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Paleolithic Fish from Southern Poland: A Paleozoogeographical Approach

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ABSTRACT: The area covered by glaciers during the Last Glacial Maximum (LGM) includes a large territory in northern Europe. In this region, Paleolithic finds are rare and fish bones fairly unique. Analysis of Paleolithic fish bones outside of the LGM range was carried out with the intention of reconstructing the paleozoogeographical distribution of this animal group before the retreat of the ice cap from the Baltic Basin. This research focuses on an archaeological fish bone assemblage from Obłazowa Cave, southern Poland. Other samples examined are from Krucza Skała Rock Shelter (Kroczyckie Rocks), Biśnik Cave (Wodąca Valley), Borsuka Cave (Szklarka Valley), and Nad Tunelem Cave (Prądnik Valley). The latter sites are considered naturally accumulated deposits, but, at Obłazowa and Krucza Skała, anthropogenic factors also played an important role. The fish bones from the Paleolithic cave deposits of Obłazowa included at least six fish genera: *Thymallus*, *Coregonus*, *Salmo*, *Salvelinus*, *Esox*, and *Cottus*. The presence of *Coregonus* was especially significant since this fish does not occur in the study area today but may have been present in some of the mountain lakes of southern Poland before the LGM. As new phylogeographic studies based on DNA analyses of different fish species are now available, such information may help in understanding the paleozoogeographical distribution of these fish during the Pleistocene.

KEYWORDS: PALEOLITHIC, FRESHWATER FISH, PALEOZOOGEOGRAPHY, POLAND, OBŁAZOWA CAVE

RESUMEN: El área cubierta por los glaciares durante el último máximo glaciar (LGM) incluía un extenso territorio de Europa septentrional. En estas regiones los hallazgos paleolíticos son infrecuentes y los de huesos de peces excepcionales. Análisis de los restos de peces paleolíticos fuera del perímetro de los glaciares fueron llevados a cabo con la intención de inferir la distribución paleozoogeográfica de este grupo antes de la retirada del casquete polar de la cuenca del Báltico. Este trabajo se centra en la muestra arqueoictiológica recuperada en la cueva de Obłazowa, en la Polonia meridional. Otros yacimientos analizados han sido los del abrigo de Krucza Skała (macizo de Kroczyckie) y los de las cuevas de Biśnick (Valle de Wodąca), Borsuka (Valle de Szklarka) y Nad Tunelem (Valle de Prądnik). Estos yacimientos se consideran acúmulos naturales, aunque tanto en Obłazowa como en Krucza Skała la actividad antrópica parece haber sido apreciable. Los restos ícticos del Paleolítico de Obłazowa incluían cuando menos seis géneros de peces: *Thymallus, Coregonus, Salmo, Salvelinus, Esox* y *Cottus*. La presencia de *Coregonus* resulta importante en la medida que este género no existe actualmente en la zona de estudio si bien pudo haber habitado lagos de montaña de la Polonia meridional antes del máximo glaciar. A medida que se dispone de nuevos datos filogeográficos basados en el ADN de las diversas especies de peces, la información obtenida servirá para esclarecer las distribuciones paleozoogeográficas de todos estos taxones a lo largo del Pleistoceno.

PALABRAS CLAVE: PALEOLÍTICO, PECES DE AGUA DULCE, PALEOZOOGEOGRAFÍA, POLONIA, CUEVA DE OBŁAZOWA

INTRODUCTION

The Postglacial colonization of fish in the Baltic Basin has been discussed by many researchers (e.g., Järvekülg & Veldre, 1963; Lepiksaar, 1984; Bănărescu, 1990, 1992; Lõugas, 1997; Paaver & Lõugas, 2003). Only after the retreat of the glaciers from the Baltic areas was it possible for fish to spread into newly formed bodies of water. Attempts to reveal the history of the early (re)colonization of fish in the previously glaciated territories of northern Europe suffer from lack of evidence. Paleogeographic reconstructions of water systems and modern distribution patterns of species alone do not give us enough information. Moreover, during recent centuries, humans have markedly changed the natural distribution ranges of fishes by means of introductions and stockings. The question of the origin of fish fauna in the early stages of the deglaciated Baltic Basin has been mainly concerned with freshwater fish since marine fish survived Glacial times in oceanic waters. Consequently, cold-adapted freshwater fish that are associated with arctic waters–such as vendace (*Coregonus albula*), European whitefish (*Coregonus lavaretus*), European smelt (*Osmerus eperlanus*), and fourhorn sculpin (*Triglopsis quadricornis*)–have received most research attention. Freshwater fishes of the Palearctic and Holoarctic which have a more widespread distribution pattern, such as grayling (*Thymallus thymallus*), burbot (*Lota lota*), pike (*Esox lucius*), perch (*Perca fluviatilis*), and roach (*Rutilus rutilus*), are also included in many studies. Of especial interest has been a group of sculpin, or bullhead, fish (*Cottus* spp.) and anadromous fish, such as salmon (Salmonidae) (Paaver & Lõugas, 2003).

