Status of the harbour seal *(Phoca vitulina)* in Southern Scandinavia

Morten Tange Olsen[1, 2], Signe May Andersen[2, 3], Jonas Teilmann[2], Rune Dietz[2], Susi Manuela Clermont Edrén[2, 3], Anton Linnet[4] and Tero Härkönen[5]

[1] *Stockholm University, Department of Genetics, Microbiology and Toxicology, Svante Arrheniusväg* 20C, *S-10691 Stockholm, Sweden*
[2] *National Environmental Research Institute, Aarhus University, Department of Arctic Environment, Frederiksborgvej 399, DK-4000, Roskilde, Denmark*
[3] *Institute of Biology, University of Southern Denmark, Campusvej 55, DK-5230 Odense M, Denmark*
[4] *Thy State Forest District, Søholtvej 6, Vester Vandet, DK-7700 Thisted, Denmark*
[5] *Swedish Museum of Natural History, Box 50007, S-10405 Stockholm, Sweden*

ABSTRACT

The harbour seal population in Southern Scandinavia has experienced repeated declines caused by hunting and epizootics. These events have shaped the current distribution and abundance of the population. This paper assesses the current status of the population. We estimate trends in abundance of harbour seals from long term survey data, compare these with historic trends inferred from previously published material, and discuss past and potential threats to the harbour seal population of Southern Scandinavia. It is evident that harbour seals have disappeared from haulout areas along the Danish shores of Kattegat and in the westernmost part of the Baltic Sea, where they were previously numerous. In the 1920-30s, when abundance was at its lowest, the population is estimated to have been only a fraction of its original size. Following 30 years of protection the population is currently approaching historic abundance and might have reached the carrying capacity in some areas. Further development depends largely on effects of future epizootics, anthropogenic disturbance, and availability of suitable haulout sites.

Olsen, M.T., Andersen, S.M., Teilmann, J., Dietz, R., Edrén, S.M.C., Linnet, A., Härkönen, T. 2010. Status of the harbour seal *(Phoca vitulina)* in Southern Scandinavia. *NAMMCO Sci. Publ.* 8:77-94.

INTRODUCTION

The harbour seals *(Phoca vitulina)* in Southern Scandinavia have experienced a turbulent history. Persisting in low numbers since the end of the last glaciation, harbour seals likely became abundant in the region only a few centuries ago (Härkönen *et al.* 2005). Once established, harbour seals were subject to hunting; first due to the value of skin and blubber and later because of conflicts with the commercial fisheries (Søndergaard *et al.* 1976, Heide-Jørgensen and Härkönen 1988). The decline during the first decades of the 20th century was driven by a coordinated Scandinavian campaign, with the objective to exterminate the seals. The population was at its lowest during the 1920s. After protection measures were taken in the 1960-70s the population started to recover, but was struck by two severe epizootics in 1988 and 2002 caused by the Phocine Distemper Virus (PDV), killing approximately half the population on each occasion (Dietz *et al.* 1989a; b, Härkönen *et al.* 2006). These events have had significant impacts on the distribution and abundance of harbour seals in Southern Scandinavia.

This paper summarizes published and unpublished data to assess the current status of the Southern Scandinavian population. Specifically, we present previously published material to account for the historic trends, and apply survey data covering the past 30 years to estimate population size and recent development. We evaluate the possible risks to the harbour seal population in Southern Scandinavian waters and provide a perspective for the future development of the population.

MATERIALS AND METHODS

Study population

The harbour seal is currently the most common seal species in Southern Scandinavia. It is a coastal, relatively sedentary seal, which-although observed in most parts of the region - is mainly found around haulout sites on undisturbed coasts, reefs, and islands, where it breeds, moults, and rests (Fig. 1). Haulout habitats vary greatly among regions, ranging from rocky shores in the Skagerrak and along most of the Swedish Kattegat coast to sandbanks, stone reefs, and single large stones in the Danish Kattegat, the Limfjord, and the western Baltic Sea. The harbour seal also occurs on the rocky shores of Kalmarsund in the Baltic proper and at the sand banks in the Wadden Sea. The harbour seals in Kalmarsund carry a unique genetic signature and appear isolated from stocks in the western Baltic and Kattegat-Skagerrak (Goodman 1998). Some genetic exchange occurs between the Limfjord and the

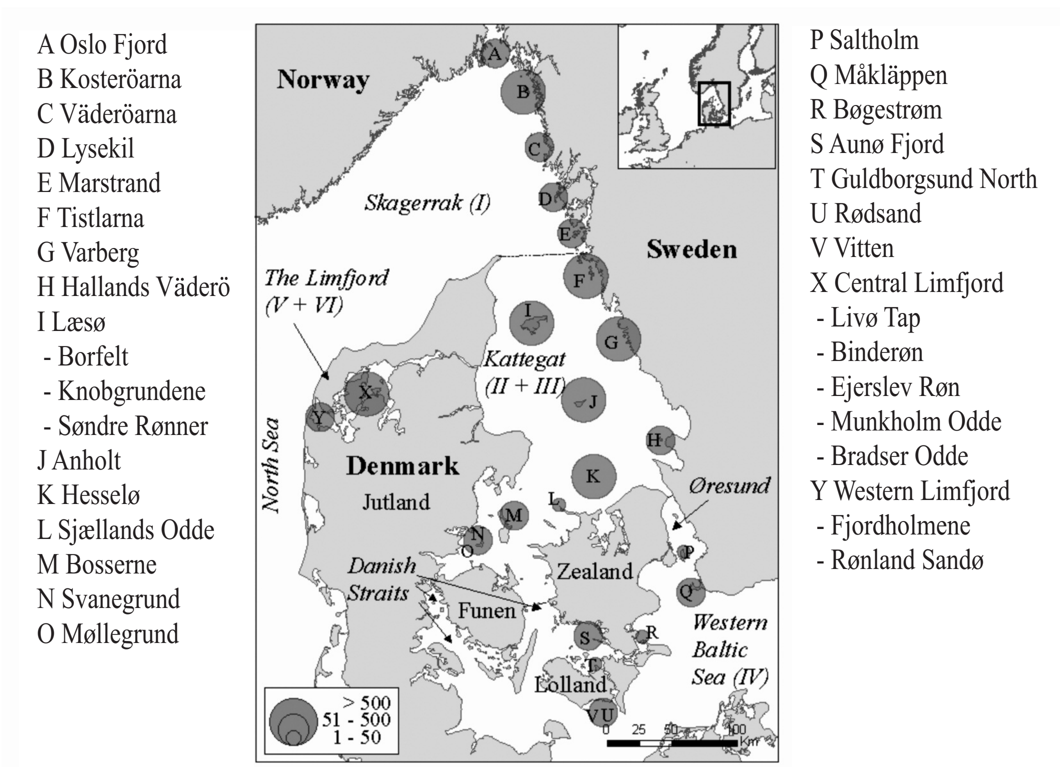

***Fig. 1.** Harbour seal haul-out sites in Southern Scandinavia. Subpopulations treated in this review are Skagerrak (I), Kattegat (II and III), western Baltic (IV), and Limfjorden (V and VI). Roman numerals refer to sub-units used for management and aerial surveys.*

Wadden Sea (Olsen *et al.* in prep.), but we assume that this is not of a magnitude to affect local population trends. Both the Kalmarsund and the Wadden Sea harbour seals are discussed elsewhere in this volume and not included here.

Within the study area, harbour seals have traditionally been divided into a number of units for management and conservation purposes, including the Skagerrak, central Kattegat, south-western Kattegat, western Baltic, the central Limfjord, and the western Limfjord (Fig. 1) (Heide-Jørgensen and Härkönen 1988, Teilmann and Heide-Jørgensen 2001). Recent genetic studies, however, documented genetic exchange between some of these units (Olsen *et al.* in prep.), suggesting the existence of 4 subpopulations within the study area: the Skagerrak, the Kattegat, the western Baltic, and the Limfjord. Although genetic studies indicate restricted historic gene flow between the central and western part of the Limfjord, there is evidence that the differentiation is in process of breaking down (Olsen *et al.* in prep.). Consequently, we treat the Limfjord as a single subpopulation.

