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New distributional data on 'glacial relict' crustaceans

Risto Väinölä & Henrik Rockas

Department of Genetics, University of Helsinki, Arkadiankatu 7, SF-00100 Helsinki, Finland

Earlier reviews on the distribution of the crustaceans *Mysis relicta*, *Pallasea quadrispinosa*, *Pontoporeia affinis*, *Gammaracanthus lacustris* and *Limnocalanus macrurus* in Finnish lakes are supplemented with 180 new records, mostly from our field work in 1985–1988. These include records of *M. relicta* and *L. macrurus* from Lake Koitere, situated above the highest ancient Baltic shoreline in eastern Finland. The present distribution of *G. lacustris*, classified as a species in need of monitoring, is reviewed. Some notes on the distribution of these crustaceans outside Finland are also given.

1. Introduction

The information on the occurrence of the crustaceans *Mysis relicta*, *Pallasea quadrispinosa*, *Pontoporeia affinis*, *Gammaracanthus lacustris* and *Limnocalanus macrurus* in Finnish lakes has earlier been summarized by Jägerskiöld (1912) and Segerstråle (1956a); Särkkä (1976) contributed new information and reviewed the data from the Kymijoki drainage area. Here, we continue the tradition of recording the present state of knowledge of the distribution of these animals, once regarded as peculiar and recent remnants of an arctic marine fauna which was supposed to have invaded the Fennoscandian lowlands in early postglacial times. Although the ideas of 'ishafsdjur' or 'marin-glazialen Relikte' have had to give way to new views on the evolutionary origin, dispersal history and ecological requirements of these species (Segerstråle 1957, Holmquist 1966, Dadswell 1974, Väinölä 1986), the concept that their distribution was determined by the late- and postglacial lentic (standing-water) connections survives. In Finland, this is equivalent to their range being restricted to areas once covered by the waters of the ancient phases of the Baltic Sea. Subsequent changes in distribution have been caused by local extinctions and dispersal downstream.

Among the new observations reported here is one from above the highest ancient Baltic coastline, which seems to challenge the current views on the colonization history of the crustaceans in Finland.

2. Material and methods

The majority of the data were obtained in connection with our field work in 1985–1988. Ninety-nine freshwater localities in Finland were visited; these included lakes already known to harbour these crustaceans and waters from which no previous information was available. The nine sites studied within the Iso-Saimaa lake complex (76 m above sea level) are not counted as separate lakes in this report, in contrast to some other similarly connected basins (e.g. Kallavesi-Suvasvesi). Some lakes in Sweden were also studied.

The peracaridan species were mainly sampled with a beam trawl (e.g. Fürst 1981) or a sled net, towed slowly along the bottom. The trawl could be adjusted to avoid or to allow the catching of bottom sediment in the sample. Several 5–10 min tows were usually made both in the deepest part of the lake and in shallower areas, up to 2–5 m. Midwater trawling was also occasionally performed. Sampling was primarily done during the afternoon hours in July–August. The records were made on live specimens in the field.

The sampling intensity varied greatly between lakes; the distribution of the animals in relation to depth and to the sediment surface was also found to vary considerably. Therefore, the value of negative observations as indicating possible absence or rarity of a species is not the same for different localities, and the data should not be taken as a complete account of the presence or absence of the species examined.

Limnocalanus macrurus was sampled using a dip net of mesh size 0.5 mm, with 1–2 vertical or oblique tows in the deepest part of the lake. A subsample was preserved and screened later for (adult) *L. macrurus* under a microscope. Tows were not made in all lakes; negative finds in the lakes studied are also indicated in Table 1.

In addition to our own results, some data were gathered from publications, but no systematic search of the literature was carried out. Some records were obtained from the collections of the Zoological Museum of the University of Helsinki, and as personal communications. Some of the new localities listed without references may also earlier have been noted by others, and resampled by us.

3. Results

3.1. New records from Finnish lakes

Table 1 gives an account of the new finds of the five crustacean species in Finnish freshwater localities; the list supplements the data given in Segerstråle (1956a) and Särkkä (1976). Altogether 180 new records are given, yielding a 55% increase in the number reported in the cited reviews (45–77% for the individual species). Fifty-six of the 86 sites in Table 1 are new 'relict' localities (none of the species listed in the earlier reviews).

