Harbour porpoises (*Phocoena phocoena*) in the North Atlantic: Distribution and genetic population structure.

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ABSTRACT

The known geographical distribution (based on ship surveys, aerial surveys, incidental sightings, stranding and bycatch data) and the population genetic structure obtained from mitochondria DNA and nuclear DNA (isozymes and microsatellites) data analyses of the harbour porpoise in the North Atlantic have recently been reviewed and revised by the International Whaling Commission. The present review builds on these documents by integrating more recent genetic and distributional studies. Studies of the genetic structure of harbour porpoise populations tend to be concentrated in areas where samples are available which coincide with areas where incidental or directed catches or stranding take place. Nevertheless, recently, several genetic studies on the population structure have been able to reveal a more comprehensive picture of the harbour porpoise population structure in the Northwest and Northeast Atlantic, although not all areas have been subjected to analyses.

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INTRODUCTION

Information on harbour porpoise distribution in the North Atlantic was reviewed comprehensively by Gaskin in 1984 and revised by the International Whaling Commission (IWC) in 1996. The present review of the distribution pattern is mainly based on these two documents and the distribution areas are listed according to their suggestions. Recently, several studies have been conducted on the genetic population structure of harbour porpoises in the North Atlantic, testing the different population structure hypotheses given in Table 1. As for the distribution patterns, the different genetic studies conducted in each of the distribution areas will be reviewed in the light of the mentioned hypothesised population structure models and the results of these studies are summarised in Table 1. In the text I have attempted to use the two terms “population” and “sub-population” to reflect the distance between the supposed “populations” and thereby their ability to exchange migrants, hence “populations” defining a low probability of exchange and “sub-population” defining a higher probability of exchange. (For genetic terminology see glossary at the end of the text)

DISTRIBUTION AND GENETIC STRUCTURE

Northwest Atlantic

Distribution

According to Gaskin (1984) harbour porpoises in the Northwest Atlantic are distributed in the

Table 1.Review of studies performed on the genetic population structure of harbour porpoises in the North Atlantic.

Population hypothesis	Populations tested	N	Method	Results	Authors
Northwest Atlantic- Northeast Atlantic	1) Northwest Atlantic (NWA) (GSTL) 2) Northeast Atlantic (NEA) (IDW (Kattegat+Belts+Øresund) Netherlands	12 93 40	Isozyme electrophoresis (2 loci)	NWA and NEA 2 separate populations. (allele frq.)	Andersen 1993
	1) Northwest Atlantic 2) Northeast Atlantic	135 194	Seq. of D-loop in mtDNA (1 locus)	2 separate populations (haplotype frq. + Phi_{ST})	Rosel *et al.* 1999b
Northwest Atlantic 1) Gulf of Maine/Bay of Fundy 2) Gulf of St Lawrence 3) E Newfoundland and Labrador	1) Gulf of Maine/Bay of Fundy 2) Gulf of St Lawrence (GSTL) 3) E Newfoundland and Labrador	93 47 48	RFLP of mtDNA	3 separate sub-populations (haplotype frq.)	Wang *et al.* 1996
1) Gulf of Maine 2) Gulf of St Lawrence 3) Newfoundland 4) mid-Atlantic states	1) Gulf of Maine (GOM) 2) Gulf of St, Lawrence (GSTL) 3) Newfoundland (NFLD) 4) mid-Atlantic states (MAS)	80 40 42 41	Seq. of D-loop in mtDNA (1 locus) + 7 microsatellites (7 loci)	3 separate sub-populations: GOM, GSTL, NFDL (haplotype frq.)	Rosel *et al.* 1999a
West Greenland	1) West Greenland 2) IDW (Kattegat+Belts+Øresund) 3) Netherlands 4) GSTL	66 93 40 12	Isozyme electrophoresis (2 loci)	A separate West Greenland population. (allele frq.)	Andersen 1993
	1) West Greenland 2) IDW -summer 3) Danish North Sea-summer	38 53 33	Isozyme electrophoresis + DNA microsatellites	A separate West Greenland population. (allele frq. + F_{ST} + assignment test)	Andersen *et al.* 1997
	1) Gulf of Maine (GOM) 2) Gulf of St, Lawrence (GSTL) 3) Newfoundland (NFLD) 4) West Greenland (WG)	80 40 42 50	Seq. of D-loop in mtDNA (1 locus) + 7 microsatellites (7 loci)	WG separate from GOM and NFLD. (haplotype frq.)	Rosel *et al.* 1999a

Population hypothesis	Populations tested	N	Method	Results	Authors
West Greenland	1) Maniitsoq	106	12 DNA microsatellites	No within structure	Andersen *et al.*
(within)	2) Nuuk	29	(12 loci)	detected.	2001
	3) Paamiut	15			
West Greenland	1) West Greenland	151	12 DNA microsatellites	A separate WG population.	Andersen *et al.*
	2) IDW (Kattegat+Belts+Øresund)	169	(12 loci)	(allele frq. + F_{ST} +	2001
	3) Danish North Sea	151		assignment test)	
	4) British North Sea	131			
	5) Norway	49			
	6) Ireland	105			
	1) Gulf of Maine (GOM)	80	Seq. of D-loop in	A separate WG population.	Tolley *et al.* 2001
	2) Gulf of St, Lawrence (GSTL)	40	mtDNA	(haplotype frq.)	
	3) Newfoundland (NFLD)	41	(1 locus)		
	4) West Greenland (WG)	50			
	5) Iceland	72			
	6) Norway	87			
Iceland	1) Gulf of Maine (GOM)	80	Seq. of D-loop in	A separate Icelandic	Tolley *et al.* 2001
	2) Gulf of St, Lawrence (GSTL)	40	mtDNA	population.	
	3) Newfoundland (NFLD)	41	(1 locus)	(haplotype frq.)	
	4) West Greenland (WG)	50			
	5) Iceland	72			
	6) Norway	87			
Faroe Islands	Not addressed				
Norway					
1) Sub-structured		20	Seq. of D-loop in	1 sub-population.	Tolley *et al.* 1999
a) Barents Sea	1) Barents Sea-females	16	mtDNA	(haplotype frq. + Phi_{ST})	
b) Northern North Sea	2) Norwegian North Sea-females		(1 locus)		
	1) North of 66° N	24	12 DNA microsatellites	1 sub-population.	Andersen *et al.*
	2) South of 66° N	25	(12 loci)	(allele frq. + F_{ST})	2001