Historic material

Information on the abundance and distribution of harbour seals in Southern Scandinavia until the 1970s was mainly obtained from reviews by Søndergaard *et al.* (1976) and Härkönen *et al.* (2005) who comprehensively gathered the information available from archaeological findings, historical scripts, and old fisheries bulletins. These reviews provide insights to the distribution of harbour seals but does not allow for estimates of abundance. The earliest detailed quantitative accounts of harbour seals stem from the hunting statistics introduced with the bounty systems in the 1890s. From 1940, information mainly originates from hunting statistics, questionnaires to hunters and fishermen issued since the 1960s, and sporadic boat or aerial based surveys initiated in the early 1960s and 1970s in Denmark and Sweden, respectively. Given the inaccessibility of much of the historic material we mainly refer to Søndergaard *et al.* (1976) and Härkönen *et al.* (2005) for references of older date.

Recent survey methods

Systematic aerial surveys were initiated in 1979 in the Skagerrak-Kattegat region to monitor the population development following the legal protection of harbour seals (Heide-Jørgensen and Härkönen 1988). In the Limfjord and the western Baltic similar surveys have been conducted since 1988. The aim was to conduct 3 surveys during the moulting season in the latter half of August each or alternate year. Survey hours were between 0900-1500 hours and under conditions standardized such that surveys were only carried out when wind speed was less than 10m/s and precipitation was absent (Heide-Jørgensen and Härkönen 1988). Timing to tidal cycle was only needed in the western Limfjord since the influence of tides is negligible in other study areas.

The seals were photographed from a single engine high-winged Cessna 172 aircraft, from an altitude of 300-500 feet (90-150 m), flying at 70-80 knots (ca 130-150 km/hr). Two observers on the same side of the aircraft took photos of haulout sites using hand held cameras equipped with 135-200 mm lenses. Afterwards the number of seals was counted on high quality photos. On the few localities where haulouts consist of single stones, seals were counted during overflight.

Statistical methods

To visualize the trend of the population index we plotted the estimated number of seals against survey year for the 4 subpopulations; Skagerrak, Kattegat, western Baltic, and the Limfjord, respectively. The number of seals in each subpopulation was estimated by applying a correction factor of 1.75, since merely 57% of the seals are estimated to haul out during surveys (Härkönen and Harding 2001). In addition to the graphic point presentation of the temporal trend of the population estimates Lowess smoother curves were applied to the 4 regions using a 25% smoothing factor. These graphics were carried out in StatView (V 5.0.1).

The average yearly growth of the subpopulations in the period before the first epizootic in 1988, between the two epizootics (1989-2001), and in the period after the second epizootic was estimated assuming an exponential growth model. Counts from both 1988 and 2002 were

Table 1. Number of seals from aerial surveys in the 4 subpopulations of Southern Scandinavia during the period 1979-2008, where Count denotes the average number of seals observed on land (for n larger than 2 the average was calculated by a trimmed mean), n is the number of surveys carried out that year, SD is the standard deviation of the counts, and Estim is the estimated number of seals in the sub-population corrected for seals in the water at the time of the survey. Note that some data in this table differs from Teilmann *et al* 2010 because of differences in data treatment. * From year 2000 it includes data from Oslo fjord.

Year	Skagerrak*				Kattegat				Western Baltic				Limfjord			
	Count	n	SD	Estim	Count	n	SD	Estim	Count	n	SD	Estim	Count	n	SD	Estim
1979	568	1	-	996	1776	1	-	3116	-	-	-	-	-	-	-	-
1980	674	1	-	1182	2096	1	-	3677	-	-	-	-	-	-	-	-
1981	709	1	-	1244	2386	1	-	4186	-	-	-	-	-	-	-	-
1982	696	1	-	1221	1491	1	-	2616	-	-	-	-	-	-	-	-
1983	1062	1	-	1863	2482	1	-	4354	-	-	-	-	-	-	-	-
1984	1127	1	-	1977	2570	2	-	4509	-	-	-	-	-	-	-	-
1985	1336	1	-	2344	3960	1	-	6947	-	-	-	-	-	-	-	-
1986	1333	1	-	2339	4458	1	-	7821	-	-	-	-	-	-	-	-
1987	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1988	748	6	24	1312	2247	3	16	3942	96	3	4	168	345	2	6	604
1989	1057	3	43	1854	2178	3	43	3820	98	1	-	172	546	3	59	958
1990	775	3	56	1359	2153	3	119	3777	175	5	11	307	510	3	29	894
1991	1180	3	28	2070	2888	3	216	5067	180	3	48	316	682	3	91	1196
1992	1036	2	325	1818	2839	3	403	5195	182	3	13	319	586	3	233	1027
1993	1910	3	115	3351	-	-	-	-	-	-	-	-	-	-	-	-
1994	2102	3	81	3687	3761	3	680	6598	181	3	32	317	650	3	194	1140
1995	2533	3	148	4444	-	-	-	-	-		-	-	-	-	-	-
1996	2338	3	47	4101	4326	3	141	7589	271	3	42	475	727	3	68	1275
1997	-	-	-	-	-	-	-	-	-	-	-	-	956	2	119	1677
1998	3201	3	414	5615	6189	3	82	10858	290	3	1	508	1044	4	316	1832
1999	2704	3	47	4743	-	-	-	-	-	-	-	-	1444	2	264	2533
2000	3979	2	239	6981	5941	3	185	10422	389	3	16	682	713	5	153	1251
2001	5981	3	406	10493	-	-	-	-	-	-	-	-	855	2	408	1499
2002	-	-	-	-	-	-	-	-	260	3	20	456	1159	3	60	2032
2003	2702	3	117	4740	4895	3	37	8587	401	3	52	704	802	2	92	1407
2004	2692	2	138	4723	4759	1	-	8349	494	3	87	866	965	1	-	1693
2005	3605	3	78	6325	5425	3	144	9518	560	3	30	982	781	3	46	1369
2006	2754	2	473	4832	5440	2	6	9544	448	2	43	785	853	3	165	1496
2007	2553	3	192	4479	5484	2	49	9620	511	3	23	896	772	2	151	1354
2008	4427	3	462	7767	-	-	-	-	737	3	21	1293	1048	3	30	1839

excluded since it is suspected that an ongoing decrease will affect the number of seals resting on land. Counts were included for 2002 for the Limfjord as surveys were carried out prior to the first observed occurrence of the disease in this area (Härkönen *et al.* 2006). The number of seals counted was $\log_e$-transformed prior to the analyses. The average annual growth rate was derived by linear regression of each subpopulation, based on a trimmed mean where the lowest count in each year was deleted. This reduce the variation in number of hauled out seals caused by disturbances during surveys and gives considerably better estimates compared to having all counts included (Teilmann *et al.* 2010). If only two surveys were conducted a given year we calculated the regular (untrimmed) mean rather than the trimmed mean, contrary to Teilmann *et al.* 2010 where the lowest of the two or three counts was deleted for trimmed mean. In years when only one survey was conducted we simply used this single observation to represent the average annual count.

TRENDS IN HISTORIC TIMES (PREHISTORY - 1970s)

The pristine abundance and distribution of harbour seals in Southern Scandinavia is uncertain. Skeletal remains in natural deposits and archaeological excavations of cultural sites in the Kattegat area suggest that seals were present in parts of Southern Scandinavia at least 8,000 years ago (Søndergaard *et al.* 1976, Aaris-Sørensen 1998, Härkönen *et al.* 2005). The abundant record of grey seal (*Halichoerus grypus*) and harp seal (*Pagophilus groenlandicus*) remains suggest that these species were previously abundant in the area. Contrastingly, harbour seal remains are scarce and totally absent for prolonged periods, suggesting that harbour seals may have colonised the area several times and subsequently become extinct (Härkönen *et al.* 2005).

