	2	1	(-)	2	2	-	-	-	+	+
375	LV	KOL1	+	2	2	2	2	2	-	-	-	+	+
377	LV	KOL1	+	2	2	2	2	2	-	-	-	+	(-)
379	LV	KOL1	+	2	1	(-)	2	2	-	-	-	+	+
381	LV	KOL1	+	2	1	2	2	2	-	(-)	-	+	(-)
Average	32% frag		100%	1.9	1.2	1.6	2.0	1.6	1.8	1.5	2.0	88%	83%
453	Perio R	KOL2	+	(-)	(-)	(-)	(-)	(-)	0	1	(-)	(-)	(-)
384	LV	KOL3	+	2	1	1	2	1	2	-	2	+	+
386	RV	KOL3	+	2	1	2	2	1	-	-	-	+	+
388	LV	KOL3	+	2	1	1	2	1	-	-	2	+	+
390	LV	KOL3	+	2	1	1	2	1	-	-	2	+	+
392	RV	KOL3	+	2	1	2	2	1	2	2	-	+	+
394	RV	KOL3	+	2	2	2	2	1	-	-	2	+	+
396	RV	KOL3	+	2	1	(-)	2	1	-	-	-	+	+
398	RV	KOL3	+	2	1	(-)	2	2	-	-	2	+	+
400	RV	KOL3	+	2	1	2	2	2	-	-	-	(-)	+
402	RV	KOL3	+	2	1	-	2	2	-	-	-	+	+
404	LV	KOL3	+	2	1	-	2	2	-	-	-	+	+
406	Frag	KOL3	+	2	2	-	-	2	-	-	-	+	+
408a	Frag	KOL3	+	1	0	(-)	(-)	2	-	-	-	(-)	(-)
408b	Frag	KOL3	+	2	1	1	(-)	2	-	-	-	(-)	(-)
408c	Frag	KOL3	+	2	2	(-)	(-)	2	-	-	-	+	+
408d	Frag	KOL3	+	2	1	(-)	(-)	2	-	-	-	(-)	(-)
410a	Frag	KOL3	+	2	2	(-)	(-)	2	-	-	-	(-)	(-)
410b	Frag	KOL3	+	2	0	(-)	(-)	2	-	-	-	(-)	(-)
410c	Frag	KOL3	+	2	1	(-)	(-)	2	-	-	-	(-)	(-)
410d	Frag	KOL3	+	2	1	(-)	(-)	2	-	-	-	(-)	(-)
412a	Frag	KOL3	+	1	0	(-)	(-)	2	-	-	-	(-)	(-)
412b	Frag	KOL3	+	2	1	2	(-)	2	-	-	-	(-)	(-)
414a	Frag	KOL3	+	1	2	2	(-)	2	-	-	-	+	(-)
414b	Frag	KOL3	+	2	0	(-)	(-)	2	-	-	-	(-)	(-)

414c	Frag	KOL3	+	2	1	(-)	(-)	2	-	-	-	(-)	(-)
414d	Frag	KOL3	+	1	1	(-)	(-)	2	-	-	-	(-)	(-)
414e	Frag	KOL3	+	2	1	(-)	(-)	2	-	-	-	(-)	(-)
414f	Frag	KOL3	+	2	2	(-)	(-)	2	-	-	-	(-)	(-)
414g	Frag	KOL3	+	2	2	2	(-)	2	-	-	-	+	(-)
414h	Frag	KOL3	+	2	1	(-)	(-)	2	-	-	-	(-)	(-)
414i	Frag	KOL3	+	1	2	(-)	(-)	2	-	-	-	(-)	(-)
416a	Frag	KOL3	+	2	1	(-)	(-)	2	-	-	-	(-)	(-)
416b	Frag	KOL3	+	2	2	(-)	(-)	2	-	-	-	(-)	(-)
416c	Frag	KOL3	+	2	1	(-)	(-)	2	-	-	-	(-)	(-)
416d	Frag	KOL3	+	1	1	(-)	(-)	2	-	-	-	(-)	(-)
416e	Frag	KOL3	+	2	2	(-)	(-)	2	-	-	-	(-)	(-)
416f	Frag	KOL3	+	2	2	(-)	(-)	2	-	-	-	(-)	(-)
416g	Frag	KOL3	+	2	1	(-)	(-)	2	-	-	-	(-)	(-)
416h	Frag	KOL3	+	1	1	2	(-)	2	-	-	-	(-)	(-)
416i	Frag	KOL3	+	2	1	(-)	(-)	2	-	-	-	(-)	(-)
416j	Frag	KOL3	+	2	2	(-)	(-)	2	-	-	-	(-)	(-)
416k	Frag	KOL3	+	2	1	(-)	(-)	2	-	-	-	(-)	(-)
416l	Frag	KOL3	+	2	2	(-)	(-)	2	-	-	-	(-)	(-)
418a	Frag	KOL3	+	2	1	(-)	(-)	2	-	-	-	(-)	(-)
418b	Frag	KOL3	+	2	2	(-)	(-)	2	-	-	-	(-)	(-)
418c	Frag	KOL3	+	2	2	(-)	(-)	2	-	-	-	(-)	(-)
418d	Frag	KOL3	+	2	1	(-)	(-)	2	-	-	-	(-)	(-)
418e	Frag	KOL3	+	1	1	(-)	(-)	2	-	-	-	(-)	(-)
418f	Frag	KOL3	+	2	1	(-)	(-)	2	-	-	-	(-)	(-)
418g	Frag	KOL3	+	2	0	(-)	(-)	2	-	-	-	(-)	(-)
418h	Frag	KOL3	+	2	1	(-)	(-)	2	-	-	-	(-)	(-)
418i	Frag	KOL3	+	1	1	(-)	(-)	2	-	-	-	(-)	(-)
418j	Frag	KOL3	+	2	2	(-)	(-)	2	-	-	-	(-)	(-)
418k	Frag	KOL3	+	1	1	(-)	(-)	2	-	-	-	(-)	(-)
418l	Frag	KOL3	+	2	2	(-)	(-)	2	-	-	-	(-)	(-)
420a	Frag	KOL3	+	1	0	(-)	(-)	2	-	-	-	(-)	(-)
420b	Frag	KOL3	+	2	1	(-)	(-)	2	-	-	-	(-)	(-)
420c	Frag	KOL3	+	2	2	(-)	(-)	2	-	-	-	(-)	(-)
420d	Frag	KOL3	+	2	2	(-)	(-)	2	-	-	-	(-)	(-)
420e	Frag	KOL3	+	1	1	(-)	(-)	2	-	-	-	(-)	(-)
Average	88% frag		100%	1.8	1.2	1.7	2.0	1.9	2.0	2.0	2.0	100%	100%
480	Perio L	KOL4	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
482	Perio L	KOL4	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
484	Frag	KOL4	+	1	2	2	2	2	2	-	2	+	+
486	Perio frag	KOL4	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
488	Perio R	KOL4	+	(-)	(-)	(-)	(-)	(-)	2	1	(-)	(-)	(-)
490	Perio frag	KOL4	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
492	RV	KOL4	+	2	2	2	2	1	1	2	1	+	+
494	LV	KOL4	+	2	2	2	2	1	1	2	2	-	-
495	RV	KOL4	+	1	2	2	2	1	1	-	1	-	+
496	Perio frag	KOL4	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
498	Perio frag	KOL4	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
500	Perio frag	KOL4	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
500	Perio frag	KOL4	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
502	Perio frag	KOL4	+	(-)	(-)	(-)	(-)	(-)	2	2	(-)	(-)	(-)
502	Perio frag	KOL4	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
504	Perio LR	KOL4	-	(-)	(-)	(-)	(-)	(-)	0	0	(-)	(-)	(-)
Average	56% frag		94%	1.5	2.0	2.0	2.0	1.3	1.7	1.4	1.5	50%	50%
437	Frag	KOL5 camp-fire	+	1	1	2	2	2	2	-	1	+	(-)
440	Frag	KOL5	+	1	2	(-)	(-)	2	1	(-)	-	(-)	(-)
442	LV	KOL5	+	1	2	2	2	1	2	-	2	+	+
447a	Frag	KOL5	+	1	2	(-)	(-)	2	1	(-)	2	-	+
447b	Frag	KOL5	+	2	2	(-)	(-)	2	1	(-)	1	-	+
447c	Frag	KOL5	+	2	2	(-)	(-)	2	2	(-)	1	-	+
Average	83% frag		100%	1.3	1.8	2.0	2.0	1.8	1.5		1.4	40%	100%
241	RV	KOL5 soil	+	0	1	0	2	0	0	1	2	-	+
243	LV	KOL5	+	0	0	0	1	0	1	2	2	-	-
245	LV	KOL5	+	0	2	2	1	0	2	2	1	-	+
247	LV	KOL5	+	1	1	2	2	0	2	-	2	-	+
249	LV	KOL5	+	0	1	2	2	0	1	-	2	+	+
251	LV	KOL5	+	1	2	1	2	1	2	2	-	+	+
253	RV	KOL5	+	1	2	2	2	1	2	2	-	+	+
255	LV	KOL5	+	0	1	1	2	1	2	-	2	-	+
257	LV	KOL5	+	1	1	2	2	2	2	-	2	+	+