Population hypothesis	Populations tested	N	Method	Results	Authors
Norway	1) Norwegian waters 2) Kattegat-Skagerrak 3) Swedish Baltic	13 25 27	RFLP of mtDNA (1 locus)	A separate sub-population (haplotype frq.)	Wang and Berggren 1997
	1) Barents Sea.females (BSF) 2) Norwegian North Sea-females (NNSF) 3) British northern North Sea-females (BNNF)	20 16 35	Seq. of D-loop in mtDNA (1 locus)	2 sub-populations. (haplotype frq. among BSF and BNNF and NNSF and BNNF)	Tolley *et al.* 1999
	1) West Greenland 2) IDW (Kattegat+Belts+Øresund) 3) Danish North Sea 4) British North Sea 5) Norway 6) Ireland	151 169 151 131 49 105	12 DNA microsatellites (12 loci)	1 separate Norwegian sub-population. (allele frq. + F_{ST} + assignment test)	Andersen *et al.* 2001
North Sea 1) Sub-structured a) Danish North Sea b) Netherlands	1) Danish North Sea-summer 2) IDW-summer 3) Netherlands	31 59 40	Isozyme electrophoresis (2 loci)	1 separate population, no sub-structure. (allele frq.)	Andersen 1993
2) Sub-structure a) Northern North Sea b) Southern North Sea	1) Northern North Sea (Shetland + E Scotland) 2) Southern North Sea (east England + Netherlands)	105 73	Seq. of D-loop in mtDNA (1 locus)	2 separate sub-populations (haplotype frq. + Phi_{ST})	Walton 1997
3) Sub-structure a) Eastern North Sea b) Western North Sea	1) Norwegian North Sea females(NNSF) 2) British northern North Sea-females (BNNF)	16 35	Seq. of D-loop in mtDNA (1 locus)	2 sub-populations. (haplotype frq.)	Tolley *et al.* 1999
	1) Danish North Sea (Skagerrak + DK North Sea 2) British North Sea (Shetland+east Scotland+east England)	151 131	12 DNA microsatellites (12 loci)	2 separate sub-populations (allele frq. + F_{ST} + assignment test)	Andersen *et al.* 2001

Population hypothesis	Populations tested	N	Method	Results	Authors
4) Separate Dutch sub-population)	1) IDW (Kattegat+Belts+Øresund) 2) Danish North Sea 3) British North Sea 4) Norway 5) Ireland	169 151 131 49 105	12 DNA microsatellites (12 loci)	Probably mixed sample from Danish North Sea and British North Sea (mixed stock analysis)	Andersen *et al.* 2001
5) North Sea	1) North Sea (German) 2) German Baltic	39 20	Seq. of D-loop in mtDNA (1 locus)	A separate North Sea sub-population. (haplotype frq.)	Tiedemann *et al.* 1996
	1) Danish North Sea-summer 2) IDW-summer 3) West Greenland	33 53 38	Isozyme electrophoresis + DNA microsatellites	A separate Danish North Sea summer sub-population. (allele frq. + F_{ST} + assignment test)	Andersen *et al.* 1997
Ireland and western British Isles					
1) Ireland/western British Isles	1) Celtic Shelf/Irish Sea 2) Northern North Sea 3) Southern North Sea	120 105 73	Seq. of D-loop in mtDNA (1 locus)	A separate Ireland sub-population. (haplotype frq. + Phi_{ST})	Walton 1997
	1) West Greenland 2) IDW (Kattegat+Belts+Øresund) 3) Danish North Sea 4) British North Sea 5) Norway 6) Ireland	151 169 151 131 49 105	12 DNA microsatellites (12 loci)	1 separate Ireland sub-population. (allele frq. + F_{ST} + assignment test)	Andersen *et al.* 2001
English Channel					
1) English Channel	1) English Channel 2) Celtic Shelf/Irish Sea 3) Northern North Sea 4) Southern North Sea	11 120 105 73	Seq. of D-loop in mtDNA (1 locus)	No structuring.	Walton 1997

Population hypothesis	Populations tested	N	Method	Results	Authors
Kattegat, Skagerrak, Belts and Swedish Baltic Sea					
1) Inner Danish waters	1) IDW-summer (Kattegat+Belts+Øresund)	59	Isozyme electrophoresis (2 loci)	A separate IDW sub-population (allele frq.)	Andersen 1993
	2) Danish North Sea-summer	31			
	3) Netherlands	40			
	4) West Greenland	38			
	5) GSTL	12			
	1) IDW-summer	53	Isozyme electrophoresis + DNA microsatellites	A separate IDW sub-population (allele frq. + F_{ST} + assignment test)	Andersen *et al.* 1997
	2) Danish North Sea-summer	33			
	1) West Greenland	151	12 DNA microsatellites (12 loci)	1 separate IDW sub-population (allele frq. + F_{ST} + assignment test)	Andersen *et al.* 2001
	2) IDW (Kattegat+Belts+Øresund)	169			
	3) Danish North Sea	151			
	4) British North Sea	131			
	5) Norway	49			
	6) Ireland	105			
Kattegat, Skagerrak	1) Kattegat-Skagerrak	25	RFLP of mtDNA (1 locus)	A separate Kattegat-Skagerrak sub-population (haplotype frq.)	Wang, and Berggren 1997
	2) Norwegian waters	13			
	3) Swedish Baltic	27			
Baltic Sea					
1) Baltic Sea	1) German Baltic	20	Seq. of D-loop in mtDNA (1 locus)	A separate German Baltic sub-population. (haplotype frq.)	Tiedemann *et al.* 1996
	2) North Sea (German)	39			
2) Swedish Baltic	1) Kattegat-Skagerrak	25	RFLP of mtDNA (1 locus)	A separate Swedish Baltic sub-population (haplotype frq.)	Wang and Berggren 1997
	2) Norwegian waters	13			
	3) Swedish Baltic	27			
2) Swedish Baltic	1) Kattegat	52	12 DNA microsatellites (12 loci)	Probably some family effect reflecting female philopatry in Kattegat and Belts. Swedish Baltic not diff. from Belts	Andersen et al. 2001
	2) Belts	85			
	3) Swedish Baltic	32			
Iberian and Bay of Biscay	Not addressed				
West Africa	Not addressed				