The first information on the occurrence of seals in the region stem from the 16-18th century, but little information regarding species, abundance, and distribution is at hand from this period

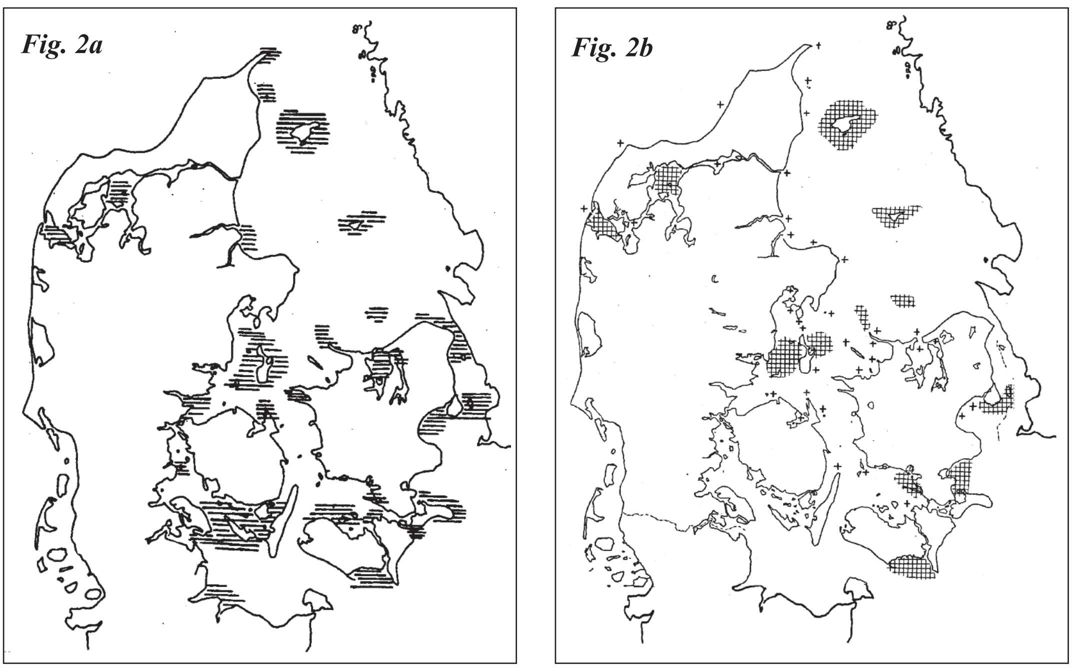

Fig. 2. *Estimated distribution of harbour seals in Denmark prior to the onset of the bounty system in 1890 (a) and in the 1970s (b). Highligted areas designate distribution of breeding sites. + designates occasional haul-out observations. Figures modified from Søndergaard et al. (1976).*

(Søndergaard *et al.* 1976). From the mid 18th century, seals were increasingly hunted, and written records describe their presence in most Scandinavian waters; often, however, without distinguishing between species of seals. Harbour seals probably colonised the region only after severe depletion of the formerly abundant grey seals during the 18th and 19th centuries (Härkönen *et al.*2005).

Increasing demands on governments were raised from commercial fisheries to control the seal population due to its presumed influence on fish stocks and damage to fishing gear. In 1889 and 1902 the Danish and Swedish governments, respectively, introduced a bounty system for hunting seals (Harding and Härkönen 1999). The number of harbour seals killed in Kattegat and Skagerrak alone during the period 1889 to 1976 is estimated to 35,300 (Heide-Jørgensen and Härkönen 1988). The effect of the campaign was unquestionable; the harbour seal population declined to a minimum in the 1920s (Søndergaard *et al.* 1976). Notably, while grey seals previously appeared to be the most abundant seal species, the proportion of harbour seals killed during the bounty system suggests that in the late 19th century the grey seal was almost extinct and the harbour seal had replaced the grey seal as the most abundant seal species in Denmark and Sweden (Härkönen *et al.* 2005). Although the bounty system was abandoned in 1927 in Denmark, the Danish government continued to provide economical support for seal harvest in some areas. In Sweden the bounty system was abandoned in 1965, and hunting bans on harbour seals were implemented in 1967 and 1977 in Sweden and Denmark, respectively (Heide-Jørgensen and Härkönen 1988, Bøgebjerg *et al.*1991). Currently, licenses can be issued at specific locations to shoot seals close to fishing gear (Dietz *et al.* 2000, Härkönen pers. comm.).

Regional trends

Skagerrak

Extrapolating from the hunting statistics of the bounty period, Heide-Jørgensen and Härkönen (1988) estimated the 1890 Skagerrak-Kattegat harbour seal population to 16,500, assuming growth rates of 5% per year in the very beginning of the 20th century, and 12% per year after 1920. According to the 1979-2006 counts given in Table 1, the Skagerrak subpopulation is about 30% (SD 4.9%) of the total size of the Skagerrak-Kattegat population. Applying this ratio to the estimate from 1890, the number of harbour seals in Skagerrak was approximately 5,500. By 1979, the Skagerrak subpopulation was estimated to about 1,000 seals *i.e.* 18% of its original size. These figures rely on a number of assumptions concerning the accuracy of the hunting statistics, the proportion of the stock killed, the ratio between the number of seals in the Kattegat and Skagerrak, and harbour seal population growth rates and are merely crude approximations. Nevertheless they serve as a guideline to the abundance of harbour seals in Skagerrak prior to the initiation of systematic hunting.

Kattegat

Records from the 18th century suggest an extensive distribution of harbour seals in Kattegat. (Søndergaard *et al.* 1976). Due to their accessibility from land and/or threat to salmon fisheries in the inlets, harbour seals were hunted and became rare at the majority of these sites by the end of the 19th century, but still abundant in areas such as Samsø, where "thousands" of seals could be observed in the 1880s (Søndergaard *et al.*1976).

The 20th century witnessed steady declines at most sites throughout the region and by the 1930s seals were more or less restricted to haulout sites on Hesselø, Læsø, Anholt, in the Samsø area, Hallands Väderö, Varberg, and Onsala. In the following period harbour seal numbers continued to decrease in the Samsø area, and is at the same time considered to have been stable at Læsø, Hesselø, and Anholt. From the 1950s numbers were increasing at the two latter sites (Søndergaard *et al.* 1976). Information on the population development at Hallands Väderö, Varberg, and Onsala during the period is limited. In 1979 the total Kattegat population was estimated to about 3,100 animals (Fig. 3b) or approximately 25% of its estimated 1890 size of 11,550 seals (see above).

Western Baltic

The single most important seal locality in the western Baltic region is the sand bar Rødsand

