Stone Age fishing strategies in Estonia. What did they depend on?

LEMBI LÕUGAS

Institute of History, Rüütli 6, EE0101 Tallinn, Estonia

(Received 10 October 1995; accepted 5 February 1996)

ABSTRACT: The paper combines zoogeographical and archaeological data in order to explore aspects of the development of Estonian fish faunas from Paleolithic times until the Neolithic. Although the main aim of this contribution is that of a regional survey, a wide variety of issues, from human paleodietary analysis to biology of the different fish groups under consideration, has been incorporated into the discussion in order to define the guidelines for a future systematic archaeoichthyological study in this particular area.

KEYWORDS: ESTONIA, THE BALTIC SEA, PALEOLITHIC, MESOLITHIC, NEOLITHIC, FISH, FISHING, C13 ANALYSIS

RESUMEN: En este trabajo se combinan datos zoogeográficos y arqueológicos al objeto de explorar aspectos referentes al desarrollo de las ictiofaunas estonas desde el Paleolítico hasta el Neolítico. Si bien el objeto primordial del estudio es el de proporcionar una perspectiva regional, una amplia gama de cuestiones, desde análisis de paleodietas humanos hasta consideraciones biológicas sobre los grupos de peces aparecidos, se integran en un intento por definir las futuras directrices de un programa sistemático de investigación arqueoictiológica en la zona.

PALABRAS CLAVE: ESTONIA, MAR BÁLTICO, PALEOLÍTICO, MESOLÍTICO, NEOLÍTICO, PECES, PESCA, ANÁLISIS C13

INTRODUCTION

The early history of Estonian fishes is poorly known. We have better knowledge about the Stone Age fishing implements, which have been found frequently in different parts of Estonia. The early history of Estonian fishes consists mainly of assumptions based on our knowledge of environmental changes during the Late Pleistocene and Holocene and the ecological requirements of different species.

A survey of the history of Estonian fish fauna is provided by Lepiksaar (1938, 1984), while comments on finds of different fish species are found in Tsepkin (1968, 1984), Jaanits (1991) and Lõugas (1995a, 1995b; Lõugas *et al.*, 1995a, 1995b).

This paper summarises finds of subfossil fish and the Stone Age fishing implements used to catch them. It describes the fishing strategies of the period and discusses the differences between the Mesolithic and Neolithic. The model relies on the development of the fish fauna in Estonian waters and on the ecology of different fish species with special emphasis on their seasonal activities and the chances prehistoric people had of catching them. In addition, a C¹³ analysis, obtained during a project on Stone Age resource utilisation in coastal Estonia, was used in order to study the diet of prehistoric people (Lõugas *et al.*, 1995a).

THE PALAEOLITHIC-LATE PLEISTOCENE

No Palaeolithic sites have been discovered in Estonia and no subfossil fish finds from that period are known. Using geological and palaeoclimatological data, an attempt can be made to reconstruct the possible migration routes of different fish species at that time. This is important because the formation of the fish fauna was one of the requirements for the colonisation of that area by man. There is reason to assume that the two sea basins, the Baltic and Sarmatian, were connected by a system of rivers and ice lakes during the Weichelian Ice Age (Kvasov, 1975, 1979) (Figure 1). The latter was fresh and partly brackish so that fish could move around freely (Lepiksaar, 1938, 1984).

During the formation of ice-dammed lakes, relict species from the Arctic Ocean could spread southwards. These species had to be both euryhaline and eurythermic, i.e. salt and cold tolerant (e.g., whitefish, *Coregonus lavaretus*; smelt, *Osmerus eperlanus*; and four-horned sculpin, *Triglopsis quadricornis*). One of the earliest immigrants from the Sarmatian basin could have been the catfish, *Silurus glanis* (Lepiksaar, 1938, 1984). The Baltic Ice Lake, corresponding to the first Baltic fresh water stage, was the region where fish species assembled and spread using the river system (Figure 2).

THE MESOLITHIC-EARLIEST PART OF THE MIDDLE HOLOCENE

The Mesolithic in Estonia spans the period from about 10000-6000 BP. and precedes the adoption of ceramic technology in the area. Climatically, the Mesolithic can be divided into three different periods: the Preboreal, which was cold and humid (10000-8500 BP.), the Boreal, which was warm and dry (8500-8000 BP.) and the Atlantic (first half), which was warm and humid. The history of the Baltic Sea during this period also went through three stages of development: a) the brackish (west part)/fresh water Yoldia Sea, b) the fresh water Ancylus Lake and c) the first part of the brackish Littorina Sea (Figures 3, 4, 5).