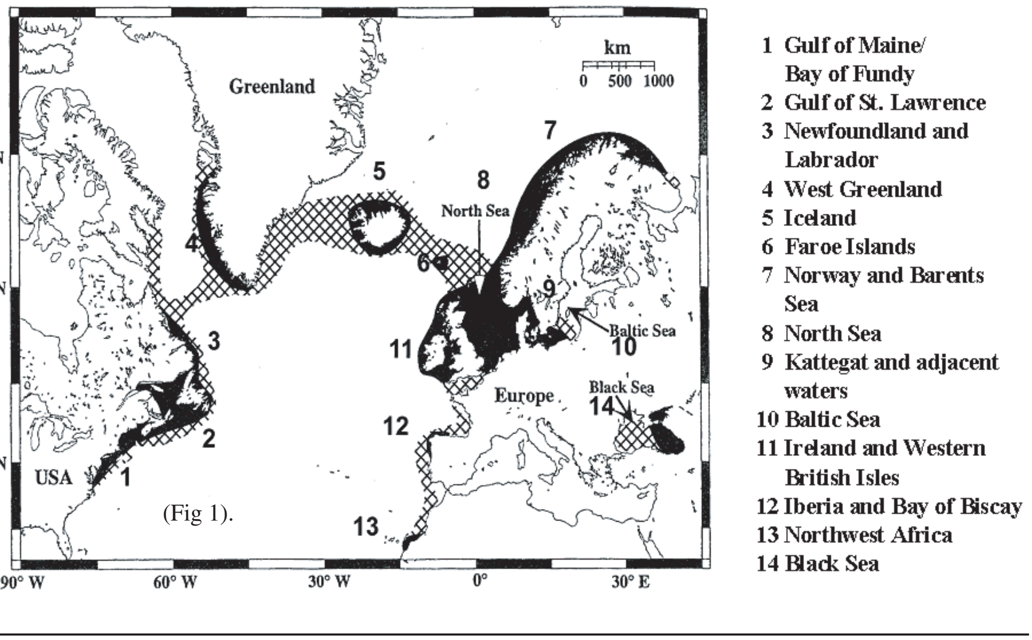
south, from Cape Hatteras (North Carolina) with a more recent observation based on two stranding records in northern Florida (IWC 1996) to the northerly limit on the Canadian coast off Baffin island at about 70^0 N (Fig 1). A seasonal migration pattern has been derived from sighting surveys within this area (Gaskin 1984, Read and Kraus MS 1991, Palka 1995, IWC 1996), where in the northern coastal waters harbour porpoises are only observed during summer. Furthermore, in the Gulf of Maine, substantial variation in the summer distribution pattern has been reported (Read and Kraus MS 1991, Read *et al.* 1993, IWC 1996) whilst little information on the winter distribution exists (Gaskin 1984, IWC 1996). On the basis of these observations IWC (1996) proposed a population structure consisting of 3 separate sub-populations 1) Gulf of Maine/Bay of Fundy, 2) Gulf of St Lawrence and 3) eastern Newfoundland and Labrador.

Implicitly Gaskin (1984) and IWC (1996) regard Northwest Atlantic and Northeast Atlantic porpoises as two distinct populations because porpoises are not expected to migrate over very long distances.

Genetic population structure

In a study of the population structure of harbour porpoises in the North Atlantic and North Pacific Wang *et al.* (1996) addressed the population structure hypothesis suggested by Gaskin (1984). Based on RFLP-analysis of mitochondrial DNA, Wang *et al.* (1996) observed significantly different haplotype frequencies between samples from Bay of Fundy/Gulf of Maine and samples from the Gulf of St Lawrence and Newfoundland, but not between the Gulf of St Lawrence and Newfoundland. The only significant difference between the Gulf of St Lawrence and Newfoundland was observed between the female samples, which indicated a male-biased migration. The Bay of Fundy and Gulf of Maine samples were pooled because no indication of sub-structure was observed. The differences detected in the results of the female-only and male-only analysis were interpreted as indications of females being more philopatric than males, which has been supported by records of annual sightings of recognisable female porpoises returning to the Bay of Fundy (Gaskin and Watson 1985, Wang *et al.* 1996). The higher genetic diversity found in the Northwest Atlantic porpoises compared to

Fig. 1. *Map showing the distribution of harbour porpoise populations/sub-populations and possible range in the North Atlantic (After IWC 1996 and Rosel et al. 1999b). Populations and sub-populations and their possible range are indicated by solid black areas, while cross-hatched areas are the possible migration routes across the North Atlantic.*



the North Pacific porpoises could well be a reflection of the differences in sample size between the two areas. Rosel *et al.* (1999a) also examined the population structure of the Northwest Atlantic harbour porpoises using sequences of the D-loop in mtDNA and microsatellite variation based on 6 polymorphic loci. Samples from 3 summer breeding areas – Gulf of Maine, eastern Newfoundland and Gulf of St Lawrence were included. The results based on variance in D-loop sequences confirmed the results from the RFLP study of Wang *et al.* (1996). Here, as in the study of Wang *et al.* (1996), the haplotype distributions of the Gulf of St Lawrence and the Newfoundland total samples were not significantly different. The results based on microsatellite variation only detected a marginally significant difference in the FST estimate between the Gulf of Maine and Newfoundland samples. Thus, Gaskin's (1984) proposed population structure hypothesis of 3 separated sub-populations: 1) Gulf of Maine/Bay of Fundy, 2) Gulf of St Lawrence and 3) eastern Newfoundland and Labrador was generally supported by the genetic data based on mtDNA markers, although it was only possible to separate the female samples from the Gulf of St Lawrence and Newfoundland in the studies of Wang *et al.* (1996) and Rosel *et al.* (1999a). By applying more than the 6 polymorphic nuclear microsatellite markers in the population structure analysis, a more contemporary picture of the population history would be obtained, which again would be associated with a higher probability of detecting the suggested population structure.

