Distribution and population structure of North Atlantic harbour seals *(Phoca vitulina)*

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ABSTRACT

A review of the known geographical distribution and current knowledge on the genetic population structure of harbour seals *(Phoca vitulina)* in the North Atlantic is presented. Based on a synthesis of the results from five different studies of neutral genetic markers (mtDNA and nuclear microsatellites, mainly) twelve genetically distinct populations were identified in the North Atlantic: USA/Canada, Iceland, west coast of Norway, Ireland-Scotland, English east coast, Channel area, Wadden Sea, Limfjord, Skagerrak, Kattegat, West Baltic, and East Baltic. Most of the studies addressed the population structure at the regional level, while only a few addressed the structuring at a local level, *i.e.* within countries. Due to the limited number of studies conducted, the identified population units were considered preliminary and more detailed, local studies would probably reveal structuring on a finer scale. The choice of genetic markers, their properties, resolution in time and applicability in population structure studies is shortly discussed and compared to ecological methods used to delineate populations.
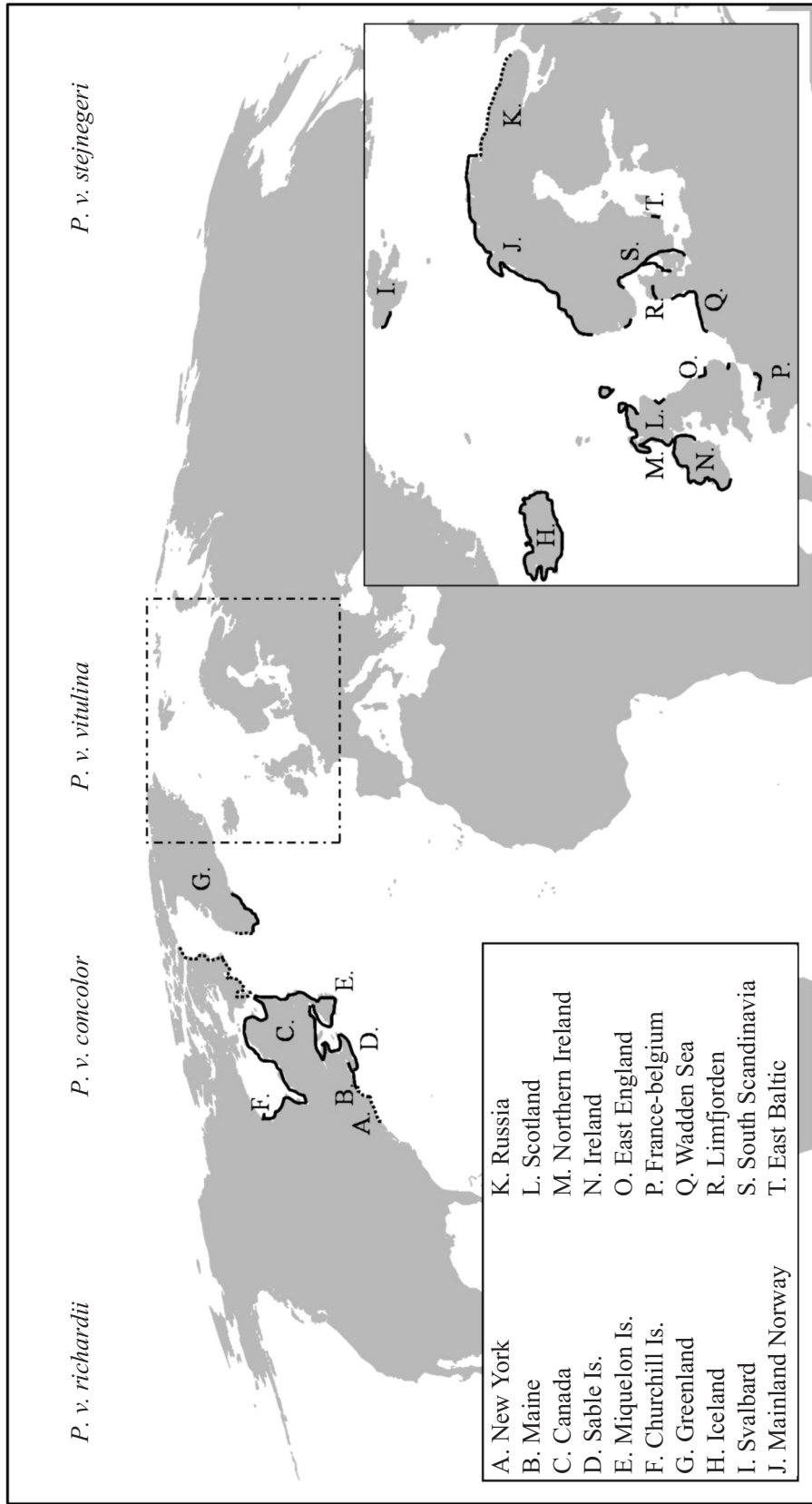
INTRODUCTION

The harbour seal (*Phoca vitulina)* is distributed along the ice-free coasts of the northern hemisphere, and exhibits one of the widest longitudinal and latitudinal spans in distribution among pinnipeds (Burns 2002). Although there is some debate regarding their precise number and taxonomy, it is generally agreed to divide harbour seals into four subspecies, including *P. v. richardii* in the northeast Pacific, *P. v. stejnegeri* in the Northwest Pacific, *P. v. concolor* in the Northwest Atlantic, and *P. v. vitulina* inhabiting the Northeast Atlantic (Árnason *et al.* 1995, Stanley *et al.* 1996, Burg *et al.* 1999, Westlake and O'Corry-Crowe 2002) (Fig. 1). The Atlantic and Pacific subspecies are estimated to have diverged 1.7 to 2.2 mya coinciding with the first record of sea ice and continental glaciations. Colonisation of the North Atlantic suggestively began 0.9 to 1.3 mya proceeding from the West Atlantic to the north and then east to Europe (Stanley *et al.* 1996).

