Status of grey seals along mainland Europe from the Southwestern Baltic to France

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ABSTRACT

The grey seal was a common species along mainland Europe during the Stone Age (8,000-5,500 BC). Along the North Sea coast populations started to decline substantially during the 11th century as a result of excessive hunting. The last breeding populations disappeared in the 16th century in the Wadden Sea, and before 1900 in the Kattegat-Skagerrak and the Southwestern Baltic as a result of an extermination campaign. No regular pupping occurred along mainland Europe until the end of the 1970s, when a breeding colony was established near Amrum in the German Wadden Sea. Somewhat later, additional breeding sites were discovered near Terschelling in the Dutch Wadden Sea (1980), at Helgoland, and off Brittany in France. Tracking of movements indicate these seal groups to be linked to the larger populations in the UK. Numbers of grey seals in the recolonised areas have increased over the years, but in the Kattegat-Skagerrak stable numbers of about 25 individuals have been observed since the 1970s, whereas more than 100 grey seals are found in the Southwestern Baltic. In the southeastern North Sea, 120 grey seals occur during moult at Helgoland, 120 in the German and over 1,130 in the Dutch parts of the Wadden Sea in 2004. Along the southern Dutch and Belgian coasts small groups are regularly observed, but no colonies have yet been established. In the colonies off Brittany in France about 105 grey seals have been counted. Successful pupping has only been recorded 3 times in the Kattegat-Skagerrak over the past 30 years, and 2-4 pups are born annually in France and the Southwestern Baltic. The relative strongholds for breeding along the European continent are the Dutch Wadden Sea, where in 2003/2004 at least 150 pups were recorded, Amrum in the German Wadden Sea (23 pups) and Helgoland (8 pups). Consequently, total numbers of counted grey seals from the Southwestern Baltic to France amounted to at least 1,600 in 2004, while about 190 pups were born in the area.

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INTRODUCTION

The history of the grey seal (*Halichoerus grypus*) stocks along the European continent serves as an illustrative example on how man exterminated a formerly abundant seal population, and how protective measures have resulted in re-colonisations in some of their former habitats. We account for the pristine situation in the area and review information on the present status of grey seals in terms of distribution, population sizes and growth rates. We mainly rely on published data from archaeological findings and population counts after the mid 1970s.

HISTORICAL DISTRIBUTION AND TRENDS UNTIL THE 20th CENTURY

The oldest subfossil grey seal remains along the mainland European coast were found in the tributaries of the Dordogne (France) and date from 18,000-14,000 BC (Capitan *et al.* 1906). The oldest subfossil remains from grey seals in the western North Sea date from some 14,000 years ago, and from about 2,000 years later in the Kattegat-Skagerrak and the Limfjord (Lepiksaar 1964, Møhl 1971). Other commonly found species of seals were harp seals (*Phoca groenlandica*) and ringed seals (*Phoca hispida*) (Clark 1946), which are typical Arctic species. Stone Age (younger period about 4,000-2,000 BC) man hunted predominantly grey seal pups, all along the European continent and also set out on seasonal hunting expeditions to more remote grey seal sites such as Hesselø in the Kattegat, where artefacts representing about 400 grey seal pups have been identified (Clark 1946, Møhl 1971). Finds of grey seals were also abundant in natural deposits from France in the south, the Limfjord, and the Kattegat-Skagerrak (Clark 1946, Lepiksaar 1964), and close to settlements in the Dutch and Schleswig Holstein parts of the Wadden Sea and the Dutch North Sea coast (Requate 1956, Reijnders *et al.* 1995). These findings indicate a continuous distribution of grey seal colonies along mainland Europe (Fig. 1).

The fact that more grey seal remains than those of other seal species have been found associated with human settlements does not necessarily imply that the species was more abundant than harbour seals (*Phoca vitulina*). The fact that young grey seal pups are land bound and cannot escape efficiently, renders them easier to hunt.