Northwest Atlantic- Northeast Atlantic

Genetic population structure

The very first genetic study of harbour porpoise population structure in Danish waters and part of the North Atlantic was based on isozymes as genetic markers (Andersen 1993). In this study a very small sample of 12 specimens sampled in Gulf of St Lawrence was included in the analysis of sub-populations in the North Atlantic. Despite the fact that only 2 polymorphic enzymes were detected and used in the study, significantly different allele frequencies were observed amongst Gulf of St Lawrence, West Greenland, Netherlands and inner Danish waters (IDW). This observation confirms Gaskin's (1984) hypothesis of 2 separate Northwest and Northeast Atlantic harbour porpoise populations even thought the sample size was low.

In a more recent paper Rosel *et al.* (1999b) analysed the evolutionary history and degree of exchange among harbour porpoise populations in the Northwest and Northeast Atlantic. The study was based on mtDNA control region sequences obtained from a pooling of 3 data sets representing the Northeast and Northwest Atlantic regions (Rosel *et al.* 1995, Tiedemann *et al.* 1996, Walton 1997). The result of the study indicated that exchange of harbour porpoises across the Atlantic rarely occurs. The observation that the genetic diversity of the 2 populations differed significantly with a higher genetic variability in the Northwest Atlantic indicated a more recent colonisation of the Northeastern Atlantic. This was supported by the star-like phylogeny displayed by the relationship among the haplotypes in this area, with a number of rare haplotypes related to the most abundant haplotype. They speculated that a disjunction in the haplotype frequencies could occur east of Greenland. This hypothesis was tested in a study by Tolley *et al.* (2001) including samples from Iceland (see later under Iceland). The result of these new studies confirms Gaskin's hypothesis of 2 separate harbour porpoise populations in the Northwest and Northeast Atlantic.

Greenland

Distribution

Further north the harbour porpoise distribution in Greenland waters, based on catch records, was described by Gaskin (1984) and more recently by Teilmann and Dietz (1998). They both describe the main distribution area as lying between Paamiut and Sisimiut in central West Greenland with a few catch records north of this area near Disko Island. Both papers mention the seasonal concentration of the catch records in the spring, summer and autumn months, although catches have been made in all months, suggesting a year-round harbour porpoise habitat (Gaskin 1984). Very few catches have been reported from eastern Greenland (Gaskin 1984, Teilmann and Dietz 1998), and the porpoises in this area, which are observed during the summer months, are most likely stragglers from West Greenland (Gaskin 1984, Teilmann and

Dietz 1998). Originally Gaskin's (1984) population model hypothesis suggested 2 sub-populations along the Greenlandic coastline: 1) a West Greenland, and 2) a Southeast Greenland sub-population; but based on the above-mentioned "straggler hypothesis" the International Whaling Commission (IWC 1996) recognised only one West Greenland harbour porpoise sub-population.

Genetic population structure

No genetic population structure study has been performed to test the hypothesis of an East Greenland and West Greenland harbour porpoise population mainly because of lack of samples from East Greenland. In a study by Andersen (1993) it was possible to differentiate amongst the West Greenland sample and the Gulf of St Lawrence sample and Dutch sample but not between the IDW sample and the West Greenland sample. This may have been a result of chance and the low number of polymorphic enzymes used. When a combined DNA-microsatellite and isozyme analysis of the porpoises in IDW, the North Sea and West Greenland was based on 3 polymorphic DNA-microsatellite loci and 2 polymorphic isozyme loci (Andersen *et al.* 1997), it was possible to differentiate between IDW and West Greenland porpoise samples and between West Greenland and the North Sea sample. Furthermore, Andersen *et al.* (1997) suggested that a significant deficiency in heterozygotes indicated a possible sub-structure within the West Greenland sample. This observation was most likely due to a sampling bias as the samples were collected from porpoises taken in a direct hunt conducted by the Inuit in different areas. Rosel *et al.* (1999a) (described above) also included a sample from West Greenland in their genetic analyses. The results showed significant different genetic variation at the mtDNA level between West Greenland and Gulf of Maine and Newfoundland for both sexes and only between West Greenland and Gulf of Maine for the females. At the nuclear level no significant population differentiation was observed. This observation could be explained by differential sex migration with a high male-mediated gene flow. In a more recent study Tolley *et al.* (2001) included the mtDNA data from the same West Greenland sample in a West-East North Atlantic study of the phylogeographic pattern of porpoise populations. In addition to the formerly described genetic differences between West Greenland and Newfoundland and Gulf of Maine, significantly different haplotype frequencies were observed between West Greenland and Norway and Iceland. Andersen *et al.* (2001) did not detect differences between the 3 locations Maniitsoq, Nuuk and Parmiut in West Greenland, but demonstrated significantly different microsatellite allele frequencies and F_{ST} estimates based on 12 loci between West Greenland and porpoise samples from Irish waters, the British and Danish North Sea, Inner Danish Waters and Norway. The overall result from these studies all support the population structure hypothesis of a separate West Greenland porpoise population as proposed by Gaskin (1984) and IWC (1996).

Iceland and Faroe Islands

Distribution

Moving southeast to the central North Atlantic towards Iceland and the Faroe Islands, there have been reported sightings of porpoises in deep waters between Greenland and Iceland and between Iceland and the Faroe Islands (Sigurjónsson *et al.* 1990, Gunnlaugsson and Sigurjónsson 1990, IWC 1996). Harbour porpoises have been reported year-round in both Icelandic and Faroese waters (Bloch *et al.* 1992, Skov *et al.* 2003). Skov *et al.* (2003) also reported the spatial distribution of harbour porpoises in relation to water depth in Faroese waters. Three major characteristics were observed in the distribution pattern: the distribution range extended to waters deeper than 600 m; the average encounter rate suggested that the abundance level varied within the 0 to 300 m depth zone (lowest frequencies over the lowest depths and the highest frequencies over the shelf edge); and finally, the encounter rate in waters shallower than 300 m was 5 times the level recorded in deeper waters (Skov *et al.* 2003). Despite the sightings in deep waters between Iceland and Faroe Islands, the IWC (1996) decided to consider Iceland and the Faroe Islands as 2 putative populations as no exchange between the 2 areas have been reported. This is a modification of Gaskin’s (1984) population structure hypothesis, which considered Iceland and Faroe Island harbour porpoises to belong to one population.