Figure 3 shows the location of the Baltic during the Yoldian Sea stage and the new route which fishes could have taken for migration into the Baltic basin. Immigration of the Atlantic forms into the Baltic at that time is quite doubtful because the influence of marine water in the Baltic was minimal and the analysis of invertebrates shows that Atlantic species (e.g., *Portlandia (Yoldia) arctica)* spread only as far as the east coast of modern Sweden and not into the Baltic. The brackish phase of the Yoldian Sea was short, 100-200 years, and more prominent in the west part of the Baltic (Björk, in press). The reasons for the short brackish water phase are not clear. The straits between the Baltic and the west coast of Sweden had gradually become more shallow and narrow due to tectonic uplift. The outflow was probably also too large to allow a saline bottom current to enter (Björk, in press).

In its fauna, the Yoldian phase did not differ very much from the previous stage of the Baltic, but it was the next opportunity for euryhaline and cold tolerant species to immigrate into the Baltic (Lepiksaar, 1984). Several freshwater species probably used the large rivers of Europe (Oder, Vistula, Niemen, etc.) for immigration into this basin during the fresh water stage of this water body.

Only one site, Pulli (Figure 6), has been discovered near the estuary of the Pärnu river, Southwest Estonia; it was C¹⁴ dated to 9285 \pm 120 (TA-284); 9600 \pm 120 (TA-245) and 9575 \pm 115 (TA-176) BP. Janis Sloka identified two species of fish, pikeperch, *Stizostedion lucioperca*, and bream, *Abramis brama* (Table 1) (Jaanits, 1991). These species derive from the ancient Sarmatian Sea and, together with other ecologically tolerant species, like pike, *Esox lucius*, perch, *Perca fluvia-tilis*, and some cyprinids, *Cyprinidae*, spread into the Baltic basin during the time of the Baltic Ice Lake or Yoldia Sea.

Because of rising temperatures, the ecological conditions for warm water fish improved during this phase. We therefore find the remains of more thermophilous fish species in the archaeological sites. Besides pike and perch, bones of tench, *Tinca tinca* (Table 1), which prefers lakes with muddy bottoms, standing water and rich vegetation, have been found at the Lammasmägi site in Kunda (Figure 6) (Lepiksaar, 1984). The Mesolithic layer of the site is dated to the Ancylus Lake stage: 8260 ± 90 (Ua-3000); 8485 ± 90 (Ua-3001) and 8515 ± 100 (Ua-3002) BP. (Åkerlund *et al.*, 1995).

At the time of the Ancylus regression a waterfall formed on the Narva river, which prevented entrance of the Baltic fish species into lake Peipsi (Figure 6). During that period smelt and whitefish inhabiting this lake split from their relatives in the sea and evolved into a new subspecies (Lepiksaar, 1938, 1984; Mikelsaar, 1984).

With the formation of the Danish Belts and the Öresund, an important route appeared for the distribution of marine species, allowing for the immigration of atlantic species into the Baltic (Fi-



FIGURE 1

Ice margin during the Weichelian Ice Age at about 14000-13000 BP. (after Kvasov, 1975, 1979). \rightarrow the possible directions (Arctic Ocean, Sarmatia basin and ice-dammed lakes) from which the first fish immigrants could have spread using the system of big rivers and ice-dammed lakes (Lepiksaar, 1984).



FIGURE 2

The Baltic Ice Lake about 11000-10300 BP. (after Björk, in press; Kvasov, 1975, 1979). → distribution possibilities through this large freshwater basin (Lepiksaar, 1984); ______ the Baltic Ice Lake; ------ the Baltic Sea.



FIGURE 3

The Yoldia Sea about 10000-9900 BP. (after Björk, in press; Kvasov, 1975, 1979). \rightarrow distribution possibility no. 2 for Arctic Ocean relicts (see also Figure 1; Lepiksaar, 1984). The immigration of Atlantic forms into the Baltic during this period is unproven. _____ the Yoldia Sea; ------- the Baltic Sea.



FIGURE 4

The Ancylus Lake about 9300-8900 BP. (after Björk, in press; Kvasov, 1975, 1979). The situation is similar to the Baltic Ice Lake stage, but due to the warmer climate the fastidious fish species could have immigrated as well (Lepiksaar, 1984). _____ the Ancylus Lake; ------ the Baltic Sea.