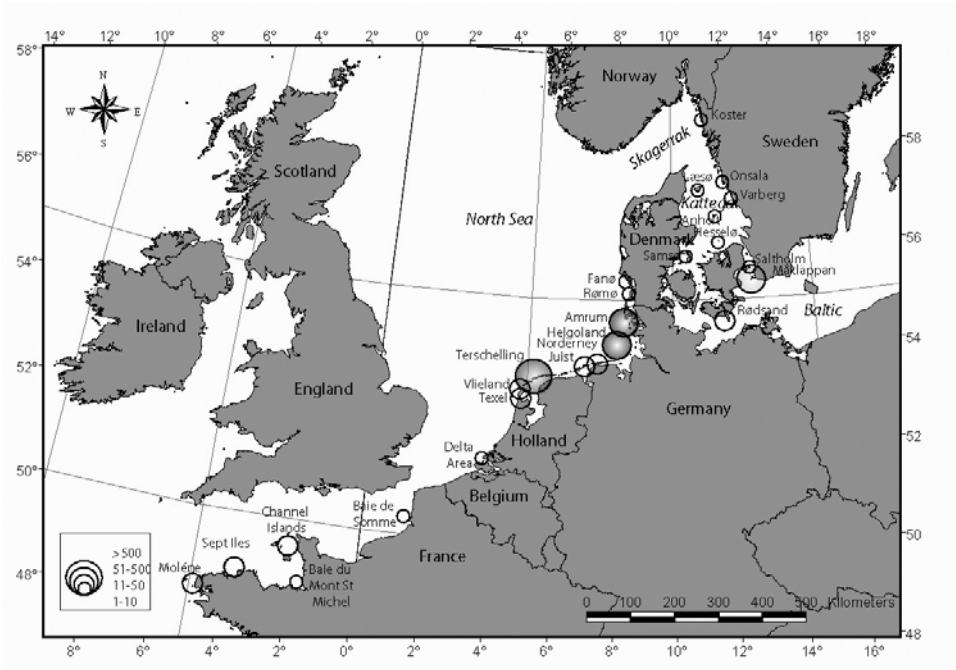

***Fig.1**. Present distribution of grey seals along mainland Europe. Shaded circles indicate regular pupping areas or sites, while hollow circles denote occurrence of grey seals. Occasional pupping also occurs at Rødsand, Måkläppen, and the 5 French localities.*

However, relative changes observed in seal remains, where the ratio between the 2 seal species grew in favour of harbour seals probably demonstrate declining grey seal numbers. Since grey seal remains dominated in natural deposits in some areas such as the Kattegat-Skagerrak, it is assumed that grey seals were more numerous in those regions (Härkönen *et al.* 2005).

The Kattegat-Skagerrak and the Limfjord

Archaeological findings indicate grey seals to have been the most common species of seals in the Kattegat-Skagerrak and the Limfjord until the Iron Age (Lepiksaar 1964, Møhl 1971). Grey seals were hunted in considerable numbers, and it is possible that man contributed to the local extinction of grey seals in the Limfjord during the late Iron Age (about 500 BC) (Møhl 1971). However, geological changes in the region closed the Limfjord off from the North Sea about 750 BC causing great changes in the salinity and ecosystem (Leth 2003). This probably also contributed to the extinction of the grey seal in the fjord. When the Limfjord opened to the North Sea in 1825 the harbour seal re-colonised the fjord but the grey seal is still only rarely seen.