Establishing the origin of the aforementioned species requires evidence in the form of fish bone remains from around the area of the Last Glacial Maximum (LGM) (Figure 1). Thus it is necessary to identify the possible Glacial refuge water bodies for these freshwater fish. Consequently, all fish bone finds of Pleistocene/Paleolithic origin have a special importance.

FIGURE 1
Study region in relation to the range of Late Glacial Maximum (LGM).

Today's hydrological and topographical situation in Poland demonstrates that almost all of the country's water bodies drain north into the Baltic Sea by way of the Vistula and Oder River systems. Poland has about 9,300 lakes which are mainly situated in the northern part of the country. This region was covered by glaciers until about 20,000 B.P., and many of these lakes were formed after the ice retreated. In southern Poland, the Tatra Mountains formed the watershed between the Vistula and Danube/Dniester River basins, separating two different catchment areas, the Baltic versus the Black Sea. This fact is important for determining the paleodistribution of aquatic fauna.

The objectives of the current study is first, to identify the fish species among the Pleistocene fauna in Poland, and, second, to reconstruct the paleozoogeographical distribution of fish species before and after the LGM, i.e. before and after the opening of the Baltic Sea Basin with the melting of the glaciers. Also, we will discuss the importance of Pleistocene evidence for and distribution of cold-adapted freshwater fish species which we recovered from southern Poland. There have been different interpretations on the migration of these fish fauna into the Baltic Sea Basin after the LGM, which are mainly based on knowledge of the geology of water bodies and on subfossil fish bone remains (e.g., Lepiksaar, 1984; Bănărescu, 1990, 1992; Lõugas, 1997; Paaver & Lõugas, 2003).

Recently, data on the variability of isozymes and mitochondrial and nuclear DNA markers provide valuable information for estimating genetic relationships among fishes of different regions and revealing ancient differentiation due to isolation in separate refugia (e.g., Bernatchez *et al*., 1999; Nesbø *et al*., 1999; Kontula, 2003). Information obtained from Pleistocene bone finds is compared with genetic data of modern fish to interpret the Late Glacial refuge areas of identified species.

MATERIALS AND METHODS

The study materials came from five caves located in southern Poland (Figure 2). Four of the caves are situated on the Krakowsko-Częstochowska Upland (Małopolska area, southern Poland): Nad Tunelem Cave, Borsuka Cave, Biśnik Cave, and Krucza Skała Rock Shelter. This research focuses on the fifth cave, Obłazowa Cave, which is the southernmost cave site discussed here and is situated in the Orawsko-Nowotarska Valley (close to the Tatra and Pieniny Mountains). Despite the presence of some cultural artifacts in the sediments of Biśnik, Borsuka, and Nad Tunelem, these caves are considered naturally accumulated deposits. At Obłazowa and Krucza Skała, however, anthropogenic factors also played an important role in the depositional process.

