Long Title: # Estimating the abundance of the critically endangered Baltic Proper harbour porpoise (*Phocoena phocoena*) population using passive acoustic monitoring

Short Title: Abundance of the Baltic Proper harbour porpoise

This paper is dedicated to the memories of Krzysztof Skóra and Vadims Yermakovs.

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Abstract

Knowing the abundance of a population is a crucial component to assess its conservation status and develop effective conservation plans. For most cetaceans, abundance estimation is difficult given their cryptic and mobile nature, especially when the population is small and has a transnational distribution. In the Baltic Sea, the number of harbour porpoises (*Phocoena phocoena*) has collapsed since the mid-20th century and the Baltic Proper harbour porpoise is listed as Critically Endangered by the IUCN and HELCOM; however, its abundance remains unknown. Here, one of the largest ever passive acoustic monitoring studies was carried out by eight Baltic Sea nations to estimate the abundance of the Baltic Proper harbour porpoise for the first time. By logging porpoise echolocation signals at 298 stations during May 2011-April 2013, calibrating the loggers' spatial detection performance at sea, and measuring the click rate of tagged individuals, we estimated an abundance of 66-1,143 individuals (95% CI, point estimate 490) during May-October within the population's proposed management border. The small abundance estimate strongly supports that the Baltic Proper harbour porpoise is facing an extremely high risk of extinction, and highlights the need for immediate and efficient conservation actions through international cooperation. It also provides a starting point in monitoring the trend of the population abundance to evaluate the effectiveness of management measures and determine its interactions with the larger neighbouring Belt Sea population. Further, we offer evidence that design-based passive acoustic monitoring can generate reliable estimates of the abundance of rare and cryptic animal populations across large spatial scales.

Introduction

Since its inception as a scientific discipline, a fundamental question in animal ecology is how many animals there are (Elton, 1927; Krebs, 1972). Based on repeated abundance estimates, trends can be inferred to determine the need for conservation actions, and to estimate the efficacy of implemented conservation measures to ensure long-term survival of a species, population or management unit. However, abundance estimation is particularly challenging for marine mammals that migrate long distances, traverse national borders, and are visible only when they come to the surface to breathe. These challenges are further compounded when the population of interest is small and widely dispersed. As a result, many abundance studies of such species/populations rely on technological and statistical advances as well as integrated international efforts (Borowicz et al., 2019; Cubaynes et al., 2019; Guazzo et al., 2019; Hammond et al., 2013; Johnston, 2019).

The harbour porpoise (*Phocoena phocoena*) is the only resident cetacean species of the Baltic Sea, the world's largest body of brackish water. Two harbour porpoise populations use the Baltic Sea: (a) the Belt Sea population, inhabiting mainly the southern Kattegat, the Belt Sea including The Sound, and the southwestern Baltic Proper; and (b) the Baltic Proper population, inhabiting mainly the Baltic Proper (Carlén et al., 2018; Galatius et al., 2012; Lah et al., 2016; Sveegaard et al., 2015; Wiemann et al., 2010) (Fig 1, S Fig 1). Although the distributions of the Belt Sea and Baltic Proper populations are likely to overlap in winter, there seems to be a geographical separation between them during the reproductive season (Carlén et al., 2018). Based on this separation, a western management border of the Baltic Proper population during May-October has been suggested between the peninsula in Hanö Bay in Sweden and the village of Jarosławiec near Słupsk in Poland (Fig 1).

There is evidence of a drastic decline in numbers of harbour porpoises in the Baltic Proper since the mid-20th century (Berggren and Arrhenius, 1995; Koschinski, 2001; Lindroth, 1962; Skóra and Kuklik, 2003). Bycatch in fishing gear has been identified as the most significant threat, and contaminant pollution as being of particular concern, in particular polychlorinated biphenyls (PCBs) (Hammond et al., 2008; HELCOM, 2013a). The distribution pattern of the Baltic Proper population has until recently been unknown (Carlén et al., 2018), and no population abundance estimate exists. However the detection rate during dedicated surveys in the southern Baltic Sea has been very low (Berggren et al., 2004; Gillespie et al., 2005; Hiby and Lovell, 1996), and the Baltic Proper harbour porpoise has been listed as Critically Endangered (CR) by the IUCN since 2008 (Hammond et al., 2008) and by HELCOM since 2013 (HELCOM, 2013a). The cryptic nature of the species, combined with its very low population density in the Baltic Proper, have precluded traditional survey methods such as mark-recapture via photo identification or visual surveys by aerial or shipboard line transects. Aerial surveys have been carried out in 1995 and 2002 (Berggren et al., 2004; Hiby and Lovell, 1996), observing a total of three and two single animals in an area covering the eastern part of the currently known management range of the Belt Sea population, and the southwestern part of the currently known management range of the Baltic Proper population (Carlén et al., 2018; Sveegaard et al., 2015). The resulting abundance estimates are thereby not to be considered as population estimates.

Fig 1. Proposed summer management borders of the harbour porpoise populations in the Baltic Sea and adjacent waters.

The May-October management border has been proposed based on the spatial distribution of harbour porpoise in the southern Baltic Sea (Carlén et al., 2018). The shaded management areas have been proposed with focus on the abundance of the Belt Sea population (Sveegaard et al., 2015).

During the last decade, passive acoustic monitoring methods have been developed to estimate the density and abundance of animals (Kyhn et al., 2012; Marques et al., 2013). The fundamental assumption is that detection rates of species-specific sounds are a reliable proxy for animal density, once factors such as the detectability of the sounds are accounted for. Harbour porpoises vocalise nearly continuously for foraging, navigation, and communication (Akamatsu et al., 2007; Linnenschmidt et al., 2013; Wisniewska et al., 2016). Like all so-called narrow-band high-frequency species, they generate sequences ("trains") of powerful, directional, stereotypic and narrow-band high-frequency clicks (Kyhn et al., 2013; Macaulay et al., 2020; Møhl and Andersen, 1973; Villadsgaard et al., 2007) in a frequency band where ambient noise is at a minimum (Richardson et al., 1995). These characteristics make the signals of narrow-band high-frequency species appropriate for passive acoustic monitoring, despite short detection ranges and a need for recorders with very high sample rate. In the Baltic Sea, the harbour porpoise is the only year-round occurring cetacean species, and its signals can be safely distinguished from those of other sporadically occurring odontocetes.

Here, the eight EU Member States surrounding the Baltic Sea (Sweden, Finland, Estonia, Latvia, Lithuania, Poland, Germany and Denmark) cooperated to conduct one of the largest passive acoustic monitoring studies to date in a joint effort, named Static Acoustic Monitoring of the Baltic Sea Harbour Porpoise (SAMBAH). The aim of the study was to estimate the density and abundance of the Baltic Proper harbour porpoise population for the first time.

Materials and methods

Survey area

The survey area encompassed the Baltic Sea from the Archipelago Sea around Åland in the north (south of 61° N) to the Darss sill (between Denmark and Germany, ca. 12° E) and the Limhamn/Drogden sill (between Sweden and Denmark, ca. 55° 50′ N) in the southwest (Fig 1Fig 1. , S Fig 1). The northern limit of the survey area was based on the current distribution of opportunistic sightings (HELCOM, 2013b). The southwestern limit followed the definition that has been used in a previous study of the population structure of the harbour porpoise in the Baltic region (Berggren et al., 2002). The waters of the Exclusive Economic Zone of the Russian enclave, Kaliningrad Oblast, and the Russian waters in the eastern-most part of Gulf of Finland were not included in the survey.

Acoustic survey

Survey design

We created a randomly positioned and oriented systematic grid of 304 survey stations, distributed over the survey area (Fig 2) in water depths between 5 and 80 m (for details, see Carlén et al., 2018). The depth data were obtained from the Baltic Sea Bathymetry Database (HELCOM, 2015). The 5-m depth limit was set for safety reasons, i.e. to make sure that boats would not hit the acoustic data loggers we deployed at each station (see below for details on the loggers), which were suspended with their hydrophones 2-3 m above the sea floor. Also, in shallower waters the loggers would be at higher risk during storms. The 80 m limit was chosen for two main reasons. This is the approximate depth of bottom areas with acute and permanent hypoxic conditions (<2ml O_2/l) in the Baltic Sea (Hansson and Andersson, 2015). Being an unsuitable bottom habitat for porpoise prey, low porpoise densities would be expected in these areas (Carlén et al., 2018). Further, an alternative rig design with acoustic data loggers suspended mid-water to monitor pelagic porpoises would have required separate detection functions (see Auxiliary data collection below), deemed to be practically out of scope of this project. The distance between primary stations was 23.55 km, which was adjusted to give the targeted number of stations. In the few cases a logger could not be deployed at the primary station, it was moved as short distance as possible, or one of four secondary stations was randomly chosen instead (Carlén et al., 2018).

Survey implementation

Our goal was to maintain a functioning acoustic data logger at each station for the full period of the survey, from 1 May 2011 to 30 April 2013. Logistical considerations meant that, in practice, some loggers were deployed before this period and some retrieved afterwards. We excluded the data from outside the core period in all results presented here.