Grey seals were more common than harbour seals in the Kattegat-Skagerrak until the beginning of the 19th century (Bynch 1801), and breeding colonies were found on the Danish islands Læsø and Anholt, and probably also at Hesselø (Joensen *et al.* 1976, Heide-Jørgensen 1980). Around the year 1800, 40-50 grey seal pups were caught each winter at Anholt, which was about half the numbers harvested some decades earlier (Bynch 1801). Throughout the 19th century a continuing decrease was observed (Tauber 1880). Breeding grey seals also occurred along the Swedish West Coast in the beginning of the 19th century at the Koster Islands, Väderöarna, Onsala, Varberg and probably at Hallands Väderö (Malm 1877, Dahlbeck 1974). The peak pupping season for grey seals in the Kattegat-Skagerrak was in January (Bynch 1801), which was suggested as an indication of a breeding population distinct both from the Atlantic grey seals (breeding in September-December) and the Baltic grey seals (breeding in February-March) (Heide-Jørgensen 1980). However, since Atlantic grey seals are known to breed in December at some other sites (Reijnders *et al.* 1995, Reijnders and Brasseur 2003a), the grey seals in the Kattegat-Skagerrak probably were part of the Atlantic stock. All of these breeding colonies probably disappeared in the end of the 19th century, suggesting that the reproducing population of grey seals in the Kattegat-Skagerrak became extinct before 1900 (Søndergaard *et al.* 1976).

The main reason for this dramatic decline, and subsequent extinction, was the introduction of bounty systems in Denmark (1889-1927) and Sweden (1908-1965). During the first year of the bounty system in Denmark (1889-1890) the take of grey seals in Kattegat was 23. The yearly catch dropped to 5 in the period 1919-1922, and remained constant in the last period with 6 caught annually in the period 1923 to 1927, after which the bounty system was abandoned. Until the complete protection of the grey seals in Denmark in 1967, very few grey seals were shot (Søndergaard *et al.* 1976).

The southwestern Baltic and the Danish straits

Grey seals dominated both in natural deposits and in remains at human settlements during the Stone Age (8,500 BC – 3,500 BC) in the area from Poland to Jutland (Clark 1946, Lepiksaar 1964, Møhl 1971, Gill 1978). Grey seals seem to have been abundant in the area until the latter half of the 19th century, when up to 700 grey seals were shot in Poland in single years (Anon. 1890). With the introduction of the bounty systems in Denmark and Sweden the breeding colonies disappeared before 1900 in Danish and Swedish waters and before 1910 in Poland and Germany (Søndergaard *et al.* 1976, Gill 1978, Harding and Härkönen 1999). The detailed Danish statistics shows that in the first year of the bounty system (1889/1890) 111 grey seals were killed in the Danish Baltic. The annual catch dropped to 52 in the period 1919-1922 and further to 50 in the period 1923-1927 (Søndergaard *et al.* 1976). A similar trend is seen in data from the Danish Straits. Here mean annual numbers shot dropped from 17 in 1889/1890 to 13 in 1919 and further to 7 in 1923-1927. However, there is no evidence of breeding colonies in the area during the 20th century.

The Wadden Sea

Sub fossil remains, of which some were dat-

ed back to 10,000 BC (van Bree *et al.* 1992), show that grey seals were present in all Wadden Sea regions and along the Dutch North Sea coast during the Neolithic and early Bronze Age (Requate 1956, Joensen *et al.* 1976, Reijnders 1978). Most of the seal remains found in Dutch deposits, dated from between 2,000 BC and 1,000 AD, originated from grey seals (van Giffen 1913, Clason 1988), which is comparable to finds in the other parts of the Wadden Sea (Reijnders *et al.* 1995). The ratio of grey seals to harbour seals seems to have gradually changed and by 1,000 AD remains of the 2 species occur in about the same quantities. This shift coincides well with growing numbers of human settlements in this area. As dykes were built, more humans settled, and more grey seals could be hunted. By the end of the Middle Ages (1400-1500 AD) grey seals virtually disappeared from the area (Reijnders *et al.* 1995).

Thus, following a long-term decline since the Neolithic, grey seals became extinct in the Wadden Sea and the Dutch North Sea coast by about 1500 AD (Reijnders *et al.* 1995). Up until the mid 20th century, only occasional animals were reported on the Dutch, German, and Danish North Sea coasts (Mohr 1952, van Haaften 1974).

