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Original research article

Defining management units for cetaceans by combining genetics, morphology, acoustics and satellite tracking

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ABSTRACT

Managing animal units is essential in biological conservation and requires spatial and temporal identification of such units. Since even neighbouring populations often have different conservation status and face different levels of anthropogenic pressure, detailed knowledge of population structure, seasonal range and overlap with animals from neighbouring populations is required to manage each unit separately. Previous studies on genetic structure and morphologic separation suggests three distinct populations of harbour porpoises with limited geographic overlap in the North Sea (NS), the Belt Sea (BS) and the Baltic Proper (BP) region. In this study, we aim to identify a management unit for the BS population of harbour porpoises. We use Argos satellite data and genetics from biopsies of tagged harbour porpoises as well as acoustic data from 40 passive acoustic data loggers to determine management areas with the least overlap between populations and thus the least error when abundance and population status is estimated. Discriminant analysis of the satellite tracking data from the BS and NS populations showed that the best fit of the management unit border during the summer months was an east–west line from Denmark to Sweden at latitude 56.95°N. For the border between BS and BP, satellite tracking data indicate a sharp decline in population density at 13.5°E, with 90% of the locations being west of this line. This was supported by the acoustic data with the average daily detection rate being 27.5 times higher west of 13.5°E as compared to east of 13.5°E. By using this novel multidisciplinary approach, we defined a management unit for the BS harbour porpoise population. We recommend that these boundaries are used for future monitoring efforts of this population under the EU directives. The boundaries may also be used for conservation efforts during the summer months, while seasonal movements of harbour porpoises should be considered during winter.

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1. Introduction

Effective management decisions rely on information on population status of a species, which implies knowledge of distribution, movements, habitat/foraging preferences, identification of population boundaries, health condition, threats and trend in abundance. Such information is rarely available for wild animal populations, and for marine animals living in the continuum of the oceans it is even more difficult to obtain. Many marine species are wide ranging animals that migrate over long distances, possibly mixing with neighbouring populations at certain seasons (e.g. Block et al., 2011). In the last decades, harbour porpoises (*Phocoena phocoena*) have been studied intensely in European waters to identify population delimitations and to monitor the status of the species (e.g., Siebert et al., 2006, Evans and Teilmann, 2009, Wiemann et al., 2010; Alfonsi et al., 2012; Fontaine et al., 2014). The main driver for this effort has been the fact that several thousand harbour porpoises are bycaught each year and drown in European gillnet fisheries (Tregenza et al., 1997; Vinther and Larsen, 2004; Bjørge et al., 2013). Reduced use of gillnets in recent years and the use of pingers has aimed to minimize bycatch, but the status of the harbour porpoises in Europe still remains unclear due to inadequate knowledge on bycatch and abundance for each of the little defined populations (Siebert et al., 2006; Hammond et al., 2013; Benke et al., 2014).

The harbour porpoise is the smallest and most numerous cetacean in European waters (Hammond et al., 2013) and has a wide distribution throughout continental shelf waters. Numerous studies have investigated the population structure of harbour porpoises in the Northeast Atlantic (Andersen et al., 2001, Fontaine et al., 2007) and in particular the waters between the North Sea and the Baltic Sea (e.g. Lockyer, 2003). This area consists of waters from the North Sea through the Skagerrak into the Kattegat, the Danish Belt Seas and the Sound, the western Baltic to the Baltic Proper (Fig. 1). Previous studies on skull morphology (Kinze, 1985; Börjesson and Berggren, 1997; Huggenberger et al., 2002), contaminant levels (Bruhn et al., 1999; Berggren et al., 1999), stable isotopes (Angerbjörn et al., 2006) and genetics (Tiedemann et al., 1996; Wang and Berggren, 1997; Andersen et al., 2001) have aimed to uncover the population structure in this area. The results are somewhat inconsistent, possibly due to small sample sizes, differences in area definitions and methodology. However, recent comprehensive genetic and morphometric studies have pointed to the existence of three harbour porpoise populations in waters between the North Sea and the Baltic Sea (Wiemann et al., 2010; Galatius et al., 2012). These populations inhabit (1) the North Sea and Skagerrak (henceforth referred to as the North Sea = NS), (2) Kattegat, Belt Sea, the Sound and western Baltic (henceforth referred to as the Belt Sea = BS), and (3) the Baltic Proper (BP), respectively (Fig. 1). The three populations are, however, not divided by geographical barriers, and their distributions overlap in so-called "transition zones" (Sveegaard et al., 2011).

The status of the harbour porpoise in the Baltic Proper has long been of concern due to the extensive population decline observed during the past 50–100 years (Skóra et al., 1988; Koschinski, 2002), and the population is listed as 'Critically Endangered' on the IUCN (the International Union for Conservation of Nature) red list (www.iucnredlist.org). Due to the limited number of abundance surveys and the wide confidence intervals the status of the Belt and North Sea populations are uncertain, however, the North Sea host a very large population with a favourable size for long term survival, while the Belt Sea population is much smaller (ASCOBANS, 2012; Hammond et al., 2013; Viquerat et al., 2014). The harbour porpoises inhabiting these three areas thus have different conservation status, occupy habitats with different oceanography, and face different anthropogenic pressures (e.g., due to different fisheries, levels of population and marine traffic) and therefore need to be managed individually.

