Post-Glacial history of the European seal fauna on the basis of sub-fossil records

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Introduction

Subfossil bones of six species of true seals (Phocidae) have been recovered during archaeological excavations in Europe: grey seal *(Halichoerus grypus)*, ringed seal *(Phoca hispida)*, harp seal *(Phoca groenlandica)*, harbour seal *(Phoca vitulina)*, bearded seal *(Erignathus barbatus)* and monk seal *(Monachus monachus)*. All of these species have a recent distribution in different European coastal waters.

In the course of climatic changes during the Late Glacial and Holocene, due to the melting ice sheets in northern Europe, new settlement areas developed along the coasts, and also newly-formed water bodies served as habitats for seals. In the past, numerous reports of bones of different European seal species have been published.

Unlike coastal regions on the Atlantic Ocean, the Barents and the Mediterranean Seas, an extensive inventory of sub-fossil bones from the Late-Glacial and Holocene were discovered in the Baltic area. Based on these records, many attempts have been made to reconstruct the temporal and spatial settlement of the Baltic Sea with recently spread seal species – or have used sub-fossil finds to demonstrate a former settlement. The works of EKMAN (1922), SALMI (1963), LEPIKSAAR (1964), FORSTÉN & ALHONEN (1975) and ERICSON (1989) are particularly valuable for this purpose.

With regard to the development of the seal fauna in different regions of the Baltic coast, there has been a considerable increase in information – a result of radiocarbon datings as well as osteological research (LINDQVIST & POSSNERT 1997; LÕUGAS 1997; 1998; 1999; UKKONEN 2002; STORÅ 2001).

With the help of all available sub-fossil records, the present study aims to portray the history of Europe's seal fauna with special reference to its development in the Baltic Basin.

Geomorphological development of the Baltic Basin in the Late-Glacial and Holocene

For migration purposes, seals are dependent on the presence of appropriately-sized bodies of water. In order to explain and understand the settlement events of individual seal species in the Baltic region, it is necessary to refer to geomorphological and climatic processes. The following is a short review of the important processes in the development of the Baltic Sea.

The Weichselian glaciation reached its peak between 21000 and 18000 BC. Following this, during the Late-Glacial, the glaciers retreated northwards in several stages. The Bølling and Allerød interstadials, left northern Germany, Denmark and a significant part of the Baltic States ice-free at that time (AARIS-SØRENSEN 1992). The retreat of the glaciers from the Onega Basin took place between 12250 and 10750 BC (SAARNISTO & SAARINEN 2001), initiating the formation of the Baltic Ice Lake in the Baltic Basin (c. 13600–10300 BC, Fig. 2a), which contained freshwater and was isolated from the ocean. It was after the Allerød interstadial, though, that a connection to seawater took place. Earlier sources (e. g. SAURAMO 1958) report that, in the Late-Glacial, there was still a connection between the Baltic Basin (Baltic Ice Lake) and the White Sea. This viewpoint, however, has been refuted through more recent research (SAARNISTO et al. 1995, BJÖRCK pers. comm., SAARNISTO pers. comm.).

In the Younger Dryas, the last phase of the Late-Glacial (from c. 10300 BC on), the further retreat of the Scandinavian ice sheet caused the formation of a more complex connection between the Baltic Basin and the world's oceans. As a result, the water level of the Baltic Ice Lake in the Baltic Basin decreased by about 25 m (BJÖRCK 1996). This connection was located in the area of the Vänern Basin in southern Sweden and was characterized by the entry of seawater (Fig. 2a). The Öresund connection no longer existed at that time, but a major land bridge connecting Denmark and southern Sweden was present again (BJÖRCK 1995a). The seawater reached the area of present-day Stockholm through

Chronostratigraphy (BC/AD)					Cultural epochs		Vegetation
1000	HOLOCENE	Younger	VIII	Sub-Atlantic	Middle Ages		deciduous forests with dominance of beech
0			VII		Iron Age / Roman Times		
1000			VI		Bronze Age		
2000		Middle	V	Sub-Boreal	Neolithic	Single Grave Culture	deciduous/mixed forests (oaks, basswoods, alders)
3000						Funnel Beaker Culture	
4000			IV			Ertebølle Culture	
5000			III	Atlantic	Mesolithic	Kongemose Culture	extensive afforestation of Europe
6000							
7000		Older	II	Boreal		Maglemose Culture	hazelnut- /pine- and birch forests
8000				Pre-Boreal			
9000							
10000	PLEISTOCENE	Late Glacial	I	Dryas III	Upper Palaeolithic	Ahrensburgian Culture	heathland boulder vegetation local birch/pine forests
11000				Allerød Dryas II Bølling		Federmesser Groups	
12000						Hamburgian Culture	tundra vegetation dwarf-shrubs graminaceous dominance
13000				Dryas I		Magdalenien	
14000							

Fig. 1: Chronozones (Roman numbers) and temporal relationships during the development of the Baltic Sea in the Late Glacial and Holocene.

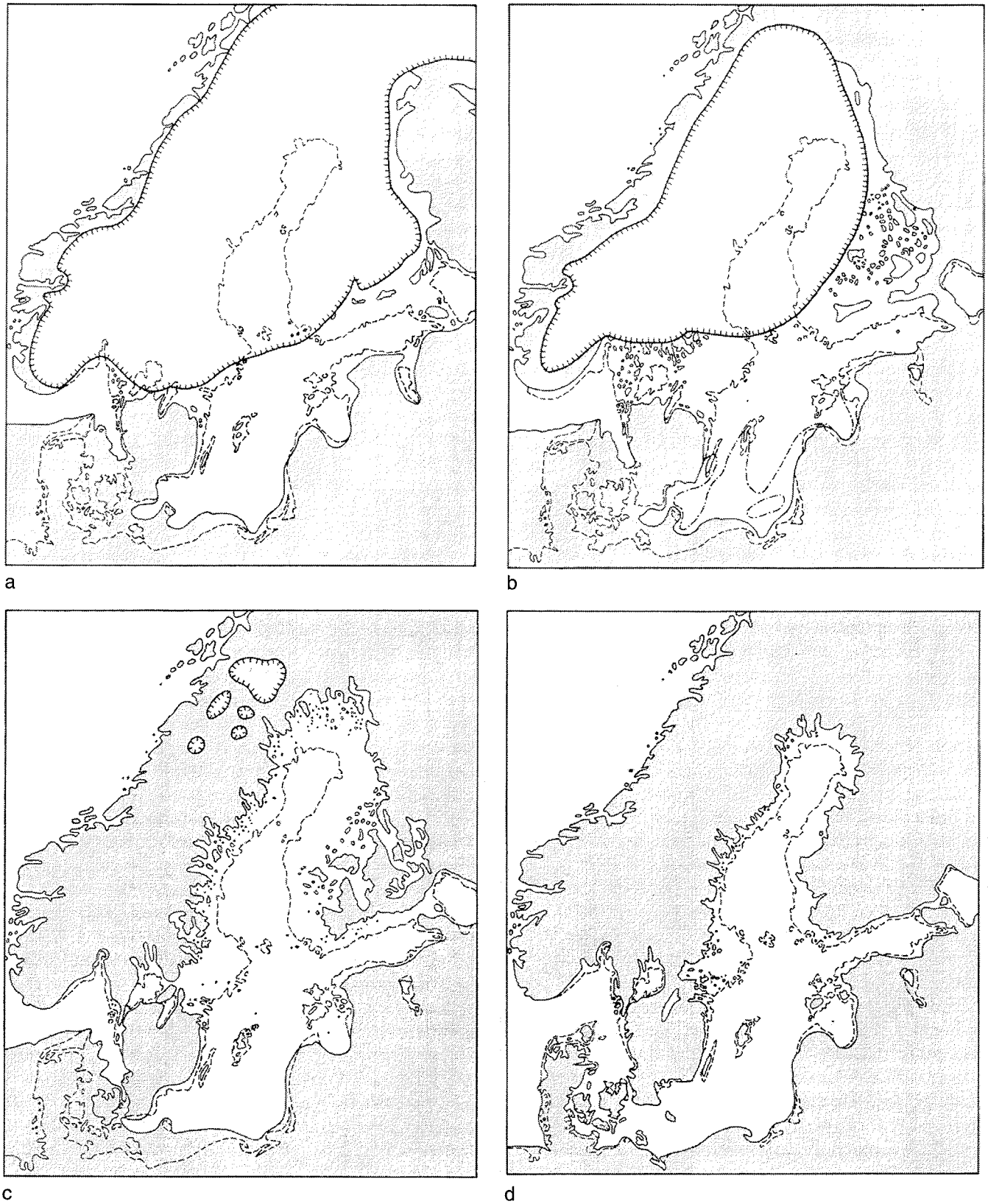


Fig. 2: Development of the Baltic Sea: a. Baltic Ice Lake; b. Yoldia stage; c. Ancylus stage; d. Litorina stage. Figures by kind permission of Lembi Loũgas (Tallinn, Estonia).

the Värnern Basin and Närkesund, respectively. *Yoldia arctica*, a bivalve mollusc, was transported to the southern Swedish Baltic area via deep water currents in the Younger Dryas; this geological stage of the Baltic Sea was therefore named after this species – »Yoldia Stage« (c. 10300–8750 BC; Fig. 2b). In the middle Pre-Boreal,

the connection of the Yoldia Sea with the ocean across the lowland west of Mt. Billingen and the depressed area of central Sweden was cut off by ongoing land uplift, so that an oligotrophic to mesotrophic freshwater lake, the Ancylus Lake, was formed from the Yoldia Sea. This lake was named after a gastropod, *Ancylus fluviatilis*, widespread at that time. By 9500 BP (8750 BC) at the latest, the Ancylus Lake was geographically completely isolated from the ocean (BJÖRCK 1995a; Fig. 2c). This period (c. 8750–7000 BC) of the later Baltic Sea lasted until the Boreal climatic epoch (c. 8000–7000 BC) and ended approximately at the beginning of the Atlantic. The area of the western Baltic Sea continued to be land at the time of the Ancylus Lake (Fig. 2c).