Obłazowa Cave is located in the southwest section of Obłazowa Rock at an altitude of approximately 7 m above the Białka River in the Orawsko-Nowotarska Valley. Two exposed limestone rocks, Obłazowa (670 m) and Kramnica (688 m), lie on the opposite bank of the Białka River. Investigations in the cave took place from 1985 to 1995 (with some breaks) and were resumed again in 2009 and 2010. The Białka riverbed was previously at a higher level where it had washed out fractured limestone, leaving a small cave along the layers of rock. The cave is a spacious chamber (9 m long, 5 m wide, and 3 m high) with a small corridor running from the mouth of the cave. The cave was inhabited during Middle and Upper Paleolithic times. Zooarchaeological analyses show that it was used only as a short-term camp by Paleolithic hunters. Obłazowa Cave is well-known for the recovery of a «boomerang» made from a mammoth tusk. The presence of the boomerang and other artifacts suggests that this site had a ceremonial function and was of ritual significance during the Upper Paleolithic period. Bone material was well preserved in this complex (Valde-Novak *et al*., 2003). During excavations, all sediments were wet-sieved, and thus a large number of small bones, including fish remains, were obtained alongside larger animal bone remains.

Many of the fish bones from Obłazowa came from layer 8, which dated to 32,000–30,000 B.P. (Valde-Novak *et al*., 2003). The other layers from this site have no ^{14}C dates, so their chronology is not well established. It is not clear if all the fish bones recovered were associated with anthropogenic activity, since they were found in almost every stratigraphic layer. The vertical profile and radiocarbon dates show some mixing of sediments. The Obłazowa fish were mostly represented by vertebrae and scales and came mainly from layers 8 to 2, i.e. those layers associated with the Upper Paleolithic occupation of this cave.

Nad Tunelem Cave is situated on the central slope of Stodoliska Ravine, 19 m above the bottom of the dry ravine, in Ojców National Park in the Krakowsko-Częstochowska Upland. In the cave, three fireplaces and archaeological materials associated with a Neolithic settlement were discovered (Rook, 1980). Below the humus was a layer of yellow clay. The fish remains analyzed in this study were recovered during excavations conducted in 2004 to 2006 by Krzysztof Sobczyk (unpublished data). All of these remains came from Holocene deposits and appear to represent a natural accumulation, demonstrating the survival of fish species from the Pleistocene to the Holocene in this region.

