Marine Biodiversity (2024) 54:42
https://doi.org/10.1007/s12526-024-01428-6

SENCKENBERG

ORIGINAL PAPER

Harbour porpoise (*Phocoena phocoena*) in the Wadden Sea World Heritage Site and requirements for trilateral monitoring

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Received: 31 December 2021 / Revised: 22 January 2024 / Accepted: 10 March 2024

Abstract
The harbour porpoise (*Phocoena phocoena*) is considered part of the 'Outstanding Universal Value' characterising the Wadden Sea World Heritage Site (WS WHS). The Trilateral Wadden Sea Plan aims to preserve the conservation status of the Trilateral Wadden Sea Cooperation Area, encompassing the WS WHS. The plan has specified two conservation targets for the harbour porpoise: (1) viable stocks and a natural reproduction capacity and (2) conservation of habitat quality for its conservation. To assess the current occurrence of the harbour porpoise in the Wadden Sea area, we collated and analysed data from regional and national research projects using telemetry, aerial surveys, strandings and passive acoustic monitoring, obtained over the years 1990–2020. The results illustrate that porpoises occur in both offshore and intertidal waters, showing seasonal movements and changes in local occurrence over time. Some porpoises displayed limited home ranges throughout the year, suggesting a possible residency for some of the animals using the Wadden Sea area. We also showed that methods, frequency and spatial coverage of monitoring activities vary among the countries Denmark, Germany and the Netherlands. We discuss the suitability of the different methods both regarding the challenges of monitoring in the complex Wadden Sea habitat as well as their ability to target the conservation aims of the WHS. We give several recommendations to assess the status of the species to meet the identified conservation aims.

Keywords World Heritage Site · Marine mammals · Harbour porpoise · MPA · Conservation · Wadden Sea · Monitoring methods · Passive acoustic monitoring · Telemetry · Strandings · Aerial surveys · Trilateral monitoring

Communicated by S. Garthe

This article is a contribution to the Topical Collection *Biodiversity and Ecology of the Wadden Sea under changing environments.*

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Introduction

The United Nations Wadden Sea World Heritage Site (WS WHS) is situated along the North Sea coastline of Denmark (DK), Germany (DE) and the Netherlands (NL). The site spans about 500 km from Blåvandshuk (DK) in the north to Den Helder (NL) in the south and covers an area of nearly 11,500 km^2 (Fig. 1).

The designation of the site was preceded by a long history of joint conservation efforts by Germany, Denmark and the Netherlands since 1978. This trilateral cooperation was formalised in 1982 with the signing of the Joint

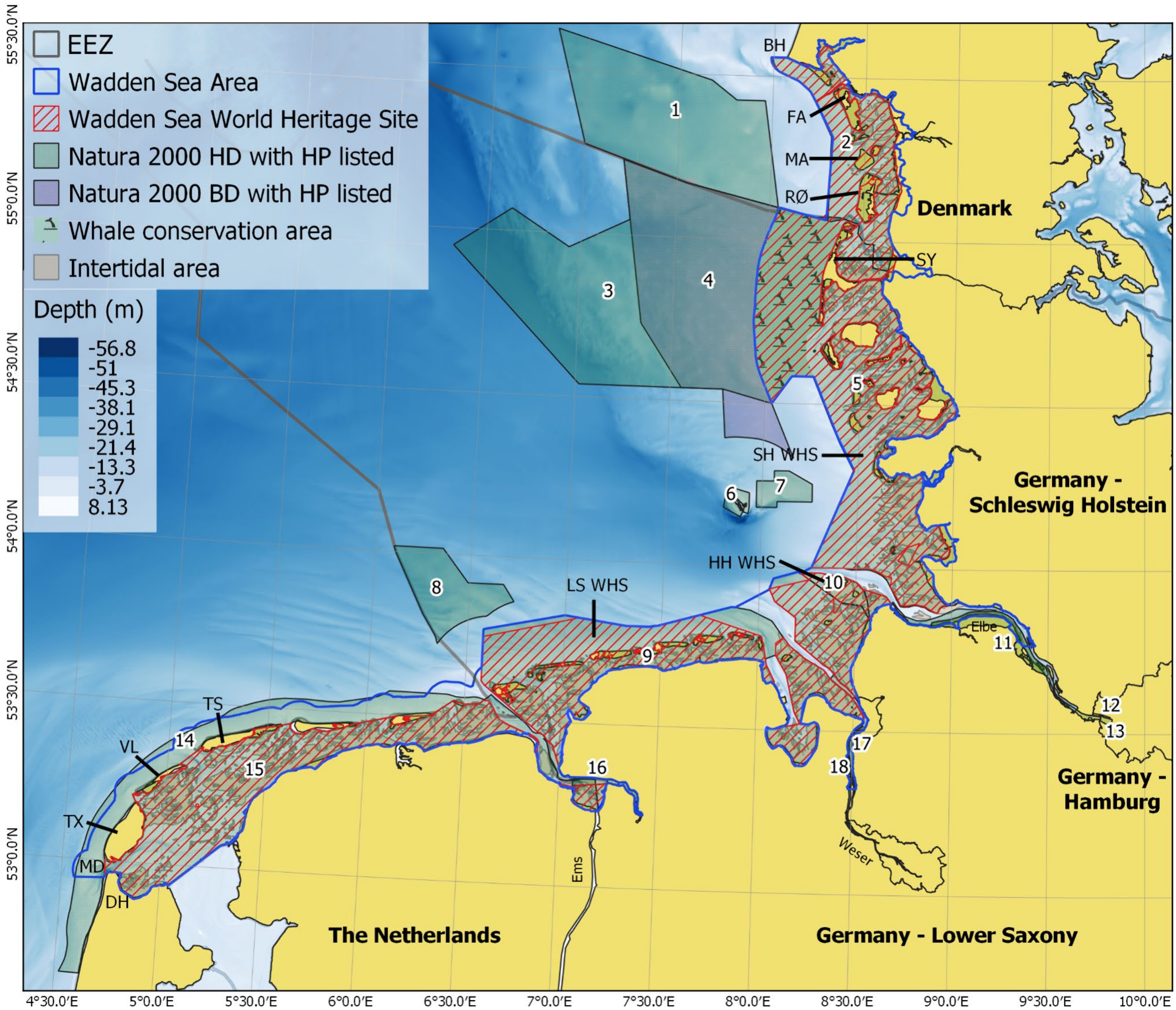

Fig. 1 The Wadden Sea World Heritage Site (WS WHS), the Trilateral Wadden Sea Cooperation Area (WSA) and adjacent or overlapping marine-protected areas (under the EU Habitats Directive (HD) and Birds Directive (BD), Natura 2000) that have listed the harbour porpoise as a species of interest. The Conservation Area (CA) is not depicted. BH, Blåvandshuk; FA, Fanø; MA, Mandø; RØ, Rømø; SY, Sylt; SH WHS, Schleswig–Holstein WHS; HH WHS, Hamburg WHS; LS WHS, Lower Saxony WHS; TS, Terschelling; VL, Vlieland; TX, Texel; MD, Marsdiep; DH, Den Helder. Natura 2000 areas: 1 = Sydlige Nordsø (HD), 2 = Vadehavet med Ribe Å, Tved Å og Varde Å vest for Varde (Danish Wadden Sea, HD), 3 = Sylter Außenriff (HD), 4 = Östliche Deutsche Bucht (BD), 5 = S–H Wattenmeer und angrenzende Küstengebiete (HD), 6 = Helgoland mit Helgoländer Felssockel (HD), 7 = Steingrund (HD), 8 = Borkum-Riffgrund (HD), 9 = Nationalpark Niedersächsisches Wattenmeer (HD), 10 = Hamburgisches Wattenmeer (HD), 11 = Unterelbe (HD), 12 = Rapfenschutzgebiet Hamburger Stromelbe (HD), 13 = Mühlenberger Loch/Neßsand (HD), 14 = Noordzeekustzone (HD), 15 = Waddenzee (HD), 16 = Unterems und Außenems (HD), 17 = Unterweser (HD), 18 = Nebenarme der Weser mit Strohauser Plate und Juliusplate (HD). Map developed in QGIS (version 3.4.3—Madeira, QGIS Development Team 2018b). Sources of data: CWSS, https://natura2000.eea.europa.eu/Environmental Agency, European Marine Observation and Data Network (EMODnet)

Declaration on the Protection of the Wadden Sea. This declaration formed the basis for the Trilateral Wadden Sea Cooperation (TWSC), which includes two levels of decision-making, the Trilateral Wadden Sea Governmental Council and the Wadden Sea Board (WSB). Both are supported by the Common Wadden Sea Secretariat (CWSS). In addition, the TWSC maintains various Expert, Networking and (ad hoc) Working Groups with specific monitoring, scientific and educational responsibilities, such as the Expert Group on Marine Mammals.

In 2009, two existing Wadden Sea National Parks in the German federal states Schleswig–Holstein and Lower Saxony and the Dutch Conservation Area were designated as a World Heritage Site (WHS). The inclusion of Hamburg Wadden Sea National Park and the Danish Wildlife and Nature Reserve followed in 2011 and 2014, respectively (Fig. 1) (Common Wadden Sea Secretariat and World Heritage Nomination Project Group 2008; WHC 2014).

The designation of a WHS is based on the presence of Outstanding Universal Values (OUV). UNESCO considered these OUVs to be so exceptional that they have a high relevance for the global community and need to be conserved for the future. The recognition of an area as a natural WHS brings increased global attention with it, and the protection of a WHS is considered the responsibility of all humankind. The practical conservation management remains the responsibility of the respective countries, including obligations such as 'to ensure that effective and active measures are taken for the protection, conservation and presentation of the cultural and natural heritage situated on its territory' (UNESCO 1972; Common Wadden Sea Secretariat and World Heritage Nomination Project Group 2008; Slob et al. 2016).

The management system of the WHS is built upon the framework of the TWSC, which has a long history of addressing the complex coordination of different legislative and regulatory bodies between and within countries as well as the integration of a multitude of stakeholders. The process to define common objectives was at times slow and challenging, but ultimately led to the development of the Trilateral Wadden Sea Plan (WSP), integrating regional, national and international obligations (Common Wadden Sea Secretariat 2010; Enemark 2021). The WSP presents the agreed conservation targets for different ecosystem components of the Trilateral Wadden Sea Cooperation Area (WSA) and WHS, and each country and federal state sets up their own management plans, either regionally or linked to national parks or Natura 2000 sites (Slob et al. 2016).

Three marine mammal species are considered important ecosystem components in the Wadden Sea: harbour seal (*Phoca vitulina*), grey seal (*Halichoerus grypus*) and harbour porpoise (*Phocoena phocoena*). The conservation targets for harbour porpoise are as follows:

- Viable stocks and a natural reproduction capacity
- Conservation of habitat quality for the conservation of the species

As part of the Trilateral Monitoring and Assessment Programme (TMAP), the Wadden Sea Quality Status Report (QSR) is published in regular intervals to assess whether the WSP targets are met (Reijnders et al. 2009; Jensen et al. 2017; Unger et al. 2022). In addition, the World Heritage Committee requests periodic reports on the status of the site (Common Wadden Sea Secretariat 2016).

For the two seal species, this assessment is based on the results of the coordinated trilateral monitoring under the Agreement on the Conservation of Seals in the Wadden Sea under the Bonn Convention (CMS 1991). The framework for this agreement is the Seal Management Plan (SMP).