Because of Scandinavia's isostatic uplifting, the Ancylus Lake gradually moved southwards at the beginning of the Atlantic and, in some places, extended as far as today's coastlines of Germany, Poland and the Baltic States (JAHNKE 1996). Around 7000 BC, the progressive isostatic uplifting of the region initiated the formation of an outlet of the Ancylus Lake into the sea, which was located within the Darss Sill and the straits Fehmarn Belt and the Store Belt. It was approximately from that time that brackish water was detected in the southern Ancylus Lake. From then on, the former land bridge between Scandinavia and the European mainland in the western Baltic region remained severed (Fig. 2d).

The water level of the Ancylus Lake dropped to below 20 m. Therefore vast areas, especially in the region of today's Gulf of Bothnia, fell dry. The drainage of a large volume of water from the Ancylus Lake was followed by a transgression of the global water level. As a result of the water level's eustatic uplifting, seawater entered the Baltic Basin through the Danish sounds. This event also had a major impact on the mainland due to the continuous rise of the water level. JAHNKE & LAMPE (2000) were able to document an increase of more than 13 m on the Western-Pomeranian coast between 8000 and 6000 BP (c. 6900–4900 BC). The brackish-water snail *Littorina littorea* also arrived with seawater in the Baltic region. From this species, the name »Litorina Sea« was derived (Fig. 2d), and is used for this sea- and/or brackish-water phase of the Baltic Sea (Fig. 1). During that time, more stepwise increases in the water level took place (JAHNKE & LAMPE 2000). At the beginning of the Litorina Stage, which is also named »Mastogloia Phase« after a characteristic algal species, the salinity was at least twice as high as it is today (LANG 1994, EHLERS 1994). The Baltic Sea started to become less saline from 2000 BC on. One mollusc species, which thrived due to the changes that had taken place, was the brackish-water gastropod *Limnea ovata*, from which the characteristic expression »Limnea Sea« is derived.

Material and methods

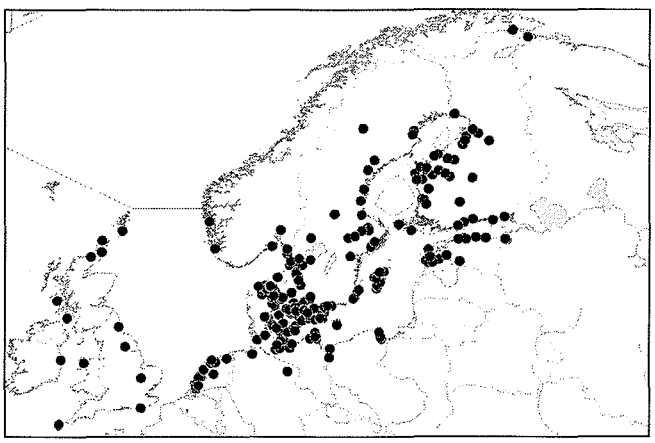
Using an extensive database, in which zoological information from both published and unpublished archaeological finds for Europe are registered (BENECKE 1999), all available information about sub-fossil true seal finds from the Late Glacial and Holocene in Europe was collected (Fig. 3). The data were revised, updated and checked.

According to their dating, the data were assigned to chronozones (Tab. 1 and Fig. 1). In most cases, sub-fossil finds were dated by assigning them to an archaeological layer. To facilitate a chronological classification of finds of individual species as exactly as possible, available ^{14}C dates for single bones were used. These were either taken directly from the sources or made available by colleagues. All ^{14}C data are listed in the appendix.

In order to chronologically assign non-^{14}C-dated remains of a species as exactly as possible, each find was temporally placed between the oldest and youngest dating of the remains of other organisms from the excavation site. This was only done, however, when it was clear from the archaeological context that, at the respective excavation, the remains were of only one settlement period. The calibration of ^{14}C data was carried out after STUIVER et al. (1998). Additionally, the PC program OxCal (Oxford University) was used. All assemblages that could not be assigned to chronozones due to unsuitable dating were chronologically arranged by their cultural epoch and included in the investigation. For the cultural epochs, the chronology of Northern Europe was applied.

With the help of a Geographic Information System (GIS), all sub-fossil assemblages from the chronozones and cultural epochs were recorded sequentially on a digital map. The localities, which were simulated temporally and spatially based on GIS, served to gain data on the Late- and Post-Glacial distribution. To accompany the detail in the text, all sub-fossil finds are presented in maps.

Fig. 3: Sites of sub-fossil seal bones from the Late-Glacial and Holocene in northern Europe.



Tab. 1: Number of sites of sub-fossil phocid records in Europe.

Chronozone/cultural period	Space of time	*H. gryp*	*P. hispi*	*P. groen*	*P. vitu*	*M. mona*	*E. barb*
I Late Glacial	(15000 BC–9000 BC)	4	2	3	1	4	7
II Pre-Boreal/Boreal	(9000 BC–7000 BC)	1	6	1			
III Atlantic	(7000 BC–5500 BC)	2	11			2	
IV Atlantic/Sub-Boreal	(5500 BC–3000 BC)	33	11	17	7		
V Sub-Boreal	(3000 BC–1000 BC)	44	28	39	12	3	1
VI Sub-Atlantic	(1000 BC–0)	8	3	3	7		1
VII Sub-Atlantic	(0–600 AD)	2	–	1	5	1	
VIII Sub-Atlantic	(600–1500 AD)	28	4	8	19		
Mesolithic	(9500–4000 BC)	23	13	4	2		
Neolithic	(5000–1800 BC)	8	10	6	2		
Bronze Age	(1800–900 BC)	1	1				
Iron Age/Roman Times	(900 BC–500 AD)	2	2	2	3		
Migration Period	(400–600 AD)	1		1	1		
Without precise dating		10	6	7	7	2	

Results

Data

Sub-fossil bones of true seals have been found at 297 places and cultural layers in Europe so far. All European localities with sub-fossil seal bones used are listed in the appendix. Available data for individual species are presented in table 1.

Ringed Seal (Phoca hispida)

Except for one record on Spitsbergen from recent times (VAN WIJNGAARDEN-BAKKER & PALS 1981) and four finds at the Varangerfjord in northern Norway from the Sub Boreal and Sub-Atlantic (RENOUF 1989), the ringed seal is documented in Europe exclusively in the Baltic area and the adjoining Kattegat and Skagerrat, in 97 sub-fossil assemblages.

For the Late-Glacial, the presence of *P. hispida* was recorded by LEPIKSAAR (1964) in the Kattegat. Based on, among others, AMS dates, the ringed seal was also found in the Gulf of Bothnia and on Gotland during the older Holocene (LINDQVIST & POSSNERT 1997; UKKONEN 2002). Finds from the middle Holocene (FORSTÉN 1972; FORSTÉN & ALHONEN 1975; 1977; FORSTÉN & BLOMQVIST 1977; EKMAN & IREGREN 1984; JONSSON 1988; TEICHERT 1989; LÕUGAS 1997) can be gathered from Fig. 4. Numerous records from the Mesolithic give supplemental information for characterizing its distribution pattern in the Post-Glacial, such as in the Gulf of Finland (AILIO 1909; FORSTÉN 1972; LÕUGAS 1997; s. Fig. 4).

For the younger Holocene (Sub-Atlantic), *P. hispida* is documented in a few faunal assemblages (LEPIKSAAR 1961; ROSENLUND 1976; REICHSTEIN 1991; LÕUGAS 1997; 1999) such as the Gulf of Bothnia and Finland as well as in the western Baltic Sea area.

Phoca hispida was the only seal species to enter the Baltic Basin through the Närke Strait during the Yoldia Stage and was able to reproduce there. Immigration of ringed seals from the White Sea during the Late Glacial was not possible, as no connection existed (SAARNISTO et al. 1995). Radiocarbon dates of ringed seal bones along the Finnish coast give a reference for the species in the region of today's Gulf of Bothnia during the period between 8750 and 7240 BC (UKKONEN 2002). At that time, the Baltic Basin was in the stage of the Ancylus Lake and isolated from the Atlantic (BJÖRCK 1995a). The shores of the Ancylus Lake were situated very far inland, especially in the early Ancylus stage. Therefore, seal remains from the older Holocene and early Atlan-