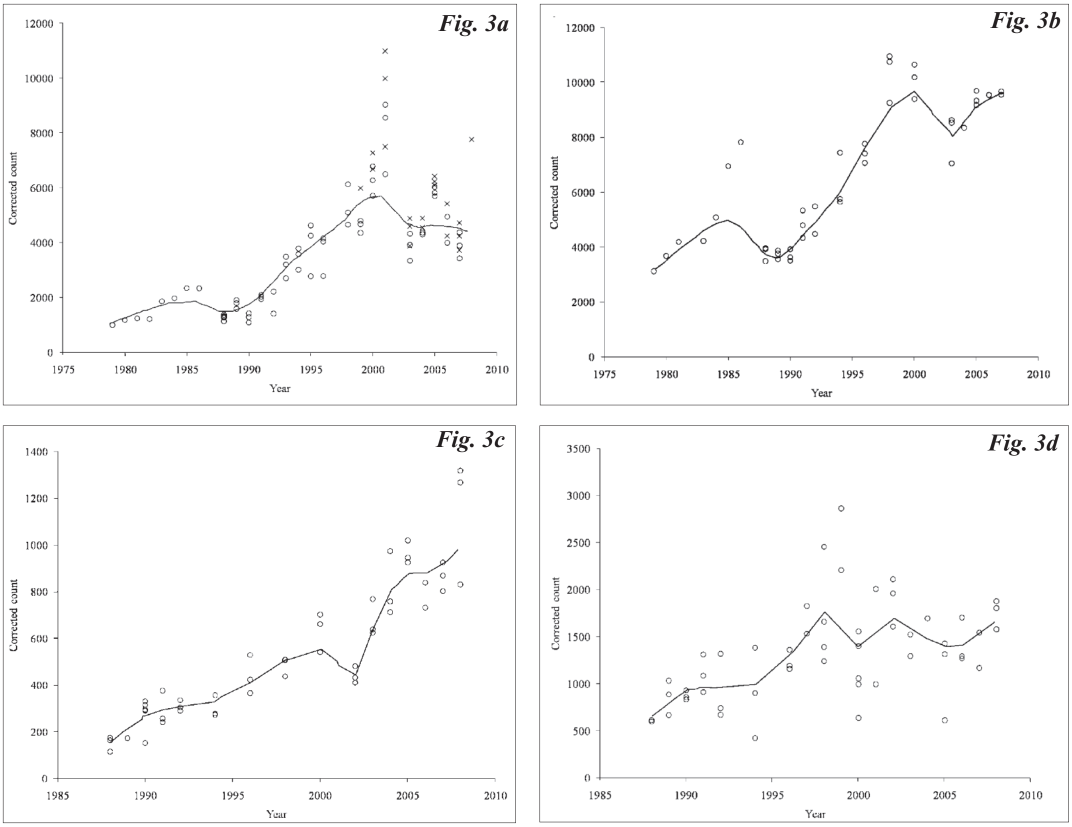

Fig. 3. *Trends in number of seals in the 4 subpopulations; Skagerak (a), Kattegat (b), western Baltic (c), and the Limfjord (d). X-axis shows year of survey and Y-axis the estimated population size corrected for the proportion of seals in the water. In addition to the graphic point presentation of the temporal trend of the population estimates Lowess smoother curves were applied to the four regions using a 25% smoothing factor. Crosses in Figure 3a is abundance including Oslo Fjord, Norway.*

in the shallow lagoon-like area south of Lolland (Fig. 1) where harbour seals and also grey seals hauled out in large numbers. Both species were subject to intensive harvest with up to 900 seals killed on single days in the spring of 1801 (Søndergaard *et al.* 1976). The intense hunting pressure gradually deprived the grey seals from the area, but harbour seals appear to have occurred in numbers as high as 200-300 seals in some years up to the 1950s. However, the repeated harvest ultimately resulted in a decline in this harbour seal population as well, with only about of 30-40 animals remaining.

Seal haulouts also existed in other parts of the Baltic. Harbour seals were abundant and widely distributed on the many islands, reefs, and islets south of Funen in the most western part of the Baltic and in the Danish Straits (Fig. 2a), but were already severely depleted by the end of the 19th century, being close to absent from the area today. Harbour seals were also abundant in Øresund between Denmark and Sweden where they, according to 18-19th century fisheries bulletins, caused significant disturbance to the fisheries and consequently were hunted intensively (Søndergaard *et al.* 1976). By the end of the 19th century, seals had disappeared from much of the area and were only relatively abundant on Saltholm in the middle of Øresund and at Måkläppen off Falsterbo in Sweden. By the 1970s, this stock had declined as well, numbering only 10-15 animals at both sites (Fig. 2b). Although estimates are associated with much uncertainty the decline in this region up until the 1970s appears to have been in the order of 80-90%, perhaps more.

Table 2. Estimated annual growth rates in the 4 subpopulations based on the exponential growth model for periods corresponding to before, between, and after the two PDV epidemics. Note that some data in this table differs from Teilmann *et al* 2010 because of differences in data treatment.
* Includes data from Oslo Fjord, Norway.

Area	Period	Growth rate (%)
Skagerrak	1979-1986	13.3
	1989-2001	13.6
	2003-2008*	6.1
Kattegat	1979-1986	12.1
	1989-2000	10.2
	2003-2007	2.9
W. Baltic	1989-2000	9.8
	2003-2008	8.5
Limfjord	1989-1999	7.9
	2000-2002	25.1
	2003-2008	2.1
Overall	1979-1986	12.4
	1989-2000	10.6
	2003-2007	2.2

The Limfjord
Harbour seals were rarely reported in the Limfjord prior to 1825, when this, hitherto largely isolated brackish water system, became connected to the North Sea. Subsequently, the harbour seal stock experienced a marked increase in abundance, becoming relatively numerous in particularly the western part of the inlet by the turn of the previous century. Although minor fluctuations likely occurred, the population is believed to have been stable at approximately 200 animals from the early 20th century to the 1970s (Søndergaard *et al.* 1976).

TRENDS IN RECENT TIMES (1970s - PRESENT)

Following the protection of the harbour seal in 1967 and 1976, the subpopulations in all areas where seals were surveyed increased exponentially by an average of 12.4% per year until the outbreak of the first PDV epizootic in 1988 (Tables 1, 2 and Fig. 3a, b). Reliable data does not exist for all areas, but the Skagerrak and Kattegat counts suggest a mortality of 7,000 seals representing a 55% decline from the years 1986 to 1989 (Dietz *et al.* 1989a, Härkönen *et al.* 2006). One year after the epizootic the total population was estimated at 6,804 seals, after correcting for seals in water at the time of the survey. Thereafter the population growth resumed increasing exponentially, reaching an estimated total of 18,886 seals for the whole study area in 2000. However, in May 2002 the PDV again appeared on Anholt in central Kattegat, from where it spread to the other subpopulations. The 2003 survey data indicate that approximately 11,300 harbour seals died during the second epizootic. However, although a greater number of seals were killed, the percentage decimation of the population was less compared to the first epizootic in 1988. On average, subpopulations declined by 20%, although more than 50% were killed in Skagerrak (Härkönen *et al.* 2006). Also this time the population started to recover, but at a much slower rate than after the first event (Table 2). In 2007, the population of the study area amounted to approximately 16,000 seals; approximately four times the size of the 1979 population and very close to the estimated pre-hunting population estimate.

Regional trends
Skagerrak
From the first surveys in 1979 to 1986, the harbour seal abundance in Skagerrak increased with an annual growth rate of 13.3% (Tables 1, 2 and Fig. 3a). In populations of true seals with even sex ratios and stable age structures the intrinsic rate of increase cannot exceed 13% per year. Larger values indicate a non-stable population structure or populations affected by migration (Härkönen *et al.* 2002). Consequently, we assume that the Skagerrak subpopulation had reached a stable age structure at the time of the first PDV outbreak. The epizootic in 1988 resulted in a population decline of 43.9%. Afterwards the subpopulation increased exponentially by 13.6% until 2002 when the second epizootic caused a decline by 53.1%. The growth has henceforth been at 6.1%

for the period 2003-2008, a rate that is influenced by a decline in 2007 caused by an as yet unidentified pathogen (Harkönën *et al.* 2008). In 2008, 4,427 harbour seals were counted in the Skagerrak. Correcting for the number of seals in the water at the time of the survey suggests a population size of 7,767 animals for the subpopulation: less than prior to the second epizootic, but about 30% more than estimated for its pre-hunting (*i.e.* 1890) size.

Kattegat
From an estimated total of 3,116 seals in 1979 the Kattegat subpopulation increased by 12.1% per year up to 1986 and 10.2% from 1989 to 2000 (Tables 1, 2 and Fig 3b). Both these rates are close to the intrinsic growth rate of harbour seals. In the period 1998-2000 the Kattegat subpopulation ceased increasing and might have reached its carrying capacity. The decline during the first epizootic was 51.1%, much more pronounced than the 17.6% observed under the second epizootic in 2002. Since then, growth has been a mere 2.9% per year in the Kattegat subpopulation and by 2007 its abundance was estimated at 9,620 seals. This estimate is close to the level observed immediately prior to the second epizootic, indicating that the Kattegat subpopulation is again approaching its current carrying capacity. Reaching an abundance of 11,500 seals as estimated for the 1890 subpopulation probably requires availability of additional suitable haulout sites.

Western Baltic
Systematic surveys of the seals in western Baltic were first initiated in 1988. Hence information on the effects of the first PDV epizootic is limited. However, 50% of seals died at the Måkläppen locality in 1988 (Dietz *et al.* 1989a; Härkönen *et al.* 2006). Until year 2000, the population grew with 9.8% per year, and hereafter declined with 33.1% as a consequence of the 2002 epizootic (Tables 1, 2 and Fig. 3c). The PDV epizootic in 2002 struck this site prior to the annual count; hence the estimated decline might be slightly higher compared to the actual mortality (Härkönen *et al.* 2006). The subpopulation increased exponentially during the first years following the epizootic, but growth appears to have ceased over the last couple of years. During 2003-2008 the annual growth rate was 8.5%, approaching 1,300 seals in 2008, substantially more than the 50-70 seals in the 1950s subpopulation. It is uncertain how the size of the current subpopulation relates to the pre-hunting size, but at those haulout sites inhabited by harbour seals today, abundance is probably similar to the abundance prior to hunting.