Acoustic data loggers were chosen instead of high-frequency full-bandwidth digital recorders, as such instruments were judged to be logistically infeasible. The logger used was the C-POD (Chelonia Ltd., Cornwall, UK). The C-POD is a click detector especially designed for logging very short, multi-cycle signals such as the narrow-band high-frequency clicks generated by the harbour porpoise. C-PODs are highly standardized to the same sensitivity by the manufacturer (Dähne et al., 2013b). Some of the C-PODs were also calibrated by SAMBAH personnel in a tank following the method described by Dähne et al. (2013) and Teilmann and Carstensen (2012), and some by using the received levels from the playback experiments (S Fig 2). Individual C-PODs were rotated between stations to distribute any error caused by instrument variation.

Acoustic processing

Since C-PODs also log other sounds besides harbour porpoise clicks, the raw data were run through an adaptive classifier, the 'KERNO' classifier, which is part of the C-POD system (Tregenza, 2014). The classifier seeks 'trains' of clicks in which successive clicks and inter-click-intervals resemble the previous and subsequent ones, and then gives each train a confidence class that the source is an actual train source, and assigns each train to a source type or 'species'. For this study an 'encounter classifier', called 'Hel1', was developed with the aim of minimizing the rate of false detections. Further, a subset of files with a low detection rate (equivalent of <60 detection positive minutes per year) was selected for visual inspection by trained experts, as this would most likely include all the files with no true positives. A total of 40,726 logging days were inspected, whereof the likely origin of false positive detections was noted for a subset of 22,689 logging days. Based on the duration of the visually inspected subset and the total dataset, and the assumptions that the spatial and temporal distribution of false positives was unrelated to porpoise detections, and that false positives were randomly distributed, we estimated a rate of 1 false detection positive minute per 247 recording days (see Supporting information).

The acoustic results for each station were aggregated into 1-second periods or 'snapshots'; for each second we recorded whether one or more harbour porpoise clicks were present or not. It was assumed that no more than one animal was recorded within each 1-second snapshot. A longer time unit would have required estimates of group size, which are not available for the Baltic Proper (Berggren et al., 2002). To avoid interference from the servicing and the playback experiment, effort and click data from the days the C-PODs were deployed or retrieved were discarded.

Auxiliary data collection

Records of CPS and survey effort seconds, both obtained from the main survey, are not sufficient on their own to estimate absolute density or abundance: we also need to know the area surveyed by the loggers (Marques et al., 2013). The probability of logging one or more clicks from a harbour porpoise over a 1-second period is, on average, a decreasing function of its horizontal distance from the sensor. Many other factors are also important, such as whether the harbour porpoise is clicking or not, the direction and depth of its swimming, and the sonar beam scanning behaviour. We therefore used a concept from the distance sampling survey literature (e.g. Buckland et al., 2001): the effective detection area (EDA). In the current context the EDA is the area of a horizontal circle centred on the logger within which, on average, as many harbour porpoises are missed in a 1-second period as are detected outside the circle. (Note that we work in 2-dimensions, rather than 3, by projecting all onto the horizontal plane – for example, animal density is per unit area of water, not volume.)

We used three auxiliary studies to estimate the EDA by month and location. First, the 'tracking experiment': in an area of relatively high porpoise density (necessarily outside the survey area), we acoustically tracked porpoises in the vicinity of C-PODs to determine the per-second probability of detection as a function of horizontal animal-logger distance. This experiment yielded estimates of EDA for clicking porpoises in one location during summer. Second, the 'tagging study': we used data from six porpoises fitted with acoustic recording tags to estimate the proportion of time porpoises are in a non-clicking (i.e., silent) state. Third, the ‘playback experiment’: we undertook playbacks of artificial porpoise click trains over a range of distances away from the C-PODs at both the tracking experiment site and most sampling locations in the main study. This allowed us to determine how distance-specific detection probability changed as a function of environmental factors, and hence generalize our results from the location and time of the tracking experiment to estimate EDA for all locations and months surveyed. Below each of these studies are described in detail. We then describe the statistical analyses that combined the results from these auxiliary studies with those from the main survey to yield estimates of porpoise density and abundance.

Tracking experiment

A challenge in using passive acoustics to detect harbour porpoises is that their echolocation signals are highly directional (Au et al., 1999; Koblitz et al., 2012; Macaulay et al., 2020), and they may adapt their source levels to different acoustic habitats (Dähne et al., 2020). Although the directionality is partly compensated by the scanning movements of the head performed by harbour porpoises (Verfuss et al., 2009), the combined effect of click directionality, source level, head-scanning behaviour, and general swim direction on the detectability of harbour porpoises needs to be measured empirically. We estimated the EDA of a C-POD by acoustically tracking free-ranging harbour porpoises with hydrophone arrays in an area where C-PODs were moored to the seabed.

This experiment was undertaken from 27 May to 22 June, 2013, in the Great Belt, Denmark (S Fig 1Fig 1.), at a water depth of 19.5 m. This site (55° 27.2’ N, 10° 50.6’ E) was selected because porpoise density was known to be high enough to yield a useable number of encounters in the time available for the experiment; the low density of porpoises in the main part of the survey area prevented us from conducting the experiments there. A harbour porpoise-tracking hydrophone array was constructed and attached to a 12.5 m research vessel. A horizontal array consisted of a cross of five hydrophones, two in port-starboard and three in bow-stern orientation. The recordings made with the horizontal array allowed us to obtain the bearing of the animal relative to the array.

In addition, we deployed a vertical array with an aperture of 13 m consisting of 10 evenly spaced hydrophones tied to a rope with a 100 kg weight at the bottom end (well above the sea floor) to assure the straight vertical orientation. The vertical array was used to determine distance and depth of the echolocating harbour porpoises. Combining this with the accurate GPS position of the boat and measuring the boat's orientation allowed us to reconstruct the geo-referenced positions from which all clicks were emitted and resulted in a swim path of the animal.

At the study site, 16 C-PODs were moored with the hydrophone approximately 2 m off the seabed in a 4x4 grid with 50 m spacing. The vessel with the arrays was anchored both by the bow and the stern at a corner of the grid. OpenTag™ inertial measurement units (Loggerhead Instruments, Sarasota, FL, USA) were placed on the array at regular intervals, measuring its 3D underwater orientation (for further details, see Macaulay et al., 2017). A vector GPS and an OpenTag™ unit were placed on the boat to precisely measure the track and heading of the vessel and its tilt and roll. In addition to the acoustic tracking of harbour porpoises swimming in the area, two visual observers were placed on the wheelhouse of the survey vessel during daylight hours. The observers scanned a sector of 180° each, recording the time, bearing, distance and number of animals of each sighting. Since click trains from different porpoises cannot be distinguished in C-POD data, only encounters where we were confident that only a single animal was present, based on the acoustic tracking data only, or in combination with the visual data, were used in the analysis.

Through the hydrophone array, the full frequency bandwidth of the animals' click trains were recorded on a computer, using a custom-made software called MALTA (Microphone Array Localisation Tool for Animals). Acoustic data from the tracking array and the spatial data of the OpenTag™, the roll and tilt sensors, and the GPS were post-processed using the PAMGUARD (https://www.pamguard.org/) and MATLAB (MathWorks Ltd, USA). The time of arrival differences from a click detected on multiple hydrophones were used to calculate the instantaneous geo-referenced 3D position of a harbour porpoise. As the porpoise swam through the survey area, multiple click positions were used to reconstruct the 3D animal tracks. These tracks were used to give an estimate of the animal's position each second of the acoustic encounter, and hence the horizontal distance from the harbour porpoise to each C-POD. C-POD data was processed in the same way as data from the main acoustic survey to yield CPS, and these were time-matched to the swim tracks. A strong diurnal pattern in detectability was noted, and each acoustic encounter was classified into whether it occurred during dawn, day, dusk, or night. Dawn is the time between beginning of civil twilight and sunrise, and dusk the time between sunset and end of civil twilight. The start and end times of the diel phases were obtained from the United States Naval Observatory (2013). The diel phase was then used as a factor in the data analysis (see below). For the five days with porpoise tracks, the average length of dawn and dusk was nearly 2 hours, of day 15 hours 24 minutes, and of night 4 hours 40 minutes.

Tagging study

The tracking experiment described above is capable of yielding a detection function (and hence EDA) for clicking harbour porpoises. However, it was unknown if harbour porpoises click all the time, something that must be taken into account. To this end, six individuals that were incidentally entrapped in Danish fixed pound nets were fitted with acoustic and depth recording tags (Wright et al., 2017). The acoustic tag was a second generation A-tag (ML200-AS2: Marine Micro Technology, Saitama, Japan; see (Kimura et al., 2013)), which is a click event logger with two hydrophones placed 105 mm apart, in line with the body axis of the animal. The tag stores the sound pressure level and the time stamp of each received click. The hydrophone detection threshold is 133 dB (peak-to-peak) re 1 μPa within a frequency range of 55-235 kHz. Neither waveform nor duration of the clicks was recorded. The time-of-arrival difference between the two hydrophones makes it possible to calculate the bearing to the source and was used to separate sounds generated by the tagged animal from those of other porpoises in the vicinity (see Wright et al. (2017) and references therein). The depth recorder (DST-Milli-F logger, Star-Oddi, Iceland) had a 1 m resolution and was set to log data at 3-second intervals. The tags remained attached for multiple days and were recovered by Argos and VHF tracking once detached from the animal using a timed releaser (Wright et al., 2017).