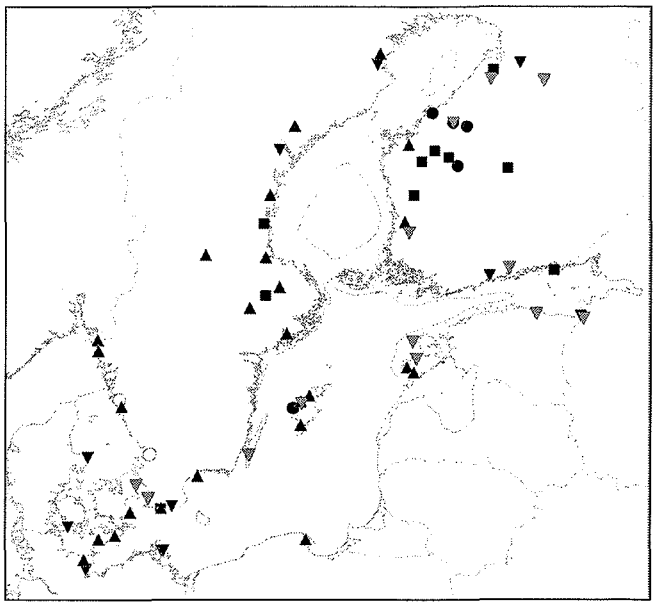


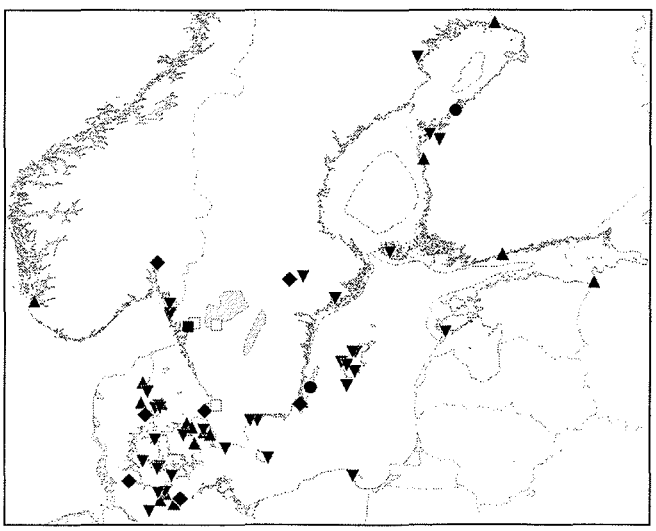
Fig. 4: Sub-fossil records of the ringed seal Phoca hispida between the Late-Glacial and the middle Holocene. – White circle: 15000–9000 BC. Black circle: 9000–7000 BC. Black square: 7000–5500 BC. Black inverted triangle: 5500–3000 BC. Black triangle: 3000–1000 BC. Grey inverted triangle: Mesolithic.

tic respectively (chronozones II and III) were, in contrast to later times, more often found far in the interior.
The vanishing connection between the Gulf of Finland and the Ladoga Lake during and at the end of the Ancylus stage (SAARNISTO et al. 1995) led to the enclosure of the population, which came to bear the name *Phoca hispida ladogensis*. Along with the isolation of the Finnish lake basins from the Baltic Basin, occurring due to land uplifting during the Ancylus period, went the separation of the animals nowadays called *Phoca hispida saimensis*. While both the Gulf of Bothnia and Finland apparently have been inhabited by *P. hispida* since the Holocene, the species seems to occur only sporadically in the western Baltic region after the Sub-Atlantic. It is unclear, though, whether the animals have immigrated from the Arctic population or whether they are members of the Baltic population that have migrated into the western Baltic. Current genetic studies confirm a gene flow into the Baltic Sea (PALO et al. 2001).
Nevertheless, it is possible since their separation that the three subspecies *P. h. botnica* (Baltic Sea), *P. h. saimensis* (Saima Lake) and *P. h. ladogensis* (Ladoga Lake) have been in contact with each other as a result of their wanderlust along rivers.

Harp Seal (Phoca groenlandica)

Except for a few records from the southern and northern Norwegian coast, *Phoca groenlandica* is documented in Europe exclusively in the Baltic area and the adjoining Kattegat and Skagerrat from 92 sub-fossil assemblages.
Harp seal bones from south-western Sweden (Bohuslän, Västergötland) are dated back to the Allerød and the Dryas III by LEPIKSAAR (1964) and FREDEN (1975) on the basis of the geological location of the sites and several ^{14}C dates. Remains of *P. groenlandica*, which were discovered during excavations of mussel shells near Uddevalla (Bohuslän, south-western Sweden), have been assigned to the Yoldia stage (LEPIKSAAR 1964). From the late Atlantic/early Sub-Boreal (chronozone IV), 15 sub-fossil records of *P. groenlandica* are known, which, beside the western Baltic, also come from the Öland Island (LINDQVIST & POSSNERT 1997), the Gulf of Finland (LÕUGAS 1999) and the Gulf of Bothnia (FORSTÉN & ALHONEN 1977) (Fig. 5). The most extensive sub-fossil material of harp seal bones in the Holocene can be attributed to the Sub-Boreal (chronozone V) (Fig. 5).
The most frequent records of *P. groenlandica* beside Gotland Island come from the western Baltic region (LEPIKSAAR 1974; ROSENLUND 1976; AARIS-SØRENSEN 1978; LINDQVIST & POSSNERT 1997; STORÅ 2001). From the Sub-Boreal the species is also documented in Finland on the Norwegian coast of the Barent Sea (RENOUF 1989).
Only a few sub-fossil finds are known from the chronozones VI and VII (SALMI 1963; SELLSTEDT 1966; RENOUF 1989; LÕUGAS 1999). In the period of chronozone VIII (600–1500 AD), which roughly corresponds with the Middle Ages, the harp seal is documented on the Swedish, Danish and German coasts (LEPIKSAAR 1966; JONSSON 1972; ROSENLUND 1976; BOESSNECK & VON DEN DRIESCH 1979; REICHSTEIN 1991; 1995).
Numerous absolute dates (see appendix) have proved that the harp seal was present in the Vänern Basin, i. e., the passage to the Baltic Ice Lake and Yoldia Sea respectively, during the Allerød and Dryas III. Immigration into the Baltic Basin during that period seems to be very doubtful due to ecological reasons (LEPIKSAAR 1964; LINDQVIST & POSSNERT 1997) and is clearly rejected, especially with regard to the analysis of available sub-fossil assemblages.
In the past, the history of harp seals in the Baltic Sea has been discussed with three different hypotheses:
(1) The relict theory by EKMAN (1922) describes the Post-Glacial Baltic harp seals as relicts from the Yoldia stage. This assumption was last expressed by REQUATE (1962). In accordance with current knowledge, this theory seems very unlikely, however.
(2) FORSTÉN & ALHONEN (1975) and LINDQVIST & POSSNERT (1997) postulate that harp seals migrated into the Baltic Sea during the Litorina phase and reproduced there.
(3) Both LEPIKSAAR (1964; 1986) and LÕUGAS (1998) consider harp seal invasions from the Barent Sea to be a likely cause for their occurrence in the Sub-Boreal. Major migrations and invasions to regions that lie outside of this area are known and have often been observed (KAPEL 1994a). LEPIKSAAR (1964; 1986) and LÕUGAS (1998) refer to the fact that no seal cubs have so far been detected in the osteological assemblages.

Fig. 5: Records of the harp seal P. groenlandica from the Late Glacial and Holocene in the Baltic region. – White square: 15000–9000 BC. Black square: 9000–7000 BC. Black triangle: 5500–3000 BC. Black inverted triangle: 3000–1000 BC. Black circle: 1000 BC – 0. Black rhomb: 600 AD – 1500 AD.



In most recent times, STORÅ (2001) proved with osteological studies on sub-fossil material of *Phoca groenlandica* from the Sub-Boreal and Neolithic that reproduction of the species did indeed happen in the Baltic. The conspicuously small phenotype of Sub-Boreal harp seals is certainly connected to this fact (LEPIKSAAR 1964, LÕUGAS 1998).

On the basis of the present ^{14}C data (see appendix), as well as bone finds from reliably-dated prehistoric settlements, it can be assumed that harp seals migrated into the Baltic Sea in the second half of the Atlantic. It is possible to make a connection between both the immigration and reproduction of *P. groenlandica* in the Baltic Sea and the development of environmental conditions in the Baltic water systems. Along with a high increase in salinity during the Litorina »sensu stricto« phase (EHLERS 1994), following the Mastogloia phase, marine fish species and thus potential prey such as cod *(Gadus morrhua)* and herring *(Clupea harengus)* arrived in the Baltic Basin (LÕUGAS 1999). Other species also benefited from this development. For example, the harbour porpoise *(Phocoena phocoena)* has occurred in the Baltic Basin since then (UKKONEN 2002).

The small size of *P. groenlandica* in the Sub-Boreal is therefore likely a result of the Baltic's changed climatic and environmental conditions on reproduction. This possibility was pointed out by LEPIKSAAR (1964).

In the Sub-Boreal, the distribution and frequency of *P. groenlandica* in the Baltic Sea apparently reached their maximum in Post-Glacial times (Fig. 5).

Compared to those from the Sub-Boreal and Neolithic, the number of finds from the Sub-Atlantic is strikingly low. This fact, however, has also been observed with grey and harbour seals, at least in the period between 1000 BC and 600 AD (chronozones VI and VII).

The species' small size can no longer be observed on skeletal remains from the Sub-Atlantic, so it can be assumed that the harp seal population reproducing in the Baltic Sea did not exist any longer. Also, the finds from the Iron Age described by LEPIKSAAR (1964) appear to be remains of animals that immigrated.

Harbour Seal (Phoca vitulina)

Among all true seals in coastal waters of Europe's temperate and boreal zones, the harbour seal is only represented in 59 sub-fossil assemblages. One record from the caverns of Altamira (coast of the Bay of Biscay, Spain) has been dated to the Late Glacial by ALTUNA (1972). *Phoca vitulina* has been documented since chronozone IV (late Atlantic/Sub-Boreal). From this time sub-fossil bones are known from coastal waters of Norway, Denmark, the Netherlands, Poland and Germany (ROSENLUND 1976, ZEILER 1995, KUBASIEWICZ 1958, TEICHERT 1989).

In the Sub-Boreal (chronozone V, 3000–1000 BC), the harbour seal is documented on northern Scotland's Orkney Islands (SUTHERLAND 1983) and at the North Cape (RENOUF 1989) (Fig. 6), while one record from the Gulf of Riga exists for the Neolithic (LÕUGAS 1999). Further records from the Sub-Atlantic are included in Fig. 6.