Nevertheless, because of the distance separating the 2 islands Gaskin (1984) suggested 2 working sub-divisions. Hence the population structure model hypothesised for porpoises in this part of the North Atlantic is 1) an Icelandic population and 2) a Faroese population.

Genetic population structure

Tolley *et al.* (2001) included mtDNA data from Icelandic harbour porpoises in a West-East North Atlantic study of the phylogeographic pattern of porpoise populations in order to analyse where the break displayed by the genetic differentiation between west and east North Atlantic could be located. No overall pattern of isolation by distance, as indicated by the correlation of geographical distance and the observed genetic variation across the North Atlantic, was observed. Furthermore, the Icelandic sample was genetically more similar to the western populations, which suggests that the observed break in the haplotype distribution probably is located between Iceland and Norway. The genetic differences detected in the haplotype frequencies between West Greenland and Iceland suggests that individuals from the same ancestral population, but from different groups, could have founded the West Greenland and Iceland populations. This result supports Gaskin's (1984) and the IWC's (1996) suggestions of a separate Icelandic harbour population. So far no genetic study has been conducted to analyse the hypothesis of a separate Faroese population.

Norwegian waters

Distribution

Moving further east to the Barents Sea and northern North Sea, porpoises are distributed from northern Norway to Lofoten-Vestfjorden waters and further south into the northern North Sea (Øien 1990, Bjørge and Øien 1995). Gaskin (1984) proposed a division of Norwegian waters into 2 working divisions, one from Skagerrak to Vestfjorden and the second from Lofoten to Varanger Fjord. Based on an apparent near-absence of porpoises in the mid-coastal region off the Norwegian west coast, the division between the Barents Sea and northern North Sea harbour porpoise distribution was defined by Bjørge and Øien (1995) and the IWC (1996) to be approximately 66° N. The northernmost distribution is at the border between Atlantic and Arctic waters. Historically, harbour porpoises have been sighted in the White Sea and at the Kola Peninsula (Gaskin 1984), but according to Gaskin (1984) no recent observations have been made in this region. Hence, the suggested population structure hypothesis in this area is 2 putative sub-populations 1) a Barents Sea and 2) a northern North Sea divided by the gap in distribution at 66° N (Bjørge and Øien 1995).

Genetic population structure

In their study of the population structure of porpoises sampled in the Swedish Baltic and Kattegat-Skagerrak, Wang and Berggren (1997) included a small sample of 13 specimens from the Norwegian West Coast. Based on RFLP analysis of mtDNA a significantly different haplotype frequency distribution was revealed between the Norwegian sample and the other 2 areas, which indicates the existence of a genetically different Norwegian sub-population as suggested by Gaskin (1984). Tolley *et al.* (1999) sequenced the D-loop in mtDNA of 38 porpoises from the Barents Sea and 45 porpoises from the Norwegian North Sea in order to test the hypothesis of a parapatric population model separated spatially with no physical barriers but with genetically different sub-populations. No significant difference in haplotype frequency between the Barents Sea and the Norwegian North Sea female samples was detected. Therefore the hypothesis of 2 parapatric sub-populations in Norwegian waters separated by the gap in distribution at 66° N as suggested by Bjørge and Øien (1995) was not supported. Tolley *et al.* (2001) included the Norwegian sample from the 1999 paper in a cross-Atlantic study of the mtDNA variation in harbour porpoises. The results indicated that the Norwegian porpoises are genetically differentiated from the western North Atlantic porpoises and from Iceland. The observed isolation by distance effect correlating geographic and genetic distance could be attributed to the pairwise distances involving the Norwegian sample. Andersen *et al.* (2001) included a Norwegian sample in the analyses of the population structure of porpoises in European waters using 12 polymorphic microsatellite loci. The Norwegian porpoises seemed to be the most genetically differentiated among the examined samples from inner Danish waters

(IDW), Danish North Sea (DKNS), British North Sea (UKNS), Ireland (EI), Netherlands (NL) and West Greenland (WG). The suggested existence (Bjørge and Øien 1995) of 2 subpopulations separated at 66^0 N was once again not supported. Furthermore, the closer relationship observed among porpoises from IDW, DKNS and Norway might indicate a common migration route going from IDW and north towards Skagerrak and the Norwegian west coast. Hence, the results from the mtDNA studies and the nuclear DNA study points to the existence of a genetically differentiated Norwegian sub-population/population separated from the western North Atlantic and from the geographically more close regions such as Scandinavian and European waters.

North Sea

Distribution

In the North Sea several shipboard and aerial sighting surveys (Heide-Jørgensen *et al.* 1993, Northridge *et al.* 1995, and Hammond *et al.* 1995) have been conducted revealing the more recent summer distribution of harbour porpoises in this area. The results of these sightings indicates a continuous distribution of porpoises across the North Sea although areas with high concentrations along the Danish and northern German coast have been reported (IWC 1996). In the Channel and north-west of the Shetland Islands very low densities of porpoises were observed in the summer months, which may indicate that these areas are the boundaries of the North Sea population (Hammond *et al.* 1995, IWC 1996). Furthermore the SCANS surveys (Hammond *et al.* 1995) recorded very few porpoises off the Dutch coast, which indicates that harbour porpoises in this area may originate from the North Sea population. Based on the oceanographic topology of the south-west and south of Norway, Yurick (1977) and Gaskin (1984) suggested an east-west division of the North Sea porpoise population resulting in an east English sub-population and a Netherlands to Denmark sub-population. These 2 putative sub-populations were not thought to be isolated but probably to have an extensive overlap (sympatrical or parapatrical) in their distribution due to the banks and shallow water across the North Sea (Gaskin 1984). Thus, 2 working areas were recognised by Gaskin: 1) east England and east Scotland; and 2) from the Channel to Skagen, which includes the majority of Skagerrak. On the other hand the population structure hypothesis suggested by the IWC (1996) for porpoises in the North Sea is one coherent North Sea population extending from southern Norway to Shetland and south to the Dutch coast, not including Skagerrak.