France

The oldest indications for the occurrence of grey seals stem from 18,000-14,000 BC, and were found in tributaries of the Dordogne. Grey seals were depicted on a reindeer antler and grey seal jaws were found as well (Capitan *et al.* 1906). Grey seal remains were found in western and southern Brittany, dating back to 5,000 years ago (A. Tresset, pers. comm., Paillet *et al.* 2004). Many finds came from young animals, suggesting the existence of reproducing grey seal colonies in the area. In more recent times, presence of seals along the French Atlantic coast has been reported since the 16th century, but reliable characteristics of grey seals were only described in 1756 (Robien 1756 in Prieur 1984). However, these later reports do not indicate permanent colonies in the area.

RECENT TRENDS

Reproducing grey seal colonies were not observed along mainland Europe and the Wadden Sea up to the 1970s, after which some sites have gradually been colonised. However, seals older than pups may not have been recognised, since especially young and to some extent female grey seals do not stand out when lying in the midst of harbour seals, when counted from a boat.

The general picture for the development of grey seal stocks, colonies and populations in the North Sea has been described (*e.g.* Reijnders and Brasseur 2003b), but here a more detailed account and a wider geographical coverage is given. The origin of the contemporary grey seals in the Kattegat-Skagerrak, the Wadden Sea, the Dutch and French coasts is not known with certainty. However, genetic studies show considerable divergence between Atlantic and Baltic grey seal populations (Boskovic *et al.* 1996), and further studies on the genetic

Table 1. Occurrence of pups born in the spring (suggesting Baltic origin) or fall-winter (suggesting Atlantic origin) in the Kattegat-Skagerrak since 1965.

Year	Locality	Spring (Feb-Apr)	Fall (Nov-Dec)	Reference
1966	Onsala		1	Dahlbeck (1974)
1967	Onsala		1	Dahlbeck (1974)
1969	Onsala		2	Dahlbeck (1974)
1982	Anholt	1		Dietz & Heide-Jørgensen (1982)
1989	Koster		1	This study
1991	Onsala	1		This study
1993	Skagen		1	Flensted (1997)
1993	Koster		1	This study
1996	Anholt	1		Heide-Jørgensen & Teilmann (1997)
1996	Hirsholmene		1	Flensted (1997)

population structure and movements are necessary to determine the relationship between the populations along mainland Europe (Fig. 1).

The Kattegat-Skagerrak

There are no reliable data on the occurrence of grey seals in the Kattegat-Skagerrak until the late 1960s and the early 1970s, when the first sporadic counts were made. Grey seal yearlings are seen occasionally, and regularly drift ashore from the end of October to late February along the West Coast of Jutland facing the North Sea. These are believed to originate from the Northeast Atlantic population breeding from mid September to mid November, which is supported by tagged pups found on the Danish North Sea coast (Hewer 1974). During the winter 2001-2002 8 grey seals were found on the Danish North Sea coast, of which at least 6 were yearlings (H. Lykke Sørensen, pers. comm.). These seals are often emaciated and therefore often shot by the game wardens if still alive. Pupping records in Kattegat-Skagerrak suggest that the present grey seals in the area originate both from the Atlantic and Baltic populations, since pupping attempts have occurred both in the winter and in the early spring (Table 1).

Grey seals have been counted more systematically in the Kattegat-Skagerrak since 1977, in connection with aerial surveys of harbour seals in August. Land-based counts over the summer period (June-August) have been carried out in some years at Anholt, Koster, Onsala, Varberg and Hallands Väderö since 1977 (Fig. 2). The maximum number counted in the entire area is 26, a magnitude that appears to have been relatively constant over the period 1977 to 2004. This is evident from the sites from where we have sufficiently long time series, such as Koster, Onsala, and Varberg. However, grey seals moult in June when they spend more time on land. Most observations are from August, so the reported numbers of grey seals in Kattegat-Skagerrak should be regarded as minimum estimates.