The Limfjord
The Limfjord subpopulation increased by 7.9% from 1989 to 1999, and was thereafter reduced by 50.6% in 2000 compared to the year before (Tables 1, 2 and Fig. 3d). The reduction was most prominent in the central part of the Limfjord. The low number of seals was confirmed by 4 additional surveys that year and neither new haulout sites nor unusual numbers of dead seals were reported. Similar declines were observed in the fisheries and in the local black cormorant population *(Phalacrocorax carbo)* (Anton Linnet, pers. comm.), which has dietary overlap with harbour seals during summer and autumn (Andersen *et al.* 2007). This indicates that food limitation might have forced the seals out of the fjord system, which was also supported by the lack of suitable seal prey in their diet during some months (Andersen *et al.* 2007). From 2000 to 2001, seal numbers increased by 25.1% indicating strong migration back into the central part of the Limfjord. Although seemingly rare, such migration supports the view that the Limfjord should be considered as a single unit when assessing harbour seal population dynamics. The epizootic in 2002 caused a 30.8% mortality from which the subpopulation has not recovered yet. The subpopulation has exhibited low growth rate (2.1%) since 2003 and amounted to 1,839 seals in 2008, which is considerably larger than the subpopulation of roughly 200 seals inhabiting the area up until the 1970s.

THREATS TO THE POPULATION

Interactions with fisheries
The conflict between fisheries and harbour seals is not new. Hunting to control seals as a competitor to fisheries was previously of major

importance to seal mortality in Southern Scandinavia, but basically ceased with the legal protection of the harbour seals in the 1960s and 1970s in Sweden and Denmark, respectively. In some areas of Sweden fishermen are allowed to kill single seals in order to protect their fishing gear (Harding and Härkönen 1999). This practice is also followed in Denmark, where dispensation to commercial fishermen can be granted to shoot a limited number of seals close to fishing gear in some regions (*e.g.* Rødsand) if serious damage to their nets or catch can be documented (Jepsen 2005). This amounts to about 10 (up to 18) seals shot per year (Dietz *et al.* 2000, Danish Forest and Nature Agency, pers. comm.), which should not be of significance for the status of the population. Also, incidental by-catch occurs, but although information is scarce this appears to have limited consequences for harbour seal abundance (Jepsen 2005).

Over the past decades high fishing pressure has resulted in depletion of fish populations and caused local changes in marine community structure (Ducrotoy and Elliott 2008). Several studies have documented the dramatic influence of these changes on mammals and birds relying on fish as food resource (Hamre 1994, Hjermann *et al.* 2004, Matthiopoulos *et al.* 2008). However, very little is known about the potential impact of fisheries in the form of reduced carrying capacity of harbour seal habitats in Southern Scandinavia. Assessing such relationship requires quantitative information on the intensity of competition, that is, whether harbour seal predation overlaps in space and time with commercial fishing. Harbour seals are opportunistic feeders showing significant regional and seasonal variation in their diet, presumably relating to prey abundance (Härkönen 1987, Brown and Pierce 1998, Andersen *et al.* 2007). Furthermore, total seal predation is often small compared to the amount taken by fisheries and many fish consumed by harbour seals are either not targeted by fishery or are under the legal minimum landing sizes (Brown and Pierce 1998, Hansen and Harding 2006, Andersen *et al.* 2007, Matthiopoulos *et al.* 2008). These observations suggest that the competitive overlap is minimal. Alternatively, it could be a consequence of adaptations by harbour seals to limited food supplies, indicating high competition pressure from the fisheries. More research is needed to address these questions.

Eutrophication

Eutrophication and seasonal oxygen deficiency can have devastating effects on benthic animals and commercial fish species (Islam and Tanaka 2004), some of which has already been observed in the North Sea-Baltic Sea region (Karlson *et al.* 2002). Feeding mainly on benthic fish species, changes in the benthic macrofauna are likely to affect the harbour seal. In 2000, large numbers of seals migrated out of the central Limfjord in what might have been a response to a collapse of the fish stock in this semi-enclosed water body (see above). The cause of the 2000 collapse is currently unknown, but eutrophication and oxygen deficiency is a frequent issue in the Limfjord system (Jensen 1990, Karlson *et al.* 2002). Eutrophication also occurs in open waters like the Kattegat, where seasonal oxygen deficiency and negative effects on the benthic macrofauna have been observed most years since the 1980s. Similarly, several fjords along the Swedish Skagerrak coast have shown declining oxygen concentrations and a seasonal lack of benthic fauna in the deeper parts (Karlson *et al.* 2002). Thus, although active management strategies in Denmark have reduced phosphorus and nitrogen levels in coastal waters by 22-57% and 44%, respectively, over the past 15 years (Carstensen *et al.* 2006), eutrophication might pose a threat to harbour seal abundance in Southern Scandinavia, at least on a local scale.

Contaminants

Several studies discuss the role of bioaccumulation and biomagnification of contaminants in relation to harbour seal health. Seals in the Dutch Wadden Sea and in the Baltic Sea have previously experienced low reproduction rates due to elevated levels of polychlorinated biphenyls (PCBs) in their diet (Rejinders 1980, Bergman and Olsson 1985, Rejnders 1986), and experimental studies have shown that levels of PCBs measured among harbour seals (20 ppm) cause impaired immunity functions (DeSwart *et al.* 1996). Harbour seals in Southern Scandinavia generally exhibit high fertility rates (Table 2) (Härkönen and Heide-Jørgensen 1990) and toxicological analyses for PCBs have revealed decreasing trends in north-eastern Atlantic marine mammals (Aguilar *et al.* 2002, Reijnders and Simmonds 2003), suggesting that these compounds might no longer be a serious issue for harbour seal health. Still, the apparent susceptibility to epizootics exhibited by the Southern Scandinavian harbour seal population (Härkönen *et al.* 2006), the regular observation of seals with wounds (Authors pers. obs.), and the continuous prevalence of bone lesions in form of alveolar exostosis (Mortensen *et al.* 1992, Härkönen pers. comm.), suggest that other compounds might be affecting the immunological response of harbour seals. Although frequencies of wounds have decreased along with the decline of some conventional POPs other compounds in the POP group could affect the immune function of harbour seals. Similarly could organohalogens as discussed in the case of alveolar exostosis (Mortensen *et al.* 1992). The role of OHC contamination, through impeding immune system function, could potentially have had an effect on the severity of the 1988 and 2002 epizootic, but no causal relation have so far been established (*e.g.* Hall *et al.* 1992a; b, Reijnders and Aguilar 2002, Härkönen *et al.* 2006, Dietz 2008).

Offshore constructions

Offshore wind farms have been established in both Denmark and Sweden as part of the national strategy for increasing the production of renewable energy. Effects of these activities on the habitat use and haulout behaviour of harbour seals were studied between 1999 and 2005 during the construction and operation of the Horns Reef and Nysted offshore wind farms in Denmark (Dietz *et al.* 2003, Teilmann *et al.* 2006, Edrén *et al.* 2010). No general change in behaviour at sea could be linked to the Horns Reef offshore wind farms. On land, the only effect detected was a short-termed alteration in seal haulout behaviour during pile drivings, which took place about 10 km from the seal locality at Rødsand in the western Baltic. However, pile driving is of limited duration and should not cause significant threats to harbour seals. The effect of wind farms on feeding behaviour of seals is still unknown.