There is, however, no framework for coordinated monitoring of harbour porpoise in the WS WHS or the WSA. The 2017 QSR recommends further research and monitoring on feeding ecology, habitat use, effects from anthropogenic activities, health status and the use of marine mammals as bio-indicators of environmental conditions, as well as harmonising of the spatial and temporal coverage of monitoring methods (Jensen et al. 2017). The Leeuwarden Declaration (2018) puts this into a larger trilateral context; Member States 'agree to duly take account of the fact that harbour porpoises are present in the Wadden Sea, thus addressing the conservation of the species' (Common Wadden Sea Secretariat 2018).

For the development and implementation of a monitoring programme, it is important to consider the 'status quo' regarding harbour porpoise occurrence in and habitat use of the Wadden Sea area. In this study, we compile trilateral data on harbour porpoises from the Wadden Sea and adjacent waters collected over the years (1990–2020) through aerial surveys, strandings, passive acoustic monitoring and satellite telemetry. We evaluate the spatial and temporal coverage of research and monitoring programmes anno 2022, as well as their suitability for the required assessment of viability, natural reproductive capacity and habitat quality. Based on this evaluation, we give advice on the best way forward to develop a coordinated and effective trilateral monitoring programme for harbour porpoise.

Material and methods

The Wadden Sea World Heritage Site

Apart from the WHS, there are two more trilateral management areas. The Trilateral Wadden Sea Cooperation Area or Wadden Sea Area (WSA, approximate size 14,700 km^2)

was defined in the Esbjerg Declaration (2001). It includes the main estuaries of the Ems, Weser and Elbe rivers; the tidal area and all barrier islands. It extends 3 nautical miles into the North Sea, with the exception of Northern Germany. There it extends 12 nm off the islands of Sylt and Amrum and encompasses a marine protected area that was designated as a 'Whale Sanctuary' as part of the National Park in 1999 (Fig. 1) (CWSS, 2008). The Conservation Area (CA) (approximate size 11,200 km^2) overlaps largely with the outline of the WHS, but in contrast to the WSA, it excludes anthropogenic structures (such as gas platforms), major rivers and estuaries. The International Maritime Organization (IMO) has also designated an area corresponding to the CA as a Particularly Sensitive Sea Area (PSSA) (IMO 2002). This recognises that the area is vulnerable to damage by maritime activities and needs special protection.

In addition, several Natura 2000 sites, designated through the European *Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora* (i.e. Habitats Directive) and *Council Directive 2009/147/EC on the conservation of wild birds* (i.e. Birds Directive), specifically list the harbour porpoise. Figure 1 shows all those sites (Nos. 1–8) that either overlap with the WHS or are directly adjacent, including several small areas in estuaries and rivers.

For the scope of this study, the term 'Wadden Sea area' refers to the combined area of the WHS, WSA and CA as well as the adjacent rivers and estuaries. This includes the 'inner' waters inside of the barrier islands, as well as the 'outer' waters beyond the islands, up to 12 nautical miles off Sylt and Amrum, and 3 nautical miles elsewhere.

Aerial surveys

Aerial surveys for harbour porpoises are, in all three countries, conducted following a standard protocol that is also applied during the large-scale SCANS (Small Cetaceans in European Atlantic waters and the North Sea) surveys (Hammond et al. 2013). Line-transect distance sampling and circle back flights are used to estimate an effective strip width (Hiby 2021), taking both perception and availability bias into account (Marsh and Sinclair 1989). Therefore, the resulting (absolute) density estimates are corrected for different sighting probabilities, for example due to increased turbidity or higher sea states, and are corrected for animals missed because they were submerged. The method allows design-based (Geelhoed and Scheidat 2018; Geelhoed et al. 2020) and model-based (Gilles et al. 2016) abundance estimation and provides information on distribution patterns and habitat use (Gilles et al. 2009). A detailed description of the method and the analyses can be found in Scheidat et al. (2008) and Hammond et al. (2013).

The data were compiled from aerial surveys conducted by Denmark (2011 to 2019), Germany (2002 to 2020) and the Netherlands (2008 to 2020), covering North Sea waters adjacent to and partly including the Wadden Sea. The analysis of aerial survey was limited to data collected in the summer months (Jun–Aug) as these had the highest survey coverage, due to better weather and longer daylight. Grid maps were produced with a cell size of 10 × 10 km, and effort (km^2) and sightings (individuals) were summed per grid cell across all years. These were then used to calculate densities per grid cell. Grid cells with a survey effort of less than 10 km of transect were removed from the analysis. Sightings of harbour porpoise calves were not aggregated but individually represented by the location of the record.

Strandings (and post-mortem examinations)

Harbour porpoises are regularly found stranded on the beaches and sandbanks in the Wadden Sea and adjacent areas. Registration of these animals can provide information on the occurrence of harbour porpoises and how this changes over time. Information on stranded animals is collected in national and regional stranding networks. Standardised procedures are followed in most regions as much as possible to ensure similar data collection between different regions (IJsseldijk et al. 2019b). Depending on the decomposition state, stranded animals can provide general information on biological parameters such as length (a proxy for age class) and sex distribution. The collection of specimens for post-mortem examinations allows researchers to investigate the cause of death, health and diseases, age, diet, potential bycatch rates and pollution, among other things.

In 1993, Denmark formalised the National Contingency Plan concerning strandings of marine mammals, which is run jointly between various institutions (Bie Thøstesen et al. 2018). The current plan (an update is due 2024) states that at least 25 porpoises are to be collected from the Danish coastline to monitor diseases, health status and general biology (Sørensen et al. 2012). One to three porpoises are collected each year from the Danish Wadden Sea area. For non-collected animals, data on location and, if possible, sex and length are registered. They are then either left on the beach or removed by the local authorities. The stranding network is funded by the Danish government but depends on public reporting of stranded marine mammals. From 2000 to 2002, the project 'Lookout for whales, dolphins and porpoises in Denmark' (Kinze et al. 2003) aimed at increasing the public's awareness about stranded porpoises and hence might have resulted in an increase in reporting stranded animals to the stranding network. Additionally, the widespread use of smartphones has increased the reporting with pictures and location, making it easier to register.

In Germany, the stranding network in Schleswig–Holstein was established after the first seal die-off in 1988/1989

(Reijnders et al. 1997). Harbour porpoises have been collected systematically with consistent effort since 1990, funded by the federal government of Schleswig–Holstein and coordinated by the National Park Administration (Siebert et al. 2001, 2006). All stranded animals are transported for post-mortem examinations to the Institute for Terrestrial and Aquatic Wildlife Research (ITAW) in Büsum, University of Veterinary Medicine Hannover (Siebert et al. 2001). The registration of porpoises in the German federal states Hamburg and Lower Saxony differs from the other regions in coverage and data storage. Post-mortem examinations have been done on single individuals on an ad hoc basis by the Lower Saxony State Office for Consumer Protection and Food Safety and the Institute of Hygiene and Environment of Hamburg.

The Dutch stranding network consists of a consortium of organisations and volunteers. Naturalis Biodiversity Center in Leiden manages the stranding records in the Netherlands in an online accessible database (www.walvisstrandingen.nl, from early 2024 onwards available on stranding.nl). Since 2008, post-mortem examinations on a selection of stranded harbour porpoises are conducted at Utrecht University. At the beginning of this programme, between 101 and 355 porpoises were necropsied per year. Since 2016, sample size is restricted to around 50 fresh animals annually (IJsseldijk et al. 2017; van Schalkwijk et al. 2022). The percentage of these originating from the Wadden Sea shore varies per year, with an average of 20.7% over the period 2016–2021 (IJsseldijk et al. 2017, 2018, 2019a, 2021b; van Schalkwijk et al. 2022). The remainder are found along the rest of the Dutch North Sea coast. For non-collected animals, data on location and, if possible, sex and length are registered. Furthermore, photographs—if available—are displayed on the website.

The strandings database used for this study was collated from stranding data from Denmark, Schleswig–Holstein and the Netherlands; the data from Lower Saxony and Hamburg were excluded due to the differences in data quality. Animals registered on shores of both the inner and outer Wadden Sea were included. A total of 6797 harbour porpoise stranding records from 1990 to 2019, both dead and alive, were included in this study. For a proportion of those records, information on the sex ($n = 3817$) and length ($n = 4933$) of the animals was available. All animals with length information are assigned to an age class based on body length, although the different countries deal with this slightly differently. For the Netherlands and Denmark, animals < 91 cm are classified as neonate, 91 to 130 cm as juvenile and > 130 cm as adult (following Lockyer 2003; IJsseldijk et al. 2020). For Germany, animals with a total length of < 100 cm are classified as neonates, animals with developed gonads as adults and the rest as juvenile. The compiled stranding data were analysed for both interannual as well as seasonal patterns. For the individuals that were sexed (M/F) and aged (adult, juvenile or neonate), ratios between categories were calculated for the three countries.

Data were explored in R (version 4.0.1, (R Core Team 2022)) following Zuur et al. (2010) and a kernel density analysis was performed in QGIS (QGIS version 3.4.3—Madeira, heatmap tool) with a cell size of $0.01 \times 0.01°$, a search radius of 0.5° and the quartic method (QGIS Development Team 2018). For roughly 1200 strandings on the Dutch Wadden islands, the exact location was not provided. In these cases, stranding locations were assigned to the centre of the islands, leading to a high kernel density on those spots on the maps.

Passive acoustic monitoring (PAM)

The use of echolocation by the harbour porpoise has made it possible to effectively monitor behaviour and occurrence of porpoises with passive acoustic monitoring (PAM) devices. The most frequently used device in the North Sea is the Continuous Porpoise Detector (C-POD). It allows the automatic collection of porpoise clicks for several months continuously and has been used in a large number of research projects (e.g. Carstensen et al. 2006; Tougaard et al. 2009b; Scheidat et al. 2011; Dähne et al. 2013; Bergès et al. 2019; Amundin et al. 2022).

As part of the monitoring programme for porpoises in Special Areas of Conservation (SACs) under the EU Habitats Directive, commissioned by the National Park Authorities and conducted by the University of Veterinary Medicine (TiHo), C-POD measuring stations were deployed in German waters (Baltzer et al. 2018). The results of six locations in the German part of the Wadden Sea were included in this study. Two stations are located in the outer Wadden Sea: Westerland (WL) and Rochelsteert (RS). Those in the inner waters are Lister Tief (LT), Meldorfer Bucht (MB), Minsener Oog (MO) and Messstelle 1 (M1) (Fig. 2). The northern stations LT, WL, RS and MB are part of Schleswig–Holstein; the two southern stations MO and M1 are part of Lower Saxony and the latter were discontinued in 2019. The four other stations have been functioning for 8 years without major problems (Baltzer et al. 2018). Stations MB, MO and M1 all have a tidal range of more than 3 m (Wehrmann 2016).