The Southwestern Baltic and the Danish Straits

At Samsø in the Danish Straits, only single grey seals have regularly been recorded over the past decades. The strait between Denmark and Sweden (Øresund) is the relative stronghold for grey seals in the area, and up to 80 grey seals have been observed in recent years (Teilmann *et al.* 2004) (Fig. 3). One or 2 pups are born annually at Måkläppen in February and March, suggesting a Baltic origin of seals at this locality. Further south at Rødsand in the Danish Baltic, maximum numbers of grey seals have amounted to 18 grey seals (Fig. 3) (Heide-Jørgensen *et al.* 1997, Dietz *et al.* 2000, Edrén *et al.* 2004). This is the highest number observed anywhere in Denmark, and Rødsand is potentially the most likely location where a re-establishment of the population can occur (Dietz *et al.* 2000). Both successful and unsuccessful breeding has taken place here. Since the first documented case, when a dead grey seal pup was found 23 February 1993 (Dietz *et al.* 2000), there have been 2 well nourished pups born, in late February 2003 (Edrén *et al.* 2004). Evidence from satellite telemetry at Rødsand show that grey seals from this area have contact with seal groups along the Swedish east coast. A tagged female from Rødsand was resighted with a pup in Estonia, confirming the connection with the large grey seal population in the Baltic proper (Dietz *et al.* 2003).

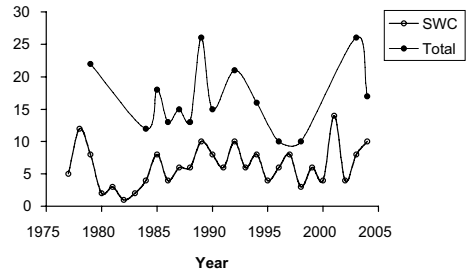

Fig. 2. *Maximum numbers of grey seals counted along the Swedish West Coast (SWC) plus total numbers including the Danish Kattegat over the period 1977-2004. No significant increase is detected in numbers along the Swedish West Coast (P=0.86).*

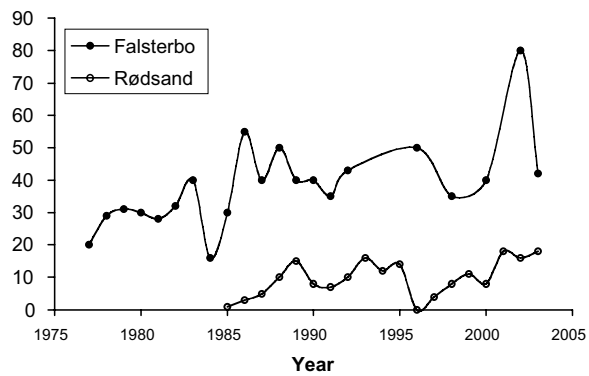

Fig. 3. *Maximum counted numbers of grey seals at the 2 main localities Måkläppen and Rødsand in the Southwestern Baltic. The mean annual rate of increase over the period was 2.7% at Måkläppen and 5.4% at Rødsand.*

The German Wadden Sea and Helgoland

A group of sandbars off the German island of Amrum was the first location in the southeastern North Sea where grey seals occurred regularly again in recent times (Scheibel and Weidel 1988). Sightings by local sailors date back to 1945, and there is 1 birth record from 1957 (Blume 1996), although pupping may not have regularly taken place until 1983 (Scheibel and Weidel, 1988). Pup production has been monitored since the autumn of 1988 through multiple boat surveys and rough age estimation of encountered pups (Abt and Koch 2000, Abt *et al.* 2002). However, survey effort was not constant. The colony has clearly increased in recent years, and since 2001 more than 20 pups per season were born (Figs. 4 and 5). During the peak of the moult in late March / early April 2004, 120 grey seals were reported (Fig. 4). Recent mid-May to early September counts (mostly 5 per year) did not normally exceed 50 seals. Summer counts have on average been increasing at 6% per year since 1976. Single animals as well as small haul-out groups (< 20), and occasional newborn pups have also been seen at other places in the German Wadden Sea, particularly in the westernmost part near the islands of Borkum, Norderney and Juist.