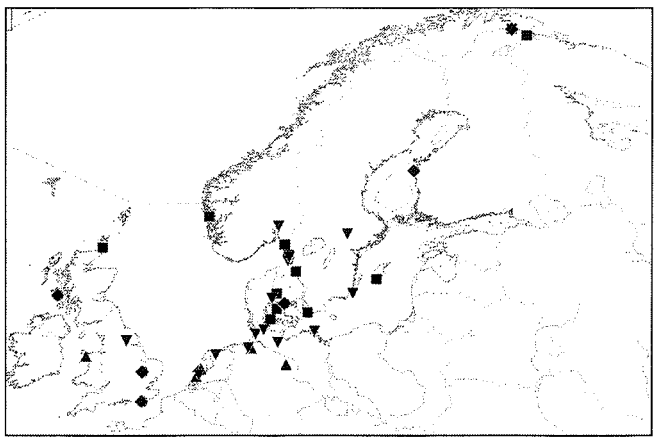


Fig. 6: Sub-fossil records of the harbour seal Phoca vitulina in European coastal waters. – Circle: 5500–3000 BC. Square: 3000–1000 BC. Rhomb: 1000–0 BC). Triangle: 0–600 AD). Inverted triangle: 600–1500 AD.

The Late Glacial record from northern Spain (ALTUNA 1972, ALTUNA & STRAUS 1976) is separated considerably in time from the remaining sub-fossil material. The bones could originate from mixed layers, as is usually the case in cave sediments, to be a mixture with layers from the Holocene. A final conclusion can only be reached through ^{14}C dating.

When looking at faunal history, the harbour seal is the most recent immigrant among the seals of northern European coastal waters. Except for the find from northern Scotland, harbour seals have not been detected along the Atlantic coast of the British Isles before the Sub-Atlantic. Even though no ^{14}C dates are available, the harbour seal is presumed to have been present in northern European coastal waters since at least the Sub-Boreal. The earliest records of *Phoca vitulina* were found in the Baltic Sea, except for one find on the Dutch coast. These relatively recent harbour seal records in the Baltic Sea therefore refer to a dispersal into the western Baltic (SOMMER & BENECKE 2002).

During the Late-Mesolithic in Europe, members of the Ertebølle culture settled in the region of the south-western Baltic Sea. From some of these settlements harbour seals have been recorded, as these people were also specialized in hunting seals. Finds from the Sub-Boreal have been discovered on the Danish islands, in the Kattegat and the Skagerrak as well as on Gotland.

With the exception of finds from Estonia and Finland, the latter of which (UKKONEN 2002) is doubtful, all further sub-fossil finds from 1000 BC–1500 AD were found in the western Baltic. This find pattern corresponds very well with the recent distribution pattern in the Baltic Sea. As the continuous settlement of the south-western Baltic Sea has been proven, it can be concluded that *Phoca vitulina* has occurred in this area since the Sub-Boreal. Harbour seals could therefore have resided

there for roughly 6000 years, representing the most recent immigrants of seal species into the Baltic Sea, as also accepted by LEPIKSAAR (1964).

Grey Seal (Halichoerus grypus)

The grey seal has been recorded in 169 sub-fossil assemblages and is by far the most frequently represented Phocidae species in Europe.
The earliest records of *H. grypus* from European coastal waters come from northern Spain's Atlantic coast, dated to the Magdalénien and Azilian (STRAUS et al. 1981; ALTUNA 1986). In Gibraltar, bone remains of the species were recovered from the Palaeolithic and Mousterian (ZEUNER 1953).
Along the North and Baltic Sea coasts, the species is recorded for the first time by two finds on the West-Swedish Skagerrak coast, which date from the Pre-Boreal and Boreal (LEPIKSAAR 1964; FREDEN 1975). From the Atlantic (chronozone III, 7000–5500 BC), only two sites are known, which represent the first confirmation for *H. grypus* in the Baltic Sea (Fig. 7), while the species was recorded in the area of the British Isles (on the west coast of Ireland) for the first time in chronozone IV (WOODMANN 1978). During the same period (5500–3000 BC), it was also found on the south-western Norwegian coast (DEGERBØL 1951), in the Gulf of Bothnia and Finland (LÕUGAS 1997; FORSTEN 1979) as well as in the entire south-western Baltic (Fig. 7). In the Sub-Boreal (chronozone V, 3000–1000 BC), *H. grypus* was first recorded on the Dutch coast (BRINKHUIZEN 1979, CLASON 1967), on Cornwall's Scilly Islands (GRAY 1983) as well as at the North Cape (RENOUF 1989).
For the early Sub-Atlantic, records exist from northern Scotland (FINLAY 1996) and the Dutch east coast (VAN GELDER-OTTWAY 1988) as well as the western Baltic Sea. All further finds from the Sub-Atlantic (chronozones VII and VIII, 0–1500 AD) come, with only a few exceptions, from the western Baltic Sea (Fig. 8).
Although *H. grypus* is much more frequently represented in sub-fossil faunal assemblages in Europe than all the other Phocidae, it is likely that only fragments of the actual prehistoric distribution in the Holocene exist. The high specialization of the Ertebølle culture alone establishes a representative picture of the seal fauna in coastal regions during the chronozone IV (the Late Mesolithic) (Fig. 7).
H. grypus is very rarely documented in northern European coastal waters during the Late Glacial, Older Holocene and early Atlantic. These finds, some of which have been dated very exactly (LEPIKSAAR 1964; FREDEN 1975), confirm the occurrence of grey seals on the Swedish west coast during the Baltic's Yoldia and Ancylus periods (Dryas III and Pre-Boreal). In this context, the settling in the Baltic Sea by *H. grypus* needs to be discussed. So far, grey seals have only been documented in the Baltic region from the Atlantic at the earliest, the time of the Litorina stage. LINDQVIST & POSSNERT

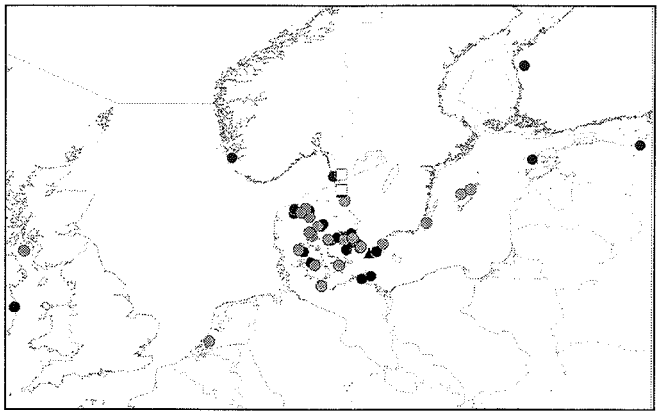


Fig. 7: Records of the grey seal H. grypus between the Late Glacial and the middle Holocene in northern Europe. – White square: 15000–9000 BC. Black square: 9000–7000 BC. Triangle: 7000–5500 BC. Black circle: 5000–3000 BC. Grey circle: Mesolithic.

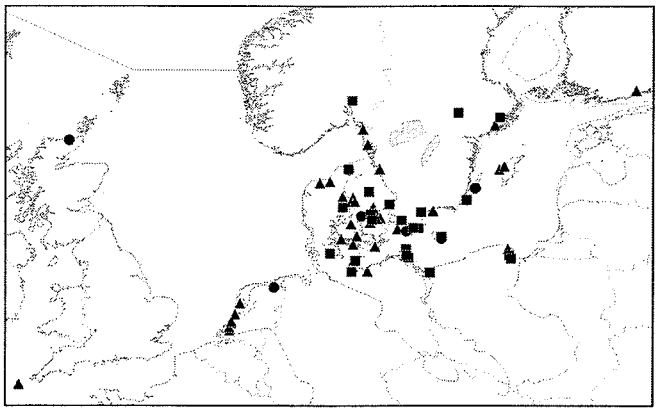


Fig. 8: Records of the grey seal H. grypus from the Sub-Boreal and Sub-Atlantic. – Triangle: 3000–1000 BC. Circle: 1000–0 BC. Square: 600 AD – 1500 AD.

(1997) describe one *H. grypus* find from Gotland, which they refer to as being from the period between 7300–6600 BC, i. e., the late Ancylus and early Litorina stage of the Baltic Basin.
Because of the temporal and spatial distribution of grey seal finds in relation to the geological development of the Baltic Basin, it seems unlikely that the species lived in the Ancylus Lake. In this case, immigration into the basin would have to have happened at the end of the Yoldia stage at the latest (c. 8750 BC). It is more plausible that the specimen in LINDQVIST & POSSNERT (1997) reached the young Baltic Basin via the Öresund at a very early time. This assumption is also discussed by LINDQVIST & POSSNERT (1997) and UKKONEN (2002). Aside from that, the find site – the Stora Fövar Cave – is also covered with Neolithic layers, so that the early dating of the find should not be overrated.
Contrary to present knowledge, a Post-Glacial isolation of grey seals in the Ancylus Lake has been declared in literature of the past (ANDERSON 1994; DAVIES 1957).

When studying sub-fossil records of *H. grypus* it can be seen that they are restricted, with only a few exceptions, to the western Baltic area. Indeed, a convergence with the Ertebølle culture that specialized on, amongst others, seal hunting, is possible in this region in chronozone IV (5300–3800 BC); however, finds from the Sub-Atlantic also show a western distribution. A further reference for the assumption of a western distribution in the middle and younger Holocene is the fact that numerous ringed and harp seals had been hunted on the coast of the Gulf of Bothnia during this period (Fig. 4 and 5), while the grey seal was hardly ever found. Only in modern times the range of the Baltic *H. grypus* population has moved to the north-eastern Baltic area.

