Agenda Item 6.1

Project Funding through ASCOBANS
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**Project Report:
Historic and present harbour
porpoise populations in the Baltic
region – geometric morphometrics
analysis**

Action Requested

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ASCOBANS

Population structure of harbour porpoises in the greater Baltic region: Evidence of separation based on geometric morphometric comparisons

Anders Galatius[1], Carl Christian Kinze[2] and Jonas Teilmann[1]

1. Department of Arctic Environment, National Environmental Research Institute, Aarhus University, Frederiksborgvej 399, 4000 Roskilde, Denmark
2. Rosenørns Allé 55 2. tv., 1970 Frederiksberg C, Denmark

Abstract

A geometric morphometric approach was employed to test a number of hypotheses regarding population structure of the harbour porpoise in the greater Baltic region. Porpoise skulls from Denmark, Sweden, Finland, Germany and Poland were measured with a suite of three-dimensional landmarks. Statistical analyses revealed highly significant shape differences between porpoises from the North Sea, Belt Sea and the inner Baltic Sea. A comparison of the directionalities of the shape vectors between these units found differences that cannot be attributed to a general, continual shape trend going from the North Sea to the inner Baltic Sea. The directionalities of the vectors indicate a morphological adaptation to the specific sub-areas. E.g., in the Belt Sea porpoises, there may be a greater reliance on benthic and demersal prey. Such adaptation may be a result of the topographic peculiarities of the area with variable topography and shallow waters. While the present results show that isolation by distance alone is an unlikely explanation for the differences found within the greater Baltic region, we cannot estimate the level of genetic isolation between areas from morphology.

Introduction

The existence of a well defined Baltic population of the harbour porpoise (*Phocoena phocoena*) is usually considered as a fact and has lead to several conservation initiatives including the "Jastarnia Plan" (ASCOBANS 2003), a recovery plan aiming to bring back the Baltic stock to former levels. The crucial question to be asked is: recovery of what from what? Are "Baltic

harbour porpoises" merely a geographical continuum of the animals dwelling in the Belt Sea, Kattegat, Skagerrak and North Sea or do they constitute a separate genetic entity?

Recently, the genetic evidence for an independent Baltic population has been reviewed by Palmé et al. (2008) who state that the differences found so far may be too small to support the hypothesis of a separate population within the Baltic Sea. However, Wiemann et al. (2010) found indications of some molecular (both mitochondrial and microsatellite DNA) differentiation between the Belt Sea and the inner Baltic. Both molecular and morphological studies have detected differences between the Belt Sea/western Baltic Sea on one side and the North Sea (Kinze 1985, Andersen 1993; Andersen et al. 1997, Andersen et al., 2001). Huggenberger et al. (2002) found significant differences between samples from the inner Baltic (east of the Darss and Limhamn underwater ridges) and the Belt Sea as well as the German Bight in the North Sea using traditional morphometrics, i.e., cranial length measurements, while Börjesson and Berggren (1997) found morphological differences between a Swedish Baltic sample and a sample from Swedish Kattegat/Skagerrak. Despite this somewhat unclear evidence which has often been based on limited sample sizes, it is usually assumed that a single independent population is present in the Baltic proper and hence that animals there originate from the same founding stock.

In recent years, geometric morphometrics have largely replaced traditional morphometrics based on length measurements (Adams et al. 2004). Geometric morphometrics is characterized by the capture of 2- or 3-dimensional coordinates from previously defined morphological landmarks from biological specimens to get an approximation of shape (Marcus, 2000). Landmark-based geometric morphometrics are superior to traditional morphometrics through more powerful statistical analyses and the facility of graphical representation of morphological change, in that original shapes are preserved throughout the analysis (Adams et al. 2004).

In this paper, we evaluate hypotheses regarding the population structure of the harbour porpoise in the Baltic at large using geometric morphometrics. We aim at providing the best possible evaluation of the

population structure in the area based on morphology, with the use of geometric morphometrics and large sample sizes.