A Contraction of the second se

FIGURE 5 The Littorina Sea about 7000 BP. (by Kvasov, 1975, 1979) → the immigration route of salt favouring species through the Öresund (Lepiksaar, 1984); ____ the Littorina Sea; -----the Baltic Sea.

gure 5). In the Baltic basin the limnic water of the Ancylus Lake was replaced by the saline waters of the Littorina Sea. This transgression, along with the rise of salinity, created hydrological conditions favourable for the production of plankton. The biomass of ichthyofauna, especially that of planktophagous herring, increased dramatically (Lepiksaar, 1986). Other species entering into the Baltic at that time were cod, *Gadus morhua*; tur-

bot, *Scophthalmus maximus*; flounder, *Pla-tichthys flesus*; sturgeon, *Acipenser sturio*; sprat, *Sprattus sprattus* and eel, *Anguilla anguilla*, among others.

The Narva and Umbusi sites (Figure 6) date to the Late Mesolithic period and the archaeozoological material contains fish species which are typical for that period, (i.e. no Atlantic forms) (Table 1). Only the recovery of salmon (or trout) requires a comment since it is not clear whether *Salmo salar/S. trutta* appeared in the Baltic at the time of the freshwater stage or at the beginning of the brackish water, Littorina, stage. The latter possibility seems more plausible, because of the migratory cycle of the former species.

THE NEOLITHIC-SECOND PART OF THE MIDDLE HOLOCENE

At the beginning of the Neolithic the modern Estonian fish fauna was already defined, notwithstanding minor details. Climatically the Neolithic is characterised as a more continental state (Subboreal) with warm summers but cold winters; this probably caused a change in the choice of camp location. A comparison of the location of sites of Neolithic hunter-fishers with those of the Mesolithic period conveys the impression that the former preferred to establish their camp directly on the coast (not on the river banks or lake shores) and probably hunted species with fatty meat (i.e., seals and pigs) instead of leaner game (as happens at the Loona site). Physiologically this may reflect the

| | PULLI | LAMMASMÄGI, KUNDA | NARVA | UMBUSI | |
|-------------------------|-------|-------------------|-----------|--------|--|
| Esox lucius | | 66 | 450 | 31 | |
| Salmo sp. | | | 1 | | |
| Perca fluviatilis | | 2 | 1 | | |
| Stizostedion lucioperca | 94 | | 259 | | |
| Abramis brama | 5 | | - | 7 | |
| Silurus glanis | | | 100 | | |
| | | 5 51 V 5 | - 10 (11) | • | |

TABLE 1

Number of fragments of fish bone from Mesolithic sites in Estonia (Lepiksaar, 1981; Tsepkin, 1984; Sloka (Jaanits 1991); Lõugas, 1995).

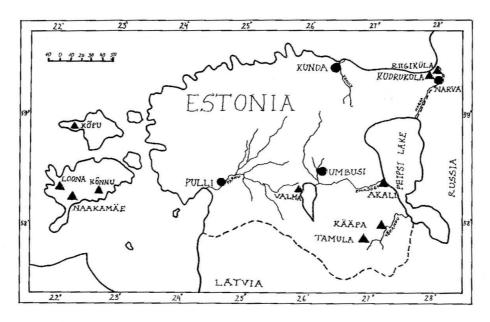


FIGURE 6 Locations of Stone Age sites in Estonia. • Mesolithic; ▲ D Neolithic.

climatic conditions of the Subboreal period (Lepiksaar, 1986). At the end of this phase there are initial signs of a deterioration of climate.

The coastal positioning of the Neolithic sites can also be explained as a result of the diversification of marine faunas in the Baltic (harp and grey seal, Atlantic fish). The island sites of Kõpu, Kõnnu, Loona and Naakamäe (Figure 6), are known as seal hunters' camps (Paaver, 1965; Lõugas *et al.*, 1995a, 1995b; Lõugas, in press) and the remains of cod, turbot and sturgeon indicate the existence and importance of Atlantic fish at that time (Table 2). The inland sites of Tamula and Kääpa (Figure 6), on the other hand, provide good examples of the freshwater fish species of the Neolithic (Table 2). Riigiküla and Kudruküla represent coastal sites which have yielded the remains of marine species as well.