Genetic population structure

Several population genetic studies based on different genetic approaches have been applied to investigate the population structure of the harbour porpoise in the North Sea. Andersen (1993), based on isozymes, found genetic differences between IDW (Kattegat, Belts and Øresund) and the Dutch sample and between IDW and the North Sea (Danish North Sea and Skagerrak) sub-populations. Kinze (1985) morphologically distinguished between porpoises from the Baltic and the Dutch coast. Andersen (1993) found a Wahlund-effect in the Danish North Sea summer sample, which was interpreted as a mixture of sub-populations in one area. This observation could be attributed to the sampling procedure, where individuals were collected over a wide geographical area, possibly representing several breeding areas (Clausen and Andersen 1988). On the basis of the genotypic distribution obtained from the 2 polymorphic loci the hypothesis of a separate Dutch and Danish North Sea – summer population was rejected. Andersen *et al.* (1997) and Andersen *et al.* (2001) used an increased number of genetic markers, thus enhancing the power of the tests for differentiation. The detection of significant allele-frequency differences, F_{ST} estimates and correct assignment of porpoises based on their multilocus genotypes to the sampling area where they had been collected, supported the hypothesis of genetically separate Danish North Sea and British North Sea sub-populations (Andersen 2001), suggesting an east-west differentiation of the porpoises in the North Sea. The Dutch sample included in the Andersen *et al.* (2001) study was genetically heterogeneous and it was hypothesised that it comprised a mixture of individuals with different origin, which was supported by a mixed stock analysis.

Tiedemann *et al.* (1996) studied the genetic differentiation between porpoises in the German

North Sea and German Baltic Sea by sequencing the mtDNA D-loop. They found a significantly different haplotype composition between the 2 populations. The nucleotide diversity in the Baltic Sea was lower compared to the North Sea, which they explained by a persisting founder effect.

Walton (1997) analysed the population structure of harbour porpoises in British and adjacent waters using direct sequencing of a portion of the control region of mtDNA. The study areas included in the North Sea were Shetland, east coast of Scotland, east coast of England and Netherlands. He divided the North Sea into a northern and southern section using a part of the Scottish coast where no stranded porpoise had been retrieved as the dividing line. The haplotype frequencies of the different sampling localities and possible poolings were compared to obtain the highest haplotype heterogeneity. This resulted in a pooling of the English and Dutch samples into a southern North Sea sub-population, while the east Scotland sample was pooled with the Shetland sample to give the northern North Sea sub-population. The significant Φ_{ST} estimate obtained between the northern North Sea and southern North Sea totals could be attributed to differences between females, indicating that females were more stationary than males (Walton 1997). These results proposed a population structure consisting of 2 separate sub-populations: southern North Sea and northern North Sea. Neither Yurick (1977), Gaskin (1984), nor IWC (1996) suggested a division of the North Sea into north and south harbour porpoise sub-populations. Tolley *et al.* (1999) included 66 porpoises sampled from the British northern North Sea that were analysed by Walton (1997). There was no significant difference in the female haplotype frequencies from the North Sea Norwegian and British northern North Sea samples. However, there was a difference between the British northern North Sea and the Barents Sea female samples. When the 9 females from the Shetlands were excluded, a significantly different haplotype distribution was observed between the British northern North Sea female sample and the Norwegian North Sea female sample. This was interpreted as a cline going east to west from Norwegian North Sea to British northern North Sea (Tolley *et al.* 1999). The east-west division of the North Sea harbour porpoises was supported by Andersen *et al.* (2001). Andersen *et al.* (2001) did not detect differences between the presumed northern and southern North Sea neither in allele frequencies nor expressed as a significant F_{ST} estimate.

Kattegat, Skagerrak and Belts

Distribution

Aerial and shipboard surveys have recorded high densities of porpoises in the Skagerrak, Kattegat and Belt waters especially in the summer months (Heide-Jørgensen *et al.* 1992, 1993, Hammond *et al.* 1995). The porpoises are distributed continuously from the border of the North Sea, which the IWC (1996) considers to be at the entrance to Skagerrak, including Skagerrak and south to the border of the Baltic Sea, which is defined by the underwater Darss ridge between Darrs, Germany and Gedser and the Limhamn underwater ridge at the inner boundary of Øresund (IWC 1996). The population model hypothesis (IWC 1996) considers the porpoise sub-population in the Skagerrak, Kattegat and Belts area to be separated from the North Sea population. Gaskin (1984) describes this area to be the western Baltic and the porpoises within this region to be a part of the Baltic Sea population. He proposed 2 working sub-divisions 1) Skagerrak, Kattegat, and Danish inland shelves to Gulf of Riga and Gulf of Finland and 2) Gulf of Bothnia, hence including Skagerrak in both the North Sea population and the Baltic Sea population.

Genetic population structure:

Great confusion about the definition of the North Sea and inner Danish waters (IDW) exists. When Andersen (1993) and Andersen *et al.* (1997) included Skagerrak with the Danish North Sea sample they were able to distinguish between the IDW (Kattegat, Belts and Øresund) and the North Sea summer samples. This observation was supported recently by Andersen *et al.* (2001). In this study the Skagerrak sample was genetically different from a combined Kattegat-Belt-Øresund-Swedish Baltic Sea sample, hence providing more evidence for the inclusion of Skagerrak porpoises into the Danish North Sea sub-population rather than into IDW sub-population.