Materials and Methods

Observations were made on skulls from the collections of the Natural History Museum in Copenhagen (n=152), the Natural History Museum in Stockholm (n=43), the Museum of Evolution in Uppsala (n=3), the Natural History Museum in Helsinki (n=7), Hel Marine Station in Poland (n=8) and the German Oceanographic Museum in Stralsund, Germany (n=77). Sexual maturity was known for 158 of the specimens from the Baltic at large (Danish North Sea, Skagerrak, Belt Sea and the Baltic Sea). In addition specimens without known maturity status, were included if they were within the size ranges of the mature specimens. Figure 1 shows geographic distribution of the samples. Therefore a total of 292 specimens were included from the greater Baltic area. The samples from the North Sea, Skagerrak and Belt Sea were collected from 1980 to the present. In order to get as large a sample as possible, the inner Baltic samples included specimens as old as the 1870s. A total of 18 animals from before 1980 is included in the inner Baltic sample. In the analyses, it is assumed that these older specimens represent the same population unit as the current Baltic porpoises and that temporal shape development in this population is negligible relative to inter-population differences.
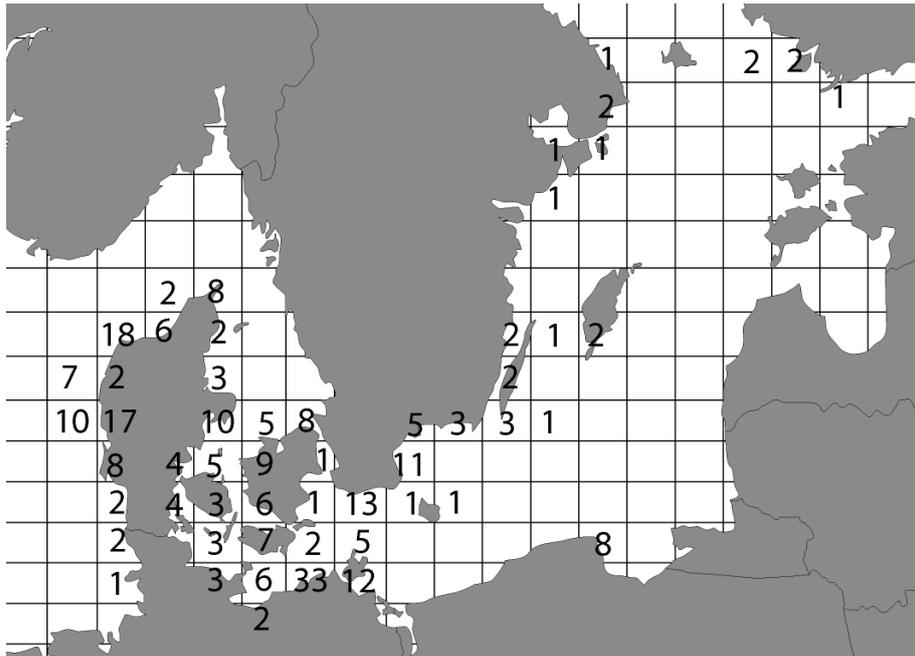
Figure 1. Map of the Baltic region. Grids defined by the International Council for Exploration of the Sea, ICES. The numbers of specimens from each grid square are given.

Figure 2. Map of the Baltic region. Grids defined by the International Council for Exploration of the Sea, ICES. Partitioning of samples are marked with bold black lines, the three alternative tested partitionings between the Belt Sea and the inner Baltic are numbered from east to west.

Based on Andersen et al. (2001), Wiemann et al. (2010) and satellite trackings of porpoise movements in Danish waters (Sveegaard et al. in press), North Sea, Skagerrak and northern Kattegat porpoises were pooled in one sample, henceforth termed North Sea / Skagerrak. There is more uncertainty

regarding partitioning between the Belt Sea and the inner Baltic. Three alternative delimitations were tested; (1) at the Fehmarn Belt and Limhamn underwater ridge, (2) at the Darss and Limhamn underwater ridges, and (3) at the German-Polish border and straight north to the Swedish southeastern corner. See Figure 2 for geographic partitioning of the samples. To relate the differences obtained within the greater Baltic region, a sample of 51 specimens from West Greenland (from the collections of the Natural History Museum, Copenhagen) were included in order to compare with a sample where complete and long-term genetic isolation can be presumed.

Shape analysis
Three-dimensional coordinates of 70 cranial landmarks were registered with a Microscribe® 3D digitizer. The following landmarks were digitized on each skull

1. Anterior tip of right premaxillary

2 and 3. The caudalmost alveoli, left and right

4 and 5. Anterior point of lacrimal, right and left

6 and 7. Anterior point of frontal, right and left

8 and 9. Tip of the antorbital process, right and left

10 and 11. Anterior base of the postorbital process of the frontal, right and left

12 and 13. Ventral point of the postorbital process of the frontal, right and left

14 and 15. Posterior base of the postorbital process of the frontal, right and left.