259	RV	KOL5	+	0	1	0	2	0	2	2	2	-	-
261	Frag	KOL5	+	0	2	(-)	(-)	2	-	(-)	2	(-)	(-)
263	RV	KOL5	+	0	1	0	2	1	2	-	-	-	+
266	RV	KOL5	+	1	0	0	1	1	-	2	2	+	+
268	RV	KOL5	+	2	0	0	2	1	2	2	-	+	+
270	Frag	KOL5	+	0	0	(-)	2	2	-	-	2	+	(-)
272	RV	KOL5	+	0	1	1	2	1	1	-	2	+	+
274	RV	KOL5	+	2	0	0	2	1	2	2	2	+	+
276	LV	KOL5	+	1	2	1	2	1	2	-	-	+	+
278	LV	KOL5	+	0	1	1	2	1	-	2	2	-	+
280	Frag	KOL5	+	2	1	2	(-)	2	-	-	2	+	(-)
282	Frag	KOL5	+	2	1	1	(-)	2	-	(-)	2	+	(-)
284	Frag	KOL5	+	1	1	(-)	(-)	2	2	(-)	-	(-)	(-)
286, 288	Frag	KOL5	+	0	1	1	(-)	2	1	2	2	+	(-)
290	Frag	KOL5	+	1	0	(-)	(-)	2	-	(-)	-	(-)	(-)
292	Frag	KOL5	+	2	1	(-)	(-)	2	-	(-)	2	(-)	(-)
294	Frag	KOL5	+	0	0	0	(-)	2	2	(-)	2	(-)	(-)
296	Frag	KOL5	+	0	0	(-)	(-)	2	2	(-)	2	(-)	(-)
298	Frag	KOL5	+	0	0	(-)	(-)	2	2	(-)	2	(-)	(-)
300	Frag	KOL5	+	1	0	(-)	(-)	2	2	(-)	2	(-)	(-)
302	Frag	KOL5	+	1	2	(-)	(-)	2	2	(-)	2	(-)	(-)
304	Frag	KOL5	+	0	0	1	2	2	2	2	2	+	+
306	Frag	KOL5	+	0	1	2	(-)	2	1	(-)	2	(-)	(-)
308	RV	KOL5	+	0	1	1	2	2	1	2	-	(-)	(-)
310	LV	KOL5	+	1	1	1	2	1	2	-	2	+	+
312	RV	KOL5	+	1	0	0	2	2	-	-	-	+	(-)
314	Frag	KOL5	+	1	1	2	(-)	2	2	(-)	2	(-)	(-)
316	RV	KOL5	+	2	0	0	2	1	-	-	-	+	+
318	LV	KOL5	+	2	0	0	2	1	-	2	-	+	+
320	RV	KOL5	+	1	1	2	2	1	2	2	2	+	+
322a	Frag	KOL5	+	1	0	(-)	(-)	2	1	(-)	-	(-)	(-)
322b	Frag	KOL5	+	1	0	(-)	(-)	2	1	(-)	-	(-)	(-)
322c	Frag	KOL5	+	1	0	(-)	(-)	2	1	(-)	-	(-)	(-)
322d	Frag	KOL5	+	2	1	(-)	(-)	2	2	(-)	-	(-)	(-)
322e	Frag	KOL5	+	2	1	(-)	(-)	2	2	(-)	-	(-)	(-)
322f	Frag	KOL5	+	2	1	(-)	(-)	2	-	(-)	-	(-)	(-)
324a	Frag	KOL5	+	0	1	(-)	(-)	2	0	(-)	2	(-)	(-)
324b	Frag	KOL5	+	0	1	(-)	(-)	2	0	(-)	2	(-)	(-)
324c	Frag	KOL5	+	0	1	(-)	(-)	2	0	(-)	2	(-)	(-)
324d	Frag	KOL5	+	1	2	(-)	(-)	2	1	(-)	2	(-)	(-)
324e	Frag	KOL5	+	1	2	(-)	(-)	2	1	(-)	2	(-)	(-)
324f	Frag	KOL5	+	1	2	(-)	(-)	2	1	(-)	2	(-)	(-)
Average	55% frag		100%	0.7	0.8	0.9	1.9	1.5	1.5	1.9	1.9	88%	90%
459	Perio R	KOL6	+	(-)	(-)	(-)	(-)	(-)	1	1	(-)	(-)	(-)
461	Perio R	KOL6	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
463	Perio frag	KOL6	+	(-)	(-)	(-)	(-)	(-)	2	2	(-)	(-)	(-)
465	Perio frag	KOL6	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
467	Perio L	KOL6	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
469	Perio frag	KOL6	+	(-)	(-)	(-)	(-)	(-)	2	2	(-)	(-)	(-)
471	Perio LR	KOL6	-	(-)	(-)	(-)	(-)	(-)	1	1	(-)	(-)	(-)
473a	Perio frag	KOL6	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
473b	Perio frag	KOL6	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
473c	Perio frag	KOL6	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
473d	Perio frag	KOL6	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
475a	Perio frag	KOL6	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
475b	Perio frag	KOL6	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
475c	Perio frag	KOL6	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
475d	Perio frag	KOL6	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
477a	Perio frag	KOL6	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
477b	Perio frag	KOL6	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
477c	Perio frag	KOL6	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
477d	Perio frag	KOL6	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
477e	Perio frag	KOL6	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
477f	Perio frag	KOL6	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
477g	Perio frag	KOL6	+	(-)	(-)	(-)	(-)	(-)	2	-	(-)	(-)	(-)
Average	82% frag		95%	(-)	(-)	(-)	(-)	(-)	1.9	1.5	(-)	(-)	(-)
427	LV	KOL7	+	2	1	2	2	1	-	-	2	+	+
429	LV	KOL7	+	2	2	2	2	1	-	2	2	+	+
431	RV	KOL7	+	2	1	2	2	1	-	-	1	+	+
Average	0% frag		100%	2.0	1.3	2.0	2.0	1	-	2.0	1.7	100%	100%