All our own records of *Mysis relicta* in Table 1 refer to the species which we have earlier provisionally designated *M. relicta I*. A closely related species (*M. relicta II*) coexists with *M. relicta I* in the Baltic Sea; the electrophoretic diagnosis of these sibling species and their distribution in the Baltic were described in Väinölä (1986).

Another *Mysis* population which was not included in the earlier reviews, or in Table 1 here, is that of Lake Pulmankijärvi (Utsjoki) in northernmost Finland, first discovered by Toivonen (1966). The lake has been isolated from the Barents Sea, and the population bears no late-glacial zoogeographical relationship to those isolated from the Baltic. The population (designated *M. relicta III*) proved to be specifically distinct from all other Fennoscandian populations (Väinölä 1986).

3.2. Other observations

The distribution of 'relict' crustaceans in Sweden was summarised by Ekman (1940), and further observations were compiled in the maps of Holmquist (1966); the expansion of distribution due to artificial introductions has been reviewed by Fürst (1981). Recently, Kinsten (1986) conducted a survey of 70 lakes, in which a number of new records were made. Our data from the province of Södermanland include additional records from Klämmingen (*P.q.*, *P.a.*), Södra Yngern (*P.q.*), Yngaren (*M.r.*, *P.q.*), and Båven (*P.a.*, *P.q.*,; in this lake, two species of *Mysis* have been found — see Väinölä 1986). *P. affinis* was also found in Hunn in Östergötland (*M.r.* and *P.q.* were recorded here by Kinsten).

Table 1. New records of 'glacial relict' crustaceans in Finnish lakes. Mr, Pq, Pa, Gl, and Lm refer to new records of the species *Mysis relicta l, Pallasea quadrispinosa, Pontoporeia affinis, Gammaracanthus lacustris* and *Limnocalanus macrurus*, respectively; (Mq) to earlier records of *Myoxocephalus quadricornis*. Other symbols: + species recorded earlier and refound in 1985–1988; x recorded earlier, not refound; – *L. macrurus* not present in a zooplankton sample.