Harbour seal populations in the North Atlantic have experienced significant fluctuations in population sizes and distribution due to local outbreaks of Phocine Distemper Virus (PDV) and anthropogenic effects such as hunting, by-catch and habitat destruction (Dietz *et al.* 1989, Heide-Jørgensen *et al.* 1992, Härkönen *et al.* 2006). Recently, harbour seal populations along the east coast of Canada and in northern Britain have declined markedly (Lucas and Stobo 2000, Thompson *et al.* 2001, Bowen

Fig. 1. *The distribution of the 12 presently identified populations of the harbour seal* (Phoca vitulina) *in the North Atlantic.*

P. v. stejnegeri

P. v. vitulina

P. v. concolor

P. v. richardii

A. New York	K. Russia
B. Maine	L. Scotland
C. Canada	M. Northern Ireland
D. Sable Is.	N. Ireland
E. Miquelon Is.	O. East England
F. Churchill Is.	P. France-belgium
G. Greenland	Q. Wadden Sea
H. Iceland	R. Limfjorden
I. Svalbard	S. South Scandinavia
J. Mainland Norway	T. East Baltic

et al. 2003, Lonergan et al. 2007). These areas were not affected by the PDV epizootic that swept the European coasts in 1988 and 2002 (Härkönen et al. 2006). Instead, the declines might be associated with factors such as anthropogenic disturbance, interspecific competition, increased predation pressure, and/or a changing climate (Lonergan et al. 2007). In Greenland, Iceland and Norway, harbour seals have declined compared to former times, and some populations appear to be in decline currently (Hauksson 1992, Teilmann and Dietz 1994, Henriksen et al. 1997, Hauksson 2006).

Identification of locally distinct genetic units is vital for a good understanding of population status and for the design of appropriate management schemes. Population units serve as a basis for monitoring and for regulating the effects of human activities. Moreover, the identification of genetic units is central to maintaining or preserving genetic diversity, ensuring the evolutionary potential of populations and thereby improving their ability to recover from local over-harvesting, environmental disturbance or disease outbreaks (Frankham 1996, Frankham 1998, Hansen et al. 1999, Frankham et al. 2002).

In the following review we present the genetic methods that have previously been applied to investigate harbour seal population structuring, summarize published and unpublished studies on the distribution and population structure of the harbour seal in the North Atlantic and shortly evaluate the advantages and shortcomings of genetic and ecological methods for population identification.

GENETIC METHODS APPLIED TO HARBOUR SEALS

The genetic markers used to assess harbour seal population structuring include the mitochondrial D-loop (Lamont et al. 1996, Stanley et al. 1996, Burg et al. 1999, Westlake and O'Corry-Crowe 2002), microsatellite markers in nuclear DNA (Goodman 1998, Burg et al. 1999), DNA fingerprinting (i.e. multilocus DNA banding patterns) and RAPDs (Random Amplification of Polymorphic DNA) (Kappe et al. 1995), and isozymes estimating genetic variation at the protein level (Swart et al. 1996). The markers used differ in the way they are inherited and consequently in their ability to detect population structure (see the subsection "Genetic methods" below). Mitochondrial DNA markers are maternally inherited while microsatellite markers, DNA fingerprinting markers, and most of the isozymes are bi-parentally. RAPDs can exhibit both modes of inheritance and should consequently always be tested prior to application.

Using microsatellites and genetic differentiation, population structure in harbour seals has been quantified using F_{ST}-like measures, either in terms of Weir and Cockerham's (1984) estimator θ, that partitions the variance in allele frequency within and among populations, or Slatkin's R_{ST} (or (ρ)) statistic estimating the variance in allele size within and among populations (Goodman 1997a). Such summary statistics quantify the distribution of the total genetic variation among populations and are in the ideal world distributed between 0 and 1, where 1 is complete differentiation.

The population structure based on mitochondrial DNA is examined by Φ statistics based on genetic distance ((Tamura and Nei 1993) nucleotide substitutions, $\alpha = 0.5$) between the haplotypes in the different sampling areas (Excoffier et al. 1992). The different geographical groupings of the populations were analysed using AMOVA (analysis of molecular variance) (Excoffier et al. 1992), a method implemented in the software package ARLEQUIN (v.3.01, Schneider et al. 2000).

Although central to fields of ecology, evolution, and conservation there is no universal agreement as to how a population is defined (Waples and Gaggiotti 2006). In reviewing the population structure of North Atlantic harbour seals we adopt the definition of Moritz's (1994) management units and define a population as a group of animals that is significantly differentiated from another group in terms of genetic variation measured at either mitochondrial or nuclear loci.