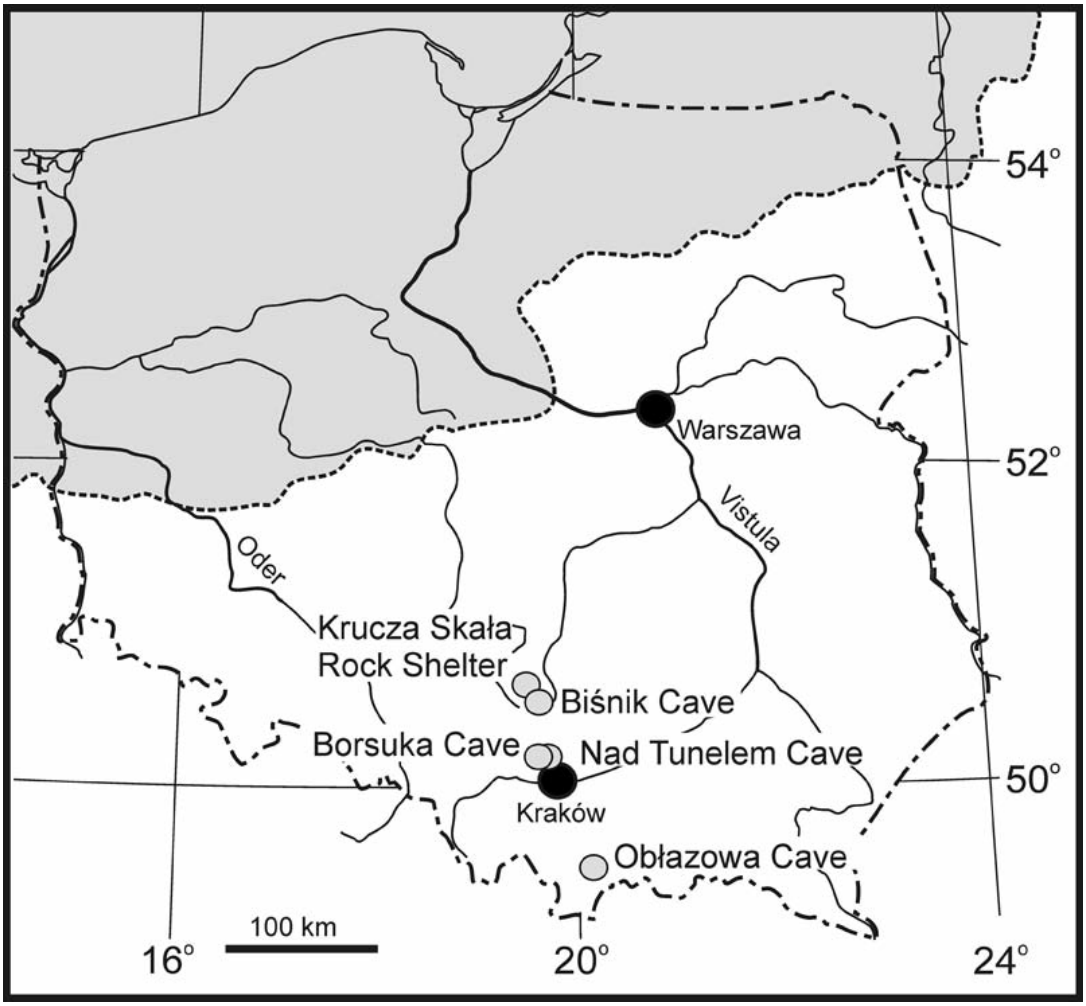

FIGURE 2

Location of study sites and maximum range of ice sheet during LGM.

Borsuka Cave is located in the Szklarka Valley, one of the hydrographic axes of the Olkusz Upland, which constitutes the southern part of the Kraków-Częstochowa Upland. The cave is situated on the northern slope of the Szklarka stream, rising about 30 m above the bottom of this narrow valley and spreading along its southwest-northeast axis. During excavations, this newly discovered site provided extraordinarily valuable material for studies on the Upper Paleolithic settlement of the region. The most interesting materials were found in layer 6, which was a unique assemblage consisting of human remains accompanied by numerous pendants made from the teeth of aurochs (*Bos primigenius*) or bison (*Bison bonasus*), and (European) elk (*Alces alces*). Due to the lack of lithic material and insufficient information from stylistic analyses of tooth pendants and from radiocarbon dates, the differentiation of materials between the Upper Paleolithic cultural complexes (Aurignacian or Pavlovian) was not clear. Faunal remains from layer 6 were dated to 27,000–24,000 B.P. Fish remains were only found in this layer, and, like the rest of the faunal remains (excluding pendants), they were the result of natural accumulation.

Biśnik Cave is located on the western slope of the Wodąca Valley, which is within the Smoleń-Niegowonice Range in the central part of the

Kraków-Częstochowa Upland. During excavations, numerous well-preserved Pleistocene layers were uncovered so that this is a very important site for both archaeology and paleoenvironmental reconstruction. The sediment chronological sequence represented the period from the Central Polish glaciation until the Holocene (Cyrek *et al*., 2009). A Middle Paleolithic sequence included at least 17 levels. Fish bones came from various layers dated from ca. 122,000-20,000 B.P.

Krucza Skała Rock Shelter is situated on the northern slope of Łysiak Hill in Kroczyckie Rock, at an elevation of 40 m above the bottom of a dry valley, and is located about 20 km northeast of Zawiercie. The sandy series of sediments mostly represent the end of the Late Pleistocene. According to ^{14}C dates, it was determined that the layers filling the shelter were formed during the short time between the Bølling and Allerød interglacials (Żarski, 2009). This corresponded well with the scarcity of flint material and art artifacts recovered, which were associated with the Magdalenian culture (Cyrek, 1994). All fish bones analyzed came from this same time period.

Fish bone identifications were carried out using the comparative reference collection housed in the Institute of History at Tallinn University, Estonia. Quantification of the fish remains was based on a count of the total number of identified specimens of each taxon, or NISP. Based upon the close association of finds and the lack of any concentration of materials within the excavation layers, we can assume that most of the fish bones came from different individuals.

RESULTS-TAXONOMY OF IDENTIFIED FISH

Most of the fish bones from Obłazowa Cave were previously studied by Eugenia K. Sytchevskaya (Valde-Novak *et al*., 2003). She identified a total of 254 fish remains, of which 144 fragments were determined to the species level. At least four fish genera were represented: *Thymallus*, *Salmo*, *Salvelinus,* and *Esox* (Table 1). The identification of *Salvelinus* was a bit uncertain (Valde-Novak *et al*., 2003). A more recent study whereby 53 additional fish remains from this site were identified yielded two more genera: *Cottus* and *Coregonus* (see Table 1, identifications by L. Lõugas).