An essential part of any management programme is monitoring of the population trend. For small cetaceans, this may be achieved by conducting continuous visual surveys from boat or aircraft (e.g., Hammond et al., 2013) following the "Distance sampling methodology" (Buckland et al., 1993). If not accounted for, abundance estimates for the individual population may be artificially inflated by including animals from a neighbouring population. Consequently, identifying geographical borders for each management unit with minimum overlap between populations is of major importance.

Separation of the NS and the BS populations with an east–west border within a transition zone in the Kattegat (waters South of the 58°N and North of 56°N latitudes) is supported by 3D geometric morphometric measurements of 277 skulls (Galatius et al., 2012), satellite tracking of 64 harbour porpoises (Sveegaard et al., 2011) as well as microsatellite and mitochondrial genetic analysis of 497 genetic samples (Andersen et al., 2001; Wiemann et al., 2010). A combination of these studies suggests a transition zone between the BS and BP populations between Fehmarn Belt and 14°20′E.

The genetic evidence for a division between the BS and the BP populations is not as strong as the division between the NS and the BS population, but Wiemann et al. (2010) nevertheless advocated a precautionary division into two separately management units. Furthermore, the less pronounced genetic and morphological difference found between BS and BP compared to the difference found between the NS and the BS population may be due to the young age of the Baltic Proper population: a recent investigation indicates immigration and establishment of harbour porpoises in the Baltic Sea around 9000 years ago when the previously closed connection to the Atlantic Ocean was established through the Danish straits as a result of ice melting in the Arctic, following the last Ice Age (Sommer et al., 2008). Without geographical seclusion, 9000 years is a relatively short time for evolutionary divergence.

In Germany, studies using static acoustic monitoring (SAM) have suggested a seasonally variable boundary between the BS and the BP populations in the Pomeranian Bay area (13°30′E–14°45′E) (Gallus et al., 2012; Benke et al., 2014). These authors hypothesize that the Baltic harbour porpoises move south–west into the Pomeranian Bay from November to March, possibly to avoid ice cover in the inner Baltic, but that the same area is occupied by BS harbour porpoises from July to October and that the two populations thus may be geographically overlapping but separated temporally.

This study aims at defining a management unit based on biological evidence for the BS harbour porpoise population during summer. This management unit should encompass the majority of the population while limiting the bias from neighbouring populations in order to estimate reliable trends in abundance and thereby conservation status. The harbour porpoises inhabiting the BS management unit is of particular interest and importance since (1) its conservation status is uncertain, (2) the influence of bycatch on the population status is unknown, (3) it represents the most probable source of new gene flow into the endangered BP population, and (4) it is probably one of the best studied cetacean populations in the world and could therefore demonstrate the potential of using a suite of methods to delineate management borders of overlapping populations.

2. Material and methods

2.1. Study area

The waters ranging from the North Sea to the Baltic Proper extend over a varied bathymetry with relatively shallow water (<50 m) in the Kattegat, the Belt Sea, the Sound and the western Baltic and deeper waters (∼700 m) in the Norwegian Trench in the Skagerrak and in the Eastern and North-Eastern part of the Baltic Proper (∼600 m). Furthermore, the salinity changes from brackish water in the Baltic Proper (majority <10 psu) to Atlantic water in Skagerrak and the North Sea (∼30 psu) (www.helcom.fi).

The transition zone between the North Sea and the Belt populations is located in Kattegat. Based on genetic and morphometric data we define this as the waters south of 58°N and north of 56°N (Fig. 1). This area encompasses all BS–NS population borders investigated by Wiemann et al. (2010) and Galatius et al. (2012).

For the transition zone between the Belt and the Baltic populations, borders are set along the Limhamn Ridge, Darss Sill and at 15°E (Fig. 1).

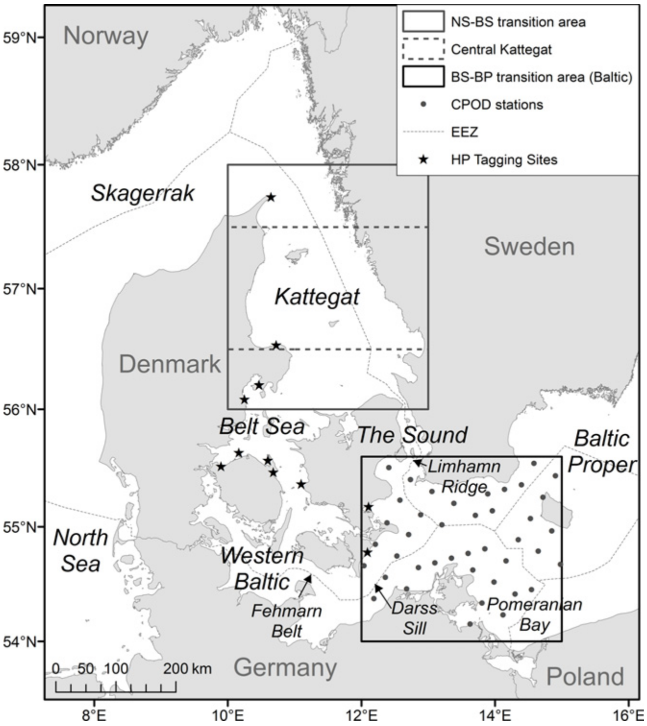

Fig. 1. Map of study area. The two transition areas separating the North Sea and the Belt Sea harbour porpoise populations as well as the Belt and the Baltic Proper populations are indicated with squares. The central Kattegat is shown with dotted lines. The harbour porpoise (HP) tagging sites are indicated with stars. Black dots signify the static acoustic data logger stations (part of the EU LIFE+ SAMBAH project). NS = North Sea, BS = Belt Sea, BP = Baltic Proper.