Human disturbance

Human disturbance in the form of urban development, sea-, land- and air-based traffic, and recreational activities (*e.g.* seabird hunting and leisure crafts during winter and summer, respectively) affect harbour seal distribution and abundance (Allen *et al.* 1984, Watts 1996, Montgomery *et al.* 2007). In the densely populated Southern Scandinavia, harbour seals have disappeared from haulout sites close to human developments and are currently restricted to undisturbed coasts in sanctuaries or relatively remote areas. It is therefore of outmost importance to harbour seal viability that haulout sites are protected and disturbance kept to a minimum to allow the population to increase or remain stable. Detailed studies evaluating the effects of human disturbance on harbour seal haulout patterns in central Kattegat are in progress (Andersen *et al.* in prep).

Interspecific competition

Interspecific competition might be another factor that affects the distribution and abundance of harbour seals in Southern Scandinavia. Grey seals and harbour seals have overlapping habitats and might also be competitors for food sources (Bowen *et al.* 2003). Both species have been subject to severe anthropogenic impacts, but responded very differently (Søndergaard *et al.* 1976, Wolff 2000, Härkönen *et al.* 2005). The previously dominating grey seal population suffered severe declines whereas harbour seals gradually increased in abundance and distribution. Contrary to harbour seals, grey seal pups are immobile for the first weeks after birth and are easily hunted. Thus, grey seals appear more vulnerable to disturbances at breeding sites, providing an advantage to harbour seals in periods of disturbance. As a consequence of conservation and management efforts during the past decades, the grey seal stock in Southern Scandinavia is currently growing and might become a competitor to harbour seals. The declines observed recently in British harbour seals might result from competition with the grey seal (Lonergan *et al.* 2007). Moreover, seeming to be more or less unaffected by PDV, the grey seal might act as an indirect competitor to harbour seals by carrying the PDV-like viruses affecting harbour seal populations

(Härkönen *et al.* 2006). Locally, competition might also occur with the great cormorant. Andersen *et al.* (2007) studied the interactions between cormorants and harbour seals in Limfjorden and observed dietary overlap of the two species during summer and autumn. Diet overlap has also been documented for the Southern Kattegat area (Härkönen 1988). However, it is unknown if this overlap results in competition. Although not studied in details the habitat selection and diet composition of harbour seals and harbour porpoises *(Phocoena phocoena)* are quite similar and may also result in interspecific competition (*e.g.* Aarefjord *et al.* 1995, Teilmann *et al.* 2007).

Genetic effects
Population declines and fragmentation might influence individual fitness through loss of genetic diversity, inbreeding depression, and reduction of the adaptive potential of individuals (Nei *et al.*1975, Hoelzel *et al.* 2001, Acevedo-Whitehouse *et al.* 2003). As discussed in the contaminant paragraph a number of observations indicate that the Southern Scandinavian harbour seal population experience reduced immunological response. This could be due to contaminants but it might result from low levels of genetic diversity. Valsecchi *et al.* (2004) found that inbred dolphins were less resistant to morbillivirus infections. So far no such correlation has been documented in harbour seals (Härkönen *et al.* 2006) and levels of genetic diversity in the Southern Scandinavian population appear similar to those observed in other populations (Goodman 1998, Olsen *et al.* in prep). However, detecting a relationship between inbreeding and immunity might require larger genetic resolution than the 7 and 15 microsatellite loci applied in the two studies, respectively. Recently Rijks *et al.* (2008) used 27 microsatellite loci to document a correlation between low genetic diversity (*i.e.* heterozygosity) and lung worm burdens in Wadden Sea harbour seals, suggesting that although remaining to be tested thoroughly, genetic diversity might also influence immune response in Southern Scandinavian harbour seals. In theory, such effects should be most prominent in harbour seals at apparently isolated localities like Rødsand (Dietz *et al.*2003) and less so in *e.g.* the Skagerrak-Kattegat area where movements among haul-out sites are more frequent (Olsen *et al.* in prep, Dietz *et al.* unpubl.).

Epizootics
Within the past 20 years the largest cause of harbour seal mortality in the region – and most of Europe – was the two outbreaks of PDV (Dietz *et al.* 1989a, b, Heide-Jørgensen *et al.* 1992, Jensen *et al.* 2002, Härkönen *et al.* 2006). Harding and co-authors (2002, 2003) investigated the sensitivity of projected populations under different future scenarios and found that populations with low growth rates and/or large annual variability in rates were the most vulnerable to future mass mortality events. In fast growing populations, like those in Southern Scandinavia, projections are more complicated, but there is an indication that the risk of extinction (*i.e.* declining to 10% of original size within 100 years) increase from 9% to 56% in the presence of epizootics (Harding *et al.* 2003).

In summer 2007, increased mortality among seals in central Kattegat caused the concern of a third PDV outbreak (Härkönen *et al.* 2008). By December approximately 300 dead seals had washed ashore in the Skagerrak-Kattegat region but as many as 2,300 seals were estimated to have died based on expected and observed aerial counts. Although it is now clear that the deaths were caused by an as yet unidentified pathogen and not PDV, the repeated occurrence of epizootics among the harbour seals of Southern Scandinavia indicate that epizootics might be the factor posing the greatest risk to the population and must be included in future conservation and management plans.

CONSERVATION AND MANAGEMENT

On a national level several Danish and Swedish seal sanctuaries have been established to ensure undisturbed haulout sites; some throughout the year and others only during the breeding and moulting period. Internationally, Denmark and Sweden have ratified the Bern Convention of 1979, aiming to conserve wild plants and animals including their habitats and protect them against threats (Jong *et al.* 1997). Both countries are also members of the Helsinki Commission (HELCOM) and have signed the Helsinki Convention of 1974 and 1992 working to protect the marine environment of the Baltic Sea. Also, all Baltic seals, including those in the Kattegat are listed under the EU Habitat Directive Annex II, and member countries are obliged to carry out monitoring of the status of seal populations and to establish special areas of conservation.

Denmark and Sweden have also ratified the 2006 HELCOM Seal Recommendation, where the following long-term management principles are accepted: all species and populations should have natural distribution and abundance and a health status that ensures their future persistence in the ecosystem. In practice this means that seal populations are allowed to reach their natural carrying capacities and former distributions. Furthermore, Denmark, The Netherlands, and Germany have established the Trilateral Governmental Cooperation in order to develop an overall conservation and management plan for the Wadden sea area (Kuiper and Enemark 2003).

The guidelines set by HELCOM and the Trilateral Government Cooperation were to a large extent implemented in the Danish seal management plan developed by the Danish Forest and Nature Agency (Jepsen 2005). In brief, the objectives of the plan are to i) preserve the seal population and its habitat; ii) evaluate existing seal reserves and assess the need for additional protected areas; iii) identify and solve conflicts with fisheries; iv) maintain or improve the possibility for the general public to observe seals; and v) promote exchange of information with neighbouring countries to ensure the best possible management of harbour seals in the region (Jepsen 2005). A management plan for harbour seals in Sweden is underway.

CONCLUSION

Compared to some centuries ago, the distribution of harbour seal breeding sites in Southern Scandinavia is now reduced. Harbour seals were previously widespread in the most western part of the Baltic Sea and the Danish Straits where they are now nearly absent. They have also disappeared from the western and Southern mainland shores of the Kattegat, and experienced significant declines in the Øresund. At its lowest in the 1920s, the total number of harbour seals in Southern Scandinavia probably did not exceed 2,000 animals; about 8x lower than the estimated abundance in 1890. Following their legal protection in the 1960s-70s conservation efforts have resulted in exponential growth in the harbour seal population, only interrupted by declines during the epizootics. Growth was close to the intrinsic rate in the Skagerrak and Kattegat subpopulations and a little lower in the western Baltic and Limfjord subpopulations. The population as a whole is now approaching pre-hunting abundance and appear healthy in terms of reproduction. However, the recurrent outbreak of epizootics indicates that the Southern Scandinavian population is having some fitness issues, the causes of which are poorly understood. Further, harbour seals are in large part restricted to the same haulout areas as 30 years ago and might have reached the current carrying capacity in some areas, as suggested by the slower or negative growth rates observed over the past couple of years. As several of the adverse factors observed to influence harbour seal fitness appear to be density dependent, further increases in the population will be determined by the availability of suitable harbour seal habitats and adequate food resources.