16 and 17. Posterior margin of anterior dorsal infraorbital foramen, right and left

18 and 19. Anterior margin of the posterior dorsal infraorbital foramen, right and left

20 and 21. Posterior tip of premaxillary, right and left

22. Nasal septum at the anterior end of the nasal apertures

23. Intersection of the ethmoid with the suture between the nasal bones,

24. Intersection of the interparietal with the suture between the nasal bones

25 and 26. Ventral tip of the nasal, right and left

27 and 28. Dorsal tip of the nasal, right and left

29. Anteriormost point of the sutures between the frontal and interparietal bones.

30 and 31. Dorsal tip of occipital condyle, right and left,

32. Medial point of the intercondylar notch of the basioccipital in ventral aspect.

33 and 34. Angle of the frontal-parietal suture at the lateral margin of the bones, right and left.

35 and 36. Junction of supraoccipital, exoccipital and parietal, right and left.

37 and 38. Junction of exoccipital, parietal and squamosal, right and left.

39 and 40. Anterior tip of exoccipital at the base of the zygomatic process of the squamosal, right and left.

41 and 42. Junction of the parietal, frontal and sphenoid, right and left.

43 and 44. Dorsal tip of the squamosal, right and left.

45 and 46. Tip of the zygomatic process of the squamosal.

47 and 48. Deep point of the jugular notch, right and left.

49 and 50. Medial tip of the paraoccipital process, right and left.

51 and 52. Suture of pterygoid and basioccipital at the lateral margin of the bones, right and left.

53 and 54. Deep point of the Eustachian notch, right and left.

55 and 56. Posterior tip of the pterygoid hamulus, right and left.

57 and 58. Posterior end of pterygoid-palatine suture, right and left.

59. Posterior tip of right palatine

60 and 61. Anterior margin of the ventral infraorbital foramen, right and left.

62. Junction of the left and right maxilla with the palatine.

63. Junction of vomer, right and left maxilla on the ventral side of the rostrum.

64 and 65. Posterior tip of premaxillary on the ventral side of the rostrum, right and left.

66. Anterior tip of vomer on the ventral side of the rostrum.

67 and 68. Anterior tip of the pterygoid hamulus, right and left.

69 and 70. Anterior tip of the palatine, right and left.

The landmark positions are depicted in Figure 3.
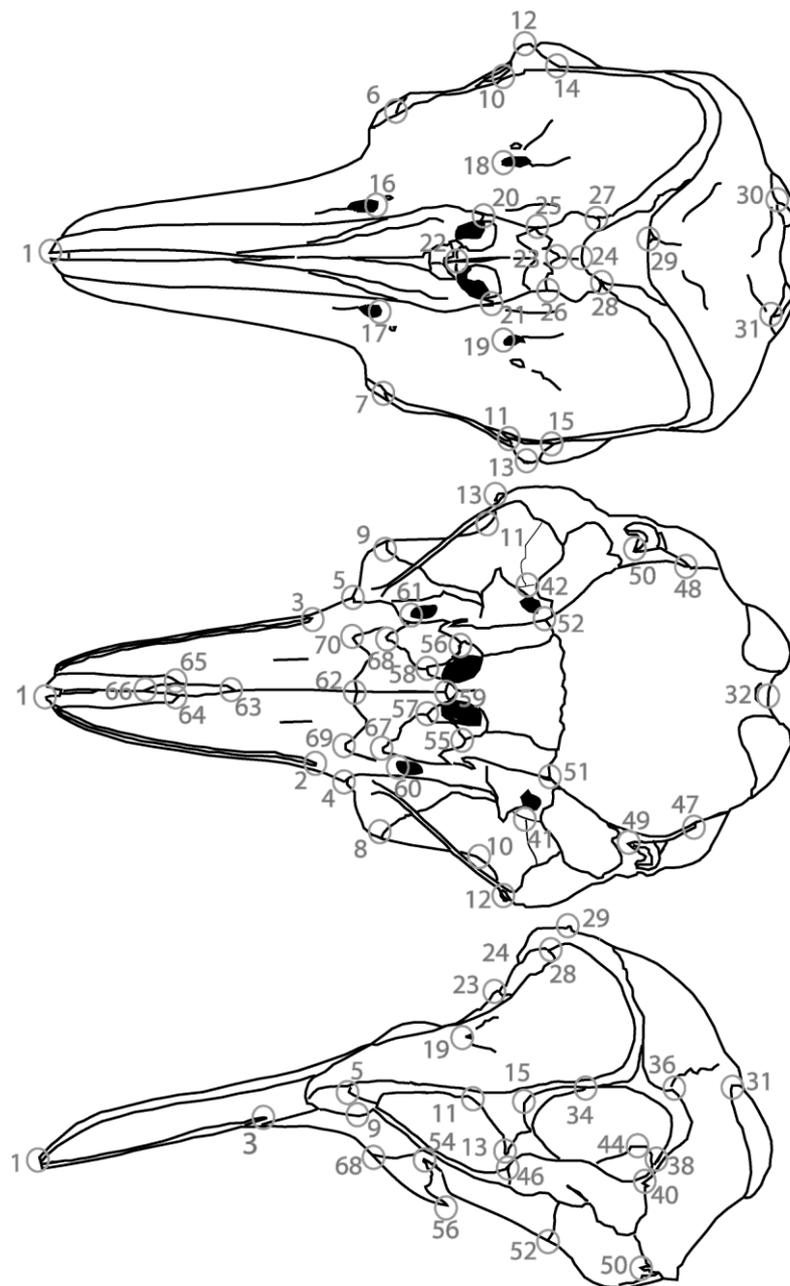
Figure 3. The three-dimensional cranial landmarks used for shape analysis defined for dorsal ventral and lateral views of the skull. See text for description of landmarks.

