Short Communication

Conservation genetics without knowing what to conserve: the case of the Baltic harbour porpoise *Phocoena phocoena*

Anna Palmé, Linda Laikre, Fred Utter and Nils Ryman

Abstract Effective conservation requires that arguments for identifying units for preservation and management are based on scientifically sound information. There is a strong conservation concern for the harbour porpoise *Phocoena phocoena* of the Baltic Sea. This concern rests on the assumption that these porpoises represent a genetically distinct population reproductively separated from adjacent populations to the west. We argue that current scientific support for this claim is weak and to a large degree speculative. Current management of Baltic harbour porpoises as a genetically separate conservation unit is premature and we urge that high priority be given towards resolving this issue.

Effective conservation management requires identification of the population's genetic structure, and genetic distinctness of a population has long been recognized as a key issue for conservation concern (Moritz, 1994). It is important, however, that arguments for genetic distinctness are based on scientifically valid information so that the efficiency of management efforts is not compromised. Here we consider the situation where genetic distinctness is used as a conservation argument but the scientific evidence appears weak: the harbour porpoise *Phocoena phocoena* of the Baltic Sea. The harbour porpoise is considered threatened in parts of its distribution range and is categorized as Vulnerable on the IUCN Red List (IUCN, 2007). It is the only cetacean occurring regularly in the Baltic Sea and in the adjacent Danish Belt, Skagerrak and Kattegat Seas (Berggren & Arrhenius, 1995; Fig. 1).

Conservation concern (ABDG, 2001; ASCOBANS, 2002; Lindahl *et al.*, 2003) for the harbour porpoise of the Baltic Sea proper (defined by the Limhamn and Darss underwater ridges; Fonselius, 1995; IWC, 2000; Fig. 1) is based on the

conjectures that the population is declining, comprises <500 animals (Berggren & Arrhenius, 1995; Hiby & Lovell, 1996; Berggren, 2003), and is genetically distinct and reproductively isolated from adjacent populations west of the Baltic, i.e. in the Belt, Kattegat and Skagerrak Seas (IWC, 2000). The population estimate for these latter regions is *c.* 40,000 animals (Hammond *et al.*, 2002).

The notion of a genetically distinct Baltic population is widely accepted by many involved in the management of the species (ASCOBANS, 2002; Huggenberger *et al.*, 2002; Koschinski, 2002; Teilmann *et al.*, 2004; HELCOM, 2006). For instance, a political agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS), ratified under the Bonn Convention by nine north European countries, largely focuses on the Baltic harbour porpoise. Considerable resources are allocated annually by the Swedish authorities to promote the conservation of harbour porpoise in Swedish waters. The Baltic porpoise is classified as 'a vulnerable geographical population' (Ingelög *et al.*, 1993; ASCOBANS, 2002), and suggestions for increased research efforts imply a genetically distinct Baltic population (Hopkins, 2005).

The scientific support for a genetically distinct Baltic harbour porpoise primarily refers to Wang & Berggren (1997) and Tiedemann *et al.* (1996). We suggest that neither provides strong evidence for such a claim. Both studies are based on mitochondrial DNA (mtDNA). Reflecting only the female genetic structuring, neither study provides insight into the variation in nuclear genes, which contain the vast majority of the genetic information. Tiedemann *et al.* (1996) compared haplotypes of 20 porpoises collected in the southern Baltic and Belt Seas area (Fig. 1) with those of 19 specimens from the North Sea, obtaining a statistically significant frequency difference (P <0.01). However, the sample referred to as Baltic also appears to have included porpoises from the Belt Seas, and this study does not therefore strictly test for genetic distinctness of a Baltic porpoise.

Wang & Berggren (1997) performed a strict comparison of samples from the Baltic proper versus animals collected in the Kattegat-Skagerrak area (Table 1) and reported a statistically significant difference of haplotype frequency distributions (using option Monte of the Restriction Enzyme Analysis Package, *REAP v.* 4.1; McElroy *et al.*, 1992). However, our recalculations do not support the notion of statistical significance. Using the data of Wang & Berggren

Anna Palmé (Corresponding author), Linda Laikre and Nils Ryman Division of Population Genetics, Department of Zoology, Stockholm University, S-106 91 Stockholm, Sweden. E-mail anna.palme@popgen.su.se

Fred Utter School of Aquatic and Fisheries Sciences, University of Washington, Box 355020, Seattle, WA 98195, USA.
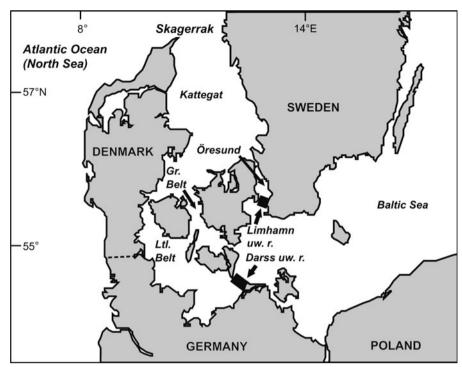
Fig. 1 The Baltic Sea and other water bodies discussed. The western borders of the Baltic proper are defined by the Limhamn and Darss underwater ridges (uw. r.).

(1997) we reanalysed the haplotype frequency difference between the Swedish Baltic and the Kattegat-Skagerrak areas, where they report a P of 0.035. We used several statistical packages (including option Monte in *REAP v.* 4.1), applying both exact calculations and simulation approaches, but did not obtain P <0.05 (P-values were 0.08 – 0.22; Table 2).

Clearly, the difference between a P of 0.035 and most of our recalculated values is not large, and strict application of the P = 0.05 limit for defining statistical heterogeneity should be exercised with caution. Nevertheless, when applying this standard criterion for statistical significance the data of Wang & Berggren (1997) do not support the idea of a Baltic population that is genetically distinct from that of the Kattegat-Skagerrak area.