2.2. Data

As harbour porpoises within the study area display seasonal variation in distribution (e.g. Gallus et al., 2012) and since all abundance surveys have taken place during the calmer weather of the summer months (Viquerat et al., 2014), we only use data from May–September to define the management units. These months also include the breeding and mating seasons of harbour porpoises (Lockyer and Kinze, 2003), and the whereabouts of harbour porpoises at this time of year are therefore relevant for both population structure and management.

2.3. Delimitation of North Sea and Belt Sea management units

2.3.1. Satellite telemetry

From April 1997 to December 2013, 96 harbour porpoises were tagged with Argos satellite transmitters within the study area. Part of these data has been described elsewhere (e.g., Teilmann et al., 2007; Sveegaard et al., 2011). Only harbour porpoises that provided positions for at least one week during May–September within the North Sea – Belt transition zone – defined as "all of Kattegat" were included in the present analysis. This resulted in a final sample size of 45 harbour porpoises. Of these, 14 were tagged at Skagen near the northern tip of Jutland, 14 harbour porpoises were tagged in central Kattegat and 17 harbour porpoises were tagged in the Danish straits (Fig. 1). Harbour porpoises were incidentally caught in pound net fishery and tagged within 36 h of being discovered by the fisherman. An Argos satellite transmitter was attached to the dorsal fin of each harbour porpoise using one, two or three 5 mm diameter polyoxymethylene pins covered with silicone tubing (for more details on tagging procedure, transmitters and effects of tagging, see Eskesen et al., 2009; Geertsen et al., 2004; Teilmann et al., 2007; Sveegaard et al., 2011). For photos of an attached transmitter see Sonne et al. (2012). Individual satellite contact persisted for up to 500 days, but mean transmission time was 96 days. Locations were filtered by the Dave Douglas SAS-routine, Argos-Filter v7.03 to avoid outliers (Sveegaard et al., 2011). To harmonize the data and reduce spatial autocorrelation, one location per day was selected for each animal using the Argos-Filter based on accuracy level and number of uplinks, resulting in a total of 7502 locations for the 96 harbour porpoises and 4165 locations for the 45 harbour porpoises. The locations were imported into ArcGIS 10.1 (ESRI) and mapped with the Zone 32 (N) Universal Transverse Mercator projection, using the WGS 1984 datum.

To determine the border between populations in "all of Kattegat" each tagged animal was provisionally assigned to either the NS or BS population or classified as having unknown population origin. To be able to assign animals within the transitions zone in "all of Kattegat" to either of the two populations a subset of "all of Kattegat" was defined as "central Kattegat" (waters south of 57°30′N and north of 56°30′N) based on the fact that none of the 14 harbour porpoises tagged in Skagen moved south of 56°30′N, similarly only few porpoises tagged south of the transition zone moved north of 57°30′N. Subsequently the population origin was based on whether the majority of an animal's locations from May to September were in (1) the central Kattegat (=unknown population origin), (2) south of the central Kattegat area (BS population) or (3) north of the central Kattegat area (NS population, Fig. 1). This method of assigning affiliation to populations resulted in 18 BS harbour porpoises (529 locations within the transition zone), 18 NS harbour porpoises (420 locations within the transition zone) and 9 harbour porpoises of unknown population origin (349 locations within the transition zone). The 9 harbour porpoises of unknown population affiliation were excluded from further analysis as the data available from these animals would not contribute to the determination of the border. Of the 36 harbour porpoises remaining in the analysis, the majority were immature (75% of all individuals) and males (61%) (Table 1). Mature females were defined as length $\geq$143 cm and mature males as length $\geq$135 cm (Lockyer and Kinze, 2003).

Table 1
Age and sex distribution of harbour porpoises (HP) tracked between 1997 and 2014 with satellite transmitters within the transition zones between populations in the North Sea (NS) and the Belt Sea (BS) and the Belt Sea and the Baltic Proper (BP), respectively. Mature females are defined as length $\geq$143 cm and mature males as length $\geq$135 cm (Lockyer and Kinze, 2003).

Population	Age	Sex	No. HP within BS–NS transition area	No. HP within BS-BP transition area
Belt Sea (BS)	Mature	Female	4	1
		Male	2	3
	Immature	Female	5	5
		Male	7	7
North Sea (NS)	Mature	Female	0	–
		Male	3	–
	Immature	Female	5	–
		Male	10	–
Total			36	16

The management boundary between the NS and the BS populations was established by conducting a linear discriminant analysis (LDA) using the MASS library in R, using the latitude and longitude coordinates of the selected harbour porpoises within the transition area. The decision boundary (orthogonal to the discriminant function) was defined as the population delimitation. Bootstrapped 95% Efron confidence intervals of the decision boundary were calculated using 1000 resamples (cf. Manly, 1991). To yield a balanced result for this purpose, the LDA requires that the positions of the two samples are balanced relative to one another within the area analysed, which is the case (Fig. 2).