ACKNOWLEDGEMENTS

This study was jointly funded by the Danish Forest and Nature Agency and the Swedish Environmental Protection Agency. We greatly thank our skilled pilots and observers participating in aerial seal surveys since 1979. Frank Rigét provided kind advice on the statistical treatment of data. Mads Peter Heide-Jørgensen and an anonymous referee provided valuable comments to the manuscript, and their help is gratefully acknowledged.

REFERENCES

Aarefjord, H., Bjørge, A., Kinze, C.C. and Lindstedt, I. 1995. Diet of the harbour porpoise *(Phocoena phocoena)* in Scandinavian waters. *Rep. int. Whal. Commn, Special Issue* 16:211-222.

Aaris-Sørensen, K. 1998. *Danmarks forhistoriske dyreverden* (3. edn.). Gyldendal, Denmark, 232 pp. (In Danish.)

Acevedo-Whitehouse, K., Spraker, T.R., Lyons, E., Melin, S.R., Guilland, F., Delong, R.L. and Amos, W. 2003. Contrasting effects of heterozygosity on survival and hookworm resistance in California sea lions pups. *Mol. Ecol.* 15:1973-1982.

Aguilar, A., Borrell, A. and Reijnders, P.J.H. 2002. Geographical and temporal variation in levels of organochlorine contaminants in marine mammals. *Mar. Environ. Res.* 53:425-452.

Allen, S.G., Ainley, D.G., Page G.W. and Ribic, C.A. 1984. The effects of disturbance on harbour seal haul-out patterns at Bolinas Lagoon, California. *Fish. Bull.* 82:493-500.

Andersen, S.M., Teilmann, J., Harders, P.B., Hansen, E.H. and Hjøllund, D. 2007. Diet of harbour seals and great cormorants in Limfjord, Denmark: interspecific competition and interaction with fishery. *ICES J. Mar. Sci.* 64:1235-1245.

Bergman, A. and Olsson, M. 1985. Pathology of Baltic grey seal *(Halichoerus grypus)* and ringed seal (*Phoca hispida*) females with special reference to adrenocortical hyperplasia - is environmental pollution the cause of a widely distributed disease syndrome? *Finn. Game Res.* 44:47-62.

Bowen, W.D., Ellis, S.L., Iverson, S.J. and Boness, D.J. 2003. Maternal and newborn life-history traits during periods of contrasting population trends: implications for explaining the decline of harbour seals *(Phoca vitulina)*, on Sable Island. *J. Zool.* 261:155-163.

Brown, E.G. and Pierce, G.J. 1998. Monthly variation in the diet of harbour seals in inshore waters along the southeast Shetland (UK) coastline. *Mar. Ecol. Prog. Ser.* 167:275-289.

Bøgebjerg, E., Tougaard, S., Madsen, J. and Nørgaard, N. 1991. Status of the harbour seal *Phoca vitulina* populations in the Danish waters, 1976-1989, and short-term effects of the epidemic in 1988. *Danish Review of Game Biology* 14 (4):2-16.

Carstensen, J., Conley, D.J., Andersen, J.H. and Ærtebjerg, G. 2006. Coastal eutrophication and trend reversal: a Danish case study. *Limnol. Oceanogr.* 51:398-408.

De Swart, R.L., Ross, P.S., Vos, J.G. and Osterhaus, A.D.M.E. 1996. Impaired immunity in harbour seals *(Phoca vitulina)* exposed to bioaccumulated environmental contaminants: review of a long-term feeding study. *Environ. Health Perspect.* 104 (S4):823-828.

Dietz, R., Heide-Jørgensen, M.P. and T. Härkönen, T. 1989a. Mass deaths of harbour seals. *Ambio* 18:258-264.

Dietz, R., Ansen, C.T., Have, P. and Heide-Jørgensen, M.P. 1989b. Clue to seal epizootic? *Nature* 338:627.

Dietz, R., Teilmann, J. and Henriksen, O.D. 2000. EIA study of offshore wind farm at Rødsand. Technical report about seals – Juli 2000. SEAS Distribution A.m.b.A. Vind Energi Center, Slagterivej 25 DK-4690 Haslev. Available at:http://www.nystedhavmoellepark.dk-/frames.asp?Page_ID=18&Page_Ref=15&Templates_ID=1

Dietz, R., Teilmann, J., Henriksen, O.D. and Laidre, K. 2003. Movements of seals from Rødsand seal sanctuary monitored by satellite telemetry. Relative importance of the Nysted Offshore Wind Farm area to the seals. National Environmental Research Institute, Denmark pp 44, NERI technical Report No 429. Available at: http://www2.dmu.dk/1-viden/2_Publikationer/3_fagrapporter/rapporter/FR429.pdf

Dietz, R. 2008. Contaminants in Marine Mammals in Greenland – with linkages to trophic levels, effects, diseases and distribution. [DSc thesis]. National Environmental Research Institute, University of Aarhus, Denmark. 120 pp + 30 articles.

Ducrotoy, J.P. and Elliott, M. 2008. The science and management of the North Sea and the Baltic Sea: natural history, present threats and future challenges. *Mar. Pollut. Bull.* 57:8-21.

Edrén, S.E.C, Andersen, S.M., Teilmann, J., Harders, P., Dietz, R. and Miller, L. A. (2010). The effect of a large Danish offshore wind farm on harbour and gray seal haul-out behaviour. *Mar. Mamm. Sci. 26:614-634.*

Goodman, S. 1998. Patterns of extensive genetic differentiation and variation among European harbour seals *(Phoca vitulina vitulina)* revealed using microsatellite DNA polymorphisms. *Mol. Biol. Evol.* 15:104-118.

Hall, A.J., Law R.J., Wells, D.E. and Harwood, J. 1992a. Organochlorine levels in common seals *(Phoca vitulina)* which were victims and survivors of the 1988 phocine distemper epizootic. *Sci. Total Environ.* 115:145-162.

Hall, A.J., Pomeroy, P.P. and Harwood, J. 1992b. The descriptive epizootiology of phocine distemper in the UK during 1988/89. *Sci. Total Environ.* 115:31-44.

Hamre, J. 1994. Biodiversity and exploitation of the main fish stocks in the Norwegian-Barents Sea ecosystem. *Biodivers. Conserv.* 3:473-492.

Hansen, B.J.L. and Harding, K.C. 2006. On the potential impact of harbour seal predation on the cod population in the eastern North Sea. *Neth. J. Sea Res.* 56:329-337.

Harding, K.C. and Härkönen, T. 1999. Development in the Baltic grey seal *(Halichoerus grypus)* and ringed seal *(Phoca hispida)* populations during the 20th century. *Ambio* 28:619-627.

Harding, K.C., Härkönen, T. and Caswell, H. 2002. The 2002 European seal plague - epidemiology and population consequences. *Ecol. Lett.* 5:727-732.

Harding, K.C., Härkönen, T. and Pineda, J. 2003. Estimating quasi-extinction risk of European harbour seal: a reply to Lonergan and Harwood. *Ecol. Lett.* 6:894-897.

Härkönen, T. 1987. Seasonal and regional variations in the feeding habits of the harbour seal, *Phoca vitulina,* in the Skagerrak and Kattegat. *J. Zool.* 213:535-543.

Härkönen, T. 1988. Food-habitat relationship of harbour seals and black cormorants in Skagerrak and Kattegat. *J. Zool.* 214:673-681.

Härkönen, T. and Heide-Jørgensen, M.P. 1990. Comparative life histories of East Atlantic and other harbour seal populations. *Ophelia* 32:211-235.

Härkönen, T. and Harding, K.C. 2001. Spatial structure of harbour seal populations and the implications thereof. *Can. J. Zool.* 79:2115-2127.

Härkönen, T., Harding, K.C. and Heide-Jørgensen, M.P. 2002. Rates of increase in age-structured populations - a lesson from the European harbour seals. *Can. J. Zool.* 80:1498-1510.

Härkönen, T., Harding, K.C., Goodman, S.J. and Johannesson, K. 2005. Colonization history of the Baltic harbour seals-integrating archaeological, behavioural and genetic data. *Mar. Mamm. Sci*. 21:695-717.