The acoustic records were processed to yield click times and these were aggregated into CPS's. The tags were programmed to duty cycle, typically recording for 10 minutes each hour. Data from the first two hours after release were discarded, as were data from seconds where the animal was <2 m from the water surface (as estimated for each second by linear interpolation between the 3-second samples of the depth records). The acoustic depth truncation was necessary because there was too much acoustic interference from the surface, such as wave noise, surface reflections, and breathing, for the tag to reliably detect the echolocation clicks generated by the tagged animal. The resulting data were analysed to produce estimates of the average probability of the tagged animal producing one or more CPS during periods of time equal to an encounter in the harbour porpoise tracking experiment (see Tracking experiment above and Statistical analysis below).

Playback experiment

The datasets from the tracking and tagging experiments can be used to estimate the EDA of harbour porpoises in the Great Belt at the time of the tracking experiment, but this may not apply to the main acoustic survey if harbour porpoise acoustic behaviour or the acoustic propagation changes over space, depth or time. We could not account for variation in acoustic behaviour, but to account for propagation differences we conducted playbacks of artificial harbour porpoise click sequences both in the Great Belt during the tracking experiment and at a sample of survey stations during the main survey.

Playbacks were conducted using omni-directional piezo-electric transducers (Denmark and Germany: TC4033, Reson A/S, Slangerup, Denmark; Sweden, Finland, Estonia, Latvia, Lithuania, and Poland: HS/150, Sonar Research & Development, Beverly, UK), suspended to a depth of ca. 5 m, at a range of up to 8 horizontal distances from the deployed C-POD, designed to span 0-500 m. Each playback consisted of a set of 11 artificial harbour porpoise-like click sequences, and each sequence consisted of 10 or 20 equally spaced clicks with an inter-click interval of 1 ms. The inter-sequence interval was 10 or 50 ms. The artificial clicks were a 100 ms pure tone at 130 kHz, shaped by a raised cosine (Hann window). The playback signals were generated by a laptop computer connected to a National Instruments D/A-converter (DAQPad 6070E, USB-6251 or USB-6361) and amplified by an A-301 HS High Voltage piezo amplifier (AA Lab Systems, Tel Aviv). The designed source level for the first click sequence was 186 dB p-p re 1µPa m, with each subsequent click sequence reduced by 3 dB, resulting in the final sequence having a source level of 156 dB p-p re 1µPa m. However, on reviewing the recordings of the playbacks made in proximity to the source, it was discovered that playbacks with the TC4033 transducer were limited in peak-peak level due to system overload for source levels greater than 181 dB p-p re 1µPa m. For the HS/150 transducer, the limitation was for levels above 169-171 dB p-p re 1µPa m (measured at two different occasions). This resulted in the highest usable source level of 168 dB p-p re 1µPa m for all playbacks; click sequences with a source level at or above 171 dB p-p re 1µPa m were excluded from further analysis. Playbacks were performed with the vessel's engine and echo sounder switched off.

After recovery of the C-PODs, time periods corresponding to the playback were examined and, for each artificial click sequence, the number of clicks that were detected (out of either 10 or 20 clicks) for a given source level and distance was recorded. Note that most of the time periods for the playbacks were discarded from the main dataset to not interfere with surveyed effort or click data.

Statistical analysis

Here we describe the estimation of harbour porpoise density and abundance, then the analyses associated with each part of the density formula, and, finally, variance estimation. Further details are given in Thomas and Burt (2016). All analyses were performed using the statistical software R version 4.0.2 (R Core Team, 2020).

Density and abundance

Density was initially estimated separately for each sampling location, month, and diel phase (dawn, day, dusk, and night, calculated using sunrise and sunset times for the 15th day of the month at each location), as follows

$$\widehat{D}_{imd} = \frac{n_{imd}}{T_{imd}\hat{v}_{imd}} \qquad (1)$$

where *D* is density, *n* the number of CPS, *T* the number of seconds of monitoring effort, ν the EDA, the hat symbol ^ indicates an estimate and subscripts *imd* indicate that all quantities are for sampling location *i* in month *m* and diel phase *d* (1=dawn, 2=day, 3=dusk, 4=night). We return to the estimation of ν below (see Effective detection area (EDA), below). Density per sampling location and month was estimated as a weighted mean of the diel phase density estimates:

$$\widehat{D}_{im} = \sum_{d=1}^{4} w_{imd}\widehat{D}_{imd} \qquad (2)$$

where w_{imd} is the proportion of the 15th day of month *m* at location *i* that is made up of diel period *d*. Density was aggregated to the level of season and country within region (northeast or southwest of the proposed management border shown in Fig 1) as the mean of the relevant location- and month-specific estimates. For this purpose, Denmark Bornholm was treated as a separate “country” from other Danish waters. Density by region was calculated as a survey area weighted mean of the relevant country-by-region estimates. Abundance was estimated as density multiplied by survey area.

Effective detection area (EDA)

The EDA for each sampling location, month and diel phase was estimated as

$$\hat{v}_{imd} = \frac{\hat{v}_d^* \hat{p}_c \hat{\xi}_{im}}{\hat{\xi}^*} \qquad (3)$$

where: $\hat{v}_d^*$ is the estimated EDA for harbour porpoises in diel phase *d* estimated from the tracking experiment (see below); $\hat{p}_c$ is the estimated probability that harbour porpoises produce one or more clicks during the time period of an acoustic encounter in the tracking experiment – this is estimated from the tag data; $\hat{\xi}^*$ is the predicted EDA for an artificial click at the tracking experiment site in the Great Belt, estimated from the playback experiment at that location; and $\hat{\xi}_{im}$ is the predicted EDA for an artificial click at sampling location *i* and month *m*, estimated from the playback experiment in the main survey area.

The motivation for this formulation is as follows. The tracking experiment enables estimation of ν_d^*, the EDA for harbour porpoises that were clicking and therefore available to be tracked acoustically and take part in the experiment. However, the EDA required is for clicking and non-clicking harbour porpoises, which is estimated by $\hat{\nu}_d^*\hat{p}_c$. To generalize this EDA to apply to sites within the main survey, we assume that the ratio of EDA for artificial clicks from playbacks at the tracking experiment site (ξ^*) to EDA of artificial clicks at a main survey site (ξ_{im}) is equal to the ratio of true harbour porpoise EDA at the tracking location site in any diel phase ($\nu_d^* p_c$) to the true harbour porpoise EDA at the main survey site in the same diel phase (ν_{imd}) – i.e. that

$$\frac{\xi^*}{\xi_{im}} = \frac{\nu_d^* p_c}{\nu_{imd}} \qquad (4)$$

yielding Equation 3.

We now describe the analyses used to estimate ν_d^* from the tracking experiment, p_c from the tagging study, and ξ^* and ξ_{im} from the playback experiment (see below).

Analysis of the tracking experiment

The goal was to estimate the EDA, ν_d^*, given input data consisting of, for each acoustic encounter, the estimated horizontal distance of the harbour porpoise from each C-POD in each second of the encounter, and whether the C-POD detected clicks or not (after processing with the KERNO and Hel1 classifiers). Each second on each C-POD during an encounter forms a binary trial, with a “success” being detection of clicks and a “failure” being non-detection. We therefore analysed the data using binary regression, with detection/non-detection as the response variable, distance and diel phase as continuous and factor covariates, respectively, and a logit link function. Our approach was similar to that of Kyhn et al. (2012), except that we did not assume a linear-logistic shape for the detection function (the relationship between detection probability and distance). Instead we used a Generalized Additive Model (GAM, (Wood, 2017)) to allow a smooth, non-linear relationship between probability of detection and distance. We used cubic regression spline bases; initial fits produced implausible shapes due to the patchy distribution of distances in some diel phases and the very small proportion of successes, so we hand-selected only three knot points (at 100, 300 and 500 m) to ensure a smooth, nonlinear function. Given the very conservative click classifier used, detection probability can be safely assumed to be zero at 500 m; this constraint was added to the model adding structural zeros to the data at 500 m so that estimated detection probability was zero at that distance with no uncertainty. Fitting was implemented using the package mgcv in R (Wood, 2017).

Trials within the same second are not independent between C-PODs, and trials within the same encounter are not independent – this will have a negligible effect on the estimated functional relationship but can strongly affect variance. To account for this effect, we used a non-parametric bootstrap (using encounter as the sampling unit) to estimate variance (see Variance estimation below).

Given the fitted detection function from the GAM, we used the following formula to give an initial estimate of EDA for each diel phase – it is based on the point transect formulae of Buckland et al. (2001); see also Kyhn et al. (2012) (although that paper uses effective detection radius rather than EDA):

$$\hat{v}_d^{**} = 2\pi \int_{r=0}^{w} r\, \hat{g}(r,d) dr \quad (5)$$

where $\hat{g}(r,d)$ is the estimated detection function for horizontal distance *r* and diel phase *d*, and *w* is some horizontal distance at which detection probability is assumed to be zero. We used *w*=500 m.