without ligaments or periostraca. The outer shell layer of the valves was much affected by dissolution. The majority of the valves contained macroscopic evidence of dissolution pits and terraces associated with decalcification of the shell material. The valves were neither bioeroded or encrusted.

Water quality

Water samples were obtained from three distinct reservoirs, namely river water, spring water and groundwater (Table 3). Measurements of their acidity showed that all the reservoirs contained acidic water of less than pH 7. The river water ranged between pH 5.1 and 5.5, whereas the spring water and the groundwater had a pH of 5.4 and 4.7, respectively. In the study region, the hydrochemical pH values remained characteristically at relatively low levels, between 6.2 and 6.6 (measured from spring and dug well waters by Lahermo et al. 1990). Our field observations support this view with indications of local pH values that are somewhat, but not critically, lower. These values can be viewed in the context of more representative regional datasets (The Finnish Environment Institute) from 36 different lacustrine sites of the Kolmosjoki River system (Fig. 4). Depth of sampling varied from 0.1 to 6.0 m. Electrometrical values of pH were measured discontinuously around 1st of October from 1989 to 2005. The values, which range between 4.8 and 7.5, showed an average of 6.5 (N=108, standard deviation 0.77). In general, waters of small lakes were more acidic than the water in Finnish streams (Lahermo et al. 1995). The water samples of the study region contained between 1.9 and 12 mg/l of total organic carbon, averaging 6.2 mg/l (N=62, std. dev. 2.38). A high humus content is known to indicate increased acidity in Finnish streams and lakes (Lahermo et al. 1995). Temperature values varied from 0 to 12.5°C, averaging 5.7°C (N=111, std. dev. 2.15).

Discussion

Taphonomic pathways

The vigorous dissolution of the shell material in the study region can be studied in a wider perspective. As discussed by Ukkonen (2001), the preservation of post-glacial mammal bones is poor in Finland. This is due to

the acidity of waters and soils, and is typical for most of the country including the study region (Lahermo et al. 1990; Kähkönen 1996). Only a few subfossil bones of terrestrial mammals have been found in Finland (Kurtén 1988; Ukkonen 1993, 2001). Heating by burning due to cooking seems to have considerably improved the preservation of mammal bones from archaeological deposits (Ukkonen 2001). One could therefore expect to find older shell material in a better state of preservation in connection with faunal remains in archaeological sites. Burning is known to decompose the *Margaritifera margaritifera* shells incrementwise (Geist et al. 2005) to such a degree that they may not serve as environmental proxies compared to naturally preserved specimens.

The remains of the river pearl mussels indicate that they went along taphonomic pathways during the transition from the biosphere to lithosphere. It is necessary to model these pathways in order to understand their present distribution and preservation (Fig. 5; Table 4). The modelling must take into account both anthropogenic and natural parameters affecting the preservation potential of shells and periostraca. These parameters are, in particular, lithology (mineralogy, grain size, sorting), local topography and human activity. Acidification of rainwater and groundwater is likely to affect the shells by dissolution and, therefore, the course of these waters may be crucial for shell preservation. The river banks and bars, which consist of coarse-grained and unconsolidated sediment at KOL2 and 4, have a higher porosity and permeability than the soil. The soil at KOL5 is relatively dense and contains a large amount of organic matter including decaying branches, leaves and roots. The organic matter appears to contain humic acids, giving the river water its brownish colour. According to Lahermo et al. (1995), particularly the acid waters in Finnish lakes and streams exhibit elevated colour values, which in turn indicates that the humic matter contributes significantly to water acidity. Organic acids dominate stream water acidity in small lakes and headwater streams in the majority of Finnish catchments (Kortelainen & Saukkonen 1995). Some of these acids are tannins that may be hydrolyzed by weak acids or bases to yield carbohydrate and phenolic acids. Even though the soil may be rich in tannins, the embedded shell material is generally less dis-

Table 3. List of water samples from the river Kolmosjoki and surrounding land areas.

Number	Locality	Water source	Date	pH
4	Upstream from KOL1	River water	Aug. 30, 2005	5.1
5	Upstream from KOL1	River water	Aug. 30, 2005	5.4
2	KOL1	River water	Aug. 30, 2005	5.5
3	KOL1	River water	Aug. 30, 2005	5.3
6	KOL4	Spring water coming up through plant debris on river bar	Aug. 31, 2005	5.4
1	KOL5	River water	Aug. 28, 2005	5.1
7	KOL6	Groundwater from excavation in old river deposits	Aug. 31, 2005	4.7
8	KOL6	River water	Aug. 31, 2005	5.3

Table 3. List of water samples from the Kolmosjoki River and surrounding land areas. The pH values were measured with paper test stickers.