Bearded Seal (Erignathus barbatus)

Only a few sub-fossil records of the bearded seal exist in Europe. The seven sub-fossil assemblages that included *Erignathus barbatus* were all recovered in the area of the former Swedish west coast on the Kattegat/Skagerrak (LEPIKSAAR 1964; FREDEN 1975). With the help of deposits in the sediment and several ^{14}C dates, these finds are assigned to the Late-Glacial (FREDEN 1975).
The Arctic bearded seal, which is especially found in areas with drift-ice (Kapel 1994b), lived along the margin of the melting Scandinavian ice sheet and ventured to the south-western glacial margin of the Baltic Ice Lake in the Allerød. During the Baltic's Yoldia phase, bearded seals reached the Vänern Basin, documented by the find from Grums with a radiocarbon age of 10105±180 BP (FREDEN 1975). Since the Yoldia stage, the species has not occurred in the Baltic Basin again.
In the Sub-Boreal and Iron Age, *E. barbatus* has been recorded in the Finland region on the Norwegian coast of the Barent Sea (RENOUF 1989). Evidence for its occurrence in modern times is provided by a find from Spitsbergen (VAN WIJNGAARDEN-BAKKER & PALS 1981); nowadays, the species can occasionally be found in these coastal regions (KAPEL 1994b).

Mediterranean Monk Seal (Monachus monachus)

Sub-fossil records of the monk seal in Europe are restricted to the Mediterranean and Black Sea. The species has been recorded from the Spanish south coast in the Late-Glacial (BATE 1928; ZEUNER 1953; BOESSNECK & VON DEN DRIESCH 1980; RODRIGO GARCÍA 1994), and cave finds exist from Sardinia in the Atlantic period (TAGLIACOZZO 1993). In the Sub-Boreal, *M. monachus* is documented in Sardinia and on the Aegean coast of southern Greece (VON DEN DRIESCH & BOESSNECK 1990; TAGLIACOZZO 1993).
In the Black Sea region only two sub-fossil assemblages include bones of the monk seal. The first was detected in western coast region (Dobrudsha) and dated to the late Atlantic (NOBIS & NINOV 2002). The other was recorded at the mouth of the Bug and assigned to the Roman Times (CALKIN 1960).
Compared to the present European distribution pattern (DUGUY & MARCHESSAUX 1994), no change in range of *Monachus monachus* seems to have taken place since the Late-Glacial. Possible local shifts of distribution within the Mediterranean Sea cannot be shown due to the small range of data available.

Summary

In sub-fossil assemblages on the European coasts, six species of Phocidae have been documented so far: grey seal (169 records), ringed seal (97 records), harp seal (92 records), harbour seal (66 records), bearded seal (10 records) and Mediterranean monk seal (12 records).
The ringed seal, *Phoca hispida*, was the only species to arrive via the Närkesund in the Baltic Basin during the Late Glacial/Pre-Boreal and to have reproduced there. Ringed seal bones from the Finnish coast confirm the presence of the species in the Gulf of Bothnia during the Ancylus phase from 8750–7240 BC. Therefore, seal remains from the Older Holocene and early Atlantic were more frequently found far away from the coasts towards the interior, compared to later time periods. While the Gulf of Bothnia and Finland have obviously been settled by *P. hispida* since the Holocene, the species seems to have occurred only sporadically in the western Baltic area since the Sub-Atlantic.
Grey seals *(Halichoerus grypus)* are much more frequently represented in the sub-fossil assemblages of Europe than all the other phocids and have been recorded in European coastal waters since the Late Glacial. During the Ancylus phase of the Baltic Sea, grey seals settled along the West-Swedish coast on the Skagerrak.
Given the temporal and spatial distribution of grey seal finds in relation to the geological development of the Baltic Basin, it seems unlikely that the species lived in the Ancylus Lake. Contrary to present knowledge, a post-Glacial isolation of grey seals in the Ancylus Lake has been argued in past literature. The range of the Baltic *H. grypus* population has only moved to the north-eastern Baltic area in modern times.
Harp seals spread to the Vänern Basin, i. e., the passage to the Baltic Ice Lake or Yoldia Sea, during the Allerød and Dryas III. Immigration into the Baltic Basin during that period appears very doubtful due to ecological reasons, and is clearly rejected by the analysis of available sub-fossil assemblages. In recent times, it was confirmed for the first time that reproduction of the species had indeed occurred in the Baltic. The conspicuously small phenotype of Sub-Boreal harp seals, which has been described as *Phoca groenlandica neolithica*, is certainly connected to this fact. It is assumed that harp seals migrated into the Baltic Sea during the second half of the Atlantic. There also seems to be a connection between both the immigration and reproduction of *P. groenlandica* in the Baltic Sea and the developing environmental

conditions in the Baltic water body. In the Sub-Boreal, the distribution and frequency of *P. groenlandica* in the Baltic Sea apparently reached their maximum in Post-Glacial times. The reproducing harp seal population vanished in the Sub-Atlantic.
The harbour seal *(Phoca vitulina)* is the most recent immigrant among the seals of northern European coastal waters. Harbour seals have spread in northern Scotland, on the Dutch coast and in the Baltic Sea since the Sub-Boreal at the latest. The relatively recent records of the species in the Baltic indicate a settlement of the western Baltic Sea. Harbour seals have occurred in the Baltic Sea for about 6000 years.
The Arctic bearded seal *(Erignathus barbatus)* lived along the margin of the melting Scandinavian ice sheet and ventured to the south-western glacial margin of the Baltic Ice Lake in the Allerød. During the Baltic's Yoldia phase, bearded seals reached the Vänern Basin. The species has not occurred in the Baltic Basin since the Yoldia stage.
The Mediterranean monk seal *(Monachus monachus)* has been recorded in the Mediterranean Sea during the Late-Glacial and in the Black Sea during the Roman Times.

Zusammenfassung

Im subfossilen Knochenfundgut der europäischen Küstengebiete konnten bisher Kegelrobbe (169 Fundstellen), Ringelrobbe (97 Fundstellen), Sattelrobbe (92 Fundstellen), Seehund (66 Fundstellen), Bartrobbe (10 Fundstellen) und Mönchsrobbe (12 Fundstellen) nachgewiesen werden.
Die Ringelrobbe *Phoca hispida* gelangte im Präboreal als einzige Robbenart durch den Närkesund in das Ostseebecken und konnte sich dort fortpflanzen. Ringelrobbenknochen der finnischen Küste belegen die Art während der Ancylusphase von ca. 8750–7240 BC im Gebiet des heutigen Bottnischen Meerbusens. Daher wurden Robbenreste aus dem Altholozän bzw. frühen Atlantikum gegenüber den späteren Zeitepochen häufiger weit im Binnenland angetroffen. Während der Bottnische und Finnische Meerbusen offensichtlich seit dem Holozän von *P. hispida* besiedelt sind, scheint die Art im westlichen Ostseegebiet seit dem Subatlantikum nur noch sporadisch vorzukommen.
Kegelrobben *(Halichoerus grypus)* sind im subfossilen Fundgut Europas wesentlich häufiger als alle anderen Phociden repräsentiert und können seit dem Spätglazial im europäischen Küstengebiet nachgewiesen werden. Während der Ancylusphase der Ostsee haben Kegelrobben an der westschwedischen Küste im Gebiet des Skagerrak gelebt.
Aufgrund der zeitlich-räumlichen Verbreitung von Kegelrobbenfunden in Verbindung mit der geologischen Entwicklung des Ostseebeckens ist es unwahrscheinlich, dass Kegelrobben im Ancylussee lebten. In der Literatur wurde in der Vergangenheit entgegen den heutigen Erkenntnissen eine postglaziale Isolierung von Kegelrobben im Ancylussee postuliert.
Das Siedlungsgebiet der Ostseepopulation von *H. grypus* hat in der Neuzeit seinen Schwerpunkt von der westlichen Ostsee in das nordöstliche Ostseegebiet verlagert.
Sattelrobben lebten während des Allerød und Dryas III im Vänernbecken, der Passage zum Baltischen Eissee bzw. Yoldiameer. Eine Einwanderung in das Ostseebecken während dieser Phase erscheint aus ökologischen Gründen höchst zweifelhaft und wird besonders im Hinblick auf die Auswertung der zur Verfügung stehenden subfossilen Knochenfunde klar abgelehnt.
In jüngster Zeit wurde erstmalig nachgewiesen, dass sich die Art im Subboreal in der Ostsee fortgepflanzt hat. Mit dieser Tatsache im Zusammenhang steht sicherlich die auffallende kleine Morphe der subborealen Sattelrobben, die als *Phoca groenlandica neolithica* beschrieben wurde. Sattelrobben sind vermutlich in der zweiten Hälfte des Atlantikums in die Ostsee eingewandert. Einwanderung und Fortpflanzung von *P. groenlandica* in der Ostsee im Atlantikum und Subboreal steht wahrscheinlich im Zusammenhang mit der Entwicklung Umweltbedingungen im Ostsee-Wasserkörper. Im Subboreal erreichen Verbreitung und Häufigkeit von *P. groenlandica* in der Ostsee offensichtlich ihren Höhepunkt in postglazialer Zeit. Der sich reproduzierende Sattelrobbenbestand der Ostsee erlosch im Subatlantikum.
Der Seehund *(Phoca vitulina)* ist der jüngste Einwanderer unter den Robben der nordeuropäischen Küstengewässer. Seehunde sind in Nordschottland, an der niederländischen Küste und in der Ostsee spätestens seit dem Subboreal verbreitet. Diese relativ jungen Belege des Seehundes in der Ostsee weisen auf eine Besiedlung der westlichen Ostsee hin. Das Seehundvorkommen in der Ostsee existiert seit etwa 6000 Jahren.
Die arktische Bartrobbe *(Erignathus barbatus)* hielt sich am Rande des schmelzenden Skandinavischen Eisschildes auf und gelangte im Allerød bis zum südwestlichen Gletscherrand des Baltischen Eissees. Während der Yoldia-Phase der Ostsee erreichten Bartrobben das Vänernbecken. In der Post-Yoldia-Phase kommt die Bartrobbe nicht mehr im Ostseebecken vor.
Die Mönchsrobbe *(Monachus monachus)* kann in Europa im Spätglazial im Mittelmeergebiet und für die Kaiserzeit im Schwarzen Meer nachgewiesen werden.