In practice, the sample size of acoustic encounters at each diel phase was small (4 in the morning phase, 21 in the day, 5 in the evening and 6 in the night), severely limiting our ability to infer accurately diurnal changes in porpoise detectability from the above analysis. Also, it is possible that diurnal behaviour was different here from other parts of the Baltic (see Discussion). We therefore used information from the main acoustic survey to inform our estimate of the relative detectability of porpoises by diel phase, as follows. The basic idea is that the number of porpoises present within each country and month does not vary by diel phase, and hence changes in porpoise encounter rate by diel phase within country and month must be due to changes in detectability. We therefore fitted a statistical model of encounter rate as a function of diel phase (with day as the base level) plus the interaction of month (as a factor) and country. We used a Generalized Linear Model (GLM) with encounter rate modelled as a Tweedie random variable (Tweedie, 1984) to accommodate for overdispersion relative to a Poisson variable, and using a log link function. The estimated diel phase coefficients were exponentiated to yield estimates of proportional change in encounter rate (and hence, by assumption, in detectability) by diel phase, relative to the day phase – we denote these e_d. The EDRs calculated from Equation 5 were then scaled as follows:

$$\nu_d^* = \frac{e_d \sum_{d=1}^{4} w_d^* \nu_d^{**}}{\sum_{d=1}^{4} w_d^* e_d} \qquad (6)$$

where w_d^* is the proportion of the day at the tracking experiment site that is made up of diel period *d* (equal to 0.084, 0.660, 0.084 and 0.171 for dawn, day, dusk and night respectively). The scaled EDRs, ν_d^*, thus have the same weighted average (weighted by w_d^*) as the unscaled ones (w_d^{**}), but their relative magnitude is the same as the e_ds, so relative detectability matches that found from the main survey. These scaled EDRs were used in Equation 3.

Analysis of tagging study

Our goal was to estimate p_c, the average probability of one or more CPS during a period of time equivalent to the encounters in the tracking experiment. Input data were, for each tagged harbour porpoise, the presence or absence of a click for each second of recording where the harbour porpoise was estimated to be deeper than 2 m (acoustic data from depths <2 m had been removed, see Tagging study above). Data from each tagged harbour porpoise was analysed separately. Within this, we undertook a separate analysis for each encounter duration from the tagging experiment. For each harbour porpoise encounter duration, we divided the tag record into chunks of this duration. Only chunks where the tag was recording for the entire duration of the chunk were retained (recall that the acoustic recorder was duty cycled). For the remaining chunks, we recorded whether the chunk contained any CPS and the proportion of the chunk where depth was <2 m – i.e. of missing click data. To correct for the missing data, we fitted a binary regression of presence/absence of at least one CPS vs. a monotonic non-increasing smooth function on the logit scale of the proportion of missing data (using the package scam in R (Pya and Wood, 2015)), and predicted the probability of one or more click for zero missing data. Let $\hat{p}_{cae}$ be the predicted probability of there being at least one CPS for tagged animal *a* and exposure duration *e*. We estimated average probability of one or more CPS for each tagged animal, $\hat{p}_{ca}$, by taking the mean across all encounter durations. Finally, we estimated the overall average probability of one or more CPS, $\hat{p}_c$, by taking a weighted mean of $\hat{p}_{ca}$ over all tagged animals, weighting by the number of seconds that each animal's tag was recording and the animal was deeper than 2 m.

Analysis of playback experiment

The goal was to estimate the EDAs ξ^* and ξ_{im} for the Great Belt tracking experiment and all stations and months in the main survey area. The two datasets (tracking experiment location and main survey area playbacks) were analysed separately. Input data variables for both were detection/non-detection of each click within an artificial click sequence, together with horizontal distance and playback source level. In addition, for the main survey playbacks, a set of candidate environmental, spatial and temporal variables that potentially affect sound propagation were obtained for each month and station. These included sediment type, depth (m), temperature (°C), salinity (PSU), pycnocline depth (m), pycnocline gradient ($kg/m^3/m$), date (year and month or Julian day) and location (latitude and longitude) (see S Table 1 for full details). Oceanographic variables were acquired from the Swedish Meteorological and Hydrological Institute (SMHI). They were derived from an oceanographic model at the spatial resolution of 0.083 decimal degrees and temporal resolution of one month. Depth was derived from the Baltic Sea Bathymetry Database at the resolution of 500x500 m (HELCOM, 2015). Sea-surface salinity had a few unusually high values so to increase model robustness we trimmed the highest 1%, setting them equal to the 99^{th} percentile value.

Separate models were fit to each dataset. Both were binary GAMs, implemented using the package mgcv in R (Wood, 2017), with detection/non-detection of each click as response variable, and covariates modelled via a logit link. Both models included distance and source level as smooth continuous covariates; model selection showed that modelling these jointly as an interaction (a tensor product of cubic regression splines) produced a better fit (lower AIC). For the main study playback analysis, additional covariates were selected for inclusion in the model that were not highly correlated with one another ($|r|<0.5$) and were modelled as main effects without consideration of interaction terms. Sediment type was modelled as a factor covariate, month or Julian day as cyclic regression splines and the other variables as thin-plate regression splines. In all cases (except the tensor product), to avoid unrealistically complicated models, smooth functions were limited to a maximum of 5 degrees of freedom. Variables were added by forward selection, with those resulting in a lower AIC being retained. Environmental variables (e.g. depth and sediment type) were offered for inclusion before explicitly temporal (e.g. month) or spatial (e.g. latitude and longitude) variables (see S Table 1).

The selected models were used to estimate EDA, by integrating out distance in a similar way to Equation 5. A single source level was used – we selected to use 168 dB p-p re. 1 µPa m, the highest level consistently used in the Great Belt playbacks, it being the closest we could come to the nominal on-axis source level of a harbour porpoise (cf. Villadsgaard et al. (2007)), who report source levels of 178-205 dB p-p re. 1 µPa m). For the main study, values of the environmental covariates were sometimes outside the range of those used to fit the model; in these cases, to avoid extrapolation, we constrained them to lie within the range of values for the stations where playbacks took place.

There are several levels of potential non-independence in the playbacks. Clicks at a given source level are not independent within a playback; in the main survey, playback hardware is not independent between stations and C-PODs were re-used at multiple stations; in the Great Belt study, each playback was broadcast to multiple C-PODs. For the main survey study, we implemented variance estimation via a non-parametric bootstrap, with the sampling unit being a playback session (i.e. a set of playbacks at a station on the same date). We note that model selection is also affected by non-independence and hence it is possible that we selected a model with too many explanatory variables; this will not lead to bias but will reduce precision. For the Great Belt tracking experiment, there were few playback sessions, so we instead included in the model a random effect for playback and another for C-POD (implemented via the re smoother in the mgcv package (Wood, 2017)). Variance estimation in this case was implemented via a parametric bootstrap, using the fitted model coefficients and associated variance-covariance matrix and assuming the coefficients follow a multivariate normal distribution.

Variance estimation

Variance and confidence interval estimation was implemented via a bootstrap procedure, where each component of the density (and abundance) estimate was generated from an independent bootstrap, as follows. For encounter rate (n and T), a non-parametric bootstrap was used, resampling sampling locations within country within region. (One issue was that there was only one sampling location in the northeast region of Danish Bornholm so no variance could be computed in this stratum. However, since the abundance in this stratum was zero in May-October and two in November-April, the lack of variance had a negligible effect in practice.) For the acoustic tracking experiment EDA, ν_d^*, a non-parametric bootstrap was used, resampling harbour porpoise encounters within diel phase (in re-fitting the models, structural zeros were used to ensure that all fitted functions had an estimated detection probability of 0 at 500 m). For the tagging study, a parametric bootstrap was used, because there were too few tagged animals for a non-parametric bootstrap. The estimated average probability of one or more CPS, $\hat{p}_c$, and its associated variance, were fitted to a beta distribution by matching the first two moments. Random samples were then generated from this distribution to produce bootstrap realizations of p_c. For the playback EDA at Great Belt, ξ^*, a parametric bootstrap was used, resampling from the fitted detection function model. For the playback EDAs in the main study, ξ_{im}, a non-parametric bootstrap was used instead, resampling playback sessions, but ignoring model selection uncertainty (i.e. using only the final model selected in analysis of the original dataset rather than re-implementing model selection within the bootstrap).

In all cases, 1,000 bootstrap resamples were generated. For each bootstrap replicate, harbour porpoise density at each site and month was estimated, using Equations 1 to 6; these site and month estimates were then combined as described in the section Density and abundance above, to produce 1,000 bootstrap replicate estimates of density and abundance at the level of seasons and region. Estimates of variance in density and abundance were derived from the bootstrap replicates using the standard estimator of variance, and confidence intervals were derived using the percentile method (see Kyhn et al. (2012)).