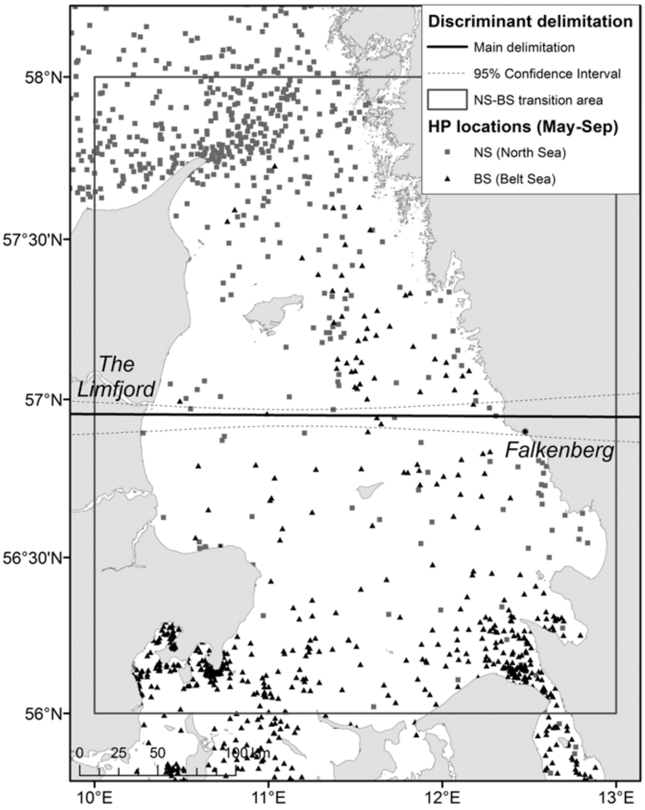

Fig. 2. Map of the transition area between the North Sea harbour porpoise population (NS) and the Belt Sea harbour porpoise population (BS) showing the locations from the satellite tracked porpoises affiliated with the population in the North Sea (grey squares) and the Belt Sea (black triangles), respectively. The management delineation is determined by discriminant analysis of the daily positions of tracked porpoises during May–September and shown with a black line. The 95% bootstrapped confidence intervals are indicated with dotted lines.

2.3.2. Genetic analysis

To test genetic support for separation in the transition area and to test for genetic differentiation between the NS and the BS population overall, genetic samples were analysed using microsatellites and mitochondrial Control Region sequence (mtCR). Genetic samples from 48 (25 BS and 23 NS) of the 96 tagged harbour porpoises were analysed based on microsatellite polymorpisms (BS-NS(48)). Of these, 47 (24 BS and 23 NS) were also analysed using mtCR (BS-NS(47)). Of the 48 harbour porpoises, 26 (13 BS and 13 NS) transmitted satellite locations for at least one week within the transition area in Kattegat (BS-N26). Observed and expected heterozygosity, deviation from Hardy–Weinberg expectations and genotypic linkage disequilibrium were tested using Genepop on the Web (Raymond and Rousset, 1995). Genetic differentiation between BS–NS(48) and BS–NS(26) was tested using STRUCTURE ver. 2.3.4 (Pritchard et al., 2000; Hubisz et al., 2009). mtCR for BS-NS(47) molecular diversity indices and FST estimates for both microsatellite and mtCR data were calculated and tested using ARLEQUIN 3.5 (Excoffier and Lischer, 2010).

The mtCR-haplotype structure between BS–NS(47) and BS–NS(26) was imaged using a two-layered haplotype networks constructed in the statistical software R running the script TempNet (Prost and Anderson, 2011). For further details see Supplementary Material 1.

2.4. Delimitation of the Belt Sea and the Baltic Proper management units

2.4.1. Satellite telemetry

Since no harbour porpoises were tagged in the Baltic Proper, the approach used for the NS—BS separation above, could not be used to establish the border between the BS and BP populations. Nevertheless, the satellite tracking data were used to investigate the annual variation in harbour porpoise density in the transition area. Of the 96 satellite tagged harbour porpoises, 24 animals (468 locations) entered the transition area and were used for this analysis.

Furthermore, data from harbour porpoises transmitting during May–September (16 harbour porpoises, 205 locations, Table 1) within the BS-BP transition area were plotted per 0.5° from 12°E to 15°E to investigate whether the gradient was smooth or had a sharp decline at a certain latitude, suggesting an eastern border of the BS population distribution.

2.4.2. Static acoustic monitoring

In addition to the analysis of the satellite tracks, the border between the BS and BP populations was investigated by analysing the harbour porpoise click train detections at 41 C-POD (Cetacean and POrpoise Detector, Chelonia Ltd, U.K.) stations spaced 25 km apart and positioned across the entire transition area (Fig. 1). These data were collected during the EU LIFE+project SAMBAH (Static Acoustic Monitoring of the Baltic Sea Harbour Porpoise, www.sambah.org). The C-POD is a stationary autonomous data logger designed to passively detect cetacean echolocation clicks within the frequency range 20–170 kHz (www.chelonia.co.uk) and has been used in numerous studies on harbour porpoise distribution (e.g. Dähne et al., 2013a; Hardy et al., 2012). The C-POD uses online digital waveform characterization to register click events and their time of occurrence, intensity, envelope centre frequency and bandwidth. This information is used as input to an off-line automated click train detection and classification algorithm. The C-POD has a maximum detection range for harbour porpoises of ca. 400 metres (www.chelonia.co.uk). For more details on C-PODS specifications, see Dähne et al. (2013b) and www.chelonia.co.uk. Data were processed using the software C-POD.exe v2.042 and the "Hel1" classifier, which is a harbour porpoise click extracting algorithm especially developed for the low harbour porpoise density in the Baltic Proper, and the train filter (the encounter classifier) "Harbour Porpoise" were chosen for analysis. Data from each station were exported as "detection positive minutes" (=Porpoise Positive Minutes, PPM) per day, and subsequently an average PPM (Av. PPM) per month was calculated.