Table 1. Genetic population status of the harbour seal in different areas of the North Atlantic

Region	Inferred population	Localities	N	Method	Reference
Atlantic	East Canada	Miquelon Is	7	mtDNA D-loop	Stanley *et al.* 1996
		Sable Is	11		
	Hudson Bay	Churchill Is	1		
	Iceland	Iceland	8		
	Scotland-N. Ireland	Moray Firth	15		
		Dornoch	16		
		West Scotland	7		
		Strangford Lough	7		
	North Sea	Norfolk	17		
		Lincolnshire	4		
		Norway	15		
		West Wadden Sea	18		
		East Wadden Sea	17		
	Southern Scandinavia	Skagerrak	9		
		Kattegat	8		
		West Baltic	9		
	East Baltic	East Baltic	8		
Northeast Atlantic	Iceland	Iceland	11	7 microsatellite loci	Goodman 1998
	Scotland-Ireland	West Scotland	18		
		East Scotland	217		
		East Ireland	11		
	East England	East England	72		
	Wadden Sea	East Wadden Sea	259		
		West Wadden Sea	147		
	Western Scandinavia	Norway	13		
		Skagerrak	133		
		Kattegat	61		

East Baltic		West Baltic	45		
		East Baltic	45		
North Sea		Dutch Wadden sea	26	RAPD and DNA fingerprinting	Kappe et al. 1995
		Eastern Scotland	20		
North Sea		Dutch Wadden sea	21	Isozyme electrophoresis	Swart et al. 1996
		The Wash (England)	17		
Southern Scandinavia	Skagerrak	Väderöarna	25	15 microsatellite loci	Olsen (pers. comm.)
	Kattegat	Tistlarna	16		
		Hallands Väderö	18		
		Læsø	14		
		Anholt	17		
		Hesselø	14		
		Samsø	31		
	Western Baltic	Falsterbo	26		
		Rødsand	15		
	Limfjord	West Limfjord	27		
		East Limfjord	28		
	Wadden Sea	Wadden Sea	28		

DISTRIBUTION AND POPULATION STRUCTURE

Northwest Atlantic
United States and Canada
In the United States and Canada, harbour seals are distributed along the coasts of eastern Canada and Maine year round and seasonally along the coasts of New England and New York (Schneider and Paine 1983). Seasonal movements southwards from Bay of Fundy to southern New England occur in autumn and early winter (Jacobs and Terhune 2000) and northwards from southern New England to Maine and eastern Canada prior to the pupping season (deHart 2002, Gilbert *et al.* 2005). Stanley *et al.* (1996) found some evidence for genetic differentiation within the region based on mitochondrial D-loop variation within the western Atlantic harbour seals from Churchill, Miquelon and Sable Island although sample sizes were low (Table 1). The population found along the eastern US and Canadian is currently considered one coherent population (Temte *et al.* 1991). Although detailed genetic studies are lacking, observations of high philopatry in other Atlantic harbour seal populations (Goodman 1998) suggest that local sub-structuring may be present within the eastern US and Canada.

Greenland
In Greenland, the harbour seal has been distributed from Avanersuaq in the Northwest to the Southeast. The main distribution area used to be between Sisimiut in central West Greenland and Nunap Isua on the southern tip, but hunting has resulted in severe declines in this region and at present harbour seals are mainly found along the Southeast coast (Teilmann and Dietz 1994). In the 1950´s catch numbers were about 200 seals per year on the west coast, but in the early 1960´s the population declined significantly, which was reflected in the catch numbers (Rosing-Asvid pers. comm.). These dropped to about 20 seals per year in the 1980´s. However, some harbour seals are still observed in the area and other still undetected groups may also congregate elsewhere along the west coast as parts of the coastline are poorly surveyed (Rosing-Asvid pers. comm.). In the southernmost part of West

Greenland hunters still catch seals (Rosing-Asvid 2010). The population structure of the harbour seals within Greenland has not yet been investigated and it is unknown whether dispersal takes place between harbour seals from the Southeast and the groups further north along the west coast.

Northeast Atlantic
The Northeast Atlantic subspecies *P. v. vitulina* is distributed from Iceland to the Baltic and the north coast of France to the Barents Sea (Fig. 1). Following the initial colonisation from the western Atlantic the population probably underwent repeated declines during the Ice Ages and recolonised the current range from more southern ice-free refugia after the ice withdrew 10,000-12,000 years ago (Stanley *et al.* 1996, Goodman 1998). Since the Middle Ages, extensive exploitation and habitat alteration have severely depleted most populations and the harbour seals have disappeared from areas where they were formerly abundant (Reijnders 1994, Härkönen *et al.* 2005). However, as a consequence of substantial conservation efforts over the past 30 years, most populations have been steadily increasing and the total abundance of harbour seals in the Northeast Atlantic is currently estimated at approximately 90,000 individuals (Härkönen 2003).

Iceland
The harbour seal is distributed along the entire Icelandic coastline but is most densely concentrated in the northwest (Hauksson 2006). The population has declined from 40,000 to approximately 10,000 animals from the 1970´s to 2003 (Hauksson *et al.* 2006), which is comparable to the decrease observed in the harbour seal populations at *e.g.* Orkney and Scotland from 1984 to1998 (Thompson *et al.* 2001). The harbour seals in Iceland were not affected by the epizootics experienced by European populations and the observed decline can most probably be ascribed to exploitation and by-catch in gill-nets (Hauksson 2006).