Acoustic detections of porpoise clicks were expressed as Detection Positive Minutes per 10 min per day (DP10min/day), to provide an index for local porpoise density (Williamson et al. 2016). To investigate the relationship between porpoise click occurrence and explanatory variables such as tide, time of day and day of the year, the frequency of harbour porpoise detections (Detection Positive Minutes per hour) was analysed by means of a generalised additive model (GAM) (Wood 2006, 2017) for each measuring station separately. In order to investigate possible effects of

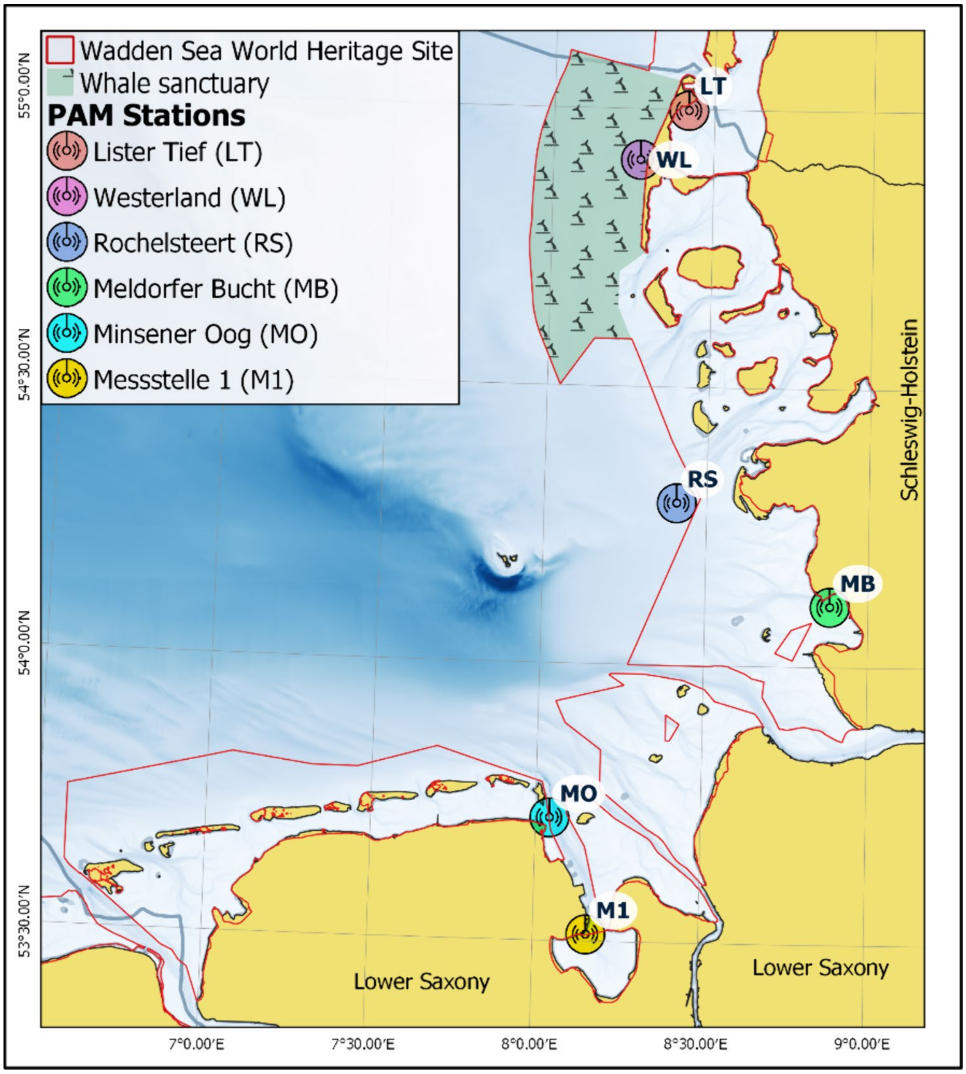

Fig. 2 Positions of the PAM stations in the German Wadden Sea area. Map developed in QGIS (version 3.4.3—Madeira, QGIS Development Team 2018b)

the tide on porpoise detections, data from nearby (< 10 km) measuring piles recording water levels were used. The data were delivered in 1-min resolution. For testing a possible impact of temporal variability over the year, the day of the year was selected as a factor. This covariate was also used as a proxy for temperature which correlates with the seasonal course over the year. All analyses were performed with R (R Core Team 2019) using the R libraries 'nlme' version 3.1–125 (Pinheiro et al. 2014) and 'mgcv' version 1.8–9 (Wood 2011). The formula of the GAM was as follows:

$$\mathrm{dpm/h} \sim \mathrm{s(dayinyear)} + \mathrm{s(daytime)} + \mathrm{s(tidaltimeinrad)}, \mathrm{family} = \mathrm{nb()}$$

A negative binomial distribution (nb) was used for the model, as well as smoothing functions s() with a cyclic cubic regression spline as a smooth term (bs = 'cc' in R) for every explanatory variable. All covariates were significant for all stations ($p < 0.05$), and no further model selection was performed. Details on the model development can be found in Baltzer et al. (2018).

Satellite telemetry

A total of 124 porpoises were tagged in the inner Danish waters by Aarhus University (AU) between 1997 and 2019. The tags were Argos satellite transmitters that logged and transmitted their locations for up to 1.5 years. Most animals have been incidentally caught in pound nets. These are fixed nets local fishers deploy in the sheltered coastal areas (without tide and strong currents) of the inner Danish waters, from the northern tip of Jutland to the southwest Baltic (Teilmann et al. 2008). Porpoises that swim into the net can move freely and are in no danger of entanglement. This provides the opportunity for researchers to tag animals when they are removed and released from the net. Such nets can, however, only be deployed in relatively sheltered areas. In open waters, drifting gillnets can be used to actively catch, tag and release porpoises. This approach has been applied successfully with Greenlandic porpoises (Nielsen et al. 2018), and in 2014 and 2016, six porpoises were caught and tagged using this method in the Danish part of the Wadden Sea area, at two locations (see the 'Results' section for exact tagging locations). One animal was an adult male (length 140 cm), and five were juvenile males (lengths 118 to 130 cm). One animal was caught in June 2014; the others in September 2016. All animals were tagged with Argos location transmitters (SPOT5, Wildlife Computers, Seattle, USA). The duration of the contact ranged from 102 to 264 days (also see Table 1 in the 'Results' section). More detailed information on tagging, data collected and methods can be found in earlier publications (e.g. Teilmann et al. 2007; Edrén et al. 2010; Sveegaard et al. 2011; Linnenschmidt et al. 2013; Wisniewska et al. 2016; van Beest et al. 2018a, b).

Results

Aerial surveys

Aerial survey effort differed over the study area. Along the Danish and Schleswig–Holstein coast, the Whale Sanctuary and adjacent waters showed the highest effort (Fig. 3a). Survey effort in the rest of the Danish and Northern German waters was less extensive, with some areas in the inner Wadden Sea waters having no or less than 5 km^2 coverage per grid cell. Porpoises have been seen all along the area and adjacent waters during the summer months, where the highest densities within the Wadden Sea area were found in the Whale Sanctuary. This pattern continues in the adjacent outer Wadden Sea/North Sea waters off the island of Sylt which showed densities > 4 individuals/km^2. Calf sightings occurred mainly in the Whale Sanctuary and further offshore (Fig. 3b).

The aerial survey effort in coastal and Wadden Sea waters in Lower Saxony and the Netherlands is lower (Fig. 4a). The effort is patchy with intensive survey coverage off the German islands of Borkum and Norderney, but low or no coverage of the inner Wadden Sea waters in Lower Saxony and the Netherlands, respectively. Harbour porpoise density is not homogenous, but areas with high densities of > 4 individuals/km^2 can be found off the island of Borkum and in the southern region off the Dutch islands of Texel, Vlieland and Terschelling. Calf sightings were recorded primarily in the two areas with higher densities and included records in the Lower Saxony area of the Wadden Sea area (Fig. 4b).

Strandings

In 1990–2019, the average number of stranded porpoises registered in the Wadden Sea area was 227 per year. This number increased in the early 2000s and slowly decreased

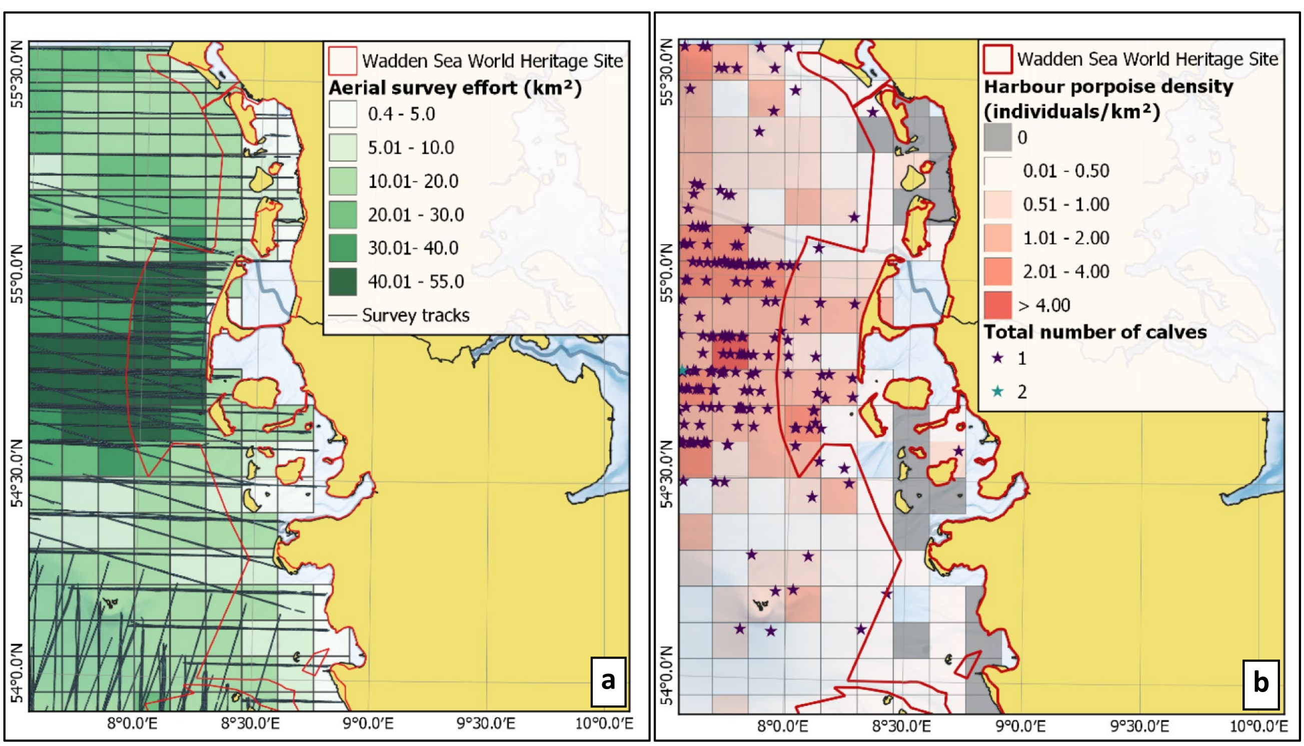

Fig. 3 Aerial survey monitoring effort (**a**) and density of harbour porpoise with locations of calf sightings (**b**) for the northern area of the Wadden Sea area and adjacent waters. Joint datasets from Germany (2002–2020) and Denmark (2011–2019) for the summer months (June, July, August). Map developed in QGIS (version 3.4.3—Madeira, QGIS Development Team 2018b)