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Literature

AARIS-SØRENSEN, K. (1978): Knoglematerialet fra den mellemneolitiske boplads ved Korsnäs. Grödinge socken. Södermanland. Riksantikvarieämbetet och Statens Historiska Museer, Rapport 8, Stockholm.

AARIS-SØRENSEN, K. (1992): Deglaciation chronology and Reimmigration of large Mammals. A south Scandinavian example from Late Weichselian-Early flandrian. Courier Forsch.-Inst. Senckenberg 153, Frankfurt/Main, 143–149.

ALTUNA, J. (1972): Fauna de Mamíferos de los Yacimientos prehistoricos de Guipuzcoa. Munibe 24, San Sebastián.

ALTUNA, J. (1986): The mammalian faunas from the prehistoric site of La Riera. In: L. G. Straus & G. Clark, La Riera Cave, Stone Age Hunter Gatherer adaptations in Northern Spain. Anthropological Papers of University of Arizona 36, 237–274, 421–479, 481–497.

ALTUNA, J. & L. G. STRAUS (1976): The solutrean of Altamira. The artifactual and faunal evidence. Zephyrus 26/27, 175–182.

ANDERSON, S. S. (1994): *Halichoerus grypus* (Fabricus 1791) – Kegelrobbe. In: J. NIETHAMMER &. F. KRAPP (Hrsg.), Handbuch der Säugetiere Europas 6/II. Wiesbaden, 97–115.

AILIO, J. (1909): Die steinzeitlichen Wohnplatzfunde in Finland 1 und 2. Helsingfors.

BATE, D. M. A. (1928): The Animal Remains. In: D. A. E. Garrod, L. H. D. Buxton, G. Elliot Smith & D. M. A. Bate, Excavation of a Mousterian Rock-Shelter at Devil's Tower, Gibraltar. The Journal of the Royal Anthropological Institute of Great Britain and Ireland 58, 33–113.

BENECKE, N. (1999): The Project »The Holocene History of the European Vertebrate Fauna«. In: N. Benecke (Hrsg.), The Holocene History of the European Vertebrate Fauna. Archäologie in Eurasien 6. Rahden/Westf., 151–161.

BJÖRCK, S. (1995a): Late Weichselian to early Holocene development of the Baltic Sea – with implications for coastal settlements in the southern Baltic region. In: A. Fischer (Hrsg.), Man and Sea in the Mesolithic. Oxford, 23–34.

BJÖRCK, S. (1995b): A review of the history of the Baltic sea, 13.0–8.0 ka BP. Quarternary International 27(1), 19–40.

BJÖRCK, S. (1996): Late Weichselian/Early Preboreal Development of the Öresund Strait; a Key Area for northerly Mammal Migration. Acta Archaeologica Lundensia, Series in 8°, 24, 123–134.

BOESSNECK, J. & A. VON DEN DRIESCH (1979): Die Tierknochenfunde mit Ausnahme der Fischknochen. In: Eketorp. Befestigung und Siedlung auf Öland/Schweden. Die Fauna. Stockholm, 24–421.

BOESSNECK, J. & A. VON DEN DRIESCH (1980): Tierknochenfunde aus vier südspanischen Höhlen. Studien über frühe Tierknochenfunde von der Iberischen Halbinsel 7. München, 1–83.

BRINKHUIZEN, D. C. (1979): Preliminary notes on fish remains from archaeological sites in The Netherlands. Palaeohistoria 21, 83–90.

CALKIN, V. I. (1960): Domašnie i dikie ivotnye severnogo Pričernomor'ja v ėpochu rannego eleza. In: Materialy i issledovanija po archeologii SSSR 53. Moskva, 7–109.

CLASON, A. T. (1967): Animal and Man in Holland's Past. Palaeohistoria 13. Groningen.

DAVIES, J. L. (1957) : The geography of the Gray Seal. J. Mammal. 38, 297–310.

DEGERBØL, M. (1951): Det osteologiske materiale. Knoglemateriale fra en ny udgravning i Vistehulen i Norge. In: H. Egenæs, Fangst-boplassen i Vistehulen på Vist, Randaberg, Nord-Jæren. Stavanger, 52–93.

DRIESCH, A. VON DEN & J. BOESSNECK (1990): Die Tierreste von der mykenischen Burg Tiryns bei Nauplion/Peloponnes. Tiryns. Forschungen und Berichte 11. Mainz, 87–164.

DUGUY, R. & D. MARCHESSAUX (1994): *Monachus monachus* (Hermann 1779) – Mönchsrobbe. In: J. Niethammer & F. Krapp (Hrsg.), Handbuch der Säugetiere Europas 6/II. Wiesbaden, 250–267.

EHLERS, J. (1994: Allgemeine und historische Quartärgeologie. Stuttgart.

EKMAN, S. (1922): Djurvärldens utbredningshistoria på Skandinaviska halvön. Upsala.

EKMAN, J. & E. IREGREN (1984): Archaeo-Zoological Investigations in Northern Sweden. Early Norrland 8, Stockholm.

ERICSON, P. (1989): Säl och säljakt I Österjöområdet under stenåldern. University of Lund, Report Series 33, 57–64.

FINLAY, J. (1996): Human and animal bone. In: R. J. Mercer, The excavation of a succession of prehistoric round-houses at Cnoc Stanger, Reay, Caithness, Highland, 1981–2. Proceedings of the Society of Antiquaries of Scotland 126, 183–184.

FORSTÉN, A. (1972): The Refuse Fauna of the Mesolithic Suomusjärvi Period in Finland. Finskt Museum 1972, 74–84.

FORSTÉN, A. (1979): Subfossil grey seal *(Halichoerus grypus)* from Teuva, W. Finland. Memoranda Soc. Fauna Flora Fennica 55, 10.

FORSTÉN, A. & P. ALHONEN (1975): The subfossil seals of Finland and their relation to the history of the Baltic Sea. Boreas 4, 143–155.

FORSTÉN, A. & P. ALHONEN (1977): Additional subfossil seals from Finland. Commentationes Biologicae 84. Helsinki, Helsingfors.

FORSTÉN, A. & L. BLOMQVIST (1977): Refuse Faunas of the Vantaa Mesolithic and Neolithic Periods. Finskt Museum 1974, 50–55.

FREDÉN, C. (1975): Subfossil finds of arctic whales and seals in Sweden. Sveriges Geologiska Undersökning, Serie C NR 710.

GELDER-OTTWAY, S. VAN (1988): Animal bones from a pre-roman iron age coastal marsh site near Middelstum (province of Groningen, the Netherlands). Palaeohistoria 30, 125–144.

GRAY, A. (1983): The animal remains. In: P. Ashbee, Halangy Porth, St. Mary's, Isles of Scilly, Excavations 1975–76. Cornish Archaeology 22, 38–39.

JAHNKE, W. (1996): Eustasie und Isostasie und ihre Auswir-

kungen auf den Meeresspiegel. In: Warnsignale aus der Ostsee. Berlin, 30–47.

JAHNKE, W. & LAMPE, R. (2000) : Zu Veränderungen des Meeresspiegels an der vorpommerschen Küste in den letzten 8000 Jahren. Zeitschr. geol. Wiss. 28 (6), 585–600.

JONSSON, L. (1988): The vertebrate faunal remains from the Late Atlantic settlement Skateholm in Scania, South Sweden. In: L. Larsson (Hrsg.), The Skateholm Project. I. Man and Environment. Acta Regiae Societatis Humaniorum Litterarum Lundensis 79. Stockholm, 56–88.

JONSSON, R. (1972): Osteologisk analys av benmaterial från det vikingatida-tidigmedeltida Köping på Öland. Tor 15, 234–236.

KAPEL, F. O. (1994a): *Phoca groenlandica* (Erxleben, 1777) – Sattelrobbe. In: J. Niethammer & F. Krapp (Hrsg.), Handbuch der Säugetiere Europas 6/II. Wiesbaden, 196–224.

KAPEL, F. O. (1994b): *Erignathus barbatus* (Erxleben, 1777) – Bartrobbe. In: J. Niethammer & F. Krapp (Hrsg.), Handbuch der Säugetiere Europas 6/II. Wiesbaden, 80–96.

KUBASIEWICZ, M. (1958): Szczątki zwierzęce ze stanowiska neolitycznego w Ustowie, pow. Szczecin. Materiały Zachodniopomorskie 4, 41–48.

LANG, G. (1994): Quartäre Vegetationsgeschichte Europas. Jena.

LEPIKSAAR, J. (1961): Tierreste der Siedlungen von Valleberga und Rinkaby. In: M. Strömberg, Untersuchungen zur jüngeren Eisenzeit in Schonen. Acta Archaeologica Lundensia, Series in 8°, 4, 220–229.

LEPIKSAAR, J. (1964): Subfossile Robbenfunde vor der Schwedischen Westküste. Zeitschr. Säugetierkd. 29 (5), 257–266.

Lepiksaar, J. (1966): Zahnwalfunde in Schweden. Bijdragen tot de Dierkunde 36, 3–16.

LEPIKSAAR, J. (1974): Djurrester från den mellanneolitiska (gropkeramiska) boplatsen vid Äs, Romfartuna sn, Västmanland. In: L. Löfstrand, Yngre stenålderns kustboplatser. Archaeological studies, Uppsala University Institute of North European Archaeology, Uppsala, 140–156.

LEPIKSAAR, J. (1986): The holocene history of theriofauna in Fennoscandia and Baltic countrys. Striae 24, 51–70.