Assumptions

We here summarize the assumptions used in estimating abundance. (1) At most one individual porpoise is detected in each one-second snapshot at each location. (2) There are no false positive detections. (3) Porpoise density at sampling locations within each country and region are representative of the density in that country and region. (4) Missing C-POD data at sampling locations are missing at random within location and month. (5) Only single porpoises were part of the Great Belt tracking experiment. (6) Acoustic behaviour of porpoises in the Great Belt tracking experiment is representative of acoustic behaviour of porpoises in the main survey area. (7) Animals with acoustic tags have temporal click patterns representative of animals within both the Great Belt and the main study area. (8) The temporal pattern of clicks in sections of the tag record that are missing is the same, on average, as that in the sections we used for analysis. (9) The statistical models used to estimate EDA of porpoises in the trials at the Great Belt, and EDA of playbacks at Great Belt and in the main survey area, produce unbiased estimates.

In deriving estimates of uncertainty (variance and confidence intervals), we made the following additional assumptions. (10) The sampling locations are located independently and at random within region within country. (11) Porpoise encounters in the Great Belt tracking experiment are independent of one another. (12) The beta distribution fitted to the estimate of proportion of time clicking from the tagging study accurately represents uncertainty on that parameter. (13) The model used to estimate EDA of playbacks in the Great Belt study produces an unbiased estimate of parameter variance and covariance; parameters follow a multivariate normal distribution. (14) Playback sessions in the main survey area are independent.

Results

Survey effort

During the survey period from 1st May 2011 to 30th April 2013, C-POD click loggers were deployed and data were successfully retrieved from 298 of the designed 304 survey stations (Fig 2). The recorded data corresponded to a total of 377 logging years, representing 62% of the total possible effort if all 304 stations had been active for the entire two-year survey period. There was strong spatial variation in effort, with considerably lower effort primarily in Estonia, Latvia and Lithuania (Fig 2). There, loggers were removed by trawling and the coast is very exposed to foul weather and ice, which interfered with servicing to exchange batteries and memory cards. There was also temporal variation in effort, with lower survey coverage in late 2011 and early 2012 (Fig 3).

Fig 2. Recording effort per station May 2011-April 2013.

The radius of each dot is proportional to the number of days of survey effort; crosses are stations with no survey effort. The shading shows the survey area.

Acoustic encounter rates

The mean acoustic encounter rate (CPS per 1,000 seconds of survey effort) from 1 May 2011 to 30 April 2013 showed a strong spatio-temporal pattern (Fig 3, S Fig 4). During May-October, the highest mean detection rates (>1 CPS/1,000 s) were recorded at the westernmost stations in Danish, Swedish and German waters, and at one station at the Northern Midsea Bank in the Baltic Proper (for geographical terms, see S Fig 1). The second highest mean rates ([>0.05]-1 CPS/1,000 s) were recorded at the adjacent stations in the southern Swedish waters, most of the remaining stations in German waters, and two stations in western Polish waters. These rates were also recorded at five stations at and around Hoburg's and the Midsea Banks in the Baltic Proper. With few exceptions, the remaining stations with detections were adjacent to these two clusters. There were no or few detections in Finnish, Estonian, Latvian and Lithuanian waters. During November-April, the highest mean detection rates (>1 CPS/1,000 s) were again recorded in the southwest and at the same station at the Northern Midsea Bank. However, detections made at a higher number of stations at lower rates (primarily ≤0.05 CPS/1,000 s), including along the east coast of Sweden, in Finnish, Latvian and Lithuanian waters, and along the coast of Poland. Detections were made in all countries surveyed except Estonia. Note that Russian waters were not included in this study for administrative reasons.

Fig 3. Mean acoustic encounter rate of harbour porpoises during May-October and November-April.

The radius of each dot is proportional to the number of click-positive seconds (CPSs) per 1,000 seconds of monitoring for the entire survey period; open circles are stations with no detections, and crosses are stations with no survey effort. The shading shows the survey area. The May-October management border was proposed by Carlén et al. (2018).

Estimation of effective detection area (EDA)

Tracking experiment

A total of 36 free-ranging single harbour porpoises were tracked acoustically with a hydrophone array in the Great Belt, Denmark, where 16 C-PODs were moored to the seabed. Summing across all C-PODs and encounters, there was a total of 26,207 s of monitoring effort, of which 137 s contained harbour porpoise detections on C-PODs. The median encounter duration was 56 s (mean 64 s, range 5-263 s). Although most encounters occurred during the day (58.3%), most CPS's were at night (73.7%), suggesting that acoustic activity and hence detectability varies by diel phase (dawn, day, dusk or night.

Detection probability was estimated to be approximately constant within each diel phase beyond around 150 m, declining at longer ranges; within 150 m, detection probability was estimated to be approximately 5-25 times higher at night than the other three diel phases (Fig 4).

Fig 4. Detection function for free-swimming porpoise from the tracking experiment.

Estimated probability of detection (solid lines) and 95% bootstrap confidence limits (dashed lines) of tracked harbour porpoise in a 1-second period in each diel phase as a function of horizontal distance. Vertical ticks at the top and bottom of each plot show the raw data: ranges at which detections were made in a 1-second period (top of plot) or at which detections were not made (bottom of plot). Circles show a summary of these data: the proportion of positive detections in ten distance bands equally spaced through the data. The shape of the detection function (on the scale of the logit link) was constrained to be the same in all diel phases, and the function was constrained to be zero at 500 m. Note the different scales on the y-axes.

The EDA for tracked porpoises was derived from this fitted detection function and the relative acoustic encounter rates in each diel phase from the main Baltic survey. Estimated EDA using just the detection function (Equation 5) ranged from 4,973 m^2 (SE 2,784) at night to 188 m^2 (SE 76) during the day (Table 1), i.e. a 25-fold difference. However, the relative acoustic encounter rates in the main survey varied only by a factor of 2.07 between day and night (Table 1). Using this information (see Materials and Methods Equation 6 and Discussion) yielded scaled estimates of EDA for tracked porpoises by diel phase that ranged from 1,847 m^2 (SE 786) at night to 891 m^2 (SE 379) during the day (Table 1). The scaled EDAs are equivalent to an effective detection radius ranging from 24 m at night to 17 m in the day.

Table 1. Estimated effective detection area (EDA), proportional change in encounter rate, and resulting scaled EDA.

Estimates are for a free-swimming harbour porpoise in a 1-second period from the tracking experiment. Values in brackets are standard errors. Symbols used ($\hat{\boldsymbol{v}}_{\boldsymbol{d}}^{**}$, $\hat{\boldsymbol{e}}_{\boldsymbol{d}}$ and $\hat{\boldsymbol{v}}_{\boldsymbol{d}}^{*}$) are defined in Equations 5 and 6, which also show how the EDAs are calculated.

Diel phase	**EDA $\hat{v}_d^{**}$ [m²]**	**Proportional change (relative to Day) in encounter rate $\hat{e}_d$**	**Scaled EDA $\hat{v}_d^{*}$ [m²]**
Dawn	351 (224)	1.42 (0.18)	1,268 (540)
Day	188 (76)	1 (0)	891 (379)
Dusk	1,138 (242)	1.20 (0.15)	1,068 (455)

Night	4,973 (2,784)	2.07 (0.25)	1,847 (786)
Weighted mean	1,101 (469)	-	1,101 (469)

Tagging study

Six harbour porpoises were opportunistically entrapped in Danish stationary pound nets. Duty cycled acoustic tags, recording 10 minutes each hour on five animals and 45 minutes each hour on one animal, were attached to the dorsal fins (Wright et al., 2017). Mean tag deployment duration was 5.6 days (range 2.1-11.1 days), yielding a mean of 97,362 s of recording data per animal (range 29,160-159,930 s). After truncation of data from times corresponding to when the tags were closer to the surface than 2 m (S Fig 5), we calculated the probability of one or more CPS for each tagged animal given each encounter duration in the tracking experiment (S Fig 6). Averaging these probabilities across encounter durations, the mean probability of one or more CPS varied between the six porpoises from 0.68 to 0.95 (S Table 2). In other words, the estimated probability of a porpoise remaining silent and being missed in the tracking experiment, assuming the tagged porpoises were representative of the population sampled in the tracking experiment, ranged from 0.05 to 0.32. The average weighted probability over all animals of one or more CPS during a tracking encounter (denoted $\hat{p}_c$ in Materials and methods) was 0.82 (SE 0.06). A beta distribution was used to represent this uncertainty when calculating variance in abundance estimates, and the corresponding beta parameters were a=40.5 and b=9.4.

Playback experiment

A total of 253 successful playback experiments of artificial porpoise click sequences were performed at 181 sampling locations within the main survey area (S Table 3). Playbacks took place in all months of the year except January and September (S Table 4). The number of distances per experiment at which playbacks were performed varied for operational reasons between 1 and 8, with a mean of 4; playback distances ranged from 5 to 500 m with a mean of 209 m. The general goal was to perform a playback at each survey station in each of the summer and winter seasons, but due to practical constraints with equipment failure and availability, this was not achieved.