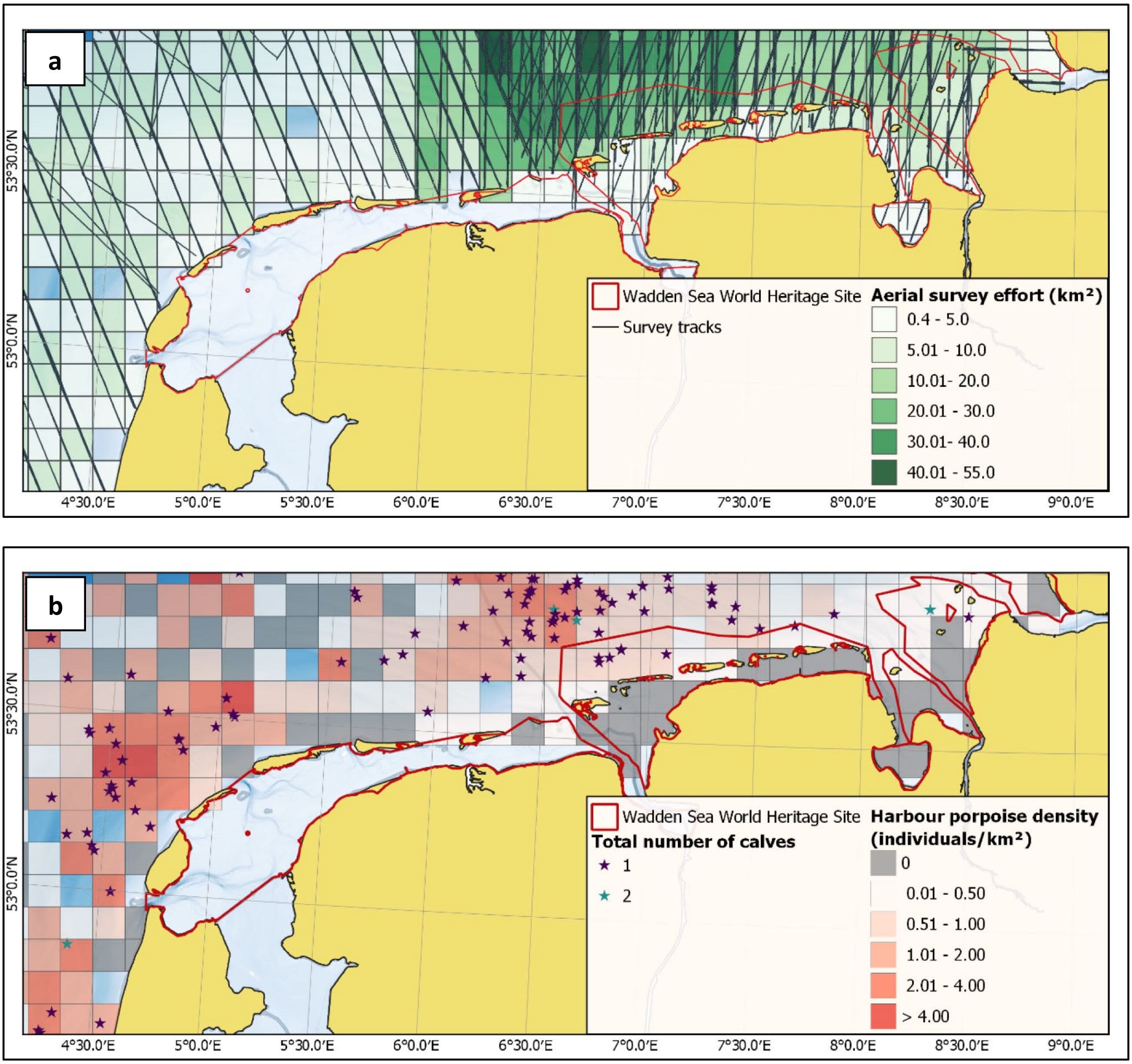

Fig. 4 Aerial survey monitoring effort (**a**) and density of harbour porpoise with locations of calf sightings (**b**) for the southern area of the Wadden Sea area and adjacent waters. Combined datasets from Germany (2002–2020) and the Netherlands (2008–2020) for the summer months (June, July, August). Map developed in QGIS (version 3.4.3—Madeira, QGIS Development Team 2018b)

again from 2011 onwards (Fig. 5). In the Danish area, hardly any strandings were registered from 1990 to 1996. Most years, the annual numbers in Denmark were around 7, apart from a distinct increase between 1998 and 2002, with a maximum of 43 in 2000 (Fig. 5). In Schleswig–Holstein (SH) (Northern Germany), annual numbers varied between years, with an average of 88 animals (range 27 to 150). The increase of total stranding numbers is mainly due to an increase in strandings in Dutch waters, rising from an annual average of 21 in 1990–1998 to an average of 272 per year in the period 2008–2014. It declines in the years after that.

The seasonal distribution of the strandings shows a distinct peak in the summer months for Germany and Denmark (Fig. 6). In the Netherlands, strandings occur throughout the year with peaks in March and summer (Fig. 6).

In all three countries, slightly more male strandings are reported (Germany 54%, the Netherlands 57% and Denmark 53%) (Fig. 7). In Germany, most strandings are qualified as neonates, while in the Netherlands, juveniles make up the largest proportion (Fig. 7). The slightly different classifications of neonates between the countries could explain these different proportions.

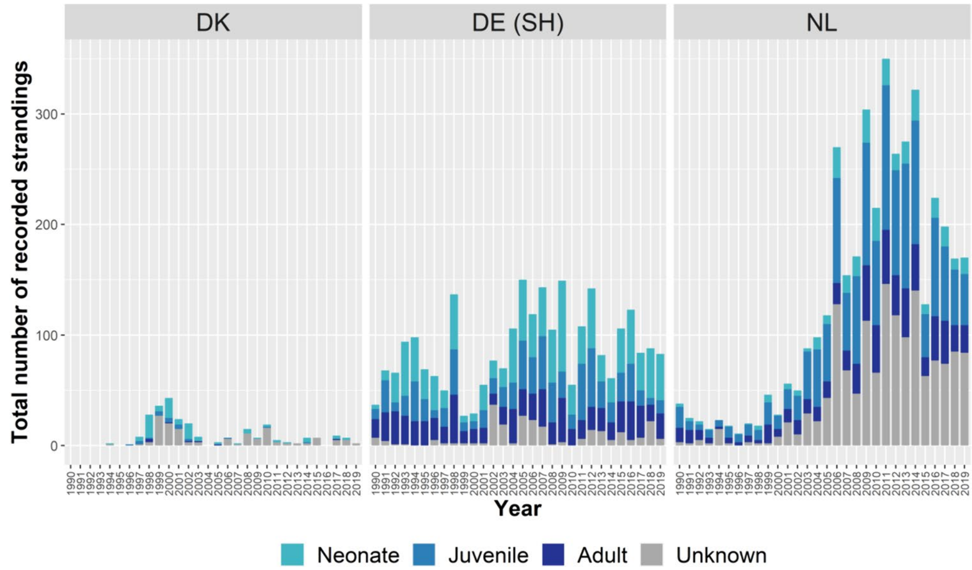

Fig. 5 Total number of reported harbour porpoise strandings from 1990 to 2019, per country and per age class. DK, Denmark; DE (SH), Germany (Schleswig–Holstein); NL, the Netherlands

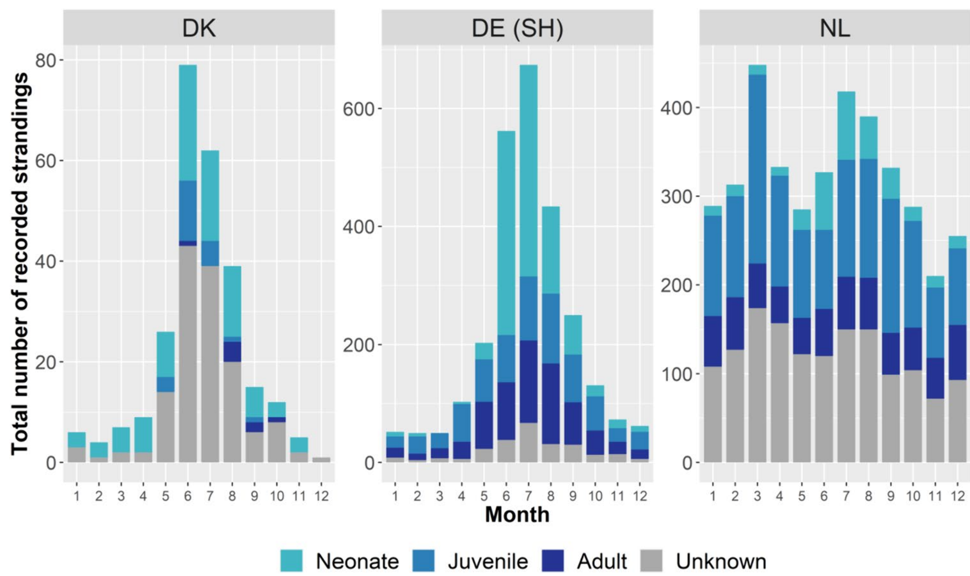

Fig. 6 Total number of strandings per month, per country and age class. DK, Denmark; DE (SH), Germany (Schleswig–Holstein); NL, the Netherlands. Note the difference in *y*-scales between areas

The spatial distribution shows that most strandings in the northern part of the Wadden Sea area (DE-SH and DK) occur on the German island of Sylt, bordering the Whale Sanctuary (Fig. 8). It is also notable that the number of strandings in the inner waters seems to have decreased in this northern part of the Wadden Sea area in the last decade (Fig. 8). In the southern part of the Wadden Sea area (NL), the overall numbers of strandings have increased, with most strandings occurring on the western Dutch Wadden Sea islands (Texel and Vlieland) (Fig. 9).

Passive acoustic monitoring (PAM)

The porpoise clicks were analysed per station and year (Fig. 10). Acoustic activity differed between stations, but porpoise clicks were detected year-round at all stations. The lowest detection rate was found for Lister Tief (LT), where porpoises were detected with a median of less than 5% DP10min/day each year. The WL station, located on the North Seaside of the island of Sylt, showed highest values, with median values varying between about 7 and 15% DP10min/day (Fig. 10).

The GAM analyses provided insights into seasonal patterns and the influence of time of day and tide on porpoise click occurrence (Fig. 11). All stations showed a pronounced increase in porpoise click occurrence in spring (Fig. 11). For the rest of the year, the pattern varied depending on the station. The stations with the highest tidal range (MB, M0 and M1 (Wehrmann 2016)) showed a link between acoustic activity and tide, although the patterns were not consistent between stations. Time of day showed much weaker but also site-specific patterns.

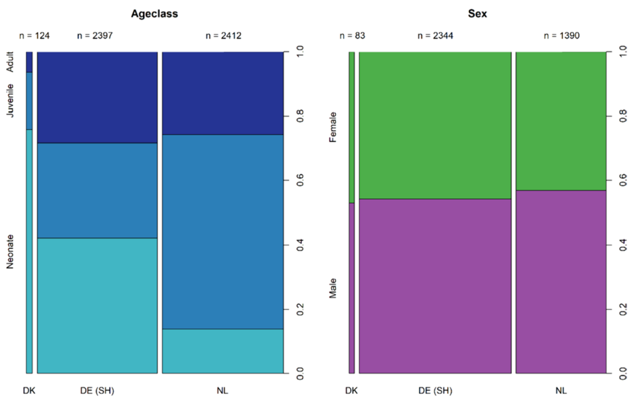

Fig. 7 Proportion of age class (left) and sex (right) for the strandings for which sex or age class was available. DK, Denmark; DE (SH), Germany (Schleswig–Holstein); NL, the Netherlands. The width of the column reflects the sample size

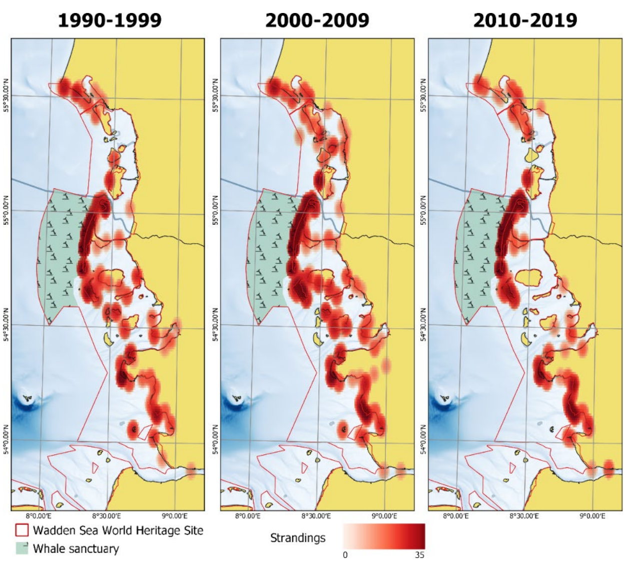

Fig. 8 Kernel densities of strandings per decade for the northern part of the Wadden Sea area (Germany (Schleswig–Holstein) and Denmark). Kernel density estimation performed in QGIS version 3.4.3—Madeira (heatmap tool) with a cell size of 0.01 × 0.01°, a search radius of 0.5° and the quartic method (QGIS Development Team 2018)

The explained deviance of the models was 4.96% (LT), 14.6% (M1), 9.25% (MB), 4.95% (M0), 9.09% (RS) and 8.3% (WL), with an R^2 adjusted of 0.01 (LT), − 0.11 (M1), 0.09 (MB), 0.03 (M0), 0.09 (RS) and 0.07 (WL) for each station.