LINDQVIST, C. & G. POSSNERT (1997): The subsistence economy and diet at Jakob/Ajvide, Eksta Parish and other prehistoric dwelling and burial sites on Gotland in long term perspective. In: Burenhult (Hrsg.), Remote Sensing. Applied techniques for the study of cultural resources and localization, identification and documentation of sub-surface prehistoric remains in Swedish archaeology. I. Thesis and Papers in North-European Archaeology 13:a. Hässleholm.

LÕUGAS, L. (1997): Post-Glacial development of vertebrate fauna in Estonian water bodies – a palaeozoological study. Dissertationes Biologicae Universitatis Tartuensis 32. Tartu.

LÕUGAS, L. (1998): Postglacial invasions of the harp seal *(Pagophilus groenlandicus)* into the Baltic sea. Proceedings of the Latvian Academy of Sciences, Section B 25 (1/2), 63–69.

LÕUGAS, L. (1999): Postglacial development of fish and seal faunas in the Eastern Baltic water systems. In: N. Benecke (Hrsg.), The Holocene History of the European Vertebrate Fauna. Archäologie in Eurasien 6. Rahden/Westf., 185–200.

NOBIS, G. & L. NINOV (2002): Zur Fauna der prähistorischen Siedlung Durankulak, Bez. Tolbuchin (NO Bulgarien) II. Die Kupferzeit. Bonner zool. Monogr. 51, 29–59.

PALO, J. U., H. S. MÄKINEN, E. HELLE, O. STENMAN & R. VÄINÖLÄ (2001): Microsatellite variation in ringed seals *(Phoca hispida)*: genetic structure and history of the Baltic Sea population. Heredity 86, 609–617.

REICHSTEIN, H. (1991): Die wildlebenden Säugetiere von Haithabu (Ausgrabungen 1966–1969 und 1979–1980). Berichte über die Ausgrabungen in Haithabu 30, Neumünster.

REICHSTEIN, H. (1995): Erste Nachweise zum Vorkommen von Hauseseln im mittelalterlichen Schleswig-Holstein. Ausgrabungen in Schleswig, Berichte und Studien 11. Neumünster, 179–187.

RENOUF, M. A. P. (1989): Prehistoric Hunter-Fishers of Varangerfjord, Northeastern Norway. Reconstruction of settlement and subsistence during the Younger Stone Age. British Archaeological Reports, International Series 487. Oxford.

REQUATE, H. (1962): Über nacheiszeitliche Säugetiere und die Geschichte der Haustiere in Schleswig-Holstein. Zeitschr. Tierzüchtung u. Züchtungsbiologie 77, 242–253.

RODRIGO GARCÍA, M. J. (1994): Remains of Melanogrammus aeglefinus (Linnaeus, 1758) in the Pleistocene-Holocene passage of the Cave of Nerja, Málaga/Spain. Offa 51, 348–351.

ROSENLUND, K. (1976): Catalogue of subfossil Danish vertebrates. Fishes. København.

SAARNISTO, M., T. GRÖNLUN & I. EKMAN (1995): Lateglacial of Lake Onega – contribution to the history of the eastern Baltic basin. Quaternary International 27 (1), 111–120.

SAARNISTO, M. & T. SAARINEN (2001): Deglaciation chronology of the Scandinavian Ice Sheet from the Lake Onega Basin to the Salpausselka End Moraines. Global and Planetary Change 31 (1–4), 387–405.

SALMI, M. (1963): Drei subfossile Sattelrobben aus Ostbottnien. Geologische Datierung der Funde und einige chronologische Beobachtungen. Archivum Soc. Zool. Botanicae Fennicae »Vanamo« 18, 82–95.

SAURAMO, M. (1958): Die Geschichte der Ostsee. Ann. Acad. Sci. Fennici (Ser. A), 1–522.

SELLSTEDT, G. (1966): Djurbensmaterial från järnåldersboplatserna vid Ormöga och Sörby-tall på Öland. Fornvännen 61, 1–13.

SOMMER, R. & N. BENECKE (2002): Postglacial history of the harbour seal *(Phoca vitulina)* in the Baltic sea. Mammalian Biology 67 (Suppl.), 37.

STRAUS, L. G., J. ALTUNA, G. A. CLARK, M. GONZÁLEZ MORALES, H. LAVILLE, A. LEROI-GOURHAN, M. MENÉNDEZ DE LA HOZ & J. A. ORTEA (1981): Paleoecology at La Riera (Asturias, Spain). Current Anthropology 22 (6), 655–682.

SUTHERLAND, S. (1983): Microfauna identified in the sieve residue from the floor of ST3. In: J. W. Hedges, Isbister. A chambered tomb in Orkney. British Archaeological Reports, British Series 115, Oxford, 149–150.

STORÅ, J. (2001): Reading Bones. Stone age hunters and seals in the Baltic. Stockholm Studies in Archaeology 21.

STUIVER, M., P. J. REIMER, E. BARD, J. W. BECK, G. S. BURR, K. A. HUGHEN, B. KROMER, F. G. MCCORMAC, J. VAN DER PLICHT & M. SPURK (1998): Intcal 98 Radiocarbon Age Calibration, 24,000-0 cal BP. Radiocarbon 40, 1041–1083.

TAGLIACOZZO, A. (1993): Archeozoologia della Grotta dell'Uzzo, Sicilia. Boll. Paletn. Ital. N. S. II Suppl. 84. Roma.

TEICHERT, L. (1989): Das Tierknochenmaterial der ertebölle-zeitlichen Fundorte von Ralswiek-Augustenhof und Lietzow-Buddelin, Kr. Rügen. Veröff. Mus. Ur- u. Frühgesch. Potsdam 23, 59–73.

UKKONEN, P. (2002): The early history of seals in the northern Baltic. Ann. Zool. Fennici 39 (in press).
WIJNGAARDEN-BAKKER, L. H. VAN & J. P. PALS (1981): Life and work in Smeerenburg. The bio-archaeological aspects. I. P. P. Publicatie 300. Amsterdam, 133–151.
WOODMAN, P. C. (1978): The chronology and economy of the Irish Mesolithic: some working hypotheses. In: P. Mellars, The Early Postglacial Settlement of Northern Europe. An Ecological Perspective. London, 333–369.
ZEILER, J. T. (1995): Hunting, fowling and stock-breeding at neolithic sites in the western and central Netherlands. Dissertation, Groningen.
ZEUNER, F. E. (1953): The Chronology of the Mousterian at Gorham's Cave, Gibraltar. Proceedings of the Prehistoric Society 19, 180–189.

Appendix a: ^{14}C datings of subfossil seal bones.

No.	seal-species	locality	^{14}C dating	Reference
1	*Phoca groenlandica*	Våxtorp	11720 ± 175 BP	Fredén 1975
2	*Phoca groenlandica*	Sköttorp	11280 ± 165 BP	Fredén 1975
3	*Phoca groenlandica*	Hästefjorden	10875 ± 160 BP	Fredén 1975
4	*Phoca groenlandica*	Hästefjorden	10235 ± 155 BP	Fredén 1975
5	*Phoca groenlandica*	Ottörn	3215 ± 100 BP	Fredén 1975
6	*Phoca groenlandica*	Närpiö	5890 ± 70 BP	Ukkonen 2002
7	*Phoca groenlandica*	Espoo	5290 ± 175 BP	Ukkonen 2002
8	*Phoca groenlandica*	Alatornio	4810 ± 70 BP	Ukkonen 2002
9	*Phoca groenlandica*	Vaasa	2995 ± 70 BP	Ukkonen 2002
10	*Phoca groenlandica*	Pietarsaari	2800 ± 65 BP	Ukkonen 2002
11	*Phoca groenlandica*	Kudruküla	4835 ± 100 BP	Lõugas 1997
12	*Phoca groenlandica*	Loona	4270 ± 75 BP	Lõugas 1997
13	*Phoca hispida*	Kudruküla	4750 ± 100 BP	Lõugas 1997
14	*Phoca hispida*	Nurmo	9505 ± 85 BP	Ukkonen 2002
15	*Phoca hispida*	Ylistaro	8495 ± 80 BP	Ukkonen 2002
16	*Phoca hispida*	Kovjoki	8270 ± 80 BP	Ukkonen 2002
17	*Phoca hispida*	Ähtävä	8195 ± 135 BP	Ukkonen 2002
18	*Phoca hispida*	Muhos	5115 ± 75 BP	Ukkonen 2002
19	*Phoca hispida*	Laholm	13425 ± 160 BP	Fredén 1975
20	*Phoca hispida*	Mölndal	10760 ± 270 BP	Fredén 1975
21	*Phoca hispida*	Bjärtrå	6085 ± 115 BP	Fredén 1975
22	*Halichoerus grypus*	Uddevalla	10170 ± 215 BP	Fredén 1975
23	*Halichoerus grypus*	Göteborg	10140 ± 150 BP	Fredén 1975
24	*Halichoerus grypus*	Västra Frölunda	9410 ± 100 BP	FREDÉN 1975

Appendix b: Localitys of subfossil seal-bone finds in europe.