The raw landmark coordinates were run through the generalized least-squares Procrustes superimposition (Rohlf and Slice 1990) using the MorphoJ-program (Klingenberg 2010). The Procrustes procedure used here was amended by the suggestions of Klingenberg at al. (2002) in order to deal with the redundancy of data points caused by the object symmetry of the vertebrate skull.

To exclude size-related variation, all further analysis was performed on the residuals of a multivariate regression of shape (Procrustes coordinates) on

the centroid size (CS - the square root of the summed squared distances of each landmark the averaged coordinates of the configuration). Since the amounts of explained variance of regressions using CS and log (CS) as dependent variables were almost identical, it was assumed that allometric shape development was linear. Thus, CS without log-transformation was used for the regression.

Sexual dimorphism was investigated for each geographical sample by testing the significance of the Mahalanobis distance between the sexes with a permutation test with 10,000 iterations. This revealed no significant differences for any of the areas ($\alpha=0.05$), and the sexes were thus pooled within each area for further analysis. To test if porpoises migrated between areas from spring/summer to autumn/winter specimens collected from April-September were tested against specimens from October-March in each sample in the same manner as the test for sexual dimorphism. Furthermore, the geographical analyses were also performed using only females or spring/summer samples (April-October) or bycaught animals.

Differences between the North Sea/Skagerrak, inner Danish waters, inner Baltic and West Greenland were analyzed with a permutation test of the significance of Mahalanobis distances (10,000 iterations) and discriminant function analysis using leave-one-out cross-validation (Lachenbruch 1967) for reclassification of specimens. Beside the traditionally used population delimitation (reviewed by Koschinski et al. 2002) at the Darss/Gedser and Limhamn/Dragør ridges, Wiemann et al. (2010) found some indications of a split of haplotypes south of Fyn. We tested two alternatives to the Darss and Limhamn delimitation: a more westerly delimitation at Fehmarn Belt, and a more easterly alternative, a split at the German-Polish border and straight north to the Swedish southeastern corner (Figure 2).

The hypothesis that shape differences across the three entities represent a continuum from the North Sea to the inner Baltic was tested by comparing the directionality of the vector describing shape differences between the North Sea/Skagerrak and Belt Sea to the vector between the Belt Sea and the inner Baltic using the program Veccompare of the IMP-package (Sheets 2001). Veccompare compares between-group vector directionality with the 95% confidence interval (CI) of within-group ranges assessed by a

bootstrap procedure with 4,900 resamples. If the observed between-group angle is larger than the CI-ranges of the two within-group angles, the directions of the two compared vectors are significantly different at α=0.05.