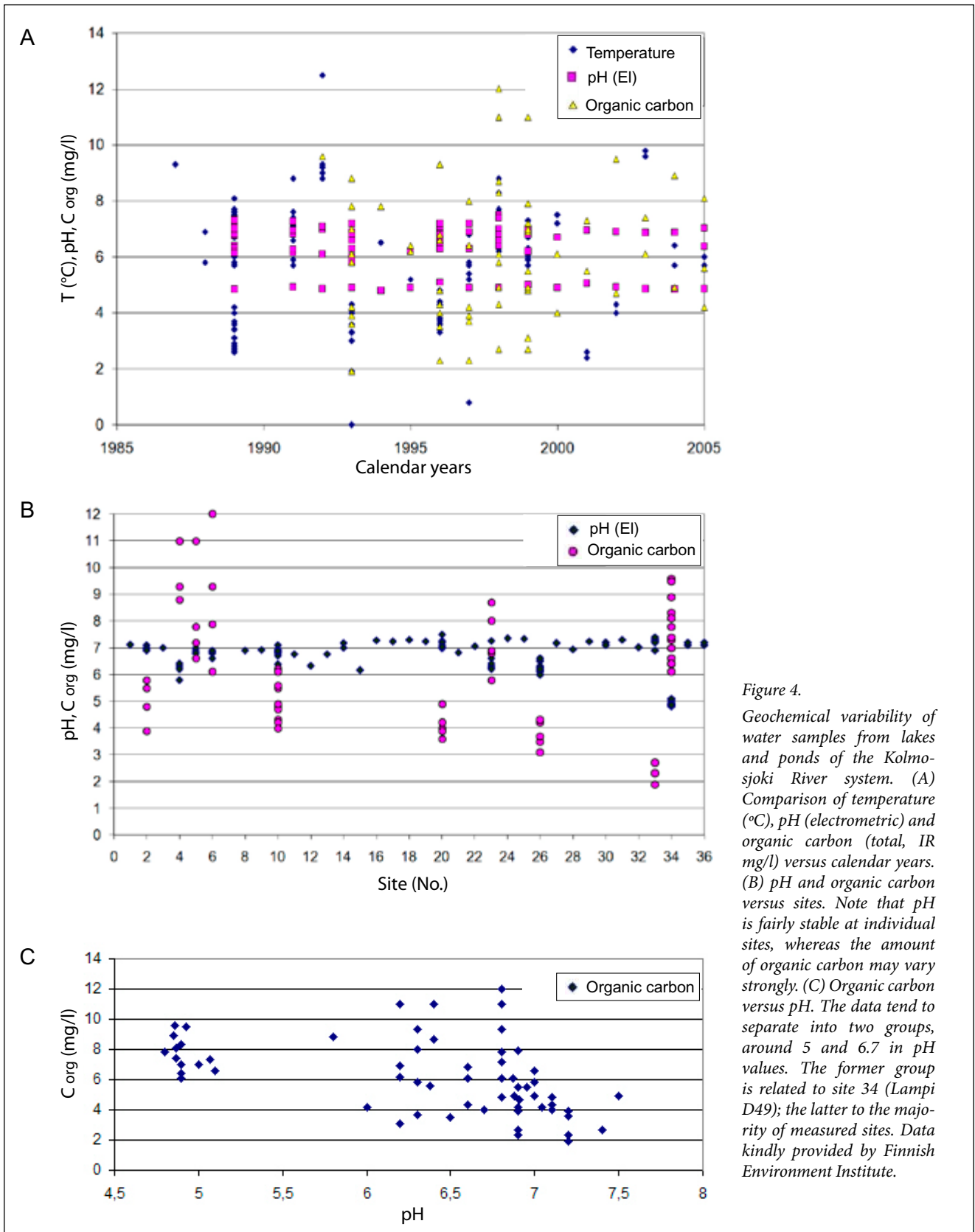


Figure 4. Geochemical variability of water samples from lakes and ponds of the Kolmo-sjoki River system. (A) Comparison of temperature (°C), pH (electrometric) and organic carbon (total, IR mg/l) versus calendar years. (B) pH and organic carbon versus sites. Note that pH is fairly stable at individual sites, whereas the amount of organic carbon may vary strongly. (C) Organic carbon versus pH. The data tend to separate into two groups, around 5 and 6.7 in pH values. The former group is related to site 34 (Lampi D49); the latter to the majority of measured sites. Data kindly provided by Finnish Environment Institute.

solved than in the river deposits. The tannins could have been leached out from the soil into the pore water of the river deposits. Water which penetrated river deposits was probably high because of better permeability and closer to the present river water level.

The sediment at the camp-fire sites KOL1, 3 and 5 is lithologically similar to the glaciofluvial sandy gravel of the local eskers and is coarse-grained like the river deposits. Shells found at these sites were uncovered or only partly covered by the sediment. They show signs of partial dis-

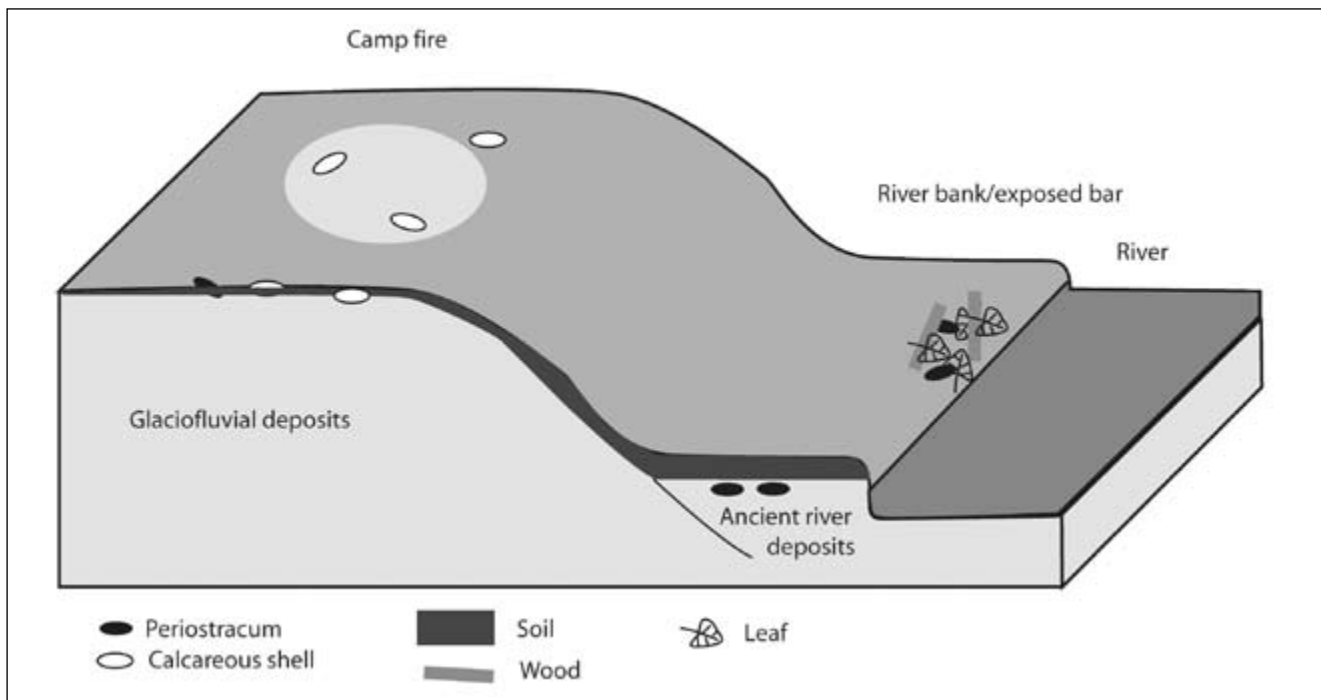


Figure 5. Sketch showing the typical distribution of calcareous shell material and periostraca of *Margaritifera margaritifera* in relation to lithology and topography. The latter may vary, however, between the sites of anthropogenic and natural occurrences. Not to scale.

solution, particularly on outer shell surfaces. The findings at the camp-fire sites rarely included periostracal fragments. As the camp-fire sites are located at topographically higher levels, the shells were probably unaffected by acidic river water. Instead, acidic rainwater is more likely to have caused the minor shell dissolution. These aerial conditions appear to have been unfavourable for the preservation of periostraca. The calcareous shell material shows no signs of burning that could have destroyed the periostraca. In summary, the absence of soil cover appears to reduce the preservation potential of calcareous shells and their periostraca. Podzolization of the mineral soils is a typical soil-forming process in forested areas of Lapland and influences the water chemistry in that the pH of the percolation water gradually increases as it passes down through the eluvial horizon of podzol soil. Kähkönen (1996) studied 90 podzol horizons in Finnish Lapland and found that a median pH of 3.4 (range of 3.0-5.1) in humus-rich organic debris but through the zone of eluviation it rose up to 4.6 (4.1-5.4). Soil may have thus provided better protection against shell dissolution than just coarse-grained sand and

gravel. Greater topographical height above river water level reduces the exposure to the acidic river water.