The other four cave sites yielded mainly bones of burbot (*Lota lota*) and salmon (*Salmo* spp.). Among the salmon, brown trout (*Salmo trutta* m. *fario*) was probably represented. Species of the

Stratigraphic unit/layer	**Early Vistulian**			**42-22,000 B.P.**				**22-18,000 B.P.**	**Late Vistulian**				**Holocene**	
Taxon	**XX**	**XVI**	**XV**	**XI**	**X**	**IX**	**VIII**	**VII**	**VI**	**IV**	**III**	**II**	**I**	**no stratigraphy**
Salmo spp. (salmon)					1		3+(10)			(1)				
Salmo salar (Atlantic salmon)						6						2	1	
Salmo trutta (brown trout)		(1)					(3)	2	1	3		8+(3)	1+(1)	(1)
Salvelinus sp. (char)						1(?)								
Coregonus spp. (whitefish)			(1)	(1)	(2)		(3)			(2)		(5)	(1)	
Thymallus thymallus (grayling)	1					3	25	25+(1)		6+(1)	5	37	2	(2)
Esox lucius (pike)						2	3	1		2		2		
Cottus spp. (bullhead)			(1)				(2)	(1)		(1)	(1)	(1)	(2)	(4)
Indet. fish		(2)				7	16	13		12+(1)	18	39+(1)	(1)	

TABLE 1

Taxonomic distribution of fish bones from Obłazowa Cave by stratigraphic unit. Numbers in brackets mark the specimens identified by L. Lõugas, others by E.K. Sytchevskaya (Valde-Novak *et al*., 2003).

genus *Coregonus* were also found. Other species, including grayling (*Thymallus thymallus*), pike (*Esox lucius*), perch (*Perca fluviatilis*), and some cyprinids, were represented by only a few bones each (Table 2).

DISCUSSION

The identified fish species show that southern Poland is an important area for understanding the distribution of cold-adapted fish in the Pre- and Postglacial periods. This region could have been a refuge area for these fish during the last glaciation (Weichselian, Vistulian), and, after the retreat of the glacier, they may have possibly spread into the Baltic Basin via the Vistula River. Even though most of the identified fish species are still present in the rivers and lakes of southern Poland today, such a long-lasting population history is interesting. Of all the fish species identified, *Coregonus* requires special attention because this fish no longer occurs in the region but may have populated the mountain lakes before the LGM.

Paleozoogeography of fish in light of DNA studies

In northern Europe, the paleozoogeography of terrestrial animals has been interpreted in relation to Pleistocene glacial events. Aquatic fauna, especially freshwater fish, directly depended on the development of glacial and post-glacial lakes and rivers. Their distribution in areas previously covered by continental ice was only possible due to the formation of new water systems. Although most fish species of Danubian origin in the Baltic Basin are well represented by subfossil bone finds (see e.g., Lepiksaar, 1984; Lõugas, 1997; Paaver & Lõugas, 2003), there is a lack of evidence for cold-adapted fish species. Therefore, DNA studies of extant populations may give us valuable data for the reconstruction of paleozoogeographical (phylogeographical) patterns of these fish.

Fish with widespread distributions such as burbot, perch, and pike were represented in all studied sites. They were probably quite common in ice-free areas during the Late Pleistocene and are still present in the rivers and lakes of Poland and elsewhere today. The DNA analyses of Eurasian burbot have shown that the maximum divergence

Taxon	Obłazowa Cave				Borsuka Cave	Nad Tunelem Cave	Biśnik Cave	Krucza Skała Rock Shelter			
	Before LGM	After LGM	Holocene	No stratigraphy	after LGM	Holocene	Before LGM	Before LGM	After LGM	Holocene	No stratigraphy
Salmo spp.	14	1			1	4	1	1	5		7
Salmo salar	6	2	1								
Salmo trutta	6	15	2	1			3				
Salvelinus sp.	1										
Coregonus spp.	7	7	1		1						5
Thymallus thymallus	55	49	2	2			2				
Esox lucius	6	4								1	1
Cottus spp.	4	3	2	4							
Lota lota					2	8	10		11	10	15
Perca fluviatilis					1						
Cyprinidae					3						1
Indet. fish	38	71	1								1

TABLE 2

Taxonomic distribution of fish bones at different cave sites.

between burbot haplotypes was very low (1.82%), and, in general, this value is within the range of intra-specific divergence, supporting the current view of a single Holarctic species, *Lota lota* (Van Houdt *et al*., 2003).