The resulting detection/non-detection data were used to fit the detection probability as a function of horizontal distance, source level and other environmental factors. The selected model included a 2-D smooth of distance and source level, plus depth, month, sea surface temperature and sea surface salinity as continuous covariates and sediment type as a 5-level factor (S Table 1 and S Table 5; S Fig 7 and S Fig 8 top plots). Detectability of artificial porpoise clicks decreased with distance and increased with source level (S Fig 8 top plots). Detectability was generally lower in deeper locations, in winter months, at moderately high sea surface temperature (15 °C) and higher sea surface salinity (6.5 and 8.5 PSU), although none of these relationships were monotonic (S Fig 7).

The fitted model was used to predict EDA of artificial clicks at a source level of 168 dB p-p re 1 μPa m for each sampling location and month in the main survey area. The mean EDA over all stations and months was 0.219 km^2 (SE 0.0291); but there was considerable variation among sites and months, ranging from 0.034 km^2 (SE 0.031, station #1097 (Sweden) in December) to 0.742 km^2 (SE 0.213, station #3026 (Estonia) in August). In general, EDA was highest in March and August and lowest in December/January and June; it tended to be higher in the northeastern sites and lower in the more western sites (S Fig 9).

During the tracking experiment in the Great Belt, playbacks were performed on 7 days over the study period, with 85 playbacks generated at distances ranging from 4 to 426 m (mean 155 m). Note that, unlike the main study playbacks, multiple C-PODs were exposed to each playbacks. Again, the detection probability was modelled as a function of horizontal distance and source level, with C-POD identifier and playbacks included as random effects (see Materials and methods for justification). As with the main survey, detectability of artificial porpoise clicks decreased with increasing horizontal distance and increased with increasing source level (S Fig 8 bottom plots); however, overall detection probability was lower than for most sites in the main survey: estimated EDA (denoted $\hat{\xi}^*$ in the Methods) was 0.062 km^2 (SE 0.009).

Density and abundance

The above elements were combined to yield estimates of density and abundance of harbour porpoise, with associated variance, by region and season (Table 2). We detected two density clusters during May-October, separated by the proposed management border (Fig 3; Carlén et al., 2018). One cluster was centred on and around the offshore banks in the central and southeastern Baltic Sea, south and southwest of the island of Gotland, Sweden (for geographical terms, see S Fig 1). Given their distribution during the breeding season, these animals most likely belonged to the Baltic Proper population, and their total abundance in this northeast region was estimated to be 66-1,143 individuals (95% CI, point estimate 490; Table 2). Using the 20th lower percentile as a precautionary minimum abundance estimate (Wade, 1998), this was equal to 130 individuals (all age classes). Assuming 50% mature individuals (Taylor et al., 2007), the mature group was estimated to be 33-572 individuals, with a 20th lower percentile of 65 individuals. The other cluster was located in the southwestern survey area, west of the island of Bornholm, Denmark, with an increasing density towards the west. Given their distribution, these animals most likely belonged to the Belt Sea population, and their abundance was estimated to be 11,511-39,046 individuals (95% CI, point estimate 21,096; Table 2). Estimates of density and abundance at the level of country, region and season are given in S Table 6 and S Table 7.

Table 2. Estimates of density and abundance of harbour porpoises in the Baltic Sea survey area (northeast and southwest of the May-October management border as well as total area) during May-October and November-April.

Region	**Season**	**Density (animals/1,000 km^2)**		**Abundance**		**CV (%)**
		Estimate	**95% CI**	**Estimate**	**95% CI**	

Northeast	May-Oct	3.70	0.49-8.62	490	66-1,143	69.4
Northeast	Nov-April	1.83	0.65-3.94	243	87-522	51.9
Southwest	May-Oct	620.80	338.74-1,139.03	21,096	11,511-39,046	33.3
Southwest	Nov-April	315.79	156.25-700.08	10,731	5,310-23,790	44.9
Total	May-Oct	129.58	72.95-239.02	21,586	12,153-39,818	32.9
Total	Nov-April	65.88	33.45-145.60	10,974	5,572-24,255	44.4

CI = confidence interval; CV = coefficient of variation.

The distribution was more scattered during November-April, but still with the highest density in the southwest, albeit lower than during May-October, and still with a considerable number of harbour porpoises on the offshore banks in central Baltic Proper (S Fig 4). In the entire surveyed area during November-April, the total abundance was estimated to be 5,572-24,255 animals (95% CI, point estimate 10,974; Table 2). During November-April, the number of porpoises remaining northeast of the May-October management border in Fig 1 was estimated to be 87-522 (95% CI, point estimate 243), and southwest of this line, 5,310-23,970 animals (95% CI, point estimate 10,731). The wide confidence intervals of the abundance estimates mean that the November-April estimates were not statistically different from the May-October estimates (bootstrap 95% CIs on the difference between winter and summer estimates include zero for the northeast (-835 to 306) and southwest (-26,852 to 4,371) regions).

Discussion

Abundance estimates

Separate populations (May-October)

We successfully estimated the density and abundance of a rare odontocete population. During May-October, i.e. during the breeding season, 66-1,143 harbour porpoises (95% CI, point estimate 490) were identified in the northeast region of the survey area, northeast of the proposed management border shown in Fig 1. We believe these represents the main part of the Critically Endangered (CR) Baltic Proper population. The animals were centred on and around the shallow offshore banks south and southwest of the Island of Gotland, Sweden (Carlén et al., 2018). Prior studies on genetics, morphology, acoustics, and movement (Galatius et al., 2012; Lah et al., 2016; Sveegaard et al., 2015; Wiemann et al., 2010) support the assumption that this cluster represents the “true” Baltic Proper population. At the same time, 11,511-39,046 harbour porpoises (95% CI, point estimate 21,096) were found in the southwest region of the survey area, primarily west of the island of Bornholm, Denmark. We believe that the main part of these animals belong to the Belt Sea population, which is centred in the Belt Sea (Carlén et al., 2018; Sveegaard et al., 2015). The estimated density in this region was 0.34-1.14 animals per km^2 (95% CI, point estimate 0.62). Visual surveys have been carried with partial overlap with the southwest region. The latest visual surveys covering the major part of the Belt Sea population in July 2012 (Viquerat et al., 2014) and 2016 (Hammond et al., 2017) estimated densities of 0.50-1.24 animals per km^2 (95% CI, point estimate 0.79), and 0.58-1.85 (95% CI, calculated by us from CV=0.30 and point estimate 1.04 assuming a log-normal distribution). Further, eight German surveys have been carried out during May-October 2002-2006, with 32% overlap with the southwest region (stratum G, Scheidat et al., 2008). During four of these visual surveys, no harbour porpoise was observed in the overlapping area. For the remaining four surveys, the density was estimated to 0.06-3.19, 0.00-0.03, 0.00-0.20 and 0.00-0.02 animals per km^2 (95% CI, point estimates 0.004, 0.008, 0.058 and 1.016). Due to the limited overlap in time and space, and the fact that the visual surveys represents days and the acoustic monitoring years, the results cannot be directly compared. However, since the distribution pattern of Belt Sea porpoises equipped with satellite transmitters shows a sharp decrease from the Belt Sea towards Bornholm (Mikkelsen et al., 2016; Sveegaard et al., 2015), the true density in the southwest region of the acoustic survey area is more likely to be in the lower than the upper end of our confidence interval.

Mixed populations (November-April)

During November-April, the harbour porpoises were more dispersed and showed no clear spatial separation between the Baltic Proper and Belt Sea populations (Carlén et al., 2018). Even though the overall detection rates decreased, there was still a relatively high detection rate of porpoises on the shallow banks in the central Baltic Proper, and the detection rates increased along the Polish coast as well as in Hanö Bay, Sweden, on both sides of the May-October management border in Fig 1 (S Fig 1). The number of animals remaining northeast of the May-October management border was 87-522 porpoises (95% CI, point estimate 243), around half the estimated number during May-October, but the wide confidence intervals in both periods mean these values are not statistically different. Earlier studies have shown movements of porpoises into the German Pomeranian Bay during winter, proposed to be Baltic Proper animals (Benke et al., 2014; Gallus et al., 2012). Our results neither confirm nor reject this hypothesis, yet it seems likely that there is a net migration of Baltic Proper porpoises from the northeast to the southwest region during November-April. This movement would imply that conservation measures for the Baltic Proper porpoise population, such as bycatch mitigation, should cover the waters from the southwestern Baltic Sea to the Åland and Archipelago Seas during November-April (ICES, 2020a). Management measures that only cover the offshore banks and surrounding areas during the summer months would not be adequate to protect the population.

Even though Baltic Proper animals move into the southwest region during November-April, the majority of the animals in this region still belongs to the more abundant Belt Sea population. During these months, the abundance in the southwest region decreased to 5,310-23,790 individuals (95% CI, point estimate 10,731). Although this number is considerably lower than the May-October estimate, it is not statistically different due to the wide confidence intervals. Nevertheless, such a seasonal migration pattern is consistent with earlier studies (Benke et al., 2014; Gallus et al., 2012; Sveegaard et al., 2015; Verfuβ et al., 2007) that found movement of Belt Sea harbour porpoises from the southwest region to the northwest, into the Belt Sea during the winter.