Wang and Berggren (1997) included in their RFLP study a sample from the Kattegat-Skagerrak area without defining whether the Kattegat-Skagerrak sample belonged to the North Sea or the inner Danish/Swedish sub-population. Thus the Kattegat-Skagerrak sample may be a mixture of 2 separate sub-populations. Hence, the observed haplotype distributions are not representative of either the Skagerrak (Danish North Sea) or the Kattegat (inner Danish water) population. The obtained results of a significantly different haplotype distribution amongst the Swedish Baltic, Kattegat-Skagerrak and Norwegian west coast samples might as well be a reflection of the mixture of the suggested inner Danish waters (Kattegat) and Danish North Sea (Skagerrak) sub-populations. If the authors consider the Kattegat-Skagerrak sample to be a part of the North Sea sub-population the results of the mtDNA study supports the population structure hypothesis suggested by Andersen (1993, Andersen *et al.* 1997, Andersen *et al.* 2001) of a genetically different inner Danish water (Kattegat+Belts+Øresund) sub-population and a Danish North Sea sub-population. If they consider the Skagerrak-Kattegat sample to belong to the inner Danish water sub-population, they indirectly assume 2 different sub-populations within the Skagerrak-Kattegat-Belt waters and Baltic Sea region, *i.e.* a Swedish Baltic Sea and an inner Danish/Swedish water sub-population.

Thus the suggested population structure hypothesis of a genetically separate Kattegat, Skagerrak and Belts sub-population (IWC 1996) are not supported by the 3 studies of Andersen (1993, Andersen *et al.* 1997, Andersen *et al.* 2001) but only by Wang and Berggren's (1996) study. In the latter case, Skagerrak is considered to belong to inner Danish waters and not the North Sea.

Baltic Sea

Distribution

Very few porpoises have been observed in the Baltic Sea recently, although a few year-round strandings and incidental catches have been reported from Polish waters which indicates the existence of at least a small resident Baltic Sea population (Skora *et al.* 1988). A few sightings and incidental catches have likewise been reported from the Swedish Baltic Sea (Berggren 1995). According to Gaskin (1984) a reported seasonal migration of porpoises out of the Baltic in winter (Møhl-Hansen 1954) has practically ceased indicating a decline in population size. Some porpoises may have wintered in the western Baltic and the Great Fisher Bank (Gaskin 1984). Whether the population structure model for the Baltic Sea and Skagerrak, Kattegat, Belts was hypothesised to constitute 2 separate sub-populations or if the hypothesis considered the Skagerrak, Kattegat and Belts sub-population to be a relict of a former Baltic Sea population could not be clarified from the IWC (1996) report.

Genetic population structure

Tiedemann *et al.* (1996) was able to differentiate the German Baltic porpoise sample from the German North Sea, genetically. The observed differentiation between these 2 areas, despite the known winter migration pattern of porpoises out of the Baltic into an area in which there is a high probability of mixing with North Sea individuals, was explained by female philopatry (Tiedemann *et al.* 1996). According to the definition of the Baltic Sea given by the IWC (1996) (See **Kattegat, Skagerrak and Belts**) the main part of the samples constituting the German Baltic in this study does not belong to the Baltic Sea. Nevertheless, this area is referred to as the western Baltic so the German Baltic porpoise sample should be considered to represent Baltic porpoises. How these porpoises are related to the Kattegat, Øresund and Belts porpoises has not yet been investigated. In general, Tiedemann *et al.* (1996) supported the separation of a North Sea and a Baltic Sea sub-population, as suggested by Gaskin (1984).

Ireland and western British Isles

Distribution

Results from sightings, incidental catches and strandings (Yurick 1977, Rogan and Berrow 1996, Hammond *et al.* 1995) have shown that harbour porpoises are distributed in the waters from the Celtic Shelf, Irish Sea and western England to northwest Scotland. They are observed year round off the Irish coast (Rogan and Berrow 1996, IWC 1996)) although a seasonal movement northward in spring has been observed (Gaskin 1984). The proposed population structure hypothesis is one Ireland/western British Isles sub-population separated from the North Sea population (IWC 1996).

Genetic population structure

Walton (1997) found significant Φ_{ST} estimates among the Celtic/Irish Sea and northern North Sea, for both sexes and for males only, and amongst the Celtic/Irish Sea and both northern and southern North Sea females. However, after applying the Bonferroni correction (Rice 1989) in this study, the significance obtained in the pairwise comparison between the Celtic/Irish Sea and northern North Sea males and southern North Sea females disappears. The significant sub-structure observed in the total and the female samples between the Celtic/Irish Sea and northern North Sea persist. This indicates the existence of genetically separate North Sea and Celtic/Irish Sea sub-populations. Andersen *et al.* (2001) included an Irish sample consisting of porpoises from Cornwall, Ireland/Wales and the Irish Sea. The Irish sample was genetically different from IDW, Danish North Sea, British North Sea, West Greenland and Norway supporting the earlier findings of Walton (1997). These observations support the proposed hypothesis of an Ireland/western UK sub-population separated from a North Sea sub-population (Gaskin 1984, IWC 1996).

English Channel

Distribution

Although sightings of porpoises in the English Channel have been reported in the past (Gaskin 1984) the more recent SCANS survey did not produce any sightings in this area (Hammond *et al.* 1995). Because no sightings of porpoises in the Channel have been recorded during the summer surveys, it is not possible to determine if the suggested sub-population in this area (Gaskin 1984) belongs to the Ireland/western British Isles sub-population or the North Sea population (IWC 1996), or is a separate sub-population that has become very rare.

Genetic population structure

A very small sample of 11 specimens from the English Channel was included in Walton's (1997) study. The comparison of haplotype frequencies between the English Channel and the northern and southern North Sea and the Celtic/Irish Sea did not reveal a further sub-structuring. This could be interpreted as supporting Gaskin's (1984) hypothesis; *i.e.* no separate Channel sub-population.

Iberian and Bay of Biscay

Distribution

Porpoises are observed throughout the year in the northern part of the Bay of Biscay (Collet MS 1995, IWC 1996). Furthermore, as indicated from incidental catches sightings and strandings in winter and early spring, porpoises are distributed further south off the Galician coast in Spain to Portuguese waters (IWC 1996). No sightings from the Mediterranean, Canary Islands and Azores have been reported (IWC 1996). The population structure hypothesis proposed by the IWC (1996) suggested a separate Iberian harbour porpoise population. This was supported by the observation of longer Iberian porpoises compared to North Sea specimens and by the difference in habitat between the Bay of Biscay and North Sea (IWC 1996).