Perch from the Baltic Sea Basin showed a higher level of intrapopulation variation, possibly reflecting Postglacial colonization from several different refugia (Nesbø *et al*., 1999). The same was true for brown trout (García-Marín *et al*., 1999). Three main refugia have been suggested for these species (Figure 3): Danubian (Black Sea), southeastern Europe, and western Europe (Bănărescu, 1990, 1992; Nesbø *et al*., 1999). Also, an eastern European refugium has been suggested (Osinov & Bernatchez 1996; Bernatchez *et al*., 1999; Kontula, 2003). The haplotypes of perch common for western Europe have been found in major rivers, including the Vistula and upper Danube, which support the idea of a Postglacial connection between these river systems via periglacial rivers during deglaciation. The Postglacial colonization of the Baltic Sea probably involved fish populations from all of these refugia, except the southern one (Nesbø *et al*., 1999).

It is very likely that salmon also survived glacial times by inhabiting freshwater refugia and glacial lakes. The high degree of genetic differentiation of Baltic and Atlantic salmon, for instance, indicate that Baltic salmon formed a distinct genetic race of this species and probably colonized the Baltic from an inland refugium (Nilsson *et al*., 2001; Paaver & Lõugas, 2003). Grayling, which belongs to the common European freshwater fish fauna, could have lived in a rather cold zone during the Ice Age and was probably already widely distributed before the last glaciation.