Genetic studies of Icelandic harbour seals have so far focused on the status of the Icelandic seals compared to other harbour seals in the North Atlantic (Stanley *et al.* 1996, Goodman 1998). Both studies found the Icelandic popu-

lation genetically divergent from all other populations examined (Stanley *et al.* 1996, Goodman 1998) (Table 1). Stanley and co-authors (1996) found a haplotype diversity of *H*= 0.75 (N=8), representing three different haplotypes, where one (G29) was a unique haplotype not observed in the other eastern North Atlantic areas studied. No study addressing population structure within Iceland has been performed.

Svalbard
The harbour seals in Svalbard are at the northern edge of the species range, and constitute the world's most northerly harbour seal population (Henriksen *et al.* 1997, Gjertz *et al.* 2001, Lydersen and Kovacs 2005). In Svalbard the seals are distributed mainly along the west coast of Prins Karls Forland and on islands in the northwestern part of Svalbard. They can be found even more northerly (Wiig 1989), but their distribution is to a large extent limited by the occurrence of sea-ice (Mansfield 1967). Surveys conducted in the 1980's suggested that the population size in Svalbard is around 500-600 individuals (Prestrud and Gjertz 1990), but more recent estimates based on direct counts suggest that there are 1,000 or more individuals (Lydersen pers. comm.). The genetic status of the Svalbard harbour seal has so far not been studied. Some connection exists between the Norwegian harbour seal populations and the Svalbard population as indicated by the recapture of a tagged Svalbard seal on the Norwegian mainland (Gjertz *et al.* 2001), however such movements are believed to be very rare and Svalbard probably constitutes a distinct unit.

Mainland Norway
The coastline of the Norwegian mainland is divided into three zoogeographic sub-provinces; Skagerrak (between the Swedish-Norwegian border and Vest-Agder), western Norway (from Rogaland northward along the Norwegian west coast including Troms in the north) and Finnmark (Finnmark north of Troms) (Bjørge *et al.* 2007).

The harbour seals are distributed all along the coastline, excluding a stretch in the southwestern part. In a nationwide survey covering most known haulout sites Bjørge *et al.* (2007) estimated a population size of 613 for the Skagerrak sub-province, 8,714 for the western Norway sub-province and 826 for the Finnmark sub-province, a total of 10,153 along the Norwegian coastline (Bjørge *et al.* 2007). Harbour seals have also been reported from the Barents Sea at Novaja Zemlja and rarely along the Murman coastline, Russia, but their numbers are unknown (Henriksen *et al.* 1997).

The harbour seals in the Skagerrak sub-province have suffered mass mortality as a result of the 1988 and 2002 phocine distemper virus epizootics (Härkönen *et al.* 2006). The epizootic did not reach the seals in the other sub-provinces. In northern Norway (Nordland and Finnmark counties) the harbour seals were depleted in the beginning of the 20th century due to hunting (Nilssen *et al.* 2010) however the seal hunt decreased from the mid 1960's allowing the harbour seals to recover in many areas. Following the introduction of a bounty system in 2003, the population has declined and current catch levels are unlikely to be sustainable Bjørge *et al.* 2007, Nilssen *et al.* 2010).

Population structure of Norwegian harbour seals has been studied by Stanley *et al.* (1996) and Goodman (1998) (Table 1). The analyses of Goodman (1998) and Stanley *et al.* (1996) indicated connection between harbour seals from Froan in southcentral Norway and Skagerrak, and seals from Oslo fjord and the Wadden Sea-East England region, respectively. Stanley *et al.* (1996) observed a haplotype diversity *H*= 0.248, representing two haplotypes, that were characteristic for the eastern North Atlantic harbour seals, but no genetic differentiation was observed between harbour seals representing different areas in the North Sea (Table 1). Goodman (1998) found that the seals in Norway were genetically different from West Baltic and Kattegat and other examined populations (Table 1). No comprehensive study of the genetic population structure of harbour seal within Norway has been conducted. However, the fact that the phocine distemper virus did not spread from the Skagerrak province and further north indicates that sub-structuring might be present in the region.

British Isles

In Great Britain, harbour seals are widespread and numerous around the west coast of Scotland and throughout the Hebrides and Northern Isles. The distribution is more restricted on the east coast with concentrations in the Moray Firth, the Firth of Tay, and the Wash (JNCC 2007). In Ireland, harbour seals are more or less continuously distributed along the west coast and the part of the north eastern coast facing Isle of Man (Cronin *et al.* 2007). Only few colonies exist along the east coast from the Northern Ireland-Ireland border and south. The minimum population estimate obtained from counts is 31,200 seals totalled for Ireland and Great Britain (Cronin *et al.* 2007, JNCC 2007).

Over the past years, harbour seals in Great Britain have exhibited substantial declines in Scotland and Orkney, the cause of which is presently unknown (Lonergan *et al.* 2007). Although the detailed genetic structuring of harbour seals in the British Isles is still to be investigated some information exists from the studies of Stanley *et al.* (1996) and Goodman (1998). Sampling the same four areas around the Isles, neither study found significant genetic differentiation among harbour seals from the east coast of Northern Ireland, the Scottish west coast, and the Scottish east coast (F_{ST}=0.019-0.077, Goodman 1998). However, both studies found significant differences between seals from these three areas and animals sampled in the Wash (F_{ST}=0.226-0.295, Goodman (1998)). Stanley *et al.* (1996) found that seals from the Wash exhibited genetic resemblance to Norwegian and Wadden Sea harbour seals, a pattern that was not supported by the approach of Goodman (1998, F_{ST} = 0.049-0.107). Such patterns could be due to sex-biased dispersal, but is more likely to be a consequence of the limited resolution of mitochondrial markers, as discussed below in "Recommendations".