The C-PODs were deployed for two years (May 2011–April 2013) two metres above the sea floor and anchored either in combination with surface buoys or by acoustic releasers with no surface buoy. Only data from May to September were included in the analyses, which gave a maximum of 306 days of recordings per C-POD station. Of the 41 stations, one was lost and provided no data in this period. The remaining 40 stations recorded for an average of 247 days (range: 57–303 days).

3. Results

3.1. Delimitation of North Sea and Belt Sea management units

3.1.1. Satellite data

The discriminant analysis between the BS and NS populations showed that the best fit of the management border was an East–West line from Denmark to Sweden at latitude 56.95°N (Fig. 2).

Of the original 96 satellite tracked harbour porpoises, 45 (4363 locations) were categorized as belonging to the BS population. When implementing the delineation at latitude 56.95°N, 33 harbour porpoises (4098 locations) stayed south of this line during the entire tracking period, corresponding to 94% of the total number of locations from BS harbour porpoises, while 12 harbour porpoises passed north of this line for some period of time.

3.1.2. Genetic analysis

No significant deviations from Hardy–Weinberg expectations (Supplementary Material 2) or genotypic linkage disequilibrium were observed. No population differentiation based on microsatellite variation was detected between the NS and the BS harbour porpoises based on the genetic cluster analysis performed in STRUCTURE, K equalled 1 over ten runs. Furthermore, no significant pairwise multilocus Fst-estimates for microsatellites was observed between BS and NS in the overall sample (BS–NS(48)), nor in the transition zone sample (BS–NS(26)). mtCR genetic diversity (Table 2) tended to be higher in the NS samples compared to the BS samples, which was most evident in the comparison of the samples with the higher sample sizes. In BS–NS(26) $\theta(S)$ and $\theta(\pi)$ were slightly higher in NS compared to BS. $\theta(S)$ and $\theta(\pi)$ are based on nucleotide variation which holds a higher resolution than estimates based on haplotypes. Haplotype networks comparing the mtCR structure for the BS–NS(47) and the BS–NS(26), (Fig. 3(a), (b)) suggest a split in haplotype distribution between BS and NS. Only haplotype Pho7 and Pho1 are shared but disproportionally. Together with the substantial structural shift in haplotype composition there was decrease in molecular diversity from NS to BS (illustrated by distance in Fig. 3(a), (b)). A significant population differentiation was detected between the BS and NS in the total sample BS–NS(47) ($p < 0.001$) using exact test based on mtCR sequences in ARLEQUIN. However, the significance disappeared when focusing on the smaller dataset from the transition zone (BS–NS(26), $p = 0.055$) probably due to the small sample size. The Fst based on haplotype frequencies between the BS and NS was significant both for BS–NS(47) (Fst $= 0.262$, $p < 0.001$) and BS–NS(26) (Fst $= 0.186$, $p < 0.05$), indicating different mitochondrial genetic composition between the BS and NS samples. For further details see Supplementary Material 1.

3.2. Delimitation of the Belt Sea and the Baltic Proper management units

3.2.1. Satellite data

The number of harbour porpoises and the number of harbour porpoise locations plotted per 0.5° longitude for each month indicate some monthly variation, and a clear decline is demonstrated from west to east for both individual months and when data was pooled for May–September (Fig. 4 and Supplementary Material 3). For the pooled data, a split at 13.5°E resulted in 85% of the number of harbour porpoises and 90% of the locations being west of this split (Fig. 4).

Table 2
MtCR haplotypes and molecular diversity indices calculated in ARLEQUIN. BS = Belt Sea, NS = North Sea. GD is gene diversity as a percentage probability of getting the same haplotype if two are randomly chosen $\theta(k)$ = based on observed haplotype number, $\theta(S)$ = based on number of segregating sites in haplotypes, $\theta(\pi)$ = based on pairwise nucleotide differences per site. SD is ± standard deviation. CL is $P < 0.05$ confidence interval limits. NS(47) and BS(47) are subsamples of BS-NS(47) and NS(26) and BS(26) are subsamples of BS-NS(26). See text for further description.

Sample	n	Pho 1	Pho 4	Pho 7	Pho 14	Pho 19	Pho 50*	Pho 51*	Pho 52*	Pho 53*	GD (SD)	$\theta(k)$ (CL)	$\theta(S)$ (SD)	$\theta(\pi)$ (SD)
NS (47)	23	13	3	3		1		1	1	1	0.67 (0.10)	3.04 (1.3–7.1)	2.71 (1.20)	1.91 (1.26)
BS (47)	24	7		15	1		1				0.54 (0.09)	1.11 (0.4–3.0)	0.80 (0.51)	0.60 (0.55)
NS (26)	13	9		2				1	1		0.53 (0.15)	1.57 (0.5–4.7)	2.90 (1.41)	1.51 (1.09)
BS (26)	13	4		7	1		1				0.65 (0.11)	1.57 (0.5–4.7)	0.97 (0.63)	0.77 (0.68)