Satellite telemetry

Many of the animals that were tagged in the northern Kattegat, and especially Skagen, moved into the North Sea, ranging as far west as northern England, mainland Scotland and Shetland (UK) and as far north as 64°N (Fig. 12). A few

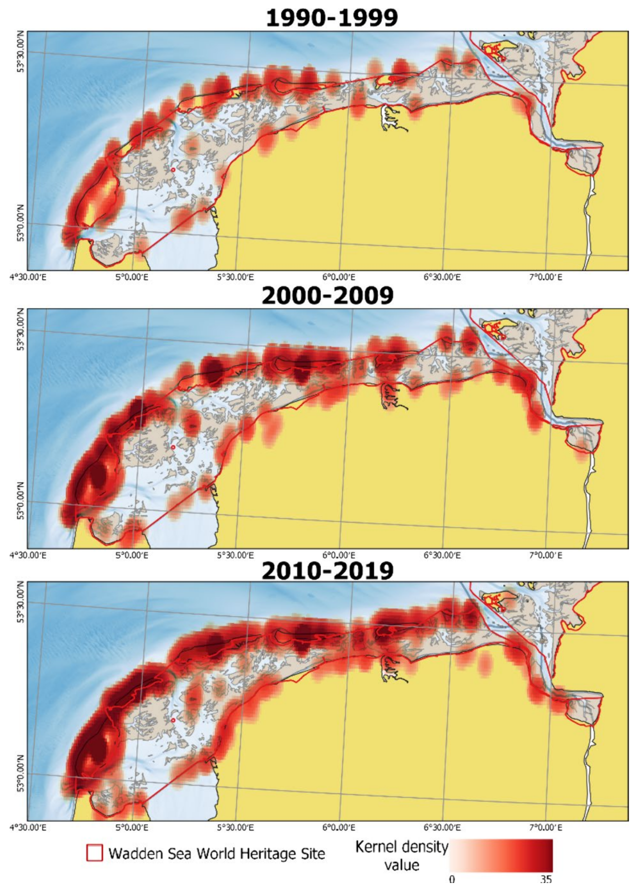

Fig. 9 Kernel densities of strandings per decade for the southern part of the Wadden Sea area (the Netherlands). Kernel density estimation performed in QGIS version 3.4.3—Madeira (heatmap tool) with a cell size of 0.01 × 0.01°, a search radius of 0.5° and the quartic method (QGIS Development Team 2018)

animals also moved into the southern North Sea, entering the Wadden Sea area and adjacent waters (black dots, Fig. 12).

For the six porpoises caught and tagged in the Wadden Sea, most locations were registered in or in close vicinity of the Wadden Sea area. On average 67% (31–98%) of the locations recorded per animal were within the Danish or German part of the Wadden Sea area (Fig. 13 and Table 1). The depth distribution of the porpoise locations reflected their occurrence in the shallow coastal habitat; all occurred primarily in water depths of less than 10 m (Table 1). The locations showed some areas that were often visited, such as the coastal waters from Blåvand to the island of Sylt. Tagged porpoises mainly used the passages between Fanø-Mandø and Rømø-Mandø when entering the tidal channels to the very shallow part of the inner Wadden Sea (Fig. 13).

The individual porpoises showed differences in the spatial and temporal use of the area (Fig. 14). Five animals (2014–138067, 2016–149166, 2016–149167, 2016–149170, 2016–149171) showed a strong site fidelity to the Wadden Sea during the period they were tracked (102–264 days).

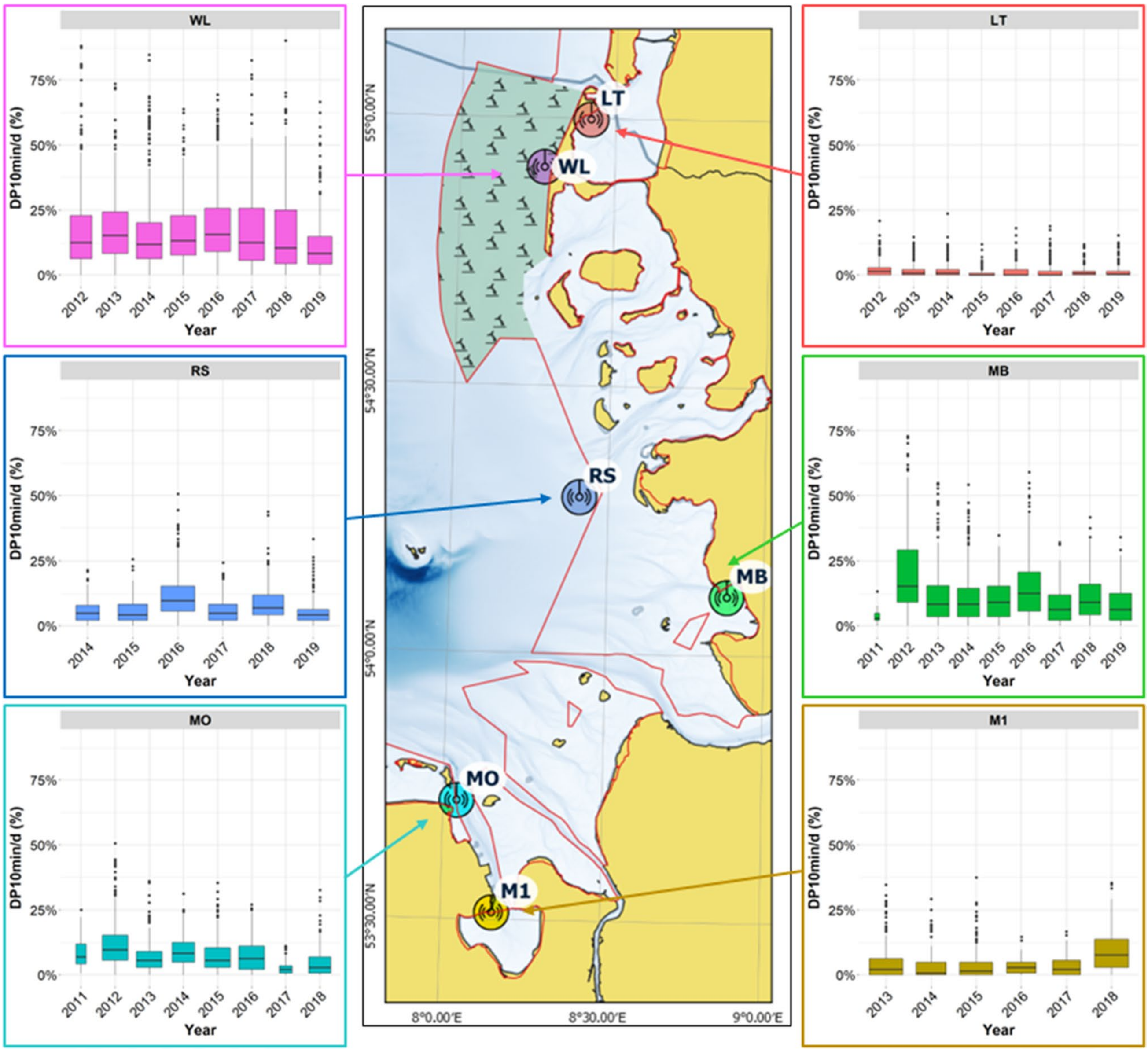

Fig. 10 Percentage of time where echolocating porpoises were recorded, shown as box plots of the DP10min/day per measurement position per year. Median drawn (black horizontal line, box—25 and 75% quantile), with whiskers (1.5 × interquartile range according to (Tukey 1977), the length of the whiskers is determined by the maximum and minimum value) and outliers (represented by black dots). The width of the individual boxes reflects the sample size. Map developed in QGIS (version 3.4.3—Madeira, QGIS Development Team 2018b)

One animal (2016–149165) covered a slightly larger range moving out into offshore waters during winter and spring.

Discussion

Harbour porpoise in the Wadden Sea

Our study collated and analysed several long-term datasets on harbour porpoise occurrence and habitat use in the Wadden Sea area, collected by research institutes from Denmark, Germany and the Netherlands. The results illustrate that harbour porpoises are regular inhabitants of the coastal and intertidal waters of the Wadden Sea area and adjacent waters, showing seasonal movements and changes in local occurrence over time.

The SCANS (Small Cetacean Abundance in the North Sea) surveys, covering the North Sea, estimated the population size to be similar in 1994 (289,000; CV = 0.14), 2005 (355,000; CV = 0.22), 2016 (345,000; CV = 0.18) and 2022

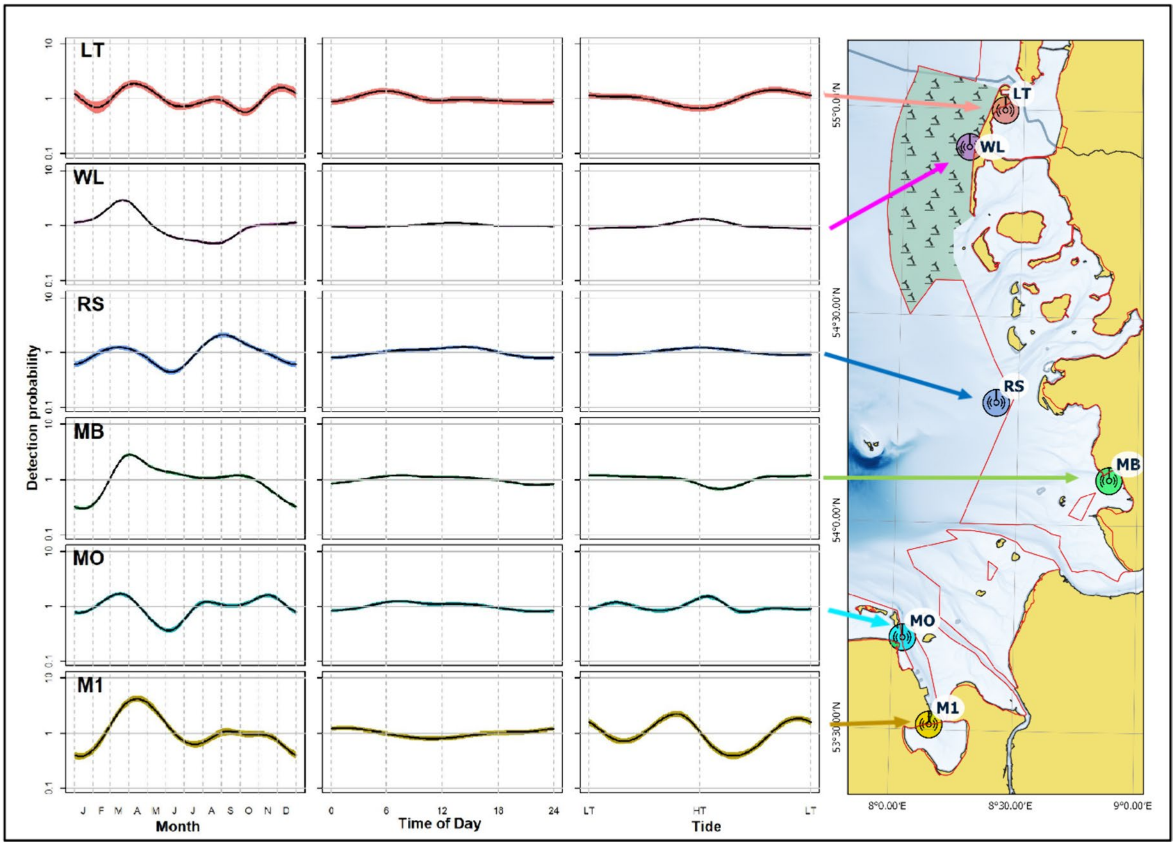

Fig. 11 Relationships between month, time of day and tide with the registration of porpoises at the six measuring positions (averaged over the monitoring period). The coloured area around the smoother function marks the 95% confidence interval. The detection probability of porpoises being present is represented relative to the y axis, with any values $y > 1$ indicating a higher likelihood of porpoises being detected (positive effect) and values $y < 1$ a lower likelihood of porpoises being detected (negative effect). A visual interpretation of the patterns was used to determine if the effect is significant; when the curve with confidence intervals includes the horizontal 1-line, there is no significant effect. Map developed in QGIS (version 3.4.3—Madeira, QGIS Development Team 2018b)