Another stronghold of grey seals in Germany is the island of Helgoland. Regular occurrence of the species is known since 1989 (Graner and Hartwig 1993) and pupping since the mid 1990s (Graner 2000). Fewer pups are born at Helgoland than off Amrum, i.e. 6 records in the winter of 1999/2000 and 8 in 2003/2004. However, as many as 120 moulting seals were counted in April 2004, smilar to numbers seen off Amrum. It is likely that many of these belong to larger breeding colonies elsewhere.

The Dutch Wadden Sea and the Delta area

Grey seals were virtually absent from the Dutch waters until around 1950. This is evident as Ijsseling and Scheygrond (1950) did not consider the species to belong to the Dutch fauna. From then on, observations of individual animals or small groups became more frequent (van Haaften 1974), though they were not using fixed areas, let alone forming colonies. In the early 1980s grey seals established a colony on the sandbank between the Islands of Vlieland and Terschelling (Reijnders *et al.* 1995). As opposed to other

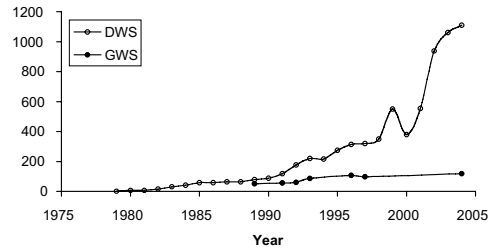

Fig. 4. *Maximum numbers of grey seals counted in the Dutch (DWS) and German (GWS) Wadden Sea, from1979 through 2004. The mean annual rate of increase in Dutch part was 19% (based on spring counts), and in Germany 6% (based on summer counts).*

sandbanks in the Dutch Wadden Sea, this particular site is only occasionally flooded. The development of the colony was successful. By 1985, 60 seals were counted and the first few pups were born, and in the winter 2003/2004 at least 150 pups were born and the total number amounted to over 1,100 animals in the moulting season (April) in 2004 (Reijnders and Brasseur 2003a, Fig. 4). In addition to the relatively large colonies in the Western Wadden Sea, small groups of 2-8 animals are regularly seen in the eastern Dutch Wadden Sea, especially on the sandbanks nearer to the North Sea. Some grey seals are also regularly seen in the southern Netherlands (the Delta area) though numbers remain very low (Fig. 1).

As described by Reijnders *et al.* (1995), regular counts of the seal colony which had settled between the Dutch islands of Vlieland and Terschelling were made by boat until the end of last century. Even though the colony had to move to a more southern sandbank, as the first 1 virtually disappeared, the colony grew steadily to over 500 animals during the moult in March-April 1999 (Fig. 4). In 2000 the numbers counted were only around 400. However, it was discovered (this study) that from 2000 onwards the founding pupping colony remained but also spread out over several sites to the west and the south, around the island of Texel. In these new colonies, around 20-40 km away from the original colony, a single pup is observed only once in a while (Fig. 1).

As boat surveys no longer appeared to be adequate to survey the larger area and numbers

would become considerably underestimated, aerial surveys were initiated in the western part of the Dutch Wadden Sea from 2002 onwards. These surveys take place during pupping in December-January and moult in March-April.

By 2004 the maximum number of grey seals observed in the western Dutch Wadden Sea during 1 survey amounted to over 1,100 animals. In summertime much lower numbers of grey seals are seen, though they are still concentrated around the same general area in the western Wadden Sea. Grey seals also use tidal sandbanks that flood every high tide. It is evident that grey seals in the Netherlands are using sub-optimal sites for pupping (Reijnders 1978). The main pupping site is frequently flooded as a result of spring tides and storms. Pups are then washed off and in some cases rescued and rehabilitated. For example in the winter of 2003-2004 the number of seal pups in rehabilitation (70 pups) exceeded the maximum pup count (61 pups). It therefore remains problematic to correctly estimate total pup production. Hauling out on the islands, which would provide a suitable habitat, is unintentionally discouraged by humans through disturbance and their feeling that seals on land are in distress and need rescue. The discrepancy between the numbers of births and growth rate of the colony can be explained by an influx of seals, most probably from the British Isles. Animals tagged in the Farne Islands in the 1970s were observed to stray to the Wadden Sea including the Netherlands (Hewer 1974, van Haaften 1974) and more recently grey seals tagged on the Isle of May were observed in the Netherlands (Hall *et al.* 2001). The relative importance of this immigration becomes less as pup production in the local colonies increases.