Differential preservation

Most *Margaritifera margaritifera* shells contain macroscopic evidence of dissolution of their umbos. The dissolution features are present in the shells of live as well as dead mussels (Linné 1806: p. 176; see Knudsen et al. 2003: fig. 1), indicating that the shell material may have been subjected to dissolution on the river floor. Pre-mortem dissolution of the outer shell layer is known to progress as a function of mussel ontogenetic age with a larger umbonal area being dissolved in older specimens (Helama & Valovirta 2007). Similar features commonly occur in aragonitic unionid shells in death assemblages on lake and river bottoms, where the water is unsaturated in aragonite (e.g., Cummins 1994). Smaller (ontogenetically younger) shells are likely to become dissolved in the post-mortem phase more rapidly than larger ones, varying with the size distribution of the shells (e.g., Cummins et al. 1986; Cummins 1994). This may explain the lack of small shells at camp-fire sites along Kolmosjoki River. A

Table 4. Different types of depositional environments that could be linked to differentiated preservation of the shell layers in *Margaritifera margaritifera*

Depositional environment	Periostraca	Prismatic layer	Nacreous layer
Exposed to river water	preserved	not preserved	not preserved
Aerially exposed (partially)	not preserved	preserved	preserved
Soil above groundwater level	preserved	preserved	preserved

Table 4. Different types of depositional environment that could be linked to differentiated preservation of the shell layers in *Margaritifera margaritifera*.

better explanation is probably size selectivity by human pearl hunters, who probably preferentially collected the biggest mussels (Keltikangas 1991; Hastie 2006). The presence of dorso-posterior fractures in many shells (Table 2) suggests the use of a knife to open the shells by cutting adductor muscles (see also Helama et al. 2007). In addition, the musquash (*Ondatra zibethica*), a beaver-like rodent, eats mussels including *M. margaritifera* and leaves piles of shells behind (Keltikangas 1991). The musquash, which was introduced by humans to parts of Europe, shows a preference for shells between 75 and 110 mm in length (Zahner-Meike & Hanson 2001). However, the mussel populations of Kolmosjoki River may also have been non-reproductive and, therefore, did not leave behind any juveniles for a long period of time.

Differential post-mortem preservation of the various shell portions is obvious from the camp-fire sites. In coarse-grained subaerial sites (KOL1, 3, 7), the outer shell layer shows a tendency to become more dissolved than the inner shell layer. Differences in the structural arrangement of crystallites and organic matrix among shell layers may well be the cause of this (e.g., Nielsen 2004). Shells of *Margaritifera margaritifera* consist of two principal aragonitic layers and organic matrix (e.g., Carell et al. 1987; Nyström et al. 1995; Liao et al. 2000). The outer shell layer has a simple prismatic structure, where the prisms (20–50 µm in diameter) are oriented perpendicular to the outer shell surface (Liao et al. 2000). Each prism is enclosed by a comparatively thick, insoluble organic sheet. The prism consists of aciculate crystallites with a feathery arrangement. The inner shell layer consists of nacreous lamellae of aragonitic tablets (1 µm thick); the lamellae are sub-parallel to the shell surface (e.g., Nyström et al. 1995; Liao et al. 2000). Thin sheets of insoluble organic matrix separate the individual lamellae, whereas each tablet is enclosed in a soluble glycol-protein matrix (Liao et al. 2000). Because of the arrangement of crystallites and organic matrix, the inner shell layer of shells from the Kolmosjoki River area appears to be more resistant to dissolution than the outer layer. The nacreous lamellae between the organic sheets are closely spaced and are less soluble than the prismatic layer. Only the large prisms are surrounded by organic sheets (Liao et al. 2000). However, the time factor must also be taken into consideration. The outer shell layer is generally exposed to etching by water for a longer period of time; the umbonal areas are typically dissolved during life. Furthermore, the shells from the camp-fire sites were exposed for shorter periods of time (up to some decades) than those from the ancient river deposits.

Water geochemistry and shell preservation

Taphonomic processes may be different in other geological settings with different water chemistries (e.g., Cummins 1994). Geochemical mapping of groundwater in Finland has been carried out during the last decades and enabled Lahermo et al. (1990) to compile a pH map of Finnish groundwater. This map shows that the ground-

water in northeastern Finland (i.e., the study region) is acidic, which is consistent with the pH measurements of available water samples. Previous studies of dug well waters and springs in the investigated region show pH values of 6.4 and 6.6, respectively. Only minor regions of Finland are characterized by pH values reaching 7.0 for dug well waters and springs. These are located sporadically in northern Finland (see Lahermo et al. 1990). Because acidic groundwater has a deteriorative effect on calcareous shells, we expect that the preservation potential is higher in these regions. The preservation potential of skeletal material is highly variable in freshwater environments where the preservation is dependent on initial water composition, methanogenesis and iron reduction, and to a lesser degree upon sulphate reduction (Canfield & Raiswell 1991). Chemical buffering capacity of freshwater systems is mainly a function of the underlying bedrock (Drever 1982). When the bedrock is non-calcareous, overlying waters may be severely undersaturated with respect to carbonates (e.g., Cummins 1994). These conditions are similar to those found in our study area.

The investigation by Ribi et al. (1986) of the prosobranch snail *Viviparus ater* from Swiss lakes showed that undersaturation with regard to calcium carbonate was the main reason for shell dissolution. Indication of shell repair is also common among snails from Lake Maggiore. Shell damage was augmented by a stony ground surface and wave action. These features were a more likely cause of death than predation (Ribi et al. 1986). Physical damage of river mussels can similarly be related to water currents (Newell et al. 2007); however, our shells of *Margaritifera margaritifera* were mainly found at campfire sites, indicating that the activities of human beings were a possible cause of the fragmentation. Shell dissolution in acidic water has also been reported to be a major cause of mortality in the freshwater bivalve *Corbicula fluminea* (Kat 1982).