FISHING AND FISHING EQUIPMENT

The absence of finds of marine fishes in the Mesolithic indicates that sea fishing was not important. Moreover, marine fishes were not available at the beginning of this period (i.e., prior to the Littorina stage). Fishing during the Mesolithic seems to have been connected mainly with the littoral zone; this does not exclude fishing from a boat or on the ice farther offshore. The ecology of pike and perch is dependant on reeds in the water body and it is easy to catch them there with a fish spear or traps of wickerwork. A number of Stone Age fishing implements have been found in Estonia. The Stone Age fish spears (more than 300 fragments are known in Estonia) are made from tubular bones of big game (cervids, aurochs). About two thirds of these belong to the Kunda type (Figure 7: 1, 2), which occurs in different sizes (8-24 cm), with either triangular (Figure 7: 2) or quadrangular (Figure 7: 1) teeth. These are first found in the Boreal period. In the 1930s Indreko (1948) discovered a skeleton of a pike with a spear in the lake marl at Kunda.

The pikeperch and the catfish inhabit the deeper portions of lakes and rivers. The former species prefers clear waters, the latter muddy bottoms. These species were probably caught with spears, harpoons or hooks. The number of harpoons from archaeological sites is about 60. They were probably used to catch beavers and seals, but perhaps also large fishes like catfish (Figure 7: 3, 4).

Fish spears and harpoons occur throughout prehistoric times, as do hooks (Figure 8: 1-5) and hook weights (Figure 8: 6-9) (Jaanits, 1991). The first evidence for fishing nets derives from the Late Mesolithic or Early Neolithic. Stone weights and bone needles for fishing nets are known from both coastal and inland sites (Jaanits, 1991).

LEMBI LÕUGAS

| | А | В | С | D | E | F | G | Н |
|-----------------------------|--------|----|-----|----|-----|----|----|------|
| Acipenser sturio | | | | | | | 15 | |
| Esox lucius | 1 | 12 | 667 | 95 | 424 | 92 | 3 | 127 |
| Salmo sp. | | | | | | 11 | | |
| Gadus morhua | 4 | | | | | 4 | 11 | 5268 |
| Thymallus thymallus | | | | | | 1 | | |
| Perca fluviatilis | | 5 | 4 | 4 | 449 | 18 | | 6 |
| Stizostedion lucioperca | | | 593 | | | 16 | 3 | |
| Anguilla anguilla | | | | | | | | 3 |
| Leuciscus idus | . 18 J | | | | 23 | | | |
| Scardinius erythrophthalmus | - | | | | 3 | | | |
| Abramis brama | 2 | | 38 | 4 | 180 | 3 | | |
| Abramis ballerus | | | | | 67 | | | |
| Tinca tinca | | | 1 | | 29 | | | |
| Rutilus rutilus | | 7 | | | 49 | 1 | | |
| Silurus glanis | | | 13 | 41 | 159 | 1 | | |
| Triglopsis quadricornis | | | | | | | | 10 |
| Scophthalmus maximus | 1 | | | | | | 14 | 25 |
| Platichtys flesus | | | | | | | | 3 |

TABLE 2

Number of fragments of fish bone from Neolithic sites in Estonia (Tsepkin, 1968, 1984; Sloka(Jaanits 1991); Lõugas, 1995). A: Kõpu; B: Kõnnu; C: Riigiküla; D: Kääpa; E: Tamula; F: Kudruküla; G: Naakamäe; H: Loona.

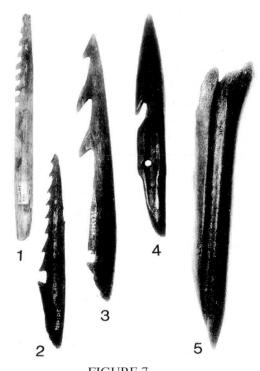


FIGURE 7 Fishing implements: 1-2 spears; 3-4 harpoons; 5 ice pick. Lake marl (1); Lammasmägi site (2, 3, 5); Kunda and Tamula (4). Photo: E. Väljal. Size: 2:3.



FIGURE 8 Neolithic fishing implements: 1-5 hooks; 6-9 hook weights; 10-12 trolls. Tamula (1, 2, 6, 7); Valma (3-5; 8-11); and Akali (12). Photo: E. Väljal. Size: 1:1.

Winter fishing took place on the ice. The naturally pointed tubular bones of big game which are often recovered at sites could have been used as ice picks (Figure 7: 5). This interpretation is based on the fact that seventy such implements were recovered from what appears to be a primary context at the bottom of lake Kunda, not far from the Lammasmägi site (Indreko, 1948; Jaanits *et al.*, 1982). To catch catfish and most cyprinids in winter is quite difficult due to their inactivity. However, if the prehistoric fishermen knew the wintering habits of these species they had the possibility of catching them. The winter shoals of bream make them easier to catch than most cyprinids.