Germany: Alt Lübeck/Schleswig Holstein, Elisenhof/Nordfriesland, Feddersen Wierde/Wesermünde, Haithabu/Schleswig-Flensburg, Oldenburg/Ostholstein, Marienbad/Ostholstein, Rosenhof/Ostholstein, Schleswig/Schleswig-Flensburg, Starigard/Ostholstein, Süssau/Ost holstein, Wolkenwehe/Stormarn, Alt Lübeck/Lübeck, Zirkow/Kr. Rügen, Ralswiek/Kr. Rügen, Lietzow/Kr. Rügen, Arkona/Kr. Rügen, Niens/Lkr. Westliche Altmark, Wangels/Ostholstein, Prohn/Kr. Nordvorpommern, Wismar, Rerik/Kr. Bad Doberan, Heidmoor/Segeberg, Neustadt/Ostholstein, Timmendorf/Nordwestmecklenburg.
Denmark: Ågab/Fyns Amt/Langeland, Århus/Århus Amt, Øgaarde/Holbæk Amt, Bjørnsholm/Ålborg Amt, Bundsø/Sønderborg Amt, Dalshøj/Bornholm Amt, Dyrholmen/Randers Amt, Ertebølle/Ålborg Amt, Hesselø, Kainsbakke/Djursland, Koustrup/Randers Amt, Langø/Odense Amt, Lidsø/Maribo Amt, Næsholm/Holbæk Amt, Norsminde/Århus, Sølager/Frederiksborg Amt, Sølager/Frederiksborg Amt, Spodsbjerg/Fyns Amt/Langeland, Svaleklint/Frederiksborg Amt, Tybrind Vig/Fyn, Vedbæk Boldbaner/Københavns Amt, Lyø/Svendborg Amt, Lindø/Svendborg Amt, Kolind/Randers Amt, Sorte Muld/Bornholm Amt, Holbæk (Fst. Ahlgade/Holbæk Amt, Havnø/Ålborg Amt, Aggersund/Nordjylland, Fannerup/Randers Amt, Mejlgaard/Randers Amt, Aamølle/Randers Amt, Virksund/Viborg Amt, Blegkilde/Ålborg Amt, Gudumlund/Ålborg Amt, Klintesø/Holbæk Amt, Jægerspris/Frederiksborg Amt, Havelse/Frederiksborg Amt, Sejrø/Holbæk Amt, Ørum/Randers Amt, Ålborg (Fst. Signalbakken/Ålborg Amt, Munkholm/Holbæk Amt, Frennemark/Bornholm Amt, Eltang Vig/Vejle Amt, Borrebjerg/Holbæk Amt, Svaneke/Bornholm Amt, Ølby Lyng/Københavns Amt, Villingebæk/Frederiksborg

Amt, Argusgrunden/Maribo Amt, Nivå/Frederiksborg Amt, Bloksbjerg/Københavns Amt, Ordrup Næs/Holbæk Amt, Kassemose/Frederiksborg Amt, Næbbet/Ærø, Stigtehave/Svendborg Amt, Nexelø/Holbæk Amt, Norslund/Århus Amt, Dragør (Fst. Stakhaven)/Københavns Amt, Rugholm/Hjørring Amt, Gjessingård/Randers Amt, Strandgård/Frederiksborg Amt, Strandby/Hjørring Amt, Øland/Hjørring Amt, Vegger/Ålborg Amt, Anholt/Ålborg Amt, Trørød/Københavns Amt, Vordingborg/Præst Amt, Nagelsti/Maribo Amt, Havnelev/Præstø Amt, Møllegabet/Svendborg Amt, Brabrand/Århus Amt, Nymølle/Bornholm Amt, Øsløs/Thisted Amt, Kolding/Vejle Amt, Anholt/Ålborg Amt

*Spain:*Cueva de Altamira/Santander, Cueva de La Riera/Asturias, Gorham's Cave/Gibraltar, La Riera.

Estonia: Kunda/Rakvereskij r., Narva I (Schicht 3 u. 2), Riigiküla, Loona/Kingiseppskij r., Naakamäe/Kingiseppskij r., Asva/Kingiseppskij r., Kõpu/Hiiumaa, Kõnnu/Saaremaa, Kroodi, Kudruküla, Kaseküla, Rebala, Reiu, Lodja, Ilmandu/Tallinskij r., Võhma/Saaremaa, Tõugu/Tallinskij r.

UnitedKingdom: Dun Bhuirg/Iona/Hebriden, Knap of Howar/Westray/Orkney, Newcastle upon Tyne/Tyne and Wear, Segontium/Caernarfon/Gwynedd, Isbister/Orkney, Dun Cul Bhuirg/Iona/Hebriden, Haddenham/Cambridgeshire, Nornour/Cornwall/Isles of Scill, Rattray/Aberdeenshire, Jarlshof/Shetland, Bishopstone/East Sussex, Millknowe/Kintyre, Stanger/Highland, Halangy Porth/St. Mary's/Cornwall, Isles of Scill, May's Hill/St. Martins/Cornwall/Isles of Scill, York (Fst. Tower Street 1–2)/Yorkshire

Ireland: Dalkey (Fst. II u. V)/Dublin.

Norway: Advik/Finnmark, Angsnes/Finnmark, Gropbakkeengen/Finnmark, Høybukt/Finnmark, Oslo (Fst. Gamlebyen, Mindets), Nyelv Nedre Vest/Finnmark, (Fst. Gamlebyen, Sønd), Gressbakken (Fst. Haus 4)/Finnmark, Smeerenburg/Spitzbergen, Viste/Rogaland, Frebergsvik/Vestfold, Ruskenesset/Hordaland

Netherlands: Hekelingen III/Zuid Holland, Leidschendam/Zuid Holland, Rijnsburg/Zuid Holland, Swifterbant/Oostelijk Flevoland, Velsen (Fst. 1)/Noord Holland, Vlaardingen/Zuid Holland, Vogelenzang/Noord Holland, Voorschoten/Zuid Holland, Waterworks of Amsterdam/Noord Holland, Zeewijk/Noord Holland, Bergschenhoek/Zuid Holland, Middelstum (Fst. Boerdamsterw/Groningen, Kolhorn/Noord Holland, Wijnaldum/Friesland, Marsumer Terp/Friesland, Pingjum/Friesland, Den Haag (Fst. Scheveningsewe)/Zuid Holland, Wijnaldum (Fst. Tjitsma)/Friesland, Leeuwarden (Fst. Speelmansstr)/Friesland. *Poland*: Wolin (Stadt, Fst. 4)/Woj. Szczecin, Szczecin (Ustowo, Fst. 1)/Woj. Szczecin, Gdansk (Fst. 1, Wyk. I-V), Sopot/Woj. Gdansk, Rzucewo (Fst. 1)/Woj. Gdansk.

Sweden: Alby/Öland, Äs/Romfartuna, Bjurselet/Västerbotten, Eketorp/Öland, Stockholm (Fst. Helgeandsholm, Ire/Gotland, Köping/Öland, Korsnäs/Södermanland, Varberg (Fst. Kloster)/Halland, Östra Torp (Fst. 19: 1)/Skåne, Rinkaby/Schonen, Segebro/Skåne, Siretorp/Blekinge Amt, Skateholm/Skåne, Skedemosse/Öland, St. Tjikkiträsk/Lappland, Uddevalla/Bohuslän, Valleberga/Skåne, Lund/Skåne, Tankbåten (Ot. von Ystad)/Malmöhus, Sandeplan/Skåne, Leksand/Dalarna, Valbo (Fst. 10, 44, 49, 86 un)/Gästrikland, Jättendal, Håcksta (Fst.)/Hälsingland, Anundsjö Yttersel/Ångermanland, Anundsjö Mellansel/Ångermanland, Otterö/Bohuslän, Rotekärrslid/Bohuslän, Rörvik/Bohuslän, Sotenkanal/Bohuslän, Burgsvik/Gotland, Sjöholmen/Skåne, Bredasten/Stora Herrestad, Rävgrav/Skåne, Dafter/Bohuslän, Rottjärnslid/Bohuslän, Skållehus/Bohuslän, Hermanö-Insel, Gröninge/Halland, Lahebiahöhle/Skåne, Lundfors/Västerbotten, Broberg/Bohuslän, Stora Förvar/Gotland, Gullrum/Gotland, Hemmor/Gotland, Visby/Gotland, Visborgs Kungsladugård/Gotland, Hoburgen (Fst. II)/Gotland, Alvena/Gotland, Ormöga/Öland, Gualöv/Skåne, Limhamn/Skåne, Ravlunda/Skåne, Stehag/Skåne, Löddesborg/Skåne, Överstekvarn/Gotland, Gisslause/Gotland, Lagmansered/Västergötland, Karlstad (Fst. Grums)/Värmland, Sköttorp/Västergötland, Våxtorp/Skåne, Hästefjorden/Bohuslän, Laholm/Halland, Mölndal/Bohuslän, Bjärtrå/Ångermansland, Tuve/Bohuslän, Västra Frölunda/Bohuslän Sotmyra/Uppland, Trönö/Hälsingland, Norrköping/Östergötland, Grums/Värmland, Sandbacken (Ot. von Uppsala)/Upland, Skattmansö/Uppland, Ölmanäs/Halland

Finland: Otterböte/Kökar/Åland, Askola/Uusimaa, Kerava/Kymi, Alavus (Fst. Rautalanvainio)/Suomi, Honkajoki/Turku-Pori, Kuortane/Vaasa, Vantaa/Uusima, Korsnäs (Fst. Orrmoan)/Vaasa, Trofastbacken/Vaasa, Kolsvidja/Åland, Teuva/Vaasa, Ähtävä/Vaasa, Kovjoki/Vaasa, Ylistaro/Vaasa, Nurmo/Vaasa, Ilmajoki/Vaasa, Muhos (Fst. Honkala)/Oulu, Ulvila/Turku-Pori, Laihia/Vaasa, Vaasa/Vaasa, Pori/Turku-Pori, Pietersaari/Vaasa, Närpio/Vaasa, Oulainen/Oulu, Lapua/Vaasa, Alatornio/Lappi, Espoo/Kirkkonummi/Uusima, Ruukki/Oulu, Vähäkyrö/Vaasa, Kiukainen (Fst. Uotinmäki)/Turku-Pori, Säräisniemi (Fst. Sillankorwa/Oulu, Wihanti (Fst. Pitkäsaari)/Oulu, Oulujoki/Oulu, Luopioinen (Fst. Hietaniemi)/Häme, Liljendal (Fst. Kvarnbacken)/Kymi