Results

We found no significant (α=0.05) differences between males or females or sampling seasons within any of the samples. Carrying out discriminant analyses with only females, summer samples or bycaught animals did not enhance discrimination of geographic areas over analyses using pooled samples.

Distances

We obtained very similar results from each of the three delimitations (Fehmarn Belt, Darss and Limhamn ridges, and the line from the German/Polish border and north to Sweden) between the Belt seas and the inner Baltic. Somewhat greater morphological distance and more successful reclassification of individuals were obtained with the more westerly border at Fehmarn Belt and these results are presented below.

Distances and significance of distances are listed in Table 1. Highly significant differences (p<0.0005) were detected among all the geographic entities using either geographic delimitation. The greatest distances were detected between the West Greenland population and the samples from the Baltic area. Within the greater Baltic area, the North Sea/Skagerrak porpoises were most divergent. Within the greater Baltic area, the Mahalanobis distance between the Belt Sea and the inner Baltic was comparable to that between the Belt Sea and the North Sea/Skagerrak.

Description of differences

Shape differences between the geographic samples are shown in Figure 4. The differences between the Greenlandic porpoises and the three respective samples from the Baltic at large were very similar, due to the relative similarity of the latter three samples. Greenlandic porpoises have shorter, but taller and wider skulls. The post- and antorbital processes are displaced caudally, indicating a more posterior position of the eyes. The nasals and nasal

apertures are displaced towards the rostrum, indicating a more anterior position of the blowhole. The rostrum has less ventral inclination.

In the greater Baltic region, the shape differences are subtle. Relative to the North Sea/Skagerrak porpoises, the Belt Sea sample have a shorter and wider skull, a more ventrally inclined rostrum and foramen magnum, a longer zygomatic process and larger nasal bones, shorter tooth rows. The inner Baltic porpoises are similar to the Belt Sea porpoises in terms of orientation of the foramen magnum and rostrum while they have a narrower skull, with a broader rostrum, shorter and less robust zygomatic processes and smaller nasal bones.
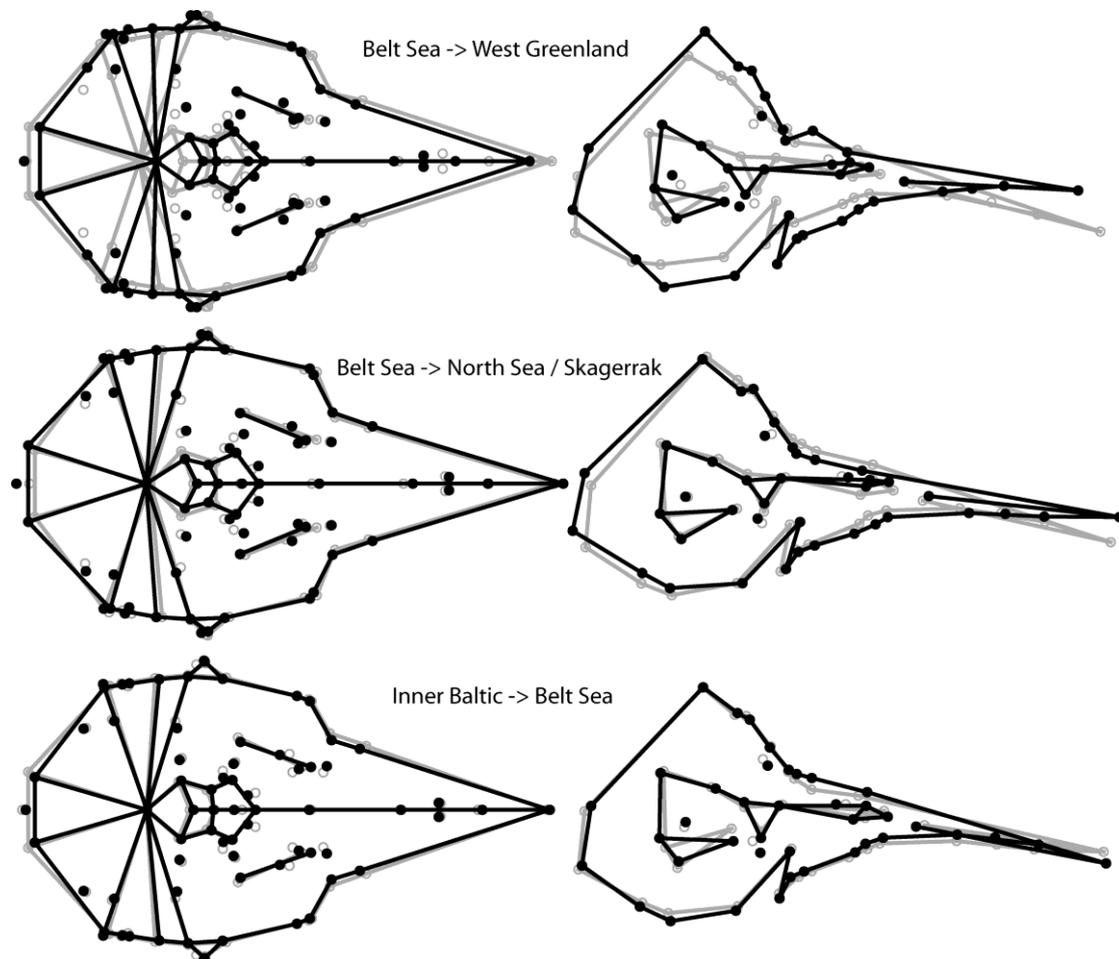
Figure 4. Shape changes associated with discriminant vectors between the samples. Dorsal aspect to the left, lateral aspect to the right. Grey outline and markers represent the shape of the sample mentioned first, black outline and markers, the shape of the sample mentioned last. Shape differences between the samples are exaggerated by a factor 6.