One of the reasons why Mesolithic people did not use the Baltic Sea resources of their time was the small difference between the fauna of the freshwater Baltic Sea and inland lakes or rivers. Seal hunting did not have an important role in the economy of Mesolithic people at that time. Only the ringed seal was hunted, accounting for less than 1% of the total amount of mammal bones in the archaeozoological material of the Kunda-Lammasmägi and Narva sites (Paaver, 1965; Lõugas, 1995b; Lõugas *et al.*, 1995a). ¹³C analyses on human bones from Kunda and Narva produced δ^{13} C

values of -21.1 (Lammasmägi at Kunda) and -21.9 (Narva), indicating that these individuals ate terrestrial food and/or freshwater fish species (Lidén, 1995; Lõugas et al., 1995a). The zooarqueological analyses reinforced this hypothesis. This result could have been anticipated because the Baltic Sea of that period was a freshwater body. Faunal and isotopic data from Neolithic sites on the Estonian islands indicate a dependence on marine resources. The sample from Naakamäe shows a typical marine value of -16.0; the Loona sample, however, has an intermediate value of -18.7. The samples from Kudruküla have terrestrial values (-21.7; -20.4; -23.0), which are to be expected by the location of the site, making terrestrial resources (game and freshwater fish) the sensible prey items (Lõugas et al., 1995a).

CONCLUSION

The colonisation of the Estonian waters by fish began after the retreat of the ice during the Late Weichelian, with an invasion of species from the North and the South. The development of the postglacial fish fauna was gradual with no great changes in species composition at the beginning of the period. The first immigrants were species associated with cold water and euryhaline conditions. These were followed by fresh and/or brackish water species from the South. At the time of the invasion of Atlantic species into the Baltic during the Littorina Sea stage, the freshwater fish fauna in Estonian lakes and rivers had already reached its present day composition.

We can roughly divide the development of Estonian fish faunas into two stages: Pre-Littorina (fresh, brackish water) and Littorina (incl. Post-Littorina, brackish and/or salt water). The Mesolithic people caught fish of the first group from local lakes and rivers using primitive implements (spears, harpoons and hooks). During the Neolithic, species of the latter group became also available, since the implements, including nets and hooks, became clearly more sophisticated. The greatest change in fish exploitation in Estonia during the Neolithic was caused by an abundance of marine faunas in the Baltic which led people to colonize the coastline and islands.

Comparing the Mesolithic and Neolithic fish finds, we can see that the former derive from a limited number of species, while the latter comprise many species. The small number of fish species in the Mesolithic material is explained by the absence of marine fish in the eastern part of the Baltic Sea at that time. Also, the camps of Mesolithic hunterfishers were probably used seasonally. A good example is the Pulli site on the bank of the Pärnu river, which was used during summer (perhaps also during autumn), but the area was evidently flooded in spring (pike spawns in spring in shallow water making them an easy prey at that time; the absence of their bones proves that the site was deserted during that particular season; T. Moora, pers. comm.). At the same time, pikeperch, which spawns on the sandy bottoms of river estuaries in late spring - early summer at water temperatures above 16°C (Mikelsaar, 1984) was intensively fished in Pulli. Lammasmägi at Kunda seems to have been inhabited in spring when the water level of the shallow ancient Kunda Lake rose enough for pike to spawn in the reeds. At this site the remains of pike dominate the fish finds (Lõugas, 1995b).

Finally, the results of fish bone analyses are, to a large extent, dependant on the state of preservation and the excavation technique employed. Paaver (1965) and the author summarize the state of preservation of the bone material from the different sites as follows: excellently preserved material was found at Tamula and Kääpa, good material at Kunda, Pulli, Naakamäe and Riigiküla (I and III layer), medium at Riigiküla (II), Loona, Kudruküla and Umbusi, and bad preservation at Narva, Kõpu and Kõnnu. Finally, it must be mentioned that sieves were used occasionally during archaeological excavations prior to the 1990s in Estonia and therefore a lot of small specimens were lost.