Drainage Lake (commune)	Records Mr	Pq	Pa	Gl	Lm[1]	(Mq)
Jänisjoki						
Ylinen (Kiihtelysvaara)	Mr	Pq			Lm	
Kiteenjoki						
Iso Heinäjärvi (Kitee)	+	+	Pa		–	
Hiitolanjoki						
Torsa (Rautjärvi)	Mr	Pq	Pa			
Vuoksi						
Korpijärvi (Mäntyharju)	Mr	Pq			Lm	
Virmajärvi (Savitaipale)	Mr	Pq			Lm	
Kuolimo (Suomenniemi)	Mr	Pq	+		Lm	
Syysjärvi (Mikkeli mlk)	Mr	Pq	Pa			
Saarijärvi (Mikkeli mlk)	Mr				–	
Nurmijärvi (Rautjärvi)	Mr	Pq			–	
Kärinkijärvi (Ruokolahti)	+	Pq	Pa			
Immalanjärvi (Imatra)	Mr	Pq	Pa		Lm	
Kermajärvi (Heinävesi)	Mr	Pq	Pa	Gl	x	
Suvasvesi (Vehmersalmi)	Mr	Pq	Pa	Gl		
Kaltimojärvi (Eno)	Mr	Pq			Lm	
Viinijärvi (Liperi)	+	Pq	+		x	
Pyhäjärvi (Uukuniemi)	+	Pq	Pa			
Pielinen (Lieksa)	+	Pq			Lm	
Jeronjärvi (Lieksa)	Mr	Pq			Lm	
Salahminjärvi (Vieremä)	+	Pq			Lm	
Rytkynjärvi (Kiuruvesi)	Mr				x–	
Sulkavanjärvi (Kiuruvesi)	Mr				x–	
Juurusvesi (Siilinjärvi)	Mr	Pq	Pa	Gl	Lm	
Ala-Siikajärvi (Nilsiä)	Mr				Lm	
Syväri (Nilsiä)	Mr					
Sälevä (Varpaisjärvi)	Mr					
Juojärvi (Tuusniemi)	Mr	Pq	Pa		Lm	
Rikkavesi (Tuusniemi)	Mr	Pq	Pa			
Koitere (Ilomantsi)	Mr				Lm	
Kymijoki						
Isojärvi (Kuhmoinen)	Mr	Pq	Pa	Gl	Lm	(Mq)
Leppävesi (Laukaa)	Mr	+	x		Lm[3]	
Kuusvesi (Laukaa)	Mr	x	x		Lm[3]	
Kangasjärvi[4] (Saarijärvi)		Pq				
Naarajärvi (Äänekoski)	Mr	Pq				
Pyhäjärvi (Saarijärvi)	+	Pq	Pa			
Summasjärvi (Saarijärvi)	+	Pq				
Mahlunjärvi (Saarijärvi)	Mr					
Iso Löytänä (Saarijärvi)	+	Pq				
Niinivesi (Rautalampi)	Mr					(Mq)
Vuohijärvi (Valkeala)	Mr	Pq		Gl	Lm	
Puulavesi (Hirvensalmi)	Mr	+	+	+	+	
Kyyvesi (Haukivuori)	Mr				Lm	
Siuntionjoki						
Velskolan Pitkäjärvi[5] (Espoo)		Pq				
Karjaanjoki						
Oinasjärvi[6] (Somero)	Mr	Pq				
Fiskarsinjoki						
Iso Simi[6] (Pohja)	Mr		Pa			
Paimionjoki						
Somerojärvi[7] (Somero)	Mr	Pq				
Kokemäenjoki						
Ahvenusjärvi[4] (Mouhijärvi)	Mr					
Näsijärvi (Tampere)	Mr	Pq	Pa	Gl	+	(Mq)
Ruovesi (Ruovesi)	Mr	Pq	Pa	Gl	Lm	
Kielekänjärvi[4] (Orivesi)		Pq				
Toisvesi (Virrat)	Mr	Pq	Pa	Gl	Lm	
Ähtärinjärvi (Ähtäri)	Mr				Lm	
Kyrösjärvi (Ikaalinen)	Mr	Pq			Lm	
Aurejärvi (Kuru)	Mr				–	
Ukonselkä (Vilppula)	Mr	Pq			Lm[8]	
Valkeinen[4] (Multia)		Pq				
Herajärvi[9] (Kuorevesi)		Pq				
Längelmävesi (Orivesi)	Mr	Pq	Pa		x	
Muhujärvi[2] (Juupajoki)	x	Pq	Pa			
Iso Roinevesi (Hauho)	Mr	Pq	+		Lm	
Kukkiajärvi (Luopioinen)	Mr	Pq	Pa		Lm	
Vesijako (Padasjoki)	Mr	Pq			Lm	
Kellola spring (Koski Hl)		Pq				
Ali-Mylly[4] (Loppi)		Pq				
Vähä-Melkutin[4] (Loppi)		Pq				
Särkijärvi[4] (Loppi)		Pq				
Isojoki						
Paattikorpi spring[10] (Isojoki)		Pq				
Ähtävänjoki						
Lappajärvi (Lappajärvi)	+	+	Pa		–	
Oulujoki						
Iso Pyhäntä (Ristijärvi)	Mr	Pq				
Jormasjärvi (Sotkamo)	Mr	Pq			–	
Kiantajärvi (Sotkamo)	Mr	Pq	Pa		Lm	
Kalliojärvi (Sotkamo)	Mr				–	
Iijoki						
Jaurakkajärvi[11] (Pudasjärvi)		Pq	Pa			
Iinattijärvi[11] (Pudasjärvi)		Pq				
Pudasjärvi[11] (Pudasjärvi)		Pq				
Kemijoki						
Kemijärvi[12] (Kemijärvi)	Mr	Pq	Pa		Lm	
Sonkajärvi[13] (Rovaniemi mlk)	x		Pa			
Sinettäjärvi[13] (Rovaniemi mlk)		Pq	Pa			
Vanttausjärvi[13] (Rovaniemi mlk)		Mr		Pa		
Tornionjoki						
Vietonen[13] (Ylitornio)		Pq	Pa			
Miekojärvi[13] (Ylitornio)	x	Pq	Pa			