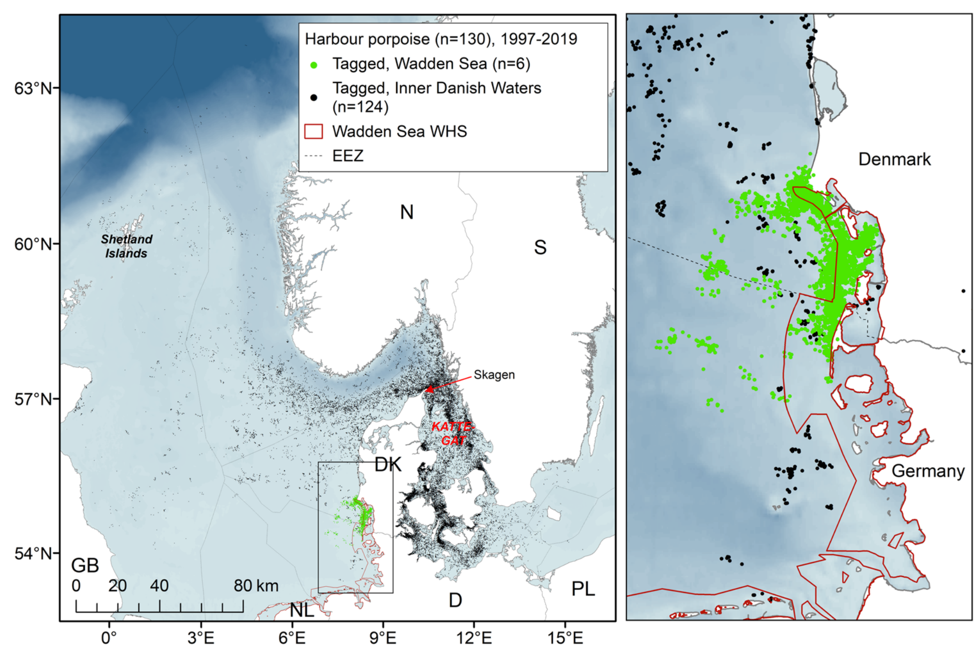

Fig. 12 Left panel shows all Argos locations of the harbour porpoises tagged by AU between 1997 and 2019. Black dots show the locations of porpoises tagged in the inner Danish waters and Skagerrak (124 individuals) and green dots represent porpoises tagged in the Wadden Sea (6 individuals). The right panel shows a closer view on the locations in and near the Wadden Sea. N, Norway; S, Sweden; DK, Denmark; D, Germany; PL, Poland; GB, UK

Table 1 Data on the six harbour porpoises tagged in the Danish Wadden Sea. All six porpoises were males. Distribution of locations is shown at different depth intervals within the study area as well as within the Wadden Sea World Heritage Site

ID no	Porpoise length (cm)	Tagging date	Contact end date	Total no. transmission days	% locations*			
					1–10 m	11–20 m	21–30 m	Inside Wadden Sea area
2014–138067	118	03/06/2014	04/10/2014	123	57	43	0	96
2016–149166	140	19/09/2016	26/04/2017	219	83	15	2	49
2016–149167	130	19/09/2016	10/06/2017	264	99	1	0	98
2016–149170	123	19/09/2016	30/12/2016	102	77	23	0	80
2016–149165	127	20/09/2016	04/06/2017	257	41	33	26	31
2016–149171	125	21/09/2016	18/03/2017	178	60	40	0	48
			Average	*190.5*	*69.5*	*25.8*	*4.7*	*67*

*In this region (Danish Wadden Sea), all inner Wadden Sea Waters fall in the 1–10-m depth category.

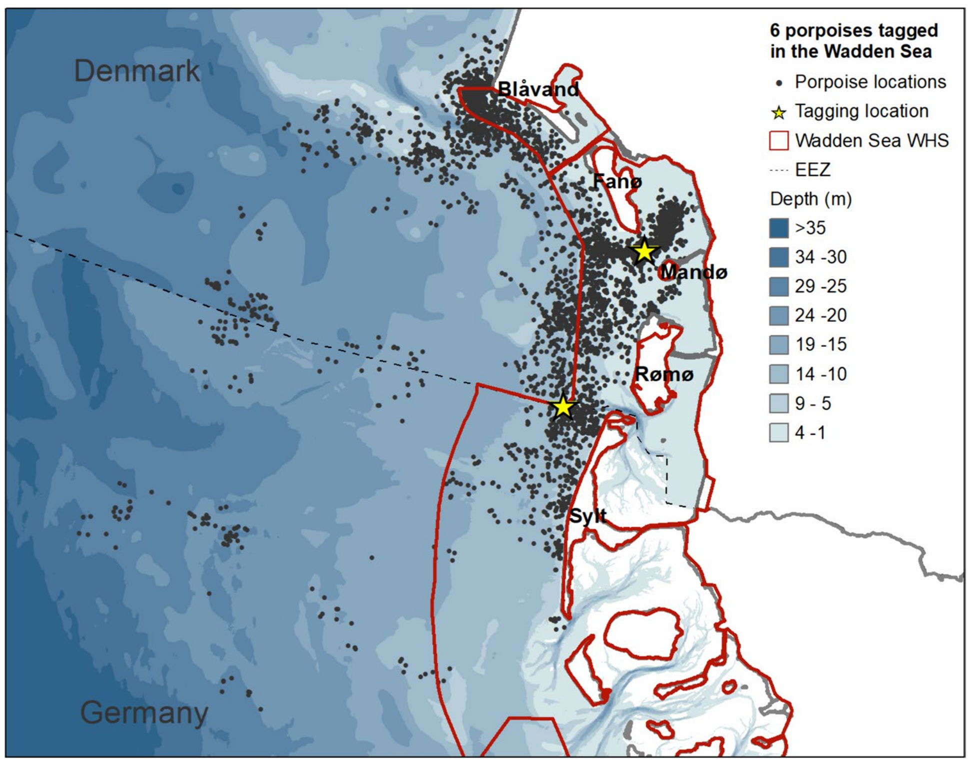

Fig. 13 Locations of the six porpoises tagged in the Wadden Sea. Depth contours and the boundary of the Wadden Sea World Heritage Site are indicated. Stars indicate the locations where the animals were tagged

(339,000; CV = 0.17) (revised from Hammond et al. 2002, 2013, 2021b; Gilles et al. 2016, 2023). The surveys also documented a large-scale southward shift in distribution within the North Sea (Hammond et al. 2002, 2013, 2021b; Gilles et al. 2016, 2023). The stranding data for the Wadden Sea area reflect this by showing an increase of stranding records along the Dutch coastline since 2000 and a peak during 2008–2014. Although reporting effort might also have increased, there is no indication that the increase in reporting effort has been different between the regions. The data are, therefore, considered comparable. Consequently, the increase seen on Dutch shores is, most likely, reflecting an actual increase in occurrence. Porpoises were common in Dutch waters up to the 1950s, then virtually disappeared. Their return from the 1990s onward has been well documented through stranding data and shore-based counts (Camphuysen 1994, 2004; Reijnders et al. 1996; IJsseldijk et al. 2021a). Their return was confirmed by aerial surveys in Germany showing an increase in numbers in waters close to the Dutch border over the period 2002–2019 (Thomsen

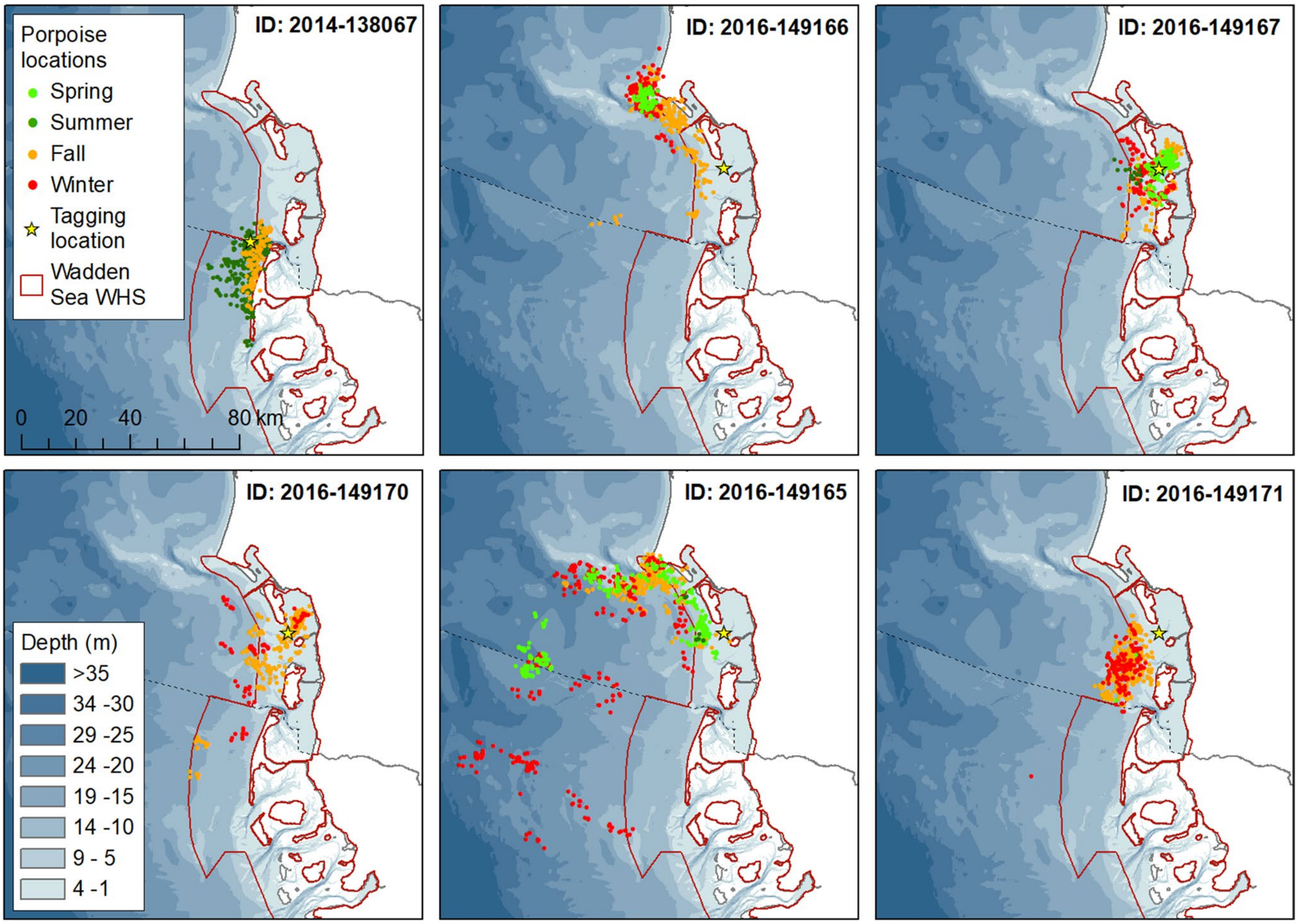

Fig. 14 Locations coloured by season (spring: March to May, summer: June to August, fall: September to November, winter: December to February) for the six harbour porpoises tagged within the Wadden Sea. Yellow stars indicate the locations where the animals were tagged

et al. 2006; Peschko et al. 2016; Nachtsheim et al. 2021). During the last decade, however, porpoise density in the northern area of the German Bight decreased (Nachtsheim et al. 2021). This decreasing trend in local abundance is not reflected in the stranding data in Schleswig–Holstein, but the distribution of stranded animals seems to have shifted from the inner to the outer shorelines of the barrier islands. On the other hand, an increased number of porpoises seem to have entered estuaries and rivers, in particular Elbe and Weser (Wenger and Koschinski 2012) as well as the Eems-Dollard area (Brasseur et al. 2010, 2011; Taupp 2021), in the last two decades. It is not clear if this phenomenon continues to date, nor whether it is linked to a larger-scale shift in distribution towards the coast or to porpoises following migratory prey species upriver (Weel et al. 2018).