Genetic population structure

No genetic population structure analyses have been applied to harbour porpoises from these waters.

West Africa

Distribution

Off the African west coast harbour porpoises are distributed continuously from the southern Morocco to Cape Verde but very little information exists on these animals (IWC 1996). The existence of a separate West African population with the Straits of Gibraltar as the northerly boundary has been proposed (Gaskin 1984, IWC 1996).

Genetic population structure

The suggested population structure hypothesis (Gaskin 1984, IWC 1996) has not been tested using genetic methods.

CONCLUSION

Many studies have analysed the genetic population structure of the harbour porpoise throughout its distribution in the North Atlantic (Table 1). These studies tend to be concentrated in areas of high incidental mortality caused by bycatch, which reflects both the growing need to fully understand the harbour porpoise sub-population/population structure and the availability of samples. Some of the studies suffer from the inconsistent application of diverse techniques such as RFLP analysis of mtDNA, sequencing of mtDNA, isozyme electrophoresis and microsatellite DNA in the different areas. This makes valid comparative analyses between nearby areas difficult. This has been overcome in more recent studies (Rosel *et al* 1999a,b, Tolley *et al.* 2001, Andersen *et al* 2001) by including harbour porpoise samples from a wider geographical range and using either or both mtDNA and nuclear markers (Rosel *et al.* 1999a). Hence a more comprehensive picture of the harbour porpoise populations in the North and Central Atlantic is emerging. Still, information about the genetic population structure is sparse from areas like East Greenland and the Baltic Sea, and in other areas like the Faroe Islands, Bay of Biscay, and West Africa no studies has been conducted.

Studies based on mtDNA reflect strictly the maternal inheritance of this organelle. This indicates that the observed sub-structuring detected in these studies where no nuclear markers have been used, might well be caused by the philopatric behaviour displayed by females, reflecting different family units and not necessarily the existence of genetically different sub-populations.

Nevertheless, the population genetic studies applied in the different regions do to some extent support the existence of genetically different harbour porpoise sub-populations/populations in the North Atlantic. Although IWC has divided the North Atlantic into 13 putative sub-populations/populations, several new studies suggest that a revision of this division to be in order. In the Northeast Atlantic the results of Walton (1997) suggested a division of the North Sea into northern and southern stock areas, while Tolley *et al.* (1999) and Andersen *et al.* (2001) suggested a division of the northern North Sea into eastern and western sub-populations. Hence, despite the high probability of mixing in the middle of the North Sea, porpoises may be associated with separate breeding areas near the coast. Such a division in sub-populations may be created by philopatric behaviour of females.

Great confusion about the definition of the North Sea and inner Danish waters (IDW) exists. The population genetic study by Andersen (1993), Andersen *et al.* (1997), and Andersen *et al.* (2001) includes the Skagerrak in the North Sea and not the inner Danish waters. All 3 studies were able to distinguish between the IDW and the North Sea, indicating at a minimum that Skagerrak porpoises are similar to those from the Danish North Sea.

Some of the studies have been hampered by small sample sizes, which lowers the power of the tests, hence increasing the probability of accepting an erroneous null hypothesis (type II error). In general, a sample size of 40 to 50 individuals, preferably not related, is a statistically "good" sample size, but another way to minimise the influence of sampling variance is to use as many independent genetic markers as possible (Hillis and Moritz 1989). In order to be able to make comparable, comprehensive analyses of harbour porpoise sub-populations/populations world-wide, future genetic studies should implement the use of different neutral markers (such as mtDNA or microsatellites or markers hypothesised to be under selection such as genes in MHC) and to calibrate genotyping between laboratories conducting the analysis. This calibration could be done by analysing identical microsatellite loci and exchanging DNA and the results of genotyping.

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GLOSSARY

Allele: A form a gene can take at a single locus. The forms differ in their DNA-sequence, which can affect the structure and form of a single product.

Allele-frequency: A measure of the relative frequency of an allele in the population. The frequency of an allele in the population is calculated as 2 x (number of homozygote individuals (AA) for the allele in question) + (the number of heterozygote individuals (Aa) for the allele in question) / 2N N= number of individuals in the sample.

Isozymes: The different electrophoretic forms of an enzyme caused by differences in sub-unit configurations of the proteins.

D-Loop: Often referred to as the control-region in mtDNA. The displacement loop is a region (qv) in which the replication of mtDNA starts. A short stretch of RNA is paired with one strand of DNA, displacing the original partner DNA strand in this region.

F_{ST}: An estimate of the relatedness of pairs of alleles between individuals within sub-populations describing the differentiation among sub-populations. It is based on the comparison of the distribution of allele-frequencies (qv).

Haplotype: A particular DNA sequece in the mtDNA molecule. A set of closely linked genetic markers present on one chromosome and which tend to be inherited together.

Haplotype-frequency: Frequency of a particular DNA sequence in the mtDNA (in the present context).

Hardy-Weinberg equilibrium: The law stating that gene frequencies remains constant from generation to generation when there is random mating in an infinitely large population with no selection, migration or mutation (qv).

Locus (loci): The position of a DNA marker or genetic marker on the chromosome.

Microsatellite: Simple nucleotide sequences composed of di-, tri- or tetra-nucleotides that are repeated. The number of repeats characterises the microsatellite-alleles. They are interspersed randomly throughout the genome.

Philopatric: Returning to a particular breeding site or area to reproduce.

Restriction site: A short region of DNA (4 to 6 basepairs) that can be recognised by a restriction enzyme (qv).

RFLP: Restriction fragment length polymorphism caused by mutations in a DNA sequence leading to creation or elimination of new restriction sites (qv).

Φ_{ST}: A measure of genetic diversity within sub-divided populations based on haplotype frequency distribution and DNA sequence differences.

Wahlund-effect: When a sub-divided population contains fewer heterozygotes than predicted, despite the fact that every sub-division is in Hardy-Weinberg equilibrium (qv).