Overall, genetic studies suggest the existence of at least two populations within the British Isles, one comprising harbour seals of Scotland and Northern Ireland, and one in the Wash on the east coast of England. However, given the absence of Irish harbour seals in the above analyses and the general lack of more detailed genetic studies, these findings are best consid-

ered preliminary. In Scotland, for instance, the non-overlapping movements of seals tagged at localities in north-eastern, western, and south-western Scotland, respectively, documented by Sharples *et al.* (2005) suggest differentiation within the presumed Scottish-Irish population. It is very likely that future genetic and ecological studies will identify additional subdivisions of the British Isles harbour seal populations.

France and Belgium

The southernmost harbour seal colonies in the Northeast Atlantic lie in northern France. The abundance of harbour seals in this area has increased since the mid-1990s with major haulout and breeding areas now existing at Baie du Mont Saint Michel, Baie des Veys, and Baie de Somme (Thiery and Kiszka 2005). By the latest survey in 2005 a total of 239 harbour seals were counted in these three areas; a five-fold increase compared to the mid-nineties (Hassani pers. com.). No major harbour seals colonies are documented for Belgium and although strandings occur regularly (Jauniaux *et al.* 2001) the number of animals in these waters is believed to be small. To our knowledge, no studies exist to date that have examined the movements and structuring of harbour seals in the region. The geographic proximity to localities in Great Britain however suggests that dispersal across the Channel might occur; as might movement from the Wadden Sea, but this awaits further analysis.

Wadden Sea

The Wadden Sea comprises a 500 km stretch along the coasts of The Netherlands, Germany (Niedersachsen and Schleswig Holstein), and Denmark. It is part of the North Sea separated by a row of barrier islands and characterised by tidal flats. The area has been heavily exploited and altered since the Middle Ages, severely affecting the distribution and abundance of the harbour seals and other marine species (*e.g.* Reijnders 1981, Wolff 2000, Lotze 2005). The overall abundance of harbour seals in this area decreased from about 40,000 animals at the beginning of the 20th century to less than 3,300 animals in the mid 1970´s. The harbour seal population has been increasing for the past 20 years (Reijnders 1981, Reijnders 1994,

Reijnders *et al.* 1997). Key areas include the Dollard embayment in the eastern Dutch Wadden Sea, the eastern part of Niedersachsen, the centre of Schleswig-Holstein, and the central Danish Wadden Sea (Ries *et al.* 1999). The genetic diversity in Wadden Sea harbour seals (H_O=0.409) is among the lowest recorded for that species (European average H_O=0.501) (Goodman 1998). This is supported by other genetic studies, finding the population to be monomorphic in 21 allozymes (Swart *et al.* 1996) and almost monomorphic in the mitochondrial D-loop (Stanley *et al.* 1996). The reduced genetic divexsrsity might be a result of a severe population decline, leading to inbreeding depression (Nei *et al.* 1975, Hoelzel *et al.* 2001) and reduced adaptive potential (Acevedo-Whitehouse *et al.* 2003, Weber *et al.* 2004, Valsecchi *et al.* 2004).The population is showing signs of reduced fitness in terms of reduced fecundity and high susceptibility to the phocine distemper virus (*i.e.* exhibited high mortality rates) (Heide-Jørgensen *et al.* 1992, Reijnders 1994), although such effects might also have resulted from the high pollution burdens measured in the population (Reijnders 1986, Swart *et al.* 1994).

Both genetic and ecological studies have indicated that harbour seals within the Wadden Sea area constitute one population. Neither mitochondrial nor microsatellite markers have revealed significant genetic differentiation among the German and Dutch Wadden Sea (Stanley *et al.* 1996) (F_{ST}=0.002, Goodman 1998) and several tagging and telemetry studies have documented extensive movements between the Dutch, German, and Danish parts (Ries *et al.* 1999, Tougaard *et al.* 2003).

Evaluating the degree of movement between Wadden Sea localities and neighbouring areas in the North Sea region is less trivial. Significant genetic differentiation in microsatellite loci compared to nearby populations made Goodman (1998) suggest that the Wadden Sea could be considered as one discrete population (F_{ST}=0.049-0.397). By contrast, mitochondrial DNA sequence data, RAPDs, minisatellites, and allozymes have shown no genetic differentiation between harbour seals sampled in the Wadden Sea and along the east coast of England

and Scotland (Kappe *et al.* 1995, Stanley *et al.* 1996, Swart *et al.* 1996). The latter observations imply that the examined localities constitute one population. However, these three studies included smaller samples sizes and employed genetic markers that probably do not have sufficient resolution to elucidate recent migration patterns compared to the markers used by Goodman (1998).

Tagging studies have documented harbour seal movements between harbour seal haulouts in the Wadden Sea and the Wash (Bonner and Whitthames 1974). Ship-based surveys suggest that the North Sea might be a very important wintering habitat for Wadden Sea harbour seals (Leopold *et al.* 1997), and several studies have documented extensive year-round northbound movements of Danish Wadden Sea harbour seals (Härkönen and Harding 2001, Tougaard *et al.* 2003). Contact with other regions is further indicated by the observed spread of the PDV from the Wadden Sea to Britain and the Limfjord (Härkönen *et al.* 2006), although grey seals also could have acted as vectors. At present, the frequency of movements does not appear sufficient to cause genetic homogenization of harbour seal populations in the Wadden Sea, southern Great Britain and the Limfjord, but with increasing population sizes in the Wadden Sea there is reason to believe that they might in the future.