Porpoise distribution shows distinct seasonal patterns in the northernmost part of the Wadden Sea, off the Danish Jutland and German Schleswig–Holstein coast, where the highest numbers of stranded animals are registered during the summer months. Aerial surveys conducted in German waters confirm this summer peak in the Sylt Outer Reef (Gilles et al. 2016). The two northernmost PAM stations located close to Sylt, however, show the highest click activity around April. This reiterates that PAM monitors local occurrence and can provide valuable site-specific information complementing occurrence inferred from larger-scale aerial surveys. The high proportion of calves in the stranding data reflects the importance of the area as a breeding area, which was already recognised in the 1990s leading to the declaration of the Whale Sanctuary (Sonntag et al. 1999).

In the southern part of the area (NL), less is known about porpoise distribution. Most strandings occur on the western Dutch Wadden Sea islands, and the number of stranding records is elevated around March and August. The peak in late summer is inconsistent with both the results from the aerial surveys, which show lowest densities during that season for this region (Geelhoed and Scheidat 2018), as well as with the sighting data collected from shore-based counts (Camphuysen 2004; Camphuysen et al. 2008). The reason for this apparent mismatch is not clear but could be related to changes in porpoise distribution, mortality or environmental factors (IJsseldijk et al. 2021). For example, sea surface temperature, current and wave height influence the decomposition time and drift behaviour of carcasses and thus the likelihood and location of a stranding (e.g. Peltier et al. 2013a, b, 2016).

In the Danish straits and the Kattegat, movement patterns differed between age classes, with juvenile males having larger home ranges than mature animals (Sveegaard et al. 2011). Home ranges of animals tagged in Greenland were even larger (Nielsen et al. 2018), and in general, porpoises showed seasonal movements to specific areas (Teilmann et al. 2008; Nielsen et al. 2018). Our study presents results from six male harbour porpoises (five juveniles, one adult) tagged in the northern Wadden Sea area, with only one animal venturing about 70 km into the North Sea during the winter months. Overall, the animals showed a high degree of residency, spending on average 67% of their time in the Wadden Sea area. Although the sample is likely not representative for all porpoises in the Wadden Sea, it is striking that their behaviour is distinct from the other tagged porpoises. Their movements could indicate a residency of porpoises in the Wadden Sea and potentially subpopulation separation. Recent genetic analyses indicate a separation of southern North Sea porpoises from the North Atlantic population, with the samples responsible for this signal mainly coming from the German Wadden Sea (Autenrieth et al. 2023). More complete DNA sampling of North Sea porpoises is necessary to assess this further and could potentially also provide information about a Wadden Sea subpopulation.

The acoustic research showed that porpoises use both the inner and outer waters of the Wadden Sea on a regular basis throughout the year. There is considerable variability in click activity between locations. All stations are similar in terms of depth and seabed characteristics, but they do show differences in tidal patterns, with strongest tidal effects in the southernmost two stations. Although tidal patterns seem to influence porpoise occurrence, the relationship is not consistent between stations. Some stations show highest click activities during low tide, whereas for others this is reversed, or click activity is highest during high tidal speeds. Relationships between porpoise occurrence and areas of high tidal energy have been shown along the coast of Scotland (Wilson et al. 2013; Benjamins et al. 2017; Waggitt et al. 2018), and Zein et al. (2019) found that the occurrence of foraging clicks of porpoises in the Wadden Sea increased with high current speed and low tide. It is likely that porpoise distribution in the Wadden Sea area is driven by prey availability. Tidal flow has been shown to aggregate phyto- and zooplankton, attracting fish (Alldredge and Hamner 1980; Simard et al. 2002). In some areas, the cohesion of fish schools is disrupted by tidal fronts, likely making them easier to catch (Cox et al. 2018) and maximising foraging efficiency (Holdman et al. 2019). In the southernmost part of the Wadden Sea area, the Marsdiep (the tidal area between the island of Texel and the mainland at Den Helder), acoustic and visual observations have shown that harbour porpoises enter the western Wadden Sea during rising tide and leave during receding tide (Boonstra et al. 2013; IJsseldijk et al. 2015) confirming a link between porpoise behaviour and tidal patterns. Extending the PAM network Wadden Sea wide could indicate whether some of these drivers also apply to other areas.

Porpoises are considered the ‘shrews of the sea’, being one of the smallest odontocetes with a high metabolism that makes it necessary to obtain a continuous calorific input (Read and Hohn 1995; Rojano-Doñate et al. 2018). Therefore, the main driver for porpoise distribution is thought to be the availability of prey (Wisniewska et al. 2016; Gilles et al. 2016). The species hunts a variety of fish and invertebrate species, benthic as well as mesopelagic and pelagic, and is considered an opportunistic feeder (Leopold 2015). The stomachs of stranded animals in the Dutch inner Wadden Sea ($n=4$) contained smelt, a freshwater species that is flushed into the Wadden Sea from lake IJsselmeer, while the stomachs of animals from the Dutch outer Wadden Sea only contained marine species ($n=12$, Leopold 2022, *pers. comm.*). Currently, the available PAM data indicates that porpoises likely use the Wadden Sea area to forage. However, the variability between the six PAM stations is too high to understand how local characteristics of a site influence porpoise feeding behaviour. A higher number of stations placed representatively in an area could help in getting more insight.

Our study presents available data on harbour porpoises in the Wadden Sea. Yet it underlines the challenges in drawing general conclusions about behaviour and habitat use of harbour porpoise in general, and specifically in the Wadden Sea. This also limits our ability to assess the role porpoises play as top predators in this ecosystem.

Potential of monitoring methods in the Wadden Sea

There are several papers evaluating survey methods for cetaceans (Evans and Hammond 2004; Hammond et al. 2021a). In the following section, we assess the potential of the current survey methods in the Wadden Sea.

Aerial surveys

Over the last decades, line transect distance sampling from aircrafts has been used as a standard monitoring method for harbour porpoise in the North Sea and adjacent waters, with the primary aim to provide unbiased abundance estimates (Hammond et al. 2002, 2013, 2021b; Scheidat et al. 2012; Peschko et al. 2016; Geelhoed and Scheidat 2018; Nachtsheim et al. 2021). Currently, aerial survey coverage of intertidal waters is limited since it is designed to representatively cover Natura 2000 sites (Denmark and Germany) and national North Sea waters (Germany and Netherlands) (Siebert et al. 2006; Gilles et al. 2009; Geelhoed et al. 2020; Nachtsheim et al. 2021).

This method includes the calculation and application of correction factors to account for changes in detection probabilities of porpoises, for example due to varying environmental conditions (Hiby and Hammond 1989; Marques et al. 2011). However, the probability of seeing submerged animals is substantially reduced when turbidity is high, which is a characteristic of the sediment-rich waters of the intertidal Wadden Sea. This makes it difficult to obtain the sample size that is needed for reliably monitoring density and distribution patterns as well as calculating absolute abundance. Another challenge is that the tidal cycle transforms this area from open water to a complex and changing habitat of sandbanks and mudflats traversed by channels and gullies. The limitations of planning aerial surveys to cover an area during specific tidal phases, e.g. during high tide, add logistic constraints.

To conclude, aerial surveys may be the most appropriate method to monitor harbour porpoise occurrence in the North Sea, but they are not best suited for intertidal Wadden Sea waters.

Strandings and post-mortem examinations

Stranding data can provide valuable information on the occurrence and health status of harbour porpoises and serve as an early warning system for unusual mortality events (IJsseldijk et al. 2020, 2021a). A stranding network relies on sufficient and regular effort to monitor the shorelines. In areas in the Wadden Sea with high human density and accessible (sandy) shorelines, sampling effort is likely consistent and high enough to register most stranded animals (Peltier et al. 2013b; Keijl et al. 2016, 2021). However, there might be seasonal variation in effort, and difficult-to access areas such as the intertidal mudflats can be under-sampled (Keijl et al. 2016, 2021). Additionally, when an animal is found dead on the shore, its exact location of death is unknown (Evans et al. 2005). Stranded animals that are found on the shorelines of the study area can thus originate from both Wadden Sea as well as North Sea waters. The likelihood of a stranding is influenced by currents, wind and temperature, as well as by individual differences in body size and body condition, all of which affect the speed of the decomposition process and the chance of animals floating, sinking or make landfall (Moore et al. 2020). This also often creates uncertainty in establishing when the animals died, although estimates can be made based on carcass freshness and local temperature. Notwithstanding, drift models have been successfully used to pinpoint the likely location where stranded small cetaceans have died (Peltier et al. 2013a, 2014, 2020) and should therefore be used more widely.

Depending on decomposition of stranded specimens and carcass completeness, information on sex and length (the latter a proxy for age class) and various health parameters can be collected directly on the stranding site. Post-mortem examinations are, however, needed to gain additional information from specimens that are difficult or impossible to obtain from animals at sea, such as population parameters on reproduction, diet, health status and cause of death. The latter two also include potential effects from anthropogenic activities, such as underwater noise, contaminants, ship strikes or bycatch (IJsseldijk et al. 2022). In Schleswig–Holstein, all stranded animals are collected and subjected to a general post-mortem examination. This allows researchers to also collect data on specimens that are in a further state of decomposition and potentially originate from offshore areas, which in other regions (e.g. the Netherlands) are discarded. Sampling of genetic material, the teeth (for ageing) and stomach contents is often still possible from (moderately) decomposed specimens. In Denmark, Lower Saxony and the Netherlands, only a (small) sample of stranded animals is collected for post-mortem examination. The selection of this sample is based on money available to collect animals, freezer capacity, post-mortem facilities and the freshness of the carcass, as well as the ease of access to the stranding location. This means that a substantial proportion of stranded specimens is discarded without sampling.

Our results demonstrate that stranding networks registering porpoises along the Wadden Sea and North Sea shorelines are an established method to monitor the occurrence of animals in the area. Systematic stranding networks with central data storage exist in Denmark, Schleswig–Holstein and the Netherlands. For the two federal states Hamburg and Lower Saxony, the registration of animals is currently not undertaken within a systematic framework, making it difficult to combine all datasets. To use strandings as a monitoring tool on a trilateral scale, the networks need to be harmonised across countries, with a comparable coverage of effort and the same data collection protocols. Furthermore, more post-mortem examinations, adhering to standardised protocols, could provide data on population parameters. The Wadden Sea Secretariat has recently conducted a trilateral workshop to provide information on the status of the stranding networks and to identify how their effectiveness can be improved (Wollny-Goerke 2023). This can be considered a very welcome first step towards a more coordinated approach.