TABLE 1 Observed haplotype frequencies of *Phocoena phocoena* from the Baltic Sea proper (see text for definition) and from the Kattegat-Skagerrak Seas (Fig. 1; data from Wang & Berggren, 1997).

Haplotype no.	Baltic Sea	Kattegat-Skagerrak Seas
2	24	20
5	0	2
53	0	1
54	0	1
55	0	1
56	1	0
58	2	0
Total	27	25

There are at least four additional molecular genetic studies of harbour porpoises in the Baltic-Belt-Kattegat-Skagerrak region but none of them address the issue of a genetically distinct Baltic population (Andersen, 1993; Andersen *et al.*, 1995, 1997, 2001), and the definition of the geographic range of the Baltic Sea varies considerably (Palmé *et al.*, 2004). The consensus from these four studies is that some general structuring exists within the region examined but the pattern has not been identified, and distinct population segments have not been recognized (Palmé *et al.*, 2004). Over all studies, only 38 specimens from the Baltic Sea have been genotyped.

The degree of genetic divergence among harbour porpoises within the Baltic-Belt-Kattegat-Skagerrak appears to be low. Using the data and sample sizes (n = 27 and 25) of Wang & Berggren (1997; Table 1) we obtain an estimate of F_{ST} (the proportion of the total genetic diversity attributable to differences between populations) between the Baltic and the Kattegat-Skagerrak of 0.007 (implying that only 0.7% of the total gene divergence is due to differences between regions). We used the software *POWSIM* (Ryman & Palm, 2006) to simulate 1,000 F_{ST} values from two samples drawn from the same population (F_{ST} = 0) and found that, with these sample sizes, the probability of obtaining an $F_{ST} \geq 0.007$ is *c.* 0.30. Therefore, this observation is not unlikely even with complete random mating (panmixia) among these waters.

Palsbøll *et al.* (2007) suggested that rejection of panmixia should not constitute the primary basis for

TABLE 2 Results of reanalyses for equal haplotype frequencies of *Phocoena phocoena* (data of Table 1) from the Baltic vs the Kattegat-Skagerrak Seas (Fig. 1) using four software packages.

Software	Type of test	P ± SE	Comments
REAP routine Monte (McElroy *et al.*, 1992)	Monte Carlo simulation	0.0812 ± 0.0028	10,000 iterations (software maximum)
GENEPOP routine STRUC (Raymond & Rousset, 1995)	Fisher's exact test (permuted)	0.0944 ± 0.0016	1,000,000 iterations
StatXact-3 (CYTEL, 1997)	Fisher's exact test (exact calculation)	0.0956	
	Fisher's exact test (Monte Carlo estimate)	0.0958 ± 0.0016	1,000,000 iterations
BIOM routine RxC (Rohlf, 1987)	Contingency χ^2 test	0.2170	

identification of conservation units. Rather, the degree of demographic independence and genetic divergence constitute the criteria for assigning such units. They suggest that with 10% or more exchange of migrants, two populations should be considered demographically connected and therefore managed jointly. With lower levels of exchange populations may be regarded as separate management units. The degree of migration between porpoises in the Baltic and those further west is unknown. However, assuming an effective population size of 200 in the Baltic (Hiby & Lovell, 1996; Berggren, 2003), that female and male effective population sizes and migration rates are equal, and migration-drift equilibrium (cf. Birky *et al.*, 1983), F_{ST} for mtDNA will be 0.05 with 20 migrants per generation (i.e. 10% migration). Using the same simulation approach as earlier we estimate the probability of obtaining the observed $F_{ST} = 0.007$ or lower as 0.35. Therefore, with these haplotype frequencies and sample sizes it is not possible to distinguish a situation of panmixia from that with a 10% exchange.

No other F_{ST} estimate between Baltic porpoises and those further west is available. However, Andersen *et al.* (2001) report an F_{ST} of 0.005 between inner Danish waters (including the Baltic, Belt and Kattegat Seas) and the Skagerrak/Danish North Sea. This low estimate indicates considerable genetic exchange between populations in this region.

Confidence in conservation genetic arguments is undermined when supporting evidence is weak. Strong opposition to protective measures almost always arises where, as in the case of the Baltic harbour porpoise, fisheries are requested to change methods and gear to protect a species. Using genetic justification for protection that may later have to be reconsidered could undermine the confidence in conservation genetics. There may be other grounds for conserving particular groupings (Taylor & Dizon, 1999), and such may exist for the Baltic porpoise, but here we are primarily concerned with the use of genetic arguments without scientific support.

A thorough investigation of the pattern of genetic substructuring of the harbour porpoises of this region is required. There are three basic types of spatial genetic differentiation: distinct local populations, continuous genetic change, or lack of differentiation (Laikre *et al.*, 2005). The management and protection required differs between these types and would also be affected by the geographic location of possible genetic groupings. If the Baltic harbour porpoise represents the same population as that of the Belt and Kattegat Seas there is no obvious genetic argument for the strong conservation efforts currently employed in the Baltic. But, if the Baltic porpoises represent a reproductively isolated population or considerable part of a cline, then strong conservation action is needed.

Acknowledgements

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Biographical sketches

ANNA PALMÉ's research focuses on spatial genetic structure over micro-geographical areas in the absence of barriers to migration. LINDA LAIKRE, FRED UTTER and NILS RYMAN share an interest in conservation genetics and the genetic effects of the human exploitation of natural populations. Linda Laikre also focuses on issues related to monitoring such effects, and Fred Utter's and Nils Ryman's research deals with the genetic structuring of natural populations and the processes that create these patterns.