Limfjord
For centuries, Limfjord in Northern Denmark was a highly isolated brackish water system with only a narrow fjord connecting it to the Kattegat in the east. In the mid 19th century, the sandbanks isolating the system from the North Sea were flooded and a permanent channel between the two water bodies established (Hylleberg 1992, Hoffmann and Dolmer 2000). It is unknown whether harbour seals occurred in Limfjorden prior to this event or colonised the area subsequently, but at present they inhabit both the western and the central part of the fjord.

A recent genetic study indicates that Limfjord harbour seals originate from the Wadden Sea area and might have been isolated or gone through a founder event in historic times, cor-

relating well with the known geological changes to the Limfjord system. Furthermore, the authors found significant genetic differentiation between seals in the central part of the fjord and those in the Wadden Sea (F_{ST}=0.081), with harbour seals sampled in the western part apparently consisting of a mix of animals from those two areas (F_{ST}=0.005-0.038). This observation fits well with the northbound movements of Wadden Sea harbour seals suggested by tagging and telemetry data (Härkönen and Harding 2001, Tougaard *et al.* 2003) and the observed spread of the PDV in 1988 and 2002 (Härkönen *et al.* 2006). Ultimately, this migration might result in the central Limfjord subpopulation being assimilated into the Wadden Sea population in the future.

Skagerrak-Kattegat-West Baltic
The fossil record suggests that harbour seals were absent from the Skagerrak-Kattegat-West Baltic region until the mid 18th century, when the area was colonized by animals dispersing southwards along the Norwegian coast (Aaris-Sørensen 1998, Härkönen *et al.* 2005). At present, harbour seals occur along the Swedish west coast, on islands and reefs in most of the Kattegat-Belt region and around Falster in the western Baltic.

Numerous genetic and ecological studies support the differentiation between harbour seals in the Skagerrak-Kattegat-West Baltic region and harbour seals in the Wadden Sea-Limfjord region (Stanley *et al.* 1996, Goodman 1998, Härkönen *et al.* 2005, Härkönen *et al.* 2006). Within the Skagerrak-Kattegat-West Baltic region, harbour seals were previously believed to constitute one large population, possibly with some connection to colonies in southern Norway (Stanley *et al.* 1996, Goodman 1998). However, a recent study employing 15 microsatellite markers and including most major haulout sites in the region revealed genetic differentiation at much finer scales. Skagerrak seals were distinct from other areas examined in the region (F_{ST}=0.010-0.058), colonies within the Kattegat-Great Belt area exhibited considerable levels of connectivity (F_{ST}=0.003-0.058), and western Baltic colonies appeared to constitute a separate entity (F_{ST}=0.004-0.057), albeit with some connection to the Kattegat via

the Øresund strait between Denmark and Sweden. Geographic differences in the movement patterns of harbour seals within the region have similarly been documented by tagging and telemetry studies (Härkönen 1987, Härkönen and Harding 2001, Dietz *et al.* 2003) and correlate well with the preliminary results of an ongoing telemetry study of harbour seals captured in central Kattegat (Dietz pers. comm.).

East Baltic
The East Baltic population of harbour seals numbers approximately 500 individuals distributed at three localities in Kalmarsund (Härkönen pers. comm.). When studied genetically the population exhibited a unique genetic signature, showing very low levels of genetic variation and marked divergence from other Northeast Atlantic populations (Stanley *et al.* 1996) (H_O=0.361, F_{ST}=0.093-0.444; Goodman 1998). It appears that this population is a remnant of the first wave of harbour seals colonising the Baltic about 8,000 years ago as the ice withdrew after the last glaciation (Härkönen *et al.* 2005). Moreover, its genetic signature indicates that in addition to experiencing one or several bottlenecks following the colonisation, the population must have had very limited contact with neighbouring populations (Härkönen *et al.* 2005). Given the current population trends in the East and West Baltic such contact might be established in the future.

SYNTHESIS

Structure of North Atlantic harbour seal populations
Reviewing population genetic studies of North Atlantic harbour seal population structuring we identified twelve distinct population units: USA/Canada, Iceland, Northern Norway, Ireland-Scotland, English east coast, Channel area, Wadden Sea, Limfjorden, Skagerrak, Kattegat, West Baltic, and East Baltic. Due to lack of data the potential population status of Greenland and Svalbard could not be determined. The indicated population structure is largely based on a few genetic studies. Of these only one was at a scale where the degree of structuring and connectivity specific to each haulout site could be inferred, suggesting sub-

divisions within an area previously thought to contain only one population unit (Table 1). In support of this finding, telemetry and tagging studies suggest that harbour seals are relatively sedentary with movements mainly being associated with foraging trips, although some juvenile mediated long-range dispersal events have been observed (Thompson *et al.*1989, Thompson and Miller 1990, Härkönen and Harding 2001, Bjørge *et al.* 2002, Dietz *et al.* 2003, Tougaard *et al.* 2006). It generally appears that harbour seals are philopatric with only limited genetic exchange. The number of different populations identified in this review may therefore be regarded as a minimum number. We expect that further sampling and improved analytical methods will reveal structuring on a much finer scale in many of the treated areas.