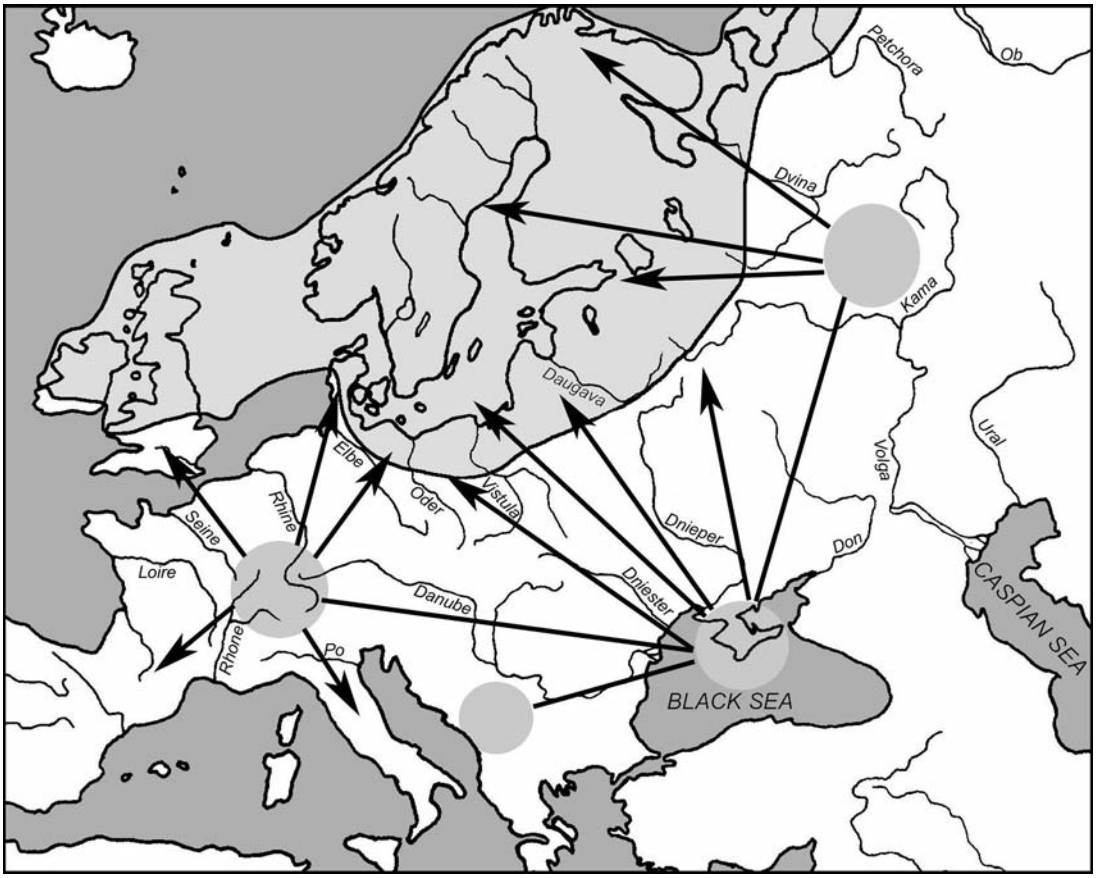

FIGURE 3

Schematic map showing the probable refugia of freshwater fish during the Ice Age and the direction of their colonization after the LGM (according to Nesbø *et al*., 1999).

Remains of fish from the genus *Cottus* (not identified to species) were represented in most of the chronostratigraphical layers at Obłazowa Cave. We can suggest that this fish was a consistent part of the aquatic fauna during the Late Pleistocene in southern Poland. Within the genus *Cottus*, two species are known in southern Poland today: the European common bullhead (*Cottus gobio*) and the Alpine bullhead (*Cottus poecilopus*). The Alpine bullhead is a cold-adapted fish, which inhabits rivers and lakes from the Russian Far East to restricted areas of northern and eastern Europe, as well as the Carpathian Mountains. The European common bullhead is also regarded as a cold-adapted species; in mountainous areas, however, it normally lives downstream from the range of the Alpine bullhead. Both species also thrive in the brackish coastal waters of the Baltic Sea.

According to studies by Tytti Kontula (2003), the mtDNA analyses of *C. poecilopus* indicate that the origin of the north European population was from the Carpathian water system (including southern Poland). These analyses showed a deep phylogeographic structuring within both European lineages of *C. poecilopus*, probably of Pleistocene or of much earlier origin. In the Carpathians, the haplotype relationships imply a more recent connection over the mountain range (i.e. Danube and Vistula versus Dnestr River) rather than through the lower reaches of the rivers draining to the Black Sea. Kontula (2003) also found that Postglacial northern Europe was colonized by *C. gobio* from three different directions by distinct western, southeastern, and eastern lineages, whereas the eastern lineage probably stemmed from a stock that survived in or near the eastern ice-lakes in northwest Russia (cf. Osinov & Bernatchez, 1996). In north European *C. poecilopus*, the northern and eastern haplotypes also clustered into an eastern mtDNA sub-lineage. Apart from indicating two sources of Postglacial colonization, this pattern also suggests glacial survival in northern Central Europe, conceivably even between the Scandinavian ice sheet and the northern Carpathian Mountain slopes. Pleistocene finds of bullhead bones from southern Poland can support this view, although it was impossible to distinguish between *C. poecilopus* and *C. gobio* among the fish bone remains.

Even though most of the study material from southern Poland came from Pre-LGM sediments, the Postglacial finds of *Coregonus* from Krucza Skała indicate a similar faunistic complex in that region before and after the LGM. It may also indicate the survival of cold-adapted fish in quite a limited area between the Scandinavian ice sheet and the northern Carpathian Mountains during the LGM. The later absence of *Coregonus* species in that region may be explained by the change in conditions after the disappearance of periglacial lake and river systems. In contrast to southern Poland, the Alpine population of lavaret (*Coregonus lavaretus*) still persists. The latter is genetically distinct from the northern European population, which indicates either different origins of postglacial whitefish populations or the splitting of populations a very long time ago (Bernatchez *et al*., 1999).

CONCLUSIONS

Pleistocene evidence for cold-adapted fish in southern Poland is very important for paleozoogeographical studies as this region represents a key area between the (Post)glacial Danubian and Baltic basins. The effect of the glaciations was far more complex than just destroying northern fish populations or splitting populations into isolated glacial refugia. For cold-adapted species, the glacial periods could also have represented times of range expansions: glacial periods created freshwater connections across present-day watersheds. Such connections probably partly explain the high level of intrapopulation variation in many fish species existing in the Baltic Basin today.

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