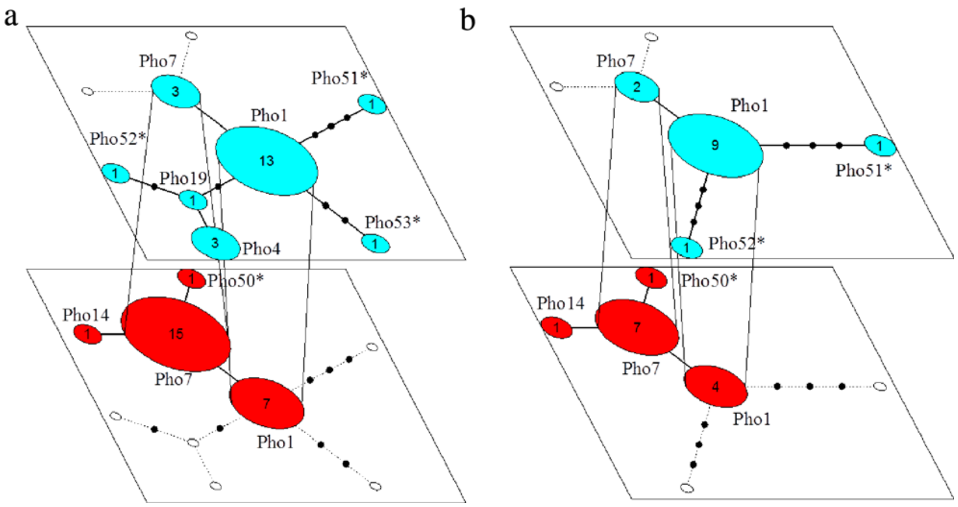

Fig. 3. Comparison of the mtCR haplotype structure in the two layered TempNet haplotype network for (a) the BS–NS(47) and (b) the BS–NS(26), top layer is NS (North Sea), bottom is BS (Belt Sea).

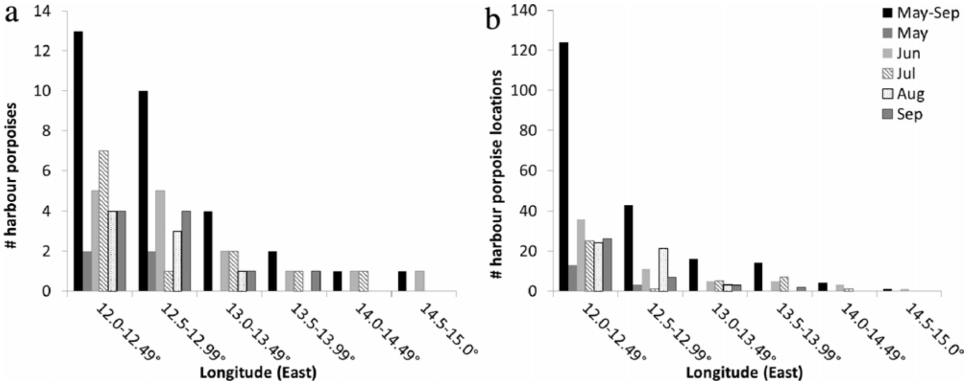

Fig. 4. Number of (a) harbour porpoises ($N = 16$) and (b) total daily harbour porpoise locations ($n = 202$) per 0.5° longitude for each month from May to September as well as pooled for May–September within the Belt Sea–Baltic Proper transition area (shown in Fig. 1).

3.2.2. Acoustic data

The static acoustic monitoring from May to September with 40 C-PODs in the BS-BP transition area showed a clear decline in detections (Average Porpoise Positive Minutes per day (Av. PPM)) from west to east (Fig. 5) and indicated a shift in density east of 13.5°E. Of the 40 stations, 23 stations detected an average of >3 PPM/day per month. Only one of these stations was located west of 13.5°E. Pooling the data west and east of 13.5°E, respectively, showed that across the year, the average daily PPM was 27.5 times higher west of 13.5°E as compared to east of 13.5°E (Fig. 6).

Average PPM per month throughout the year suggested an eastward migration of the BS harbour porpoises from around May peaking with high activity just west of 13.5°E in August–September and retracting back westward in December (Supplementary Material 4).

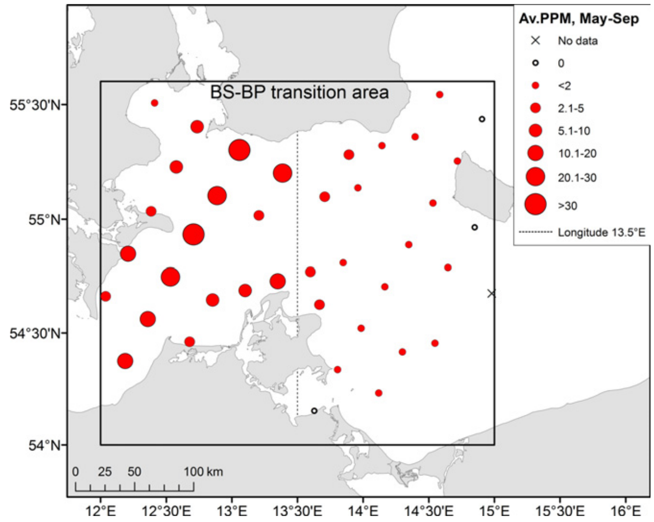

Fig. 5. Map of the Belt Sea (BS) – Baltic Proper (BP) population transition area showing average Porpoise Positive Minutes (Av. PPM) for the period May–September 2011–2013. The suggested management border at 13.5°E is indicated by a dashed line.