Conservation status, threats and management needs

IUCN and HELCOM have classified the harbour porpoises in the Baltic Proper as Critically Endangered (CR) (Hammond et al., 2008; HELCOM, 2013a). The assessments were based on an aerial survey in 1995, partially covering the currently known management range of the Belt Sea population and partially the currently known Baltic Proper management range (Carlén et al., 2018; Sveegaard et al., 2015). The aerial survey estimated a total of 599 groups of single animals (95% CI 200-3,300 groups) (Hiby and Lovell, 1996). Based on an estimation of 50% mature individuals (Taylor et al., 2007), and a precautionary approach using the lower 20th percentile of the abundance estimate (Wade, 1998), IUCN reached an estimate of 192 mature individuals. We have now estimated the population abundance of the Baltic Proper population to be 66-1,143 individuals, with a 20th lower percentile equal to 130 (all age classes). Assuming 50% mature individuals, 33-572 mature Baltic Proper harbour porpoises remain with a 20th lower percentile of 65. These low numbers strongly supports the IUCN and HELCOM assessment that the Baltic Proper harbour porpoise is facing an extremely high risk of extinction in the wild.

In its latest threat matrix for the Baltic Proper harbour porpoise, ICES Working Group on Marine Mammal Ecology (WGMME) lists the threat levels by bycatch, contaminants, and underwater noise from explosions, military sonars and seismic surveys as ‘high’, based on evidence or strong likelihood of negative population effects, mediated through effects on individual mortality, health and/or reproduction (ICES, 2019). For the years 2009-2012, the annual number of bycaught harbour porpoises of the Baltic Proper population has been estimated to 7-12 animals (North Atlantic Marine Mammal Commission & Norwegian Institute of Marine Research, 2019). This is ten times or more than the estimated limit for sustainable human-caused mortality for the population: 0.7 animals per year (North Atlantic Marine Mammal Commission & Norwegian Institute of Marine Research, 2019), using the PBR (Potential Biological Removal) approach (Wade, 1998). In the Baltic Proper, 97% or more of harbour porpoise bycatch have been reported to occur in gillnets, including driftnets (prior to 2008) and semi-driftnets (Berggren, 1994; EC-DGMARE, 2014; Skóra and Kuklik, 2003). As pingers reduce but do not eliminate bycatch of harbour porpoises (Dawson et al., 2013; Larsen and Eigaard, 2014; Palka et al., 2008), a bycatch rate close to zero can only be reached by closing all gillnet fisheries within the distribution range of the Baltic Proper harbour porpoise.

PCBs have been associated with impaired health, immunosuppression, increased disease risk and reproductive failure in harbour porpoises (Beineke et al., 2007a, 2007b, 2005; Jepson et al., 2005, 1999; Lehnert et al., 2019; Murphy et al., 2015). PCB concentrations measured in harbour porpoises collected the Baltic Sea in the 1980s and 1990s have been alarmingly high (Berggren et al., 1999; Bruhn et al., 1999; Falandysz et al., 2002; Kannan et al., 1993). The recorded levels were often well above thresholds for the onset of physiological impacts, adverse health effects, and profound reproductive impairment (Helle et al., 1976; Jepson et al., 2005; Kannan et al., 2000; Murphy et al., 2015). Since the 1990s, the PCB concentrations in Baltic herring (*Clupea harengus*) and guillemot egg (*Uria aalge*) have declined, but remain higher than for example in the North Sea (Nyberg et al., 2015). The current levels in the Baltic biota indicate that PCB contamination remains a serious impediment to the health and reproductive status of the Baltic Proper harbour porpoise population, but lack of samples prevents direct studies. The lack of samples is due to a combination of the small population size and a low willingness to report and land bycaught harbour porpoises.

Impulsive underwater noise sources occurring in the Baltic Proper can cause behavioural disturbance, hearing loss, and other physical injury to harbour porpoises (Kastelein et al., 2017, 2015; Ketten, 2004; Lucke et al., 2009; Pirotta et al., 2014; Sarnocińska et al., 2020; Thompson et al., 2013; von Benda-Beckmann et al., 2015). Data on loud sources of impulsive noise in the Baltic Sea are collated nationally and reported to an ICES registry in support of HELCOM (HELCOM, 2021; ICES, 2020b). During 2015-2019, underwater explosions have primarily been reported from a few and primarily coastal locations in the Baltic Proper, airgun arrays in offshore waters in the southern Baltic Proper, and sonars in offshore waters across the Baltic Proper (ICES, 2020b). The spatial distribution of the sonars, which primarily are used for sea floor exploration, strongly overlaps with the year-round distribution of Baltic Proper harbour porpoise. The pressure is rapidly increasing due to a raising interest in offshore wind power. In January 2020, the total number of wind farms in the stages from concept to pre-construction within the entire survey area was 58, whereof 39 are within the May-October management range of the Baltic Proper population (4COffshore, 2020; S Table 8). It is therefore concerning that there is a lack of regulations regarding underwater noise. Germany has a dual exposure limit to avoid injury and significant disturbance from pile driving, applicable only to harbour porpoises in the southern North Sea (Federal Ministry for the Environment, Nature Conservation and Nuclear Safety, 2013), while Denmark has an exposure limit to avoid hearing impairment from pile driving, together with a guideline for estimating such impact, applicable to any Danish waters (Danish Energy Agency, 2016; Skjellerup et al., 2015). In all other countries around the Baltic Sea, underwater noise exposure limits are missing, and no country has any noise guidelines that take the conservation status of the Baltic Proper harbour porpoise into account. This is despite the fact that underwater noise is listed as a pollutant in the European Marine Strategy Framework Directive (2008/56/EC), and offshore constructions and associated activities pose a high risk to negatively impact the status of the Critically Endangered Baltic Proper harbour porpoise population. However, the development of common standards for impact assessment and mitigation of impulsive noise is a prioritized action in the HELCOM draft regional action plan for underwater noise (HELCOM 2020).

A recent population viability assessment of the Baltic Proper harbour porpoise population has been carried out, applying a range of biologically realistic parameter values and three different levels of bycatch (Cervin et al., 2020). Under the baseline scenario, with biological values representing a healthy population and absence of bycatch, the annual population growth rate was estimated to 2.3% (SD ±6.4%). Under recent conditions, a more likely scenario is an intermediate fertility (60%) in combination with a bycatch of 7-15 individuals per year (7-12 bycatch per year was estimated for 2009-2012 by North Atlantic Marine Mammal Commission & Norwegian Institute of Marine

Research, 2019). The latter scenario was estimated to lead to quasi-extinction (≤50 animals) in 44-75 years. Even substantial improvements in fertility could not balance out the investigated levels of bycatch (Cervin et al., 2020).

The importance of adequate bycatch mitigation on the population development is clearly demonstrated by the examples of the vaquita (*Phocoena sinus*), a porpoise species endemic to the Gulf of California, Mexico, and the Morro Bay harbour porpoise stock in Central California, USA. The abundance estimates of both management units have been similar to our estimate of the Baltic Proper harbour porpoise, and both units have been threatened by bycatch, but differences in the efficiency of the bycatch mitigation has led to strikingly different outcomes. In 1997, the abundance of the vaquita was estimated to be 567 individuals (95% CI 177-1,073). Despite several efforts (Jaramillo-Legorreta et al., 2017; Rojas-Bracho and Reeves, 2013), bycatch in illegal gillnetting has continued (Jaramillo-Legorreta et al., 2017, 2019), resulting in fewer than 19 vaquitas remaining as of summer 2018 (Jaramillo-Legorreta et al., 2019) with extinction becoming increasingly probable without immediate elimination of all bycatch. In contrast, high levels of bycatch in set gillnets within the range of the Morro Bay harbour porpoise stock lead to increasingly restrictive closures, reaching an almost complete ban (Forney et al., 2014; Moore et al., 2009). Additional bycatch in a driftnet fishery was reduced by the use of acoustic deterrent devices (pingers) and closures (Barlow and Cameron, 2003; Moore et al., 2009). From 1990 to 2012, the Morro Bay stock increased from 571 (95% credible interval 252-2,666) to 4,191 animals (95% credible interval 1,900-11,971), indicating an average annual growth rate of 9.6% since the near elimination of gillnets (Forney et al., 2020). It should be pointed out that the Morro Bay harbour porpoise stock does not suffer from high levels of environmental pollutants as the Baltic Proper harbour porpoise population.

These two examples show that a severely reduced porpoise population may recover if the human-induced mortality is considerably reduced, while failing to implement and enforce prompt and decisive conservation measures, often requiring community acceptance, may lead to extinction.

They also show that repeated abundance surveys provide a thorough basis for informed measures. However, a major difference between the Baltic Proper harbour porpoise, the vaquita and the Morro Bay harbour porpoise stock, is that the distribution range of the Baltic Proper harbour porpoise is approximately 12 and 22 times larger and is shared by nine countries. As such, efficient international cooperation to conserve the Baltic Proper harbour porpoise is needed.