Defining population
In identifying populations we have applied a loose definition of Moritz's (1994) management units corresponding to units of significant genetic difference measured either at mitochondrial or nuclear loci. In many recent statistical models genetic divergence is interpreted in terms of rejecting panmixia among the samples studied (*e.g.* Pritchard *et al.* 2000, Guillot *et al.* 2005). As pointed out by several authors (Waples and Gaggiotti 2006, Palsbøll *et al.* 2006,) this definition suffers from the fact that with an adequate amount of highly variable markers, genetic structure can be detected even for very high migration rates, and vice versa; even if differentiation is present, insufficient sampling can result in a failure to detect it (*e.g.* Palsbøll *et al.* 2006, Waples and Gaggiotti 2006). Instead, Palsbøll *et al.* (2006) recently suggested that management units (*i.e.* populations) was defined by the amount of genetic divergence at which they become demographically independent (*i.e.* the growth of the population is determined by local birth and death rates and not immigration), rather than by the rejection of panmixia. In each specific case, a dispersal threshold level below which populations should be assigned to different management units can be set according to the biological and conservation context. The reliance on the influence of demographic characteristics on population genetic divergence rather than significant departure from panmixia makes the approach more appealing to most

management and conservation questions, and perhaps more importantly, necessitates the evaluation of both ecological and genetic data in determining the delineation of populations. Moreover, defining the demographic assumptions and delimiting criteria *a priori* makes the process of delineating units both transparent and explicit, and allows for changes as new information is obtained over time (Palsbøll *et al.* 2006). Currently, there is no general framework to determine such a threshold, *i.e.* the dispersal rate at which populations become demographically connected (Waples and Gaggiotti 2006, Palsbøll *et al.* 2006). However, the substantial amount of knowledge on harbour seal genetics and ecology already at hand suggest that with an interdisciplinary effort the threshold level can be determined within a realistic frame of time and resources, providing a valuable metric for objectively identifying the boundaries of harbour seal populations.

Methods for identification of populations
Genetic methods
The resolution in time of different genetic markers and hence their applicability to management questions depends on inheritance-mode (mentioned in the section "Genetic methods applied to harbour seals") and mutation rate. Mitochondrial markers have a mutation rate of approximately 5×10^{-5} base substitutions per generation (Sunnucks 2000), nuclear microsatellite markers 3×10^{-3} to 3×10^{-4} per generation depending on the locus (Weber and Wong 1993), and isozymes a mutation rate of about 4×10^{-6} per generation (Wagner and Selander 1974). Estimates of mutation rates for RAPD and DNA-fingerprinting have not been published. In general, markers with high mutation rates, such as microsatellites, gives the highest resolution in time *i.e.* are able to detect more subtle and recent population structures compared to the other markers mentioned.

To date, most genetic studies of harbour seals have assessed genetic differentiation and population by use of summary statistics such as F_{ST}. A limitation to these statistics is that they rely on assumptions which are very rarely met in natural populations (*e.g.* infinite population size) and might thus yield erroneous results

(Whitlock and MacCauley 1999, Pearse and Crandall 2004, Ryman and Leimar 2008). Consequently, recent studies of natural populations tend to focus on analysis methods that relax or avoid these assumptions. An approach that has received considerable attention in recent years is the Bayesian clustering method STRUCTURE (Pritchard *et al.* 2000) that groups individual genotypes to minimise Hardy-Weinberg disequilibrium and gametic phase disequilibrium within groups. Approaches such as STRUCTURE that is based on individual genotypes use much more information in the data set than the F_{ST}-like summary statistics, and often has more power to describe the demography and history of population and relationships of individuals in a detailed manner (Selkoe and Toonen 2006).

Moreover, recent advances in analyses of genetic data, primarily microsatellites, have made it possible to obtain information about movement patterns on approximately real time scale by use of assignment tests (Wilson and Rannala 2003, Paetkau *et al.* 2004) and the newest methods for identification of migrants (*e.g.* BIMr, (Bayesian Inference of Migration rates) Faubet and Gaggiotti 2008). However, these kinds of studies require good baseline information on structure of the breeding colonies which can be obtained from the population genetic studies.

Ecological methods
The considerable amount of information on harbour seal movement patterns gathered from tagging and telemetry studies currently provides the best alternative to genetic analyses of population structure (*e.g.* Thompson and Miller 1990, Thompson 1994, Thompson *et al.* 1996, Dietz *et al.* 2003, Tougaard *et al.* 2003). One advantage of telemetry data is their operation in real time, the timescale which is often most relevant to conservation and management. In addition, telemetry studies generate much important information on the behavioural aspects of harbour seal movement and how this correlates with oceanographic features. One drawback of telemetry studies is that tags have a limited lifetime (typically 7-8 months) and are mostly applied to the skin of the animal and therefore lost during the moulting period.

Consequently, researchers must choose between coverage of the long period after moulting (*i.e.* fall, winter and spring) or coverage of the short breeding period before moulting (spring and summer). If animals mix outside the breeding season but exhibit strong fidelity to their respective breeding areas, telemetry may not reveal much about breeding populations if they are only applied over the long period.

Similar to telemetry, mark-recapture studies can provide information on fidelity to breeding sites and the degree of exchange between them on the time scales of days to several years. However, the value of mark-recapture studies for delineations of breeding units depends on the timing of marking and recapturing *i.e.* individuals should be tagged and re-sighted during the breeding period, as is the case with telemetry.