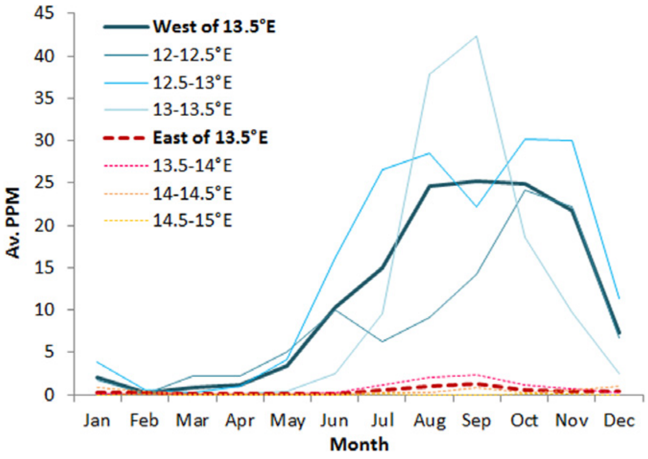

Fig. 6. Average daily Porpoise Positive Minutes (Av. PPM) per month with data pooled west and east of the proposed management unit delineation at 13.5°E and for each 0.5° longitude.

4. Discussion

This pluridisciplinary study used three different methods to investigate population structure and to define a management unit for the BS harbour porpoise population. We found that the northern management delineation separating the NS and the BS populations is best defined as an east–west line at latitude 56.95°N from the Danish coast at the mouth of the Limfjord to the Swedish west coast near Falkenberg and that the south-western management delineation of the BS population towards the BP population is best defined at the north-south line from southern Sweden to Germany at longitude 13.5°E. To obtain this spatial definition of the management unit, we first used data from comprehensive studies of population genetics and morphometrics to detect population differentiation and propose transition zones. Subsequently, distribution data for a large number of individuals were used to estimate the actual delimitations of management units among these three overlapping populations of cetaceans.

The three harbour porpoise populations have different conservation status, inhabit different habitats with different prey species and availability and face different anthropogenic pressures, and it is thus important to detect trends and manage them separately, e.g., as done by ASCOBANS (2009a,b, 2012). It is also important to note that the main focus of this study is to define the area for the BS population with least overlap and influence from the two neighbouring populations during summer. However, this does not necessarily mean that this is the best delineations for managing the NS and BP populations. Especially for the BP it is uncertain if the population may extend further west or potentially further east of the proposed lines. However, this very small population would only have little influence on the status of the larger BS population, but the BS population could have large effect on BP abundance estimates by either underestimating or overestimating this population. Further studies into the movements and habitat use of BP porpoises are needed to solve this dilemma.

The sample size of 36 satellite tagged harbour porpoises used to determine the management unit border between the BS and the NS populations was relatively small so obviously these harbour porpoises only represent a small fractions of the animals belonging to each population. Furthermore, the ratio of mature/immature and males/females were not evenly distributed especially in the NS sample that contained a large proportion of young males. However, when analysing 64 satellite tagged harbour porpoises, Sveegaard et al. (2011) showed no particular difference in movement between males and females, but immature animals had larger home ranges than mature animals. For our study, this could introduce a bias, but since the majority of the animals in the BS sample were also immature, we believe this to be minimal. This is further supported by a small variation in the discriminant analysis when data from all year were included to obtain a larger sample size and when both mature and immature harbour porpoises were analysed separately (data not shown).

The discriminant analysis of the tagging data depends on correct assignment of population affiliation for each individual tagged harbour porpoise, which was conducted, based on the location of the majority of locations from May to September. As support to this population assignment or as a possible new method of assignment, genetic data from biopsy samples of the satellite-tagged harbour porpoises were compared. Using microsatellite markers, the split between the BS and NS populations was not significant, and thus, this test did not allow for assignment of individuals to a specific population. This is unlike the results from microsatellite data reported by Wiemann et al. (2010), however, this is likely due to our much smaller dataset and the relatively small differences between populations. Although microsatellite results indicate a close genetic relationship between the BS and NS populations, the analysis of the structure of mtCR haplotype distribution and nucleotide structure in haplotypes supported a separation. A possible explanation for this apparent discrepancy in pattern would be that males migrate more than females although this is not supported by movements of the satellite tagged harbour porpoises (Sveegaard et al., 2011). Hence, this suggests male dispersal in the breeding season for mating purposes which is a mechanism that could serve to avoid inbreeding as seen in other mammals (e.g.,Handley and Perrin, 2007). Another explanation could be that the two populations are in the process of admixing, as Alfonsi et al. (2012) suggested for the harbour porpoise along the French Atlantic coast. The lack of deviation from HW expectations of the microsatellite frequencies suggested a panmictic breeding population as it only takes one generation to restore HW-expectations after two genetically different populations admix. It is not possible to pursue this further with the present dataset. Another important conclusion that can be drawn from the sparse genetic data is the structural shift in haplotype composition observed between NS and BS, with higher diversity in the private haplotypes in the NS and the decrease in molecular diversity from NS to BS, all suggesting that the BS harbour porpoises probably have diverged from migrants from the North Sea, when the Baltic Proper became accessible after the last ice age about 7000 years ago. As seen in Wiemann et al. (2010), a larger sample size and more markers showed that there is a significant nuclear differentiation between the BS and NS harbour porpoises, and although the mitochondrial haplotype composition differs between the two populations, it is not possible to assign individual tagged harbour porpoises to either population based solely on genetics. Single-nucleotide polymorphism (SNP) analysis in the future may show higher resolution and thereby provide more structure.