Living conditions and reproduction

Populations of river pearl mussels in Ireland require free running nutrient levels and water chemistry with ammonia, nitrate and phosphates below 0.10, 1.7 and 0.06 mg/l, respectively. In particular, acidity should be above pH 6.3 for the mussels to thrive (Moorkens et al. 2000). Similar requirements would be expected for the Finnish populations. The stream bottom water from the Kolmosjoki River gave pH values close to the lower tolerance limit for river pearl mussels (Table 3). Since the stream organic matter consists of mixtures of humic material, plant roots and leaf fragments, together with varying amounts of mineral matter (Bølviken et al. 1983), acidification of the river water by tannin is likely to occur. The Kolmosjoki River is a tributary of the Lutto River, which is a famous pearl mussel river that was dammed up on the Russian side in the 1960s, thus preventing salmon from moving up the stream (Oulasvirta 2006). *Margaritifera margaritifera* needs fish species of the family Salmonidae to host its larvae (glochidia) during metamorphosis. Salmon

(*Salmo salar*) and brown trout (*Salmo trutta*) are consequently important for the reproduction of *Margaritifera* (e.g., Geist et al. 2006; Preston et al. in press). After the fertilized eggs have matured, release and attachment of the glochidial larvae to fish gills is essential for their survival (e.g., Moorkens et al. 2000; Araujo & Ramos 2001; Bondø 2006; Geist et al. 2006). The glochidia, which are microscopic thin-shelled larvae (Harms 1907, 1909; Nezhlin et al. 1994), develop within females for 2-3 months from June and are present in fish gills of known European populations from August (Bauer 1987). The attachment must continue for eight to nine months before the larvae enter the next ontogenetic stage and settle on the river bottom (Bondø 2006). *Margaritifera margaritifera* are common in upper and middle river sections characterized by clean and oligotrophic fast-flowing waters. They live particularly in calcium-poor waters in granitic areas. Juvenile mussels, that is, those less than 50 mm in size, can live completely burrowed in stable substrates (e.g., Chesney et al. 1993; Araujo & Ramos 2001). Young mussels depend on the supply of plant detritus, which consists of small particles entering the waters by underground transport processes. In this way, plant detritus enters the river water from its surroundings and serves as food for the mussels (Hruska 1999). Clean gravel and sand are essential for a healthy population in order to avoid silt clogging the gills (Moorkens 1999). Younger mussels were recently found in five tributaries of the Lutto River system (Oulasvirta 2006).

Past distribution of river pearl mussels

During past centuries, *M. margaritifera* has declined due to anthropogenic influences on aquatic systems and their surroundings. These include dredging, eutrophication, river regulations, farming, water pollution, deforestation, log floating and the introduction of exotic fish (e.g., Valovirta & Yrjänä 1996; Araujo & Ramos 2001). Deforestation and river regulations result in a significant increase in river sedimentation. Soil and nutrients are lost through runoff and lead to subsequent eutrophication and silting up of the river. This affects fish breeding areas as well as the mussels. In addition, overfishing for pearls is particularly responsible for the decline of populations in European rivers (e.g., Hessling 1859; Boettger 1954). Therefore, comparison of present and ancient distributions is not directly possible.

The fossil and subfossil occurrences of the shells are not only dependent on past water quality, but also on the availability of reproduction hosts. As populations of river pearl mussels reflect a favourable coincidence of environmental and ecological parameters, absence of their shells in ancient deposits within a particular area must be interpreted with caution. Prediction of the distribution of fossil and subfossil river pearl mussels is closely dependent on reproductive conditions and anthropogenic activity, as well as pre-sedimentary to post-sedimentary dissolution (Fig. 3).

Conclusions

This study predicts where to find calcareous shells and periostraca of freshwater mussels. It also shows the taphonomic pathways the mussels followed in their transition from biosphere to lithosphere. The preservation potential is dependent upon various physical, chemical and biological parameters. In particular, the acidity of the rainwater, river water and groundwater had a major affect on the calcareous shell material. The acidity is related to the geochemistry of local bedrock and basement rocks as well as leaching of tannins from the soil into the waters. The outer shell layer is the layer most likely to dissolve, the periostracum less so; this leads to differential preservation of the shell layers. In past centuries, pearl hunters distributed mussel remains in the vicinity of elevated camp-fires. Here, the calcareous shells are generally more likely to be preserved because of a soil cover. Further search for ancient shells of *Margaritifera margaritifera* should consider the past topography, lithology, residence time of acidic water, the presence of salmonid hosts for its larvae and anthropogenic activities.

Acknowledgements

The Carlsberg Foundation kindly provided the senior author with a postdoctoral scholarship (No. 04-0256/20). The work of SH was made possible by a postdoctoral scholarship from the Koneen Säätiö Foundation. Financial support was also provided by the Department of Geology at the University of Tromsø, for JeKN. The fieldwork was partially supported by the German Research Foundation (DFG).

We are also thankful for the hydrochemical data kindly provided by the Finnish Environment Institute. The shell samples were collected under license from The Lapland Regional Environment Centre (LREC). Stephen K. Donovan and Martin Zuschin kindly reviewed the manuscript and provided constructive comments.

References

- Ansell, A.D. 1968: The rate of growth of the hard clam *Mercenaria mercenaria* (L) throughout the geographic range. *Journal du Conseil Permanent International pour l'Exploration de la Mer* 31, 364-409.
- Araujo, R. & Ramos, M.Á. 2001: Action plans for *Margaritifera auricularia* and *Margaritifera margaritifera* in Europe. In: Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention), Council of Europe Publishing. *Nature and Environment* 117, 1-64.
- Bauer, G. 1987: Reproductive strategy of the freshwater pearl mussel *Margaritifera margaritifera*. *Journal of Animal Ecology* 56, 691-704.
- Bauer, G. 1992: Variation in the life span and size of the freshwater pearl mussel. *Journal of Animal Ecology* 61, 425-436.
- Boettger, C.R. 1954: Flussperlmuschel und Perlenfischerei in der Lüneburger Heide. *Abhandlungen der Braunschweigischen Wissenschaftlichen Gesellschaft* 6, 1-40.
- Bondø, T.-H. 2006: Perlen forsvinner. *VG Helg*, 1st April 2006, 48-49.
- Bølviken, B., Bergström, J., Björklund, A., Konti, M., Lehmuspelto, P., Lindholm, T., Magnusson, J., Otteson, R.T., Steenfelt, A. & Volden, T. 1983: Geochemical Atlas of Northern Fennoscandia. Nordkalott Project, NGU-SGU-GTK 1980-1986, 19 pp., 155 maps.
- Canfield, D.E., & Raiswell, R. 1991: Pyrite formation and fossil preservation. In: Allison, P.A. & Briggs, D.E.G. (eds.): *Taphonomy: Release*