Examples of mark-recapture studies include the freeze-branding of pups carried out over a long-term period in Skagerrak (Härkönen and Harding 2001) and photo-identification and flipper-tagging (Bjørge *et al.* 2002). Photo-identification has been used to provide mark-recapture based information on site fidelity of harbour seals from the Moray Firth in Northeast Scotland. The data were also used to estimate adult survival rates (Mackey *et al.* 2008). Flipper-tagging of harbour seal pups was used to estimate dispersal and by-catch mortality of the species in Norwegian waters (Bjørge *et al.* 2002).

When using alternative methods to identify populations, such as stable isotopes (Outridge *et al.* 2003, Jay *et al.* 2008), contaminants (Hansen *et al.* 2004), and parasite loads (Balbuena *et al.* 1995) it is important to consider the time scale at which the method is operating *i.e.* contaminants operate at a scale going from days to entire life-spans depending on the compound measured and so do stable isotopes and parasite loads. Although potentially capable of revealing biological patterns undetectable by more traditional approaches these methods require further development and/or validation before they can be applied routinely to identify population units.

A disadvantage of ecological studies is that they are often time consuming, labour intensive, and

consequently expensive, unless carried out by volunteers. Contrary, genetic analysis provides valuable information on population structure quickly and at comparatively lower costs.

Recommendations
Information about the distribution and spatial structure of a species is fundamental in providing plans for management. The level of knowledge needed for proper management is determined by the management objectives and the overall factors that influence the target group. As an example, it is important to identify more subtle population structures when animals are subject to harvest while this may be less important when management aims at conservation of unharvested populations that are abundant on a large geographical scale. Consequently, when initiating a study, choice of method and sampling strategy should be carefully designed to address the objectives of a given scientific or management question at the appropriate temporal and spatial scale.

Studies operating over ecological time scale are often more relevant to management considering demographic changes and immediate extinction risks. However, the low time requirement

and cost posed by genetic studies, renders these a good first choice to get an idea of the minimum number of population units. Moreover, genetic methods will also give information on the number of evolutionary significant units which is useful for evaluation of individual population's conservation value. This is important to ensure overall genetic diversity of harbour seals and thereby the potential for long term survival in the face of recurrent disease outbreaks. A careful sampling design should be planned collecting samples from the breeding colonies preferably during the breeding season. Depending on the question asked the sampling design should consider the proximity of the breeding colonies, the number of juveniles and adults represented and the number of males and females represented in the samples.

For genetic studies, a suite of neutral markers such as microsatellites or mitochondrial DNA (depending on the level of information needed) should be applied. Contrary to mitochondrial DNA, analysis of microsatellites provides both paternal and maternal information. Microsatellites are highly polymorphic and have proven useful for studies of recently established populations due to their relatively high muta-

Table 2. Microsatellite markers applied in studies of Southern Scandinavian harbour seals and suggested for future studies of North Atlantic harbour seals.

Locus	Species of origin	Reference
BG	Elephant seal (*Mirounga leonina*)	Gemmel *et al.* (1997)
Hg6.1	Grey seal (*Halichoerus grypus*)	Allen *et al.* (1995)
Hg6.3	Grey seal (*Halichoerus grypus*)	Allen *et al.* (1995)
Hg8.10	Grey seal (*Halichoerus grypus*)	Allen *et al.* (1995)
Hl-20	Leopard seal (*Hydrurga leptonyx*)	Davis *et al.* (2002)
Lc18	Crabeater seal (*Lobodon carcinophagus*)	Davis *et al.* (2002)
Lc26	Crabeater seal (*Lobodon carcinophagus*)	Davis *et al.* (2002)
Lw7	Weddell seal (*Leptonychotes weddellii*)	Davis *et al.* (2002)
Lw11	Weddell seal (*Leptonychotes weddellii*)	Davis *et al.* (2002)
Lw18	Weddell seal (*Leptonychotes weddellii*)	Davis *et al.* (2002)
Lw20	Weddell seal (*Leptonychotes weddellii*)	Davis *et al.* (2002)
Pvc43	Harbour seal (*Phoca vitulina*)	Coltman *et al.* (1998)
SGPV2	Harbour seal (*Phoca vitulina*)	Goodman (1997b)
SGPV10	Harbour seal (*Phoca vitulina*)	Goodman (1997b)
SGPV11	Harbour seal (*Phoca vitulina*)	Goodman (1997b)
TBPV2	Harbour seal (*Phoca vitulina*)	Burg *et al.* (1999)

tion rate, detecting genetic differences on an individual and population level. Sex-biased dispersal can only be analysed using a bi-parental marker or sex-specific markers as markers on the Y-chromosome and mitochondrial markers. If site-fidelity displayed by females alone is the key question, mitochondrial markers would be preferable (Sunnucks 2000, Wink 2006).

The number and type of microsatellites used are suggested by the study of Rijks *et al.* (2008). The authors' study showed that 15 microsatellite markers applied to a sample size of 30 individuals per locality give a resolution at the substructure level separating breeding colonies at a distance of 100-150 km in the Skagerrak, Kattegat and West Baltic region (Table 2). Preferably the markers used in this study should be chosen in future studies and calibration between different laboratories conducted to be able to pool data-sets in a larger scale analysis of the relationship and gene flow patterns of North Atlantic harbour seal population.

ACKNOWLEDGEMENTS

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