Härkönen, T., Dietz, R., Reijnders, P., Teilmann, J., Thompson, P., Harding, K., Hall, A., Brasseur, S., Siebert, U., Goodman, S.J., Jepson, P.D., Rasmussen, T.D. and Thompson, P.M. 2006. A review of the 1988 and 2002 phocine distemper virus epidemics in European harbour seals. *Dis. Aquat. Org.* 68:115-130.

Härkönen, T., Bäcklin, B.M., Barrett, T., Bergman, A., Cortney, M., Dietz, R., Harding, K.C., Malmsten, J., Roos, A. and Teilmann, J. 2008. Mass mortality in harbour seals and harbour porpoises caused by an unknown pathogen. *Vet. Rec.* 162:555-556.

Heide-Jørgensen, M.P. and Härkönen, T. 1988. Rebuilding seal stocks in the Kattegat-Skagerrak. *Mar. Mamm. Sci.* 4:231-246.

Heide-Jørgensen, M.P., Härkönen, T. and Åberg, P. 1992. Long-term effects of epizootic in harbour seals in the Kattegat-Skagerrak and adjacent areas. *Ambio* 21:511-516.

Hjermann, D.Ø., Ottersen, G. and Stenseth, N.C. 2004. Competition among fishermen and fish causes the collapse of Barents Sea capelin. *Proc. Natl. Acad. Sci.* 101, 32:11679-11684.

Hoelzel, A.R., Campagna, C. and Arnbom, T. 2001. Genetic and morphometric differentiation between island and mainland southern elephant seal populations. *Proc. R. Soc. Lond., Ser. B: Biol. Sci.* 268:325-332.

Islam, M.S. and Tanaka, M. 2004. Impacts of pollution on coastal and marine ecosystems including coastal and marine fisheries and approach for management: a review and synthesis. *Mar. Pollut. Bull.* 48:624-649.

Jensen, J.N. 1990. Increased abundance and growth of the suspension-feeding bivalve *(Corbula gibba)* in a shallow part of the eutrophic Limfjord, Denmark. *Neth. J. Sea Res.* 27 (1):101-108.

Jensen, T., van de Bildt, M., Dietz, H.H., Andersen, T.H., Hammer, A.S., Kuiken, T. and Osterhaus, A. 2002. Another phocine distemper outbreak in Europe. *Science* 297:209.

Jepsen, P.U. 2005. Forvaltningsplan for spættet sæl *(Phoca vitulina)* og gråsæl *(Halichoerus grypus)* i Danmark. Miljøministeriet, Skov- og Naturstyrelsen (In Danish, English summary.)

Jong, G.D.C., Brasseur, S.M.J.M. and Reijnders, P.J.H. 1997. Harbour seal - *Phoca vitulina vitulina.* In: Reijnders, P.J.H., Verriopoulo, G. and Brasseur, S.M.J.M. (eds.); *Status of pinnipeds relevant to the European Union.* DLO Institute of Forestry and Nature Research, Wageningen, 76-97.

Karlson, K., Rosenberg, R. and Bonsdorff, E. 2002. Temporal and spatial large-scale effects of eutrophication and oxygen deficiency on benthic fauna in Scandinavian and Baltic waters: A review. *Oceanogr. Mar. Biol*. 40:427-489.

Kuiper, J. and Enemark, J.A. 2003. Introduction to the international symposium on management of North Sea harbour and grey seal populations. In: *Management of North Sea harbour and grey seal populations.* Proceedings of the international symposium at EcoMare, Texel, The Netherlands, November 29-30, 2002. Waddden Sea Ecosystem No. 17. Common Wadden Sea Secretariat, Wilhelmshaven, Germany, 9-10.

Lonergan, M., Duck, C.D., Thompson, D., MacKey, B.L., Cunningham, L. and Boyd, I.L. 2007. Using sparse survey data to investigate the declining abundance of British harbour seals. *J. Zool.* 271:261-269.

Matthiopoulos, J., Smouth, S., Winship, A.J., Thompson, D., Boyd, I.L. and Harwood, J. 2008. Getting beneath the surface of marine mammal-fisheries competition. *Mamm. Rev.* 38:167-188.

Montgomery, R.A., Ver Hoef, J.M. and Boveng, P.L. 2007 Spatial modeling of haul-out site use by harbour seals in Cook Inlet, Alaska. *Mar. Ecol. Prog. Ser.* 341:257-264.

Mortensen, P., Bergman, A., Bignert, A., Hansen, H.J., Härkönen, T. and Olsson, M. 1992. Prevalence of skull lesions in harbour seals *(Phoca vitulina)* in Swedish and Danish museum collections during the preiod 1835-1988. *Ambio* 21:520-524.

Nei M., Maruyama, T., Chakraborty, R. 1975. The bottleneck effect and genetic variability in populations. *Evolution* 29:1-10.

Olsen, M.T., Andersen, L.W., Dietz, R., Teilmann, J. and Härkönen, T. in prep. Fine scale genetic structure of harbour seals in southern Scandinavia.

Reijnders, P.J.H. 1980. Organochlorine and heavy metal residues in harbour seals from the Wadden Sea and their possible effects on reproduction. *Neth. J. Sea Res*. 14: 30-65.

Reijnders, P.J.H. 1986. Reproductive failure in common seals feeding on fish from polluted coastal waters. *Nature* 324:456-457.

Reijnders, P.J.H. and Aguilar, A. 2002. Pollution and marine mammals. In: Perrin, W.F., Würsig, B., Thewissen, J.G.M. (eds.); *Encyclopaedia of marine mammals.* Academic Press, San Diego, 948-956.

Reijnders, P.J.H. and Simmonds, M.P. 2003. Global temporal trends or organochlorines and heavy metals in pinnipeds. In: Vos, J.G., Bossart, G.D., Fournier, M., O'Shea, T. (eds.); *Toxicology of marine mammals.* Taylor and Francis, London, 491-506.

Rijks, J.M., Hoffman, J.I., Kuiken, T., Osterhaus, A.D.M.E. and Amos, W. 2008. Heterozygosity and lungworm burden in harbour seals *(Phoca viulina)*. *Heredity* 100:587-593.

Søndergaard, N.O., Joensen, A.H. and Hansen, E.B. 1976. Sælernes forekomst og sæljagten i Danmark. *Danske Vildtundersøgelser hæfte 16, Vildtbiologisk Station.* 80p. (In Danish.)

Teilmann, J. and Heide-Jørgensen, M.P. 2001. Sæler i Østersøen, Kattegat og Limfjorden 2000. In: Laursen, K. (ed.); *Overvågning af fugle, sæler og planter 1999-2000, med resultater fra feltstationerne.* NERI technical report no. 350. (In Danish.)

Teilmann, J., Tougaard, J., Carstensen, J., Dietz, R. and Tougaard, S. 2006. Summary on seal monitoring 1999-2005 around Nysted and Horns Rev offshore wind farms. Technical report to Energi E2 A/S and Vattenfall A/S. Available at: http://www.ens.dk/graphics/-Energiforsyning/Vedvarende_energi/Vind/havvindmoeller/vvm%20Horns%20Rev%202/begge%20parker/Samle%20rapport%20s%E6ler%20final.pdf

Teilmann, J., Larsen, F. and Desportes, G. 2007. Time allocation and diving behaviour of harbour porpoises *(Phocoena phocoena)* in Danish waters. *J. Cetacean Res. Manage.* 9(3):35-44.

Teilmann, J., Riget, F. and Härkönen, T. 2010. Optimizing survey design for Scandinavian harbour seals: population trend as an ecological quality element. *ICES J. Mar. Sci.* 67:952-958.

Valsecchi, E., Amos, W., Raga, J.A., Podestá, M. and Sherwin, W. 2004. The effects of inbreeding on mortality during a morbillivirus outbreak in the Mediterranean striped dolphin *(Stenella coeruleoalba)*. *Anim. Conserv.* 7:139-146.

Watts, P. 1996. The diel hauling-out cycle of harbour seals in an open marine environment: correlates and constraints. *J. Zool.* 240:175-200.

Wolff, W.J. 2000. The south-eastern North Sea: losses of vertebrate fauna during the past 2000 years. *Biol. Conserv.* 95:209-217.