Comparison of shape vectors in the Baltic region

The vectors describing the shape difference going from the North Sea/Skagerrak to the Belt Sea and the difference going from the Belt Sea to

the inner Baltic had an angle of 120.3°, while the 95% confidence intervals of the two vectors were ±55.5° and ±59.7°, respectively, and thus significantly different.

Table 1. Mahalanobis distances among the samples and percentages of specimens successfully allocated to their original sample in the respective comparisons by leave-one-out cross-validation.

	Inner Baltic	Belt Sea	North Sea/Skagerrak
Belt Sea	3.02 (69%)	X	X
North Sea/Skagerrak	3.16 (73%)	3.28 (75%)	X
West Greenland	6.12 (94%)	5.81 (95%)	5.85 (91%)

Discussion

The current study revealed highly significant morphological differences of harbour porpoises within the greater Baltic region. The detected differences were subtle, much smaller than the differences between any of the Baltic area samples and porpoises from West Greenland between which geneflow should be negligible for a very long time. The Baltic Sea has a short history as a habitat suitable for porpoises. A recent investigation indicates immigration and establishment of harbour porpoises in the Baltic Sea around 9,000 years ago (Sommer et al. 2008). This is a short time for evolution of differences and the relatively short distances and lack of obvious barriers to gene flow in the Baltic probably ensure that genetic and morphological differences will always be moderate. During these 9,000 years there has been several instances of complete ice coverage in the Baltic, which will have forced porpoises from this area into the Belt Sea (Teilmann & Lowry 1996; Koslowski & Schmelzer 2007). Sediment core analyses from the Gotland Deep indicate longer periods of anaerobic conditions in the 1300s which would have excluded all life from at least the northern part of the Baltic (Emeis et al. 2010). It has been assumed that the Baltic porpoises made annual migrations out of the Baltic Sea through the Belt Sea during the winter (Møhl-Hansen 1954; Gaskin 1984). Gaskin (1984) noted that these migrations did not occur on a large scale anymore and recently, the assumption of massive seasonal migration has been challenged by new data extracted from historical sources (Kinze

2008). Investigations of population structure in the area have not indicated migrations based on seasonal separation of samples (Huggenberger et al. 2002; Wiemann et al. 2010). The bulk of the material for the current study was collected over the last 30 years and we did not detect a signal of seasonal variation. Some of the Finnish and most easterly Swedish specimens in our sample were collected in the winter before 1950, so even if these migrations have taken place, they were probably not a ubiquitous phenomenon.