In the southern Netherlands, only small incidental groups of grey seals are observed. In 2003 the maximum number of grey seals observed amounted to 14 in June. This is by far the highest number observed, as for years maximum numbers counted amounted to 5 grey seals (Henk Zandstra pers. comm., Hoekstein *et al.* 2003). During the moult (March-April 2003) 4-6 seals were observed in this area. With an annual growth rate of 20.7% between 1980 and 2004, the colonies in the Wadden Sea numbered to over 1,100 seals in 2004. With the numbers observed in the south of the Netherlands and the ones in the rest of the Wadden Sea, the numbers of grey seals in Dutch waters amounted to at least 1,130 in 2004.

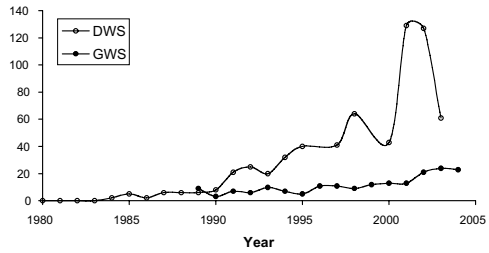

Fig. 5. *Maximum numbers of grey seal pups counted in the Dutch (DWS) and German (GWS) Wadden Sea through the period 1980-2004.*

France

Local names of sites in Brittany suggest long-term persistence of seals along the coast, without specific reference to the species. The earliest reliable records are from stranded grey seals in the 1950s, which also included many young seals tagged in Wales (Lucas 1960). From the 1970s, irregular censuses were conducted by naturalists in the 2 grey seal colonies identified in France: the Molène archipelago and the Sept Îles archipelago (Fig. 1). The maximum number of animals counted at haul-outs increased from 10 to 25 seals over the period 1975 to 1990 in the Molène archipelago (Prieur and Duguy 1981, Duguy and Hussenot 1991), and up to 17 seals were observed in the Sept Îles archipelago in the early 1990s (Siorat *et al.* 1993). Less than 20 grey seal pups were recorded overall in the 2 colonies from 1957 (first birth reported) to 1998, but numbers have been increasing during recent years (Vincent 2001). Duguy and Prieur (1980) concluded that the pup production was too low to explain the persistence of the colonies. It was suggested that the French grey seals constituted a "sink" population, supplied by juvenile seals dispersing from their British natal sites, which is supported by tag recoveries from stranded seals (Duguy and Prieur 1980, Prieur and Duguy 1981, Siorat *et al.* 1993).

Today, grey seals can be observed year-round in the 2 colonies of the Molène and the Sept Îles archipelagos (Fig. 1), with a couple of pups born every year. Many seals are observed along the

mainland coast in the vicinity of these 2 sites, sometimes hauling out on isolated rocks. Grey seals also haul-out and breed on the Channel Islands, and individuals are observed along the French mainland coast at Cotentin, probably coming from these colonies. Increasing numbers of seals are reported elsewhere in the Baie du Mont Saint Michel, and in the Baie de Somme (Fig. 1).

In addition, a significant number of yearlings strand every year along the French Atlantic coast, from the western part of the Channel to the Spanish boarder. Numbers of strandings have varied from 20 to 60 over the last ten years (CRMM, unpublished data). At the minor haul-out sites of the Baie du Mont Saint Michel and the Baie de Somme, where harbour seals are more common, the number of grey seals counted varies seasonally, with a maximum of about ten individuals in each bay. In the Sept Îles archipelago, numbers varied between 10 and 20 in the period 1997 to 2000, and increasing numbers are suggested in recent years. During the same period, the number of seals hauling out in the Molène archipelago varied between 30 and 65. These figures have increased by 7% per year since previous censuses in 1991/1993 (Fig. 6) (Vincent *et al.* 2005). Counts prior to the 1990s in the same area did not follow a strict protocol, so long-term rates of increase cannot be estimated. In 1997/2000, significant differences in seasonal abundance and sex ratio were observed in the Molène archipelago: the maximum numbers of seals were counted during the moulting season (March) and minimum numbers during the pupping season in November. This is late compared to September in South-west England, however similar to the pupping season at the Farne Islands. The sex ratio was highly biased towards males during the moult, and less so during the rest of the year.