1) In addition to the localities noted in this column, *L. macrurus* was recorded from the following lakes, from which other species were also previously known: Simpelejärvi (Parikkala), Peurunka (Laukaa), Kivijärvi (Kivijärvi), Hauhanjärvi (Luhanka) and Suontienselkä (Suonenjoki). It has also been reported (Granberg & Hakkari 1987) from Vatianjärvi (Laukaa). — 2) Segerstråle 1956b. — 3) Granberg & Hakkari 1977. — 4) Meriläinen & Hynynen 1989 and pers. comm. — 5) HM (Zoological Museum, University of Helsinki), leg. S.Segerstråle 1959. — 6) L. Koli, pers. comm. — 7) HM, leg. T. Valtonen 1968. — 8) Veijola 1983. — 9) HM, leg. J. Toivonen 1962. — 10) E. Koskenniemi, pers. comm. — 11) Haverinen 1956. — 12) Sormunen 1964. — 13) Viitala 1985.

In this connection we may note that *P. affinis* no longer seems to be present at most of its marginal southern and southwestern localities outside the main Fennoscandian range. We did not find it in 1986 in Denmark (Furesø) or SW Norway (Orrevatn and the adjacent Horpestadvatn; Frøylandsvatn was not visited). The species is probably also extinct in all the lakes where it was earlier found in Germany (Waterstraat 1988) and Poland (Żmudziński 1990). Other 'relict' crustaceans are still thriving in these areas. On the other hand, in Lithuania *P. affinis* has been found in two lakes in the 1970s; *M. relicta, P. quadrispinosa* and *L. macrurus* were reported from 15, 43 and 13 lakes, respectively (Grigelis 1977, 1980).

4. Discussion

In the light of the data accumulated so far, there is little unexpected in most of the new records in Table 1; the crustaceans have been found to be regularly present in most relatively deep lakes in the area once submerged by the waters of the Baltic basin (cf. Segerstråle 1956a, Särkkä 1976). The majority of sites visited by us were also fairly large and deep basins. However, the new *P. quadrispinosa* localities also include two springs (E. Koskenniemi and H. Salemaa, pers. comm.; another spring locality was described by Segerstråle 1958) and some rather small forest lakes (Meriläinen & Hynynen 1989).

4.1. Lake Koitere, above the highest ancient Baltic shoreline

The zoogeographically most intriguing new site is Lake Koitere (143 m above sea level) in eastern Finland, where both *M. relicta* and *L. macrurus* were encountered. The lake lies 20–30 m above the local highest Baltic shoreline, which dates back to the Yoldia phase, about 10 000 years ago (Hyvärinen 1966, 1971). Thus, according to the hypothesis of lentic and downstream dispersal only, the crustaceans cannot have entered Koitere directly from the main Baltic basin.

Shortly before the deglaciation of the Koitere basin, contemporaneously with the formation of the Salpausselkä ridges, a rather large local ice lake (the Ilomantsi Ice Lake) existed in the area south of Koitere, lying parallel with the Baltic Ice Lake and some 30–40 m higher than its level (Hyvärinen 1971, Vesajoki et al. 1986). Since the ice receded northwest and the Ilomantsi Ice Lake was drained, the waters from the area once covered by it could enter the Koitere basin (e.g. Eronen and Vesajoki 1988).Thus Koitere could have obtained its 'relict' populations from the Ilomantsi Ice Lake, provided they were present there. However, this would only move the problem one step further back in time.

There has recently been a revival of the idea of an early recession and a subsequent major readvance of the ice-sheet to the Salpausselkä I position, before the final deglaciation of the lake district (Rainio 1985); this might be thought to have caused a sluicing-up (cf. Segerstråle 1957) of the crustaceans to the supra-Baltic area. However, according to Eronen & Vesajoki (1988), the glacier oscillation probably did not affect the Ilomantsi region, and this mode of invasion from the Baltic basin thus seems unlikely. This raises the question whether the crustaceans could have reached the Ilomantsi Ice Lake independently from the east. Another (unlikely) explanation for the presence of 'relict' species in Koitere might be a recent introduction in connection with fish transplantations.