Kinze (1985) initially found no differences between the Kattegat and Skagerrak, but later (Kinze 1990) established significant differences between his Kattegat/Belt Sea sample and a Swedish Bohus Län sample, while differences between the former and a Skagerrak sample were weak. Börjesson and Berggreen (1997) found that inner Baltic porpoises had wider anterior skulls and longer toothrows than their Kattegat/Skagerrak porpoises. This does not correspond with the differences we obtained between the Belt Sea and inner Baltic, but fits better with the difference we recorded between the Baltic and North Sea/Skagerrak, so it is probable that their Kattegat/Skagerrak sample predominantly represented animals drawn from the same population as our North Sea/Skagerrak sample. Most of the significantly different length measurements of Huggenberger et al. (2002) are difficult to relate directly to our shape data, but the longer tooth row found in their North Sea and narrower rostrum base of their 'transition' sample is also found in our North Sea and Belt Sea samples, respectively.

Given the limited shape differences among the samples in the greater Baltic region, the morphometric approach is not very useful for establishing clear boundaries among different population units, should there be any. The best resolution out of three investigated hypotheses for delimitation between the Belt Sea and the inner Baltic was obtained at the Fehmarn Belt. Even if we cannot clearly define where the population split is, our results do indicate that there is a morphological segregation within the Belt Sea/inner Baltic area which is independent from the split between the North Sea/Skagerrak and the Belt Sea and thus not based on isolation by distance from the North Sea population. If morphological differences within the Baltic were the result of isolation by distance, a reasonable assumption would be that the morphological variation that was related to geography would show a

continuous change in the same direction from one end of the area to the other. The vectors describing the shape difference going from the North Sea/Skagerrak to the Belt Sea and the difference going from the Belt Sea to the inner Baltic had an angle of approximately 120°, which means that going from the Belt Sea into the Baltic, the shape vector describes a change going somewhat towards the North Sea shape. This could indicate morphological adaptation that is peculiar to the Belt Sea porpoises relative to the other samples. The Belt Sea and southern Kattegat do possess some unique qualities relative to the neighbouring areas. The area serves as the only drain from the Baltic Sea which is one of the largest estuaries in the world. It consists of mainly shallow water with deeper channels carrying saline water from the North Sea into the Baltic Sea, while the low saline water flows out of the Baltic at the surface. This creates strong halo- and thermoclines as well as strong wind and density driven currents. The unique and ever changing environment is likely the basis for the special adaptations forming the population separations. One striking feature of the Belt Sea porpoises relative to the neighbouring samples is a more ventrally inclined rostrum. The more coastal porpoise species (harbour porpoise, finless porpoise (*Neophocaena phocaenoides*) vaquita (*Phocoena sinus*) and Burmeister's porpoise *(Phocoena spinipinnis)*) also have more ventrally inclined rostra relative to the pelagic porpoises (Dall's porpoise *(Phocoenoides dalli)* and spectacled porpoise (*Phocoena dioptrica*) where it was interpreted as an adaptation to more feeding on demersal and benthic prey items (Galatius et al. in press). The Belt Sea porpoises may have adapted similarly, although on a much smaller scale. The Belt Sea including southern Kattegat and maybe part of the German Baltic seems a small area for a population of highly mobile animals without obvious restrictions to movement, but adaptation to a unique local environment would help explain this.

Satellite telemetry studies show that porpoises regularly cross the speculative borders we evaluated in this study (Teilmann et al. 2008). Almost 100 harbour porpoises have been satellite tracked in the greater Baltic region (Teilmann et al. 2008; Sveegaard et al. in press; NERI unpublished data). These data show that individual harbour porpoises may swim several hundred kilometres over short periods and stay within relatively small areas for longer

time. Although some animals from the Kattegat/Belt Sea move into the North Sea/Skagerrak and inner Baltic, they tend to stay within the region in which they were tagged or return to this area after a period. Movements and home ranges of satellite tagged porpoises suggest population segregations in the northern Kattegat and east of the Darss/Gedser underwater ridge (Teilmann et al. 2008; Sveegaard et al. in press). These extensive movements, combined with the inclusion of specimens collected outside the breeding season and stranded specimens which may have drifted after dying, mean that our samples contain specimens that would not reproduce in the area where they were collected. This implies that the morphometric distances between neighbouring populations are probably underestimated and that the actual divergence of Belt Sea porpoises may thus be greater than our estimates.

The current study gives further indication of reproductive isolation of harbour porpoises in the inner Baltic. This putative population is in acute danger of depletion (Skòra et al. 1988; Berggren and Arrhenius 1995; ASCOBANS 2003; Gillespie et al. 2005).

Acknowledgements

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