- ing the data Locked in the Fossil Record, 337–387. Plenum Press, New York.
- Carell, B., Forberg, S., Grundelius, E., Henrikson, L., Johnels, A., Lindh, U., Mutvei, H., Olsson, M., Svardström, K. & Westermark, T. 1987: Can mussel shells reveal environmental history? *Ambio* 16, 2–10.
- Chesney, H.C.G., Oliver, P.G. & Davis, G.M. 1993: *Margaritifera durrovensis* Phillips, 1928: Taxonomic status, ecology and conservation. *Journal of Conchology* 34, 267–299.
- Cummins, R.H. 1994: Taphonomic processes in modern freshwater molluscan death assemblages: Implications for the freshwater fossil record. *Palaeogeography, Palaeoclimatology, Palaeoecology* 108, 55–73.
- Cummins, H., Powell, E.N., Stanton, R.J. Jr., & Staff, G. 1986: The size-frequency distribution in palaeoecology; Effects of taphonomic processes during formation of molluscan death assemblages in Texas bays. *Palaeontology* 29, 495–518.
- Davenport, C.B. 1938: Growth lines in fossil pectens as indicators of past climates. *Journal of Paleontology* 12, 514–515.
- Drever, J.I. 1982: The Geochemistry of Natural Waters. Prentice-Hall, Inc., Englewood Cliffs New Jersey, 388 pp.
- Flessa, K.W., Cutler, A.H. & Meldahl, K.H. 1993: Time and taphonomy: quantitative estimates of time-averaging and stratigraphic disorder in a shallow marine habitat. *Paleobiology* 19, 266–286.
- Geist, J., Auerswald, K. & Boom, A. 2005: Stable carbon isotopes in freshwater mussel shells: Environmental record or marker for metabolic activity? *Geochimica et Cosmochimica Acta* 69, 3545–3554.
- Geist, J., Porkka, M. & Kuehn, R. 2006: The status of host fish populations and fish species richness in European freshwater pearl mussel (*Margaritifera margaritifera*) streams. *Aquatic Conservation: Marine and Freshwater Ecosystems* 16, 251–266. DOI: 10.1002/aqc.721.
- Goodwin, D.H., Flessa, K.W., Schöne, B.R. & Dettman, D.L. 2001: Cross-calibration of daily growth increments, stable isotope variation, and temperature in the Gulf of California bivalve mollusc *Chione cortezi*: Implications for paleoenvironmental analysis. *Palaios* 16, 387–398.
- Hallman, D.P., Flessa, K.W., Kowalewski, M., Hertweck, G., Aggen, J. & Carlton, J. 1996: Ternary taphograms and the comparative taphonomy of recent mollusks from the North Sea and the Gulf of California. *Senckenbergiana Maritima* 27, 67–75.
- Harms, W. 1907: Zur Biologie und Entwicklungsgeschichte der Flussperlmuschel (*Margaritana margaritifera* Dupuy). *Zoologischer Anzeiger* 31, 814–824.
- Harms, W. 1909: Postembryonale Entwicklungsgeschichte der Unio-niden. *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere* 28, 325–386.
- Hastie, L.C. 2006: Determination of mortality in exploited freshwater pearl mussel (*Margaritifera margaritifera*) populations. *Fisheries Research* 80, 305–311.
- Helama, S. & Valovirta, I. 2007: Shell morphometry, pre-mortal taphonomy and ontogeny-related growth characteristics of freshwater pearl mussels in northern Finland. *Annales Zoologici Fennici* 44, 285–302.
- Helama, S. & Valovirta, I. 2008: The oldest recorded animal in Finland: Ontogenetic age and growth in *Margaritifera margaritifera* (L. 1758) based on internal shell increments. *Memoranda Societatis pro Fauna et Flora Fennica* 84, 20–30.
- Helama, S., Nielsen, Jan K. & Valovirta, I. 2007: Conchology of endangered freshwater pearl mussel: Conservational palaeobiology applied to museum shells originating from northern Finland. *Bollettino Malacologico* 43, 161–170.
- Helama, S., Schöne, B.R., Black, B.A. & Dunca, E. 2006: Constructing long-term proxy series for aquatic environments with absolute dating control using a sclerochronological approach: Introduction and advanced applications. *Marine and Freshwater Research* 57, 591–599.
- Hessling, T. von 1859: Die Perlmuscheln und ihre Perlen (Naturwissenschaften und geschichtlich mit Berücksichtigung der Perlgewässer Bärns). Leipzig, 372 pp.
- Hruska, J. 1999: Nahrungsansprüche der Flussperlmuschel und deren halbnatürliche Aufzucht in der Tschechischen Republik. *Heldia* 4(6), 69–79.
- Johansson, P. 1988: Deglaciation pattern and ice-dammed lakes along the Saariselkä mountain range in northeastern Finland. *Boreas* 17, 541–552.
- Johansson, P. 1995: The deglaciation in the eastern part of the Weichselian ice divide in Finnish Lapland. *Geological Survey of Finland, Bulletin* 383, 1–72.
- Jones, D.S. 1980: Annual cycle of shell growth increment formation in two continental shelf bivalves and its paleoecologic significance. *Paleobiology* 6, 331–340.
- Jones, D.S. 1983: Sclerochronology: Reading the record of the molluscan shell. *American Scientist* 71, 384–391.
- Kähkönen, A.-M. 1996: The geochemistry of podzol soils and their relation to lake-water chemistry, Finnish Lapland. *Geological Survey of Finland, Bulletin* 385, 1–89.
- Kat, P.W. 1982: Shell dissolution as a significant cause of mortality for *Corbicula fluminea* (Bivalvia: Corbiculidae) inhabiting acidic waters. *Malacological Review* 15, 129–134.
- Keltikangas, V. 1991: Seitsemän tuntia erämaata ja muita kertomuksia. Werner Söderström Osakeyhtiö, Porvoo-Helsinki-Juva, 292 pp.
- Kennish, M.J. & Olsson, R.K. 1975: Effects of thermal discharges on the microstructural growth of *Mercenaria mercenaria*. *Environmental Geology* 1, 41–64.
- Knudsen, J., Jensen, K.R., Nielsen, C. & Johnson, R.I. 2003: Lorentz Spengler's descriptions of freshwater mussels (Mollusca: Unionacea): translation and notes. *Steenstrupia* 27, 263–279.
- Kortelainen, P. & Saukkonen, S. 1995: Organic vs. minerogenic acidity in headwater streams in Finland. *Water, Air and Soil Pollution* 85, 559–564.
- Kowalewski, M., Flessa, K.W. & Hallman, D.P. 1995: Ternary taphograms: Triangular diagrams applied to taphonomic analysis. *Palaios* 10, 478–483.
- Kurtén, B. 1988: Fossil and subfossil mammals in Finland. *Memoranda Societatis pro Fauna et Flora Fennica* 64, 35–39.
- Lahermo, P., Ilmasti, M., Juntunen, R. & Taka, M. 1990: Suomen geokemian atlas, osa 1. Suomen pohjavesien hydrogeokemiallinen kartoitus. The Geochemical Atlas of Finland, Part 1. The Hydrogeochemical mapping of Finnish groundwater. Geological Survey of Finland, Espoo, 66 pp.
- Lahermo, P., Mannio, J. & Tarvainen, T. 1995: The hydrogeochemical comparison of streams and lakes in Finland. *Applied Geochemistry* 10, 45–64.
- Liao, H., Mutvei, H., Sjöström, M., Hammarström, L. & Li, J. 2000: Tissue responses to natural aragonite (*Margaritifera* shell) implants in vivo. *Biomaterials* 21, 457–468.
- Linné, C. von 1806. A general system of nature through the three grand kingdoms of animals, vegetables, and minerals, systematically divided into their several classes, orders, genera, species, and varieties, with their habitations, manners, economy, structure, and peculiarities. Vol. 4, worms. Translated and extended edition by W. Turton from Caroli Linnaei Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Editio decima tertia, aucta, reformata (Gmelin, J.F., ed., 1791). Lackington, Allen and Co., London.
- Marchitto, T.M., Jones, G.A., Goodfriend, G.A. & Weidman, C.R. 2000: Precise temporal correlation of Holocene mollusc shells using sclerochronology. *Quaternary Research* 53, 236–246.
- Marsden, I.D., & Pilkington, R.M. 1995: Spatial and temporal variations in the condition of *Austrovenus stutchburyi* Finlay, 1927 (Bivalvia: Veneridae) from the Avon-Heathcote Estuary, Christchurch. *New Zealand Natural Sciences* 22, 57–67.
- Meriläinen, K. 1976: The granulite complex and adjacent rocks in Lapland, northern Finland. *Geological Survey of Finland, Bulletin* 281, 1–129.
- Moorkens, E.A. 1999: Conservation management of the freshwater pearl mussel *Margaritifera margaritifera*. Part 1: Biology of the spe-