Actually, there is also an observation of *P. quadrispinosa* from the supra-Baltic area in eastern Finland, from Iso Lapinjärvi (145 m a.s.l.) in Tuupovaara. The lake, draining to the Jänisjoki system, is situated between the areas of the Baltic Ice Lake and the final phase of the Ilomantsi Ice Lake as sketched by Hyvärinen (1971) and Vesajoki et al. (1986). The record was listed in Segerstråle (1956a), but the maximum extent of the Baltic waters in the area was unclear at that time. Also, unlike the other 'relict' species, *P. quadrispinosa* probably does not entirely lack the capacity of upstream movement: it has often been found in rivers (Segerstråle 1956a) and has also been reported from above the highest Baltic shore in Sweden (e.g. Kinsten 1986).

On the other hand, we note that no 'relicts' were found in our study in Lake Ruunaanjärvi (139 m a.s.l.) in Lieksa, or in the small Lake Yläpaukkajanjärvi (144 m a.s.l.) near the south end

of Lake Pielinen. Both lakes lie slightly above the highest ancient shoreline of the Pielinen basin, then part of the Yoldia phase of the Baltic (Hyvärinen 1966); they were not in communication with waters from the Ilomantsi Ice Lake, either.

4.2. Distribution of *Gammaracanthus lacustris*

In the recent report of the committee for conservation of endangered species in Finland (Rassi et al. 1986), *Gammaracanthus lacustris* is listed as a rare species in need of monitoring. Segerstråle (1956a, b) gave records from 10 lakes, Särkkä (1976) from 13; here the number is increased to 21. In addition to the eight new localities given in Table 1, we refound thriving populations of *G. lacustris* in Saimaa, Kallavesi, Maaninkajärvi, Puulavesi, Kolima, Konnevesi, Päijänne, Pääjärvi (Lammi), Lohjanjärvi and Pyhäjärvi (Artjärvi)*. The subareas of the Iso-Saimaa complex (76 m a.s.l.) where *G. lacustris* was found comprise Etelä-Saimaa, Lietvesi, Tolvanselkä, Pihlajavesi, Enonvesi and Paasivesi; it has also been reported from Pyhäselkä (Segerstråle 1956a) and Luonteri (Meriläinen 1985). Further earlier records of *G. lacustris* involve the lakes Kynsivesi and Keitele (Särkkä 1976), and Rehja (= Nuasjärvi) where it was recorded in both the 1860s and 1950s (Segerstråle 1956a) but not by us in 1985.

G. lacustris is generally regarded as the species with the most stringent ecological requirements among the crustaceans concerned. Therefore, it is interesting to note that *G. lacustris* (and the other crustaceans as well) was abundant in Lake Lohjanjärvi. Though now recovered, this relatively eutrophic lake recently underwent a period of rather heavy industrial influence; the deeper parts of the lake were severely depleted of oxygen during winter months in the 1960s (Helminen 1987).

In Finland, *G. lacustris* has been met with primarily in lakes with relatively large deep (50–60 m) basins (exception: Rehja 38 m); the trophic status and humus content of the lakes do not seem to be critical for its occurrence. The species could well be present in additional, still unstudied basins in the central parts of the major drainage systems. On the other hand, we note the absence of *G. lacustris* in samples from some apparently suitable (large, deep, clean) lakes, which may reflect its early dispersal history. Such sites include the North Karelian great lakes Pielinen and Höytiäinen, and also Juojärvi, Rikkavesi and the Puruvesi basin of Saimaa, which were all isolated relatively early during the Yoldia phase of the Baltic, and perhaps also the somewhat younger Suontienselkä and Iso Roinevesi.

Although *G. lacustris* is generally the most infrequent of the 'relict' crustaceans, and usually co-occurs with all the other species, there are some *Gammaracanthus* lakes where *P. affinis* has not been found (Maaninkajärvi, Vuohijärvi, Pääjärvi/Lammi). Like *G. lacustris*, *P. affinis* may also be absent from the North Karelian waters north of Joensuu (Höytiäinen, Pielinen).

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