The satellite tagging data suggests that a management border around 13.5°E includes the majority of the BS population migrating eastward during the summer. This result is based on a rather small sample size (13 tagged harbour porpoises), which may proportionally lend too much weight to the movements of individual animals. If the management border was based solely on data from satellite tagged harbour porpoises, it would not include considerations of the possible influence of the BP population probably also occupying this area. Thus, we used static acoustic monitoring data to support the findings from the satellite tracking data. The static acoustic monitoring data also point to a management border at longitude 13.5°E. This delimitation is slightly west of the easternmost geographical population split tested by Galatius et al. (2012), who found that a more westerly border at the Fehmarn Belt performed marginally better in the morphometric analyses, although this may have been caused by a lower sample size from the Baltic Proper. Wiemann et al. (2010) found best support for a split at the Darss and Limhamn underwater ridges west of longitude 13.5°E. It is important to note that the west to east decline in Porpoise Positive Minutes demonstrated by the acoustic data loggers and in the satellite tracking did not provide an estimate of the western boundary of the BP population. A good estimate of this boundary would require a number of BP animals to be satellite tagged and monitored over some years, which does not seem feasible nor practicable given the low density of the BP population and the lack of fishing gear that can provide opportunistic live capture of harbour porpoises. Also, it is unlikely that any of the 96 tagged harbour porpoise in Denmark originated from the BP population. The acoustic data did, however, clearly show that the density of harbour porpoises east of 13.5°E, i.e. the BS population, was sufficiently low compared to west of 13.5°E, that even if the true boundary lies further east it would not significantly inflate the BS population abundance.

In order to manage the three porpoise populations effectively it is relevant considering the possible reasons why they do not mix freely, which seems peculiar when there are no apparent geographical borders to separate them. One possible explanation is that they inhabit waters of different oceanicographic characteristics, which could contribute to lower migration rates if individual harbour porpoises adapt to specific environments. This was e.g. suggested by Fontaine et al. (2007). They examined population structure of harbour porpoises in the eastern North Atlantic and found strong evidence in their genetic data that oceanographic characteristics and physical processes have a major impact on the demographic and genetic structure of harbour porpoises even when no geographical marine barriers exists. Furthermore, Rosel et al. (1999) examined the harbour porpoise population structure using mitochondrial DNA (mtDNA) sequence and nuclear microsatellite data and found that harbour porpoises in the northwest Atlantic Ocean should not be considered one panmictic population although no geographical barriers exists. Consequently, this could be the situation in our study area as well.

Still, another explanation could be that the areas inhabited by the three populations contain different prey species composition and/or availability. Although harbour porpoises may be opportunistic feeders, it is likely that they specialize in certain prey species, as illustrated by Aarefjord et al. (1995), who found that harbour porpoises inhabiting deeper waters primarily prey on pelagic fish, while harbour porpoises in shallower waters prey on benthic species and furthermore, that harbour porpoises in the BS population prey more on benthic fish like gobies than the NS harbour porpoises (Aarefjord et al., 1995). Moreover, the morphological differences in the skull between the three populations suggested that the harbour porpoises inhabiting the Belt Sea were more adapted to feeding near the sea bottom than the other two populations (Galatius et al., 2012). These authors speculated that the unique local habitat of the Belt Sea is the reason why a population of highly mobile animals could exist in such a small area.

4.1. Management

In the present study, we defined a management unit for the BS harbour porpoise population for the summer months based on available biological evidence. We suggest that this management unit is used in future management and conservation efforts of harbour porpoises in this area by both governments and other relevant bodies during summer, while seasonal movements of harbour porpoises should be considered during winter. Here, we specifically point to ASCOBANS which have adopted three management plans related to the study area: The North Sea (ASCOBANS, 2009a), the Baltic Proper (ASCOBANS, 2009b) and the waters in between (ASCOBANS, 2012). In these plans, the boundaries between the three areas are located within the transition areas, but do not match the findings in the present study. We therefore recommend that ASCOBANS re-evaluate the status of the populations within the three areas, and that the new biologically based boundaries found in this study are considered.

In the EU, all member states are required by the Habitats Directive to take action to maintain or restore a favourable conservation status of harbour porpoises (EEC, 1992). However, since the harbour porpoise is a wide ranging species not limited by national borders, it is not sufficient for each EU country to act individually. Abundance assessments on a national scale may be influenced by temporary or permanent movement of the harbour porpoises to neighbouring countries, i.e. due to movement of food sources or in search for more favourable habitats and may thus over- or underestimate the abundance. Instead, European countries should collaborate across borders to determine population status and future surveys, e.g., future SCANS surveys should aim to include population structure into their survey strata delimitations.

This study demonstrates the combination of a suite of methods to determine the ranges of populations and management units for a complex and vulnerable cetacean species. Determining management borders for one population showed reasonable agreement between methods despite the limited sample sizes. However, it should also be emphasized that population boundaries may not be static. Populations should therefore be monitored continuously, and the management areas should be revised regularly based on changes in the animals' distributions. This is particularly important in a time when the marine environment is under pressure from anthropogenic activities and climate change that may fragmentize and degrade ecological niches.

In other marine animals, similar analyses using several methods are also needed, but usually, the data are not available. Population abundances and distribution data may therefore be based on management of either too large or too small areas. This may result in a lack of relevant indicators to respond to, or too much management action caused by alerts from natural fluctuations within a population rather than true changes in abundance or distribution. Knowledge of correctly identified population units may facilitate future efficient management of biodiversity and optimize the use of available funding.

The next step is to estimate abundance of harbour porpoises within this new management unit and to design a management plan that will ensure continuous future abundance surveys for the area to detect trends. Furthermore, the number of bycaught harbour porpoises within the management unit should be examined and monitored so that the bycatch rate may be calculated and the sustainability assessed.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.gecco.2015.04.002.

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