- cies and its present situation in Ireland. Irish Wildlife Manuals, No. 8. Dúchas, The Heritage Service, Dublin, 34 pp.
- Moorkens, E.A., Valovirta, I. & Speight, M.C.D. 2000: Towards a margaritifera water quality standard. Convention on the conservation of European wildlife and natural habitats. *Council of Europe, T-PVS/invertebrates 2000 (2)*, 1-14.
- Mutvei, H. 1996: Musselskal som miljökarkiv. *Fauna och Flora 1996 (5/6)*, 39-42.
- Mutvei, H., Dunca, E., Timm, H. & Slepukhina, T. 1996: Structure and growth rates of bivalve shells as indicators of environmental changes and pollution. *Bulletin de l'Institut océanographique, Monaco, n° special 14*, 65-72.
- Mutvei, H., Westermark, T., Dunca, E., Carell, B., Forberg, S. & Bignert, A. 1994: Methods for the study of environmental changes using the structural and chemical information in molluscan shells. *Bulletin de l'Institut océanographique, Monaco, n° special 13*, 163-186.
- Navarro, J.M. 1988: The effects of salinity on the physiological ecology of *Choromytilus chorus* (Molina, 1782) (Bivalvia: Mytilidae). *Journal of Experimental Marine Biology and Ecology 122*, 19-34.
- Nebelsick, J.H. 1999: Taphonomy of *Clypeaster* fragments: Preservation and taphofacies. *Lethaia 32*, 241-252.
- Nebelsick, J.H. & Kowalewski, M. 1999: Drilling predation on recent clypeasteroid echinoids from the Red Sea. *Palaios 14*, 127-144.
- Newell, A.J., Gower, D.J., Benton, M.J. & Tverdokhlebov, V.P. 2007: Bedload abrasion and the in situ fragmentation of bivalve shells. *Sedimentology 54*, 835-845.
- Nezlin, L.P., Cunjak, R.A., Zotin, A.A. & Ziuganov, V.V. 1994: Glochidium morphology of the freshwater pearl mussel (*Margaritifera margaritifera*) and glochidiosis of Atlantic salmon (*Salmo salar*): A study by scanning electron microscopy. *Canadian Journal of Zoology 72*, 15-21.
- Nielsen, J.K. 2004: Taphonomy in the light of intrinsic shell properties and life habits: Marine bivalves from the Eemian of northern Russia. *Paläontologische Zeitschrift 78*, 53-72.
- Nielsen, J.K. & Funder, S. 2003: Taphonomy of Eemian marine molluscs and acorn barnacles from eastern Arkhangelsk region, northern Russia. *Palaeogeography, Palaeoclimatology, Palaeoecology 191*, 139-168.
- Nyström, J., Lindh, U., Dunca, E. & Mutvei, H. 1995: A study of *Margaritifera margaritifera* shells from the river Pauliströmsån, Sweden. *Nuclear Instruments and Methods in Physics Research Section B, 104*, 612-618.
- Oulasvirta, P. 2006: Kysymyksiä ja vastauksia – ja lisää kysymyksiä. In Oulasvirta, P. (ed.) Pohjoisten virtojen raakat. Interreg-kartoitus-hanke Itä-Inarissa, Norjassa ja Venäjällä. Metsähallitus. pp. 124-135.
- Penttilä, S. 1963: The deglaciation of the Laanila area, Finnish Lapland. *Bulletin de la Commission Géologique de Finlande 203*, 1-71.
- Preston, S.J., Keys, A. & Roberts, D. in press: Culturing freshwater pearl mussel *Margaritifera margaritifera*: A breakthrough in the conservation of an endangered species. *Aquatic Conservation: Marine and Freshwater Ecosystems*.
- Ribi, G., Mutzner, A. & Gebhardt, M. 1986: Shell dissolution and mortality in the freshwater snail *Viviparus ater*. *Schweizerische Zeitschrift für Hydrologie 48*, 34-42.
- Saarnisto, M. 1973: Contributions to the late-Quaternary history of the Lutto river valley, Finnish Lapland. *Commentationes physico-mathematicae 43*, 11-20.
- Sorsa, P. 1965. Pollenanalytische Untersuchungen zur spätquartären Vegetations- und Klimaentwicklung im östlichen Nordfinland. *Annales Botanici Fennici 2*, 301-413.
- Synge, F.M. 1969. The raised shorelines and deglaciation chronology of Inari, Finland and South Varanger, Norway. *Geografiska Annaler 51 A*, 193-206.
- Tanner, V. 1936: Det senglaciala havets utbredning i Lutto och Suomu älvars dalgångar ovanför sammanflödet samt några ord om morfologin i denna trakt. Résumé: L'extension de la mer sen-glaciaire dans les vallées des rivières Lutto et Suomu en Laponie en amont de leur confluent. *Bulletin de la Commission Géologique de Finlande 115*, 107-119.
- Ukkonen, P. 1993: The post-glacial history of the Finnish mammalian fauna. *Annales Zoologici Fennici 30*, 249-264.
- Ukkonen, P. 2001: Shaped by the Ice Age: Reconstructing the history of mammals in Finland during the Late Pleistocene and Early Holocene. Doctoral dissertation, University of Helsinki, 111 pp.
- Valovirta, I. & Yrjänä, T. 1996: Effects of restoration of salmon rivers on the mussel *Margaritifera margaritifera* (L.) in Finland. In: Convention on the conservation of European wildlife and natural habitats. Colloquium on Conservation, Management and Restoration of Habitats for Invertebrates: Enhancing Biological Diversity. Killarney, Ireland, 26-29 May 1996. Council of Europe, T-PVS (96) 51, 38-48.
- Zahner-Meike, E. & Hanson, J. M. 2001. Effect of muskrat predation on naiads. *Ecological Studies 145*, 163-184.
- Ziuganov, V., San Miguel, E., Neves, R.J., Longa, A., Fernández, C., Amaro, R., Beletsky, V., Popkovitch, E., Kaliuzhin, S. & Johnson, T. 2000: Life span variation of the freshwater pearl shell: A model species for testing longevity mechanisms in animals. *Ambio 29*, 102-105.