Individual movements from the main colony of the Molène archipelago have been assessed by using Satellite Relay Data Loggers (SRDLs). Sixteen wild seals were tracked from 1999 to 2003. Fourteen seals left the archipelago, of which 9 crossed the English Channel to South-west England, Wales, or the Channel Islands (Vincent *et al.* 2005). Two out of 4 rehabilitated juvenile grey seals released in the vicinity of the Molène archipelago in 1997 crossed the Channel, with 1 seal visiting a grey seal colony in South-east Ireland (Vincent *et al.* 2002). Overall, more than half of the 20 seals tracked from western Brittany visited other grey seal colonies overseas. This, together with the seasonal variations in abundance and sex/age structure of the haul-out group of the Molène archipelago, clearly indicates that grey seals in France do not constitute a separate and "sink" population, but probably belong to a larger population in the South-west British Isles that move among sites during their annual cycle.

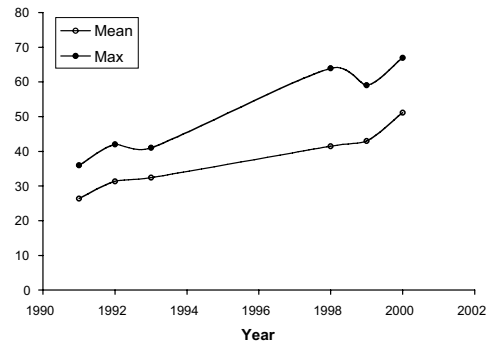

Fig. 6. *Mean and maximum numbers of grey seals counted at Molène in Brittany, France since 1992. The rate of increase, as based on mean numbers, was 7% per year.*

CONCLUSIONS

Archaeological findings show that grey seals were widespread along the European continent before they gradually disappeared around the late Middle Ages in the Wadden Sea to the late 19th century in the Kattegat-Skagerrak. It is most likely that human interference played a role in the disappearance of all of the colonies. Apparently in more remote areas such as in the Kattegat-Skagerrak and Brittany the species was eradicated later than in more accessible areas such as the Wadden Sea.

As the species became protected throughout the area in the 20th century, particularly at the Farne Islands, it gradually came back and new colonies along the North Sea and Channel Coasts were most probably supplied by grey seals from Britain, whereas seals in the Kattegat-Skagerrak are suggested to come from both the Atlantic and Baltic populations. Interestingly, the peak breeding season is in the spring in the Baltic and in the autumn in the UK, and the few pups

which are born in the new colonies in the Kattegat-Skagerrak seem to vary between spring and autumn. The grey seals in the southwestern Baltic breed synchronously with the grey seals in the Baltic proper and adult seals have been tracked far north into the Baltic. Evidently, pups born in Brittany descend from UK seals.

It is intriguing that the maximum number of pups in the Dutch Wadden Sea is observed in late December. This is relatively late compared to pupping at most colonies in the UK and early compared to the pupping in the Baltic. It is known that seals from Eastern Scotland (Farne Islands and Isle of May) regularly cross the North Sea to this colony. Planned genetic studies might reveal the origin of the seals in these colonies. Despite the suboptimal breeding sites, which are flooded regularly, the Dutch colony in the Wadden Sea seems to be the most successful, growing at an exponential rate of increase of 19% since the beginning of the 1980s, which indicates substantial immigration since the maximum rate of increase in European grey seals is about 10% per year (Reijnders and Brasseur 2003b, Harding *et al.* 2007).

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