ACKNOWLEDGEMENTS

I would like to thank the organising committee of the 8th meeting of the I.C.A.Z. Fish Remains Working Group for their general support. My special thanks are due to Johannes Lepiksaar, Gothenburg, for supervision and discussions since 1991. I thank also Prof. Anto Raukas, Institute of Geology, Estonian Academy of Sciences, Prof. Toomas Saat, Institute of Zoology and Hydrobiology, Tartu University, and Dr. Vello Lõugas, Institute of History, Estonian Academy of Sciences for their useful comments; also Liis Soon (from the latter institution) for correcting the manuscript. My participation in the Madrid Meeting was funded by the PACT Paleoecological Research Group (Council of Europe) and the Estonian Scientific Foundation (grant no. 1022). Tartu University and the Estonian Scientific Foundation (grant no. 1022) covered the flight to Madrid and back.

REFERENCES

- ÅKERLUND, A.; REGNELL, M. & POSSNERT, G. 1995: Stratigraphy and chronology of the Lammasmägi site at Kunda, in PACT, Estonia 2. Rixensart, Belgium.
- BJÖRK, S. IN PRESS: A review of the history of the Baltic Sea, 13.0-8.0 ka BP., in Quaternary International 27.
- INDREKO, R. 1948: Die mittlere Steinzeit in Estland, Uppsala, Sweden. 427 pp.
- JAANITS, K. 1991: Rybolovstvo i morskoi promysel´ na territorii Estonskoi SSR, in Gurina, N.N. (ed.): Rybolovstvo i morskoi promysel´ v epohu mesolita-rannevo metalla v lesnoi i lesostepnoi

zone vostotschnoi Evropy: 25-38. Leningrad. (In Russian).

- JAANITS, L.; LAUL, S.; LÕUGAS, V. & TÕNISSON, E. 1982: *Eesti esiajalugu*. Tallinn, Estonia.
- KVASOV, D. D. 1975: Pozdnetschetvertitschnaja istorija krupnych ozer i vnutrennich morej vostotschnoi Evropy. Leningrad. (In Russian).
- KVASOV, D. D. 1979: The Late Quaternary history of large lakes and inland seas of eastern Europe. In Annales Academiae Scientarum Fennicae A 127.
- LEPIKSAAR, J. 1938: Eesti kalastiku kujunemise loost jääajast tänapäevani. In Eesti Kalandus, 11-12: 285-290; 302-305.
- LEPIKSAAR, J. 1984: *Eesti kalastiku kujunemise loost jääajast tänapäevani*. In: Pettai, E. (ed.): *Eesti kalanduse minevikust*: 327-338. Stockholm.
- LEPIKSAAR, J. 1986: The Holocene History of Theriofauna in Fennoscandia and Baltic Countries Striae 24: 51-70.
- LIDÉN, K. 1995: *Prehistoric diet transitions*. Dissertation, Stockholm University.
- LÕUGAS, L. 1995a. Subfossil fauna complex from Narva region. Appendix to Kriiska, A.: Stone Age settlements in the lower reaches of the Narva river. In: PACT, Estonia 2. Rixensart, Belgium.

- Lõugas, L. 1995b. Analyses of animal remains from the excavations at the Lammasmägi site, Kunda, North-east Estonia. In: PACT, Estonia 2. Rixensart, Belgium.
- LÕUGAS, L.; LIDÉN, K. & NELSON, D. E. 1995a: *Resource utilization along the Estonian coast during the Stone Age.* In: *PACT, Estonia* 2. Rixensart, Belgium.
- LÕUGAS, L.; KRIISKA, A. & MOORA, H. 1995b: Coastal adaptation and marine exploitation of the island, Hiiumaa, during the Stone Age with special emphasis on the Kõpu I site. In: PACT. Rixensart, Belgium.
- LÕUGAS, L. IN PRESS: Subfossil seal finds from archaeological coastal sites in Estonia, east part of the Baltic Sea. Anthropozoologica.
- MIKELSAAR, N. 1984: *Eesti NSV kalad*, Tallinn. 432 pp.
- PAAVER, K. 1965: Formirovanie teriofauny i izmencivost´ mlekopitajuschich Pribaltiki v golocene, Tartu. (In Russian).
- TSEPKIN, E. A. 1968: Promyslovaja ichtiofauna Narvskich neolititscheskich stojanok. In: Bjull. MOIP, Otd. Biol. 73/5: 123-129. Moscow. (In Russian).
- TSEPKIN, E. A. 1984: Ostatki ryb iz drevnich poselenii na poberezhje Baltijskovo morja. In: Bjull. MOIP, Otd. Biol. 89/2: 50-58. Moscow. (In Russian).