Methodological limitations and alternatives

Acoustic survey

As we excluded waters deeper than 80 m from the survey, it was not possible to quantify the number of porpoises there. Within the surveyed depth range, most harbour porpoise detections occurred at 20–50 m depth, and tapered off on both sides, especially towards greater depths (Carlén et al., 2018). There is no information on association between harbour porpoise and fish distribution in the central Baltic Sea. However, prey availability and predictability appear to be the main driver for harbour porpoise distribution in The Sound, the strait that forms the Danish-Swedish border (Sveegaard et al., 2012a), and herring distribution explains large-scale distribution of harbour porpoises in the eastern North Sea, Skagerrak and Kattegat (Sveegaard et al., 2012b). In the southern central Baltic Sea, the most abundant subgroup of herring spawns in shallow coastal areas in spring. This behaviour is, in general, followed by a migration by older herring to the deep offshore Bornholm Basin and Gdansk Deep from July to December. Sprat (*Sprattus sprattus*) perform the opposite seasonal migration; they concentrate in the Bornholm Basin, Gdansk Deep and Gotland Basin from December to June, and transit to shallow coastal waters from June to December (Aro, 2002; Parmanne et al., 1994; Popiel, 1984; Stepputtis, 2006). Pelagic prey are thus available for harbour porpoises in both shallow and deep Baltic waters year round, while benthic prey are only available in shallow waters due to anoxic conditions (Hansson and Andersson, 2015). Regardless, future surveys are recommended to investigate the occurrence of harbour porpoises in the deep waters of the Baltic Sea.

We assumed that porpoise density at the sampled locations was, on average, representative of that in the main survey area. This was ensured by the systematic random grid design, although some adjustments had to be made in the few cases where the primary grid location could not be surveyed (Carlén et al., 2018). Overall, we believe these deviations from the ideal design will have caused a negligible bias in the abundance estimate. For stations that were surveyed, there was geographic variation in coverage (again for logistical reasons), with lower coverage in the east of the survey area. While this lower coverage was accounted for in the analysis methods, and so will not cause bias, it does mean that uncertainty is higher in this region. One assumption made in dealing with missing data is that, within station and month, it is missing at random with respect to animal density.

In using the detection metric of click positive second (CPS) as being proportional to porpoise density (Equation 1 in Materials and methods), we assumed that at most one porpoise was detected in a one-second snapshot at a sampling station. This assumption is justified because of the highly directional nature of porpoise click production: even when larger groups of porpoises are present, it is unlikely that more than one will be facing a hydrophone in the same second. Various alternative metrics have been used in passive acoustic monitoring with C-PODs and the preceding T-PODs, such as the number of detected clicks per unit time (Jaramillo-Legorreta et al., 2019; Osiecka et al., 2020), encounter rate and duration (Benjamins et al., 2016; Carlström, 2005), and detection positive time units ranging from 15-seconds or one minute (Clay et al., 2018; Kyhn et al., 2012; Nuuttila et al., 2018), to hours (Benjamins et al., 2017), waiting times or silent periods (Carstensen et al., 2006; Dähne et al., 2013a) or days (Benke et al., 2014; Palmer et al., 2019). Click counting is an example of a cue-based approach that has been recognized as a valid method for estimating absolute density (e.g. Marques et al. 2013). However, the porpoise detection algorithm used here (and generally for C-PODs) requires multiple clicks to be received, and although decreasing the risk of false positives, it complicates the process of estimating click detectability and linking it to click production rate. The number of clicks received per unit time (e.g. per second) given that at least one is detected is also highly variable, partly because click production rate varies considerably with behaviour and click type (buzz clicks, for example, are produced with a much shorter inter-click interval). Given this variability, an approach based on using acoustics to detect animal presence at “snapshots” of time was deemed preferable for this study. Using a short snapshot interval enabled us to assume that at most one animal was detected per snapshot and so bypass the need to estimate population mean group size; robust estimates of group size are not available for harbour porpoises in the Baltic Sea (Berggren et al., 2002). In addition, longer “porpoise positive” time units such as hours or days will saturate at higher density so they become no longer proportional to animal density.

The estimation method assumed no false positive CPS’s. This assumption was supported by a detailed manual analysis that showed negligible false positive detections from the classification algorithm used (see Supporting information). The disadvantage of using such a stringent algorithm is that a large number of valid detections are discarded, due to a restrictive classification criterion, contributing to an effective detection area that was much smaller than the area over which it is possible to detect porpoise clicks. Because only a small area was monitored around each station, the encounter rate variance was high. False positive detections are not a problem for abundance estimation, as long as their rate is accurately determined (Marques et al. 2013). In the current case, there was a strong impetus to minimise false detections in order to avoid incorrectly claiming the presence of the species based on false positive detections, since this would have substantial implications for the conservation obligations of the countries around the Baltic Sea. In other applications, a more liberal classification algorithm would be preferred, and would lead to a lower overall variance.

Tracking experiment, tagging study and playback experiment

Our estimates of effective detection area per station and month were based on the tracking experiment in the Great Belt, the tagging study and the playback experiment (Equation 3 in Materials and methods). In the tracking experiment, we assumed that only one animal was present during each encounter; we excluded data from times where we could visually detect multiple animals or saw evidence of multiple animals in the acoustic tracking data. We assumed that the animals were accurately localized by the acoustic tracking array; in practice there will have been some localization error but its effect on inference is likely minimal. We assumed the acoustic behaviour of porpoises tracked in the Great Belt site was representative of that in the survey area – an assumption that is unlikely to be correct. Indeed, we found that the estimation of variation in detectability with diel phase in the Great Belt tracking experiment was far greater than the diel variation in acoustic encounter rate from the main survey. This diel variation could be, for example, because porpoises were foraging on prey that is more accessible at night during the tracking experiment and so were more vocally active in that diel phase compared with other places within the main survey area. We were able to correct for this difference, but other variability in acoustic behaviour cannot be detected with our methods, and this is probably the biggest weakness of our study. Future abundance estimation surveys should collect information about detectability of wild-swimming porpoises on a larger sample of sites, and within the survey area, to increase robustness of the estimates. Our tracking experiment also had a small sample size of encounters, which did not cause bias, but contributed greatly to overall variance. Future studies should devote a bigger proportion of the overall effort to collecting detectability data from animal encounters, which will likely necessitate using lower cost detectability measurement methods than the tracking experiment. A suitable method would be multiple deployments of vertical hydrophones arrays with four or more channels, allowing distances to be calculated up to approximately 70-100 m (Dähne et al., 2020; Kyhn et al., 2013). However, to gather sufficient click data in the Baltic Proper, these systems would have to work autonomously over long times frames (at least weeks to months).

Data from tagged animals were used to account for the small proportion of animals that could have been missed from the tracking experiment because they did not emit echolocation clicks while in the vicinity of the tracking array. We assumed that the acoustic behaviour of the tagged animals was representative of those in the Great Belt. This is not something we can test directly, but we did find a relatively small variation between the six tagged animals in the mean probability of one or more CPS in a time period corresponding with the length of the tracking experiment encounters (S Table 2). This small variation indicates that the average acoustic behaviour at this time scale may not vary greatly between individuals. The relatively small variation also meant that, despite the small sample of only six tagged individuals, the estimate of mean probability of a CPS had low variance and contributed little to overall uncertainty in abundance estimates. The tags do not effectively record clicks while they are close to the surface and hence we also had to assume that click production while animals were close to the surface was the same as that while they were deeper. While it may be the case that click production is less at shallow depths (certainly no clicks can be recorded while the animal is above the surface to breathe), the periods of time at these depths are generally much shorter than the length of the tracking experiment encounters, and so mild violation of this assumption is unlikely to cause much bias in the results.

We used playbacks of artificial porpoise clicks to determine how the effective detection area calculated from wild-swimming porpoises in the tracking experiment scaled to each sampling location in the main survey area, and how the scaling changed by month. Compared with observations on wild-swimming porpoises, playback experiments are easy to perform. A hardware failure meant we obtained fewer playbacks than expected, and in some places a larger range of distances from the C-PODs would have been helpful, but overall the estimated detection functions were robust and had low variance. Playback experiments are an excellent way to estimate the effects of variation in sensor depth and changing propagation conditions, but because they do not include porpoise behaviour or (in our case) the directionality of porpoise clicks, they are no substitute for observations of wild-swimming animals. However, given the extremely low porpoise density in most parts of the Baltic Sea, it will never be possible to estimate detectability using wild-swimming porpoises in all areas, and hence some component of playback-measured calibration will be necessary also in future studies.

Conclusions

An international effort of eight European countries reliably estimated the abundance of a rare and cryptic animal population across a large spatial scale using passive acoustic monitoring. We obtained a small abundance estimate for the Baltic Proper harbour porpoise, confirming that the population is facing an extremely high risk of extinction. Given the large geographical scale in which the population is distributed, the fact that its distribution range is shared by nine different countries, and the importance in taking action promptly, we call for immediate, urgent, and efficient international cooperation in eliminating bycatch and mitigating the negative impact of underwater noise and other environmental pollutants on harbour porpoises in the Baltic Sea.

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Data Accessibility

All processed data and R code files to reproduce the results given in this paper are uploaded to Dryad, doi: *[doi not yet available, to be uploaded to Dryad upon acceptance of the manuscript and before publication]*.

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