Passive acoustic monitoring (PAM)

One of the most important advantages of passive acoustic monitoring is the possibility of almost continuous data collection (Mellinger et al. 2007), also in areas where other types of surveys are complicated. The high temporal resolution can be used to collect fine-scale information on activity patterns, as well as specific behaviour, such as foraging or socialising, and can help investigate habitat preference and the effect of human activities (Wisniewska et al. 2016; Schaffeld et al. 2016; Sørensen et al. 2018; Berges et al. 2019). A disadvantage of PAM is low spatial coverage: an individual PAM station only detects porpoise clicks in a radius of several hundred metres (Villadsgaard et al. 2007; Jacobson et al. 2017; Nuuttila et al. 2018). The detection probability varies with the location of the device, as well as with the behaviour of the porpoises. Therefore, it is important to develop a suitable deployment plan to ensure that the data collected is representative. It is currently not straightforward to calculate porpoise densities from PAM data, but there are efforts to further develop such a method (Kyhn et al. 2012; Marques et al. 2013; SAMBAH 2016; Amundin et al. 2022). The continuous and potentially long-term data collection makes PAM an appropriate tool for low density areas.

PAM can be applied when surveying by aircraft or vessel is challenging or impossible and is therefore a suitable method to monitor porpoise occurrence and behaviour in the Wadden Sea area. PAM has been applied in the Wadden Sea through a systematic monitoring programme in German waters, as well as during short-term projects in the Ems estuary (Brasseur et al. 2010) and the most southern part of the Wadden Sea area (Boonstra et al. 2013). The data is helpful to interpret local patterns in occurrence while considering complex changes in the environment, such as tidal cycles. Interestingly, porpoise click source levels and bandwidths were found to be lower in the Wadden Sea than in other waters (Dähne et al. 2020). This is possibly an adaptation to the murky and turbulent waters, as suspended particles and microbubbles lead to cluttered echoes. The consequence for PAM detections is yet unknown. It is important to ensure that a monitoring programme takes into account the locations and number of PAM devices needed to ensure robust data can be collected (Verfuß et al. 2007). Furthermore, even though porpoise acoustic monitoring is primarily done with (C)PODs, there is currently no agreed standard protocol for data collection or analyses using this method (Verfuß et al. 2008). A Wadden Sea wide PAM network and standardised protocols on collection, storage and analyses of data across the three countries would greatly benefit our knowledge on the spatial and temporal distribution of harbour porpoises in this region.

Satellite telemetry

One of the main advantages of tagging porpoises is that it can provide information on the behaviour of individuals over extended periods of time, informing on large- as well as small-scale movements and enabling porpoise occurrence to be modelled taking environmental parameters and prey occurrence into account (Edrén et al. 2010; Sveegaard et al. 2012; Nielsen et al. 2018). Some types of tags also collect detailed data on diving patterns, swimming speed (Teilmann et al. 2007; van Beest et al. 2018b) or vocalisations (Wisniewska et al. 2016, 2018). In addition, some devices can record background sounds, thereby allowing for an evaluation of effects of these sounds on animal behaviour (van Beest et al. 2018b).

Especially in the complex inner waters of the Wadden Sea, tagging can collect valuable high-resolution information on how porpoises navigate through this tidal habitat. It allows researchers to investigate how porpoises use the Wadden Sea specifically and what the relationship is with the North Sea. One caveat is that it can take some time before a sufficient number of animals are tagged, and, as a result, before representative data are available. At this point, only six males have been tagged and tracked in the northern part of the Wadden Sea area. Tagging more porpoises of different sex and age and on more locations in the Wadden Sea could provide information on habitat use, feeding behaviour and the impact of human activities. Moreover, as tagging involves handling the animal, it allows for collection of live porpoise measurements, blood samples, swabs and blubber biopsies and photo ID. Tagging should be done following ethical standards, and methods should be streamlined between the Wadden Sea countries.

Other methods

There is a suit of other methods to collect data on harbour porpoises. Of these, environmental DNA (e-DNA) sampling and analysis have shown to be a promising, non-invasive method for detecting species presence, especially for elusive species or in areas where other methods are limited (Suarez-Bregua et al. 2022). e-DNA samples can also help with population structure analyses (Parsons et al. 2018). Pilot experiments could indicate whether this is a desirable method in the Wadden Sea.

In general, genetic analyses can inform about (sub)population structure (Rosel et al. 1999; Autenrieth et al. 2023) and management units (Sveegaard et al. 2015), but also about potential (sub)population declines (Ben Chehida et al. 2023).

Assessing conservation status

The Wadden Sea Plan states two main goals for harbour porpoises in the Wadden Sea: (1) a viable stock with a natural reproduction capacity and (2) conservation of habitat quality for the conservation of the species.

In the context of the Quality Status Assessment for this species, Reijnders et al. (2009) describe a viable population as one that ‘maintains its vigour and its potential for evolutionary adaptations'. To do this, a population has to be large enough to withstand catastrophic events, such as a mass mortality event, and should have enough genetic variability so that its evolutionary potential is not hindered. The use of the term 'stock' in fishery management is to describe a living resource from which catches are taken. The term 'usually implies that the particular population is more or less isolated reproductively from other stocks of the same species and hence self-sustaining' (FAO 1997). Harbour porpoises in the Greater North Sea are considered one population and are treated as one assessment area (ICES 2014; NAMMCO 2019; Geelhoed et al. 2022). It is not clear if, within the Wadden Sea Plan, the term 'stock', for which viability and natural reproduction capacity are to be assessed, refers to the subset of the North Sea population that occurs in the Wadden Sea or to the entire North Sea population (Common Wadden Sea Secretariat 2010). While the framework of the WHS is site-specific, it considers the conservation of species in all their habitats. This is especially true for mobile species (groups) that move in and out of the area, such as harbour porpoises, seals, migratory birds and fish, and are considered part of the 'Outstanding Universal Values' that make this area so special.

The second aim addresses adequate habitat quality. The current data show that porpoises navigate the Wadden Sea, including the intertidal waters, to find prey. However, our understanding of what drives porpoise distribution in the Wadden Sea and how this is linked to habitat quality is still insufficient.

In monitoring frameworks, specific biological criteria are chosen to assess the success of management and conservation measures against the defined aims. Which criteria should be measured to allow the assessment of 'viability' and 'habitat quality' has, however, not been well defined to date.

Table 2 lists criteria often used in monitoring and assessment. We evaluated how suitable the discussed methodological approaches are for harbour porpoise in the Wadden Sea. This assumes that the monitoring schemes would be designed with sufficient sample size and spatial coverage throughout the trilateral region. There is not one single method that can inform on all the criteria listed. Depending on the selected criteria for monitoring, a combination of methods that complement each other should be chosen. Any method should be applicable all across the Wadden Sea area, collect representative data and use standardised protocols that can be implemented in a long-term monitoring programme.

Table 2 Overview of research methods and possible monitoring criteria for harbour porpoise in the Wadden Sea. Filled green circle: suitable; semi-filled circle: suitable method in part of the Wadden Sea area; grey circle: not suitable

Monitoring Criteria \ Methods	Aerial surveys	Strandings database	Post-mortem examinations	PAM	Telemetry
Abundance	◐	○	○	○	○
Index of occurrence	◐	◐	○	●	○
Diel and seasonal distribution	◐	◐	○	●	◐
Habitat use	◐	◐	◐	●	●
Behaviour	◐	○	○	◐	●
Feeding ecology	◐	○	◐	◐	◐
Reproduction	◐	◐	◐	○	○
Age structure	○	◐	◐	○	○
Health	○	○	◐	○	○

Recommendations

Harbour porpoises are an integral part of the Wadden Sea ecosystem and contribute to the Outstanding Universal Value of the WS WHS. Porpoises can also be regarded as an ambassador to the larger public, being one of the 'big five' species in the Wadden Sea (together with grey and harbour seal, white-tailed eagle (*Haliaeetus albicilla*) and European sturgeon (*Acipenser sturio*, currently being reintroduced) (Nationalpark Wattenmeer 2021; Visit Wadden 2023)) and having a prominent position on the logo (Fig. 15).

The WS WHS is part of a complex patchwork of regional, national and international protected areas. To date, monitoring and research efforts are mostly implemented nationally or regionally (e.g. by federal state), leading to a mismatch in the spatial and temporal coverage within the trilateral region.

In this paper, we presented the current data and knowledge on harbour porpoise in the Wadden Sea and related research and monitoring programmes. It becomes clear that a coherent monitoring programme is lacking. Therefore, we highlight the following first steps:

1. For the member parties to apply suitable monitoring methods that are in accordance with the conservation objectives. These should be coordinated within and between countries to fit into the framework of a single integrated management plan for the harbour porpoise and focus on filling the current monitoring gaps:
   (a) Setting up and maintaining a systematic stranding network in Lower Saxony and increasing the number of post-mortem investigations to fill knowledge gaps on population parameters like reproduction and age structure;
   (b) Extending the PAM network to Denmark, Lower Saxony and the Netherlands and increasing the number of tagged animals to collect data on distribution, habitat use and behaviour.
2. Coordinate the development of monitoring activities with the relevant authorities responsible for management of adjacent Natura 2000 sites. Sites that list harbour porpoise as a species of interest and are situated in rivers and estuaries are particularly important, as those areas are not represented in North Sea conservation frameworks.
3. Streamline monitoring efforts with the requirements of existing international law and agreements and regional conventions (such as MSFD, ASCOBANS, OSPAR) regarding reporting cycles and data formats.
4. Encourage the establishment of joint databases, preferably web-based and open-source. Where applicable, link to the use of agreed protocols on data collection to allow for a combined analysis. Data should be shared trilaterally but also externally, to ensure assessments at meaningful scales.
5. Explore other methods such as (e-)DNA studies and assess whether they could contribute to harbour porpoise monitoring in the area.

Fig. 15 The logo of the Wadden Sea World Heritage Site (left) and a harbour porpoise in the wild (right) (photo: M. Scheidat)

Furthermore, we recommend the following to help in the development of a trilateral management framework:

1. Continue the existing trilateral work on porpoises by different research groups in the Wadden Sea and promote the international exchange of knowledge, in particular through the Expert Group on Marine Mammals.
2. For the Wadden Sea Secretariat to continue the facilitation of expert knowledge, such as through workshops and symposia (e.g. Common Wadden Sea Secretariat (2019)), and to assist in developing public awareness schemes on a trilateral level where this will help improve monitoring programmes (e.g. stranding network).
3. For the trilateral agreement to evaluate the suitability of the current conservation objectives for the harbour porpoise in the WHS Wadden Sea and adapt them if needed. Provide guidance on how the terms 'viability', 'stock', 'population' and 'habitat quality' are to be interpreted and what kind of criteria should be used to assess them.

These recommendations aim to assist in progressing the goal of the Leeuwarden Declaration (2018), which states that the member countries of the WS WHS are 'Conscious that coordinated monitoring, data handling and assessment of the quality status are crucial factors for the conservation and management of the Wadden Sea, also as a World Heritage Site' (Common Wadden Sea Secretariat 2018). Applying this to the harbour porpoise in the Wadden Sea will result in a coordinated trilateral framework allowing for an adequate monitoring of its conservation status.

Acknowledgements A large part of the data presented here has been collected during long-term programmes. We would like to take this opportunity to acknowledge especially the many enthusiastic volunteers that have contributed to this work over decades. We would like to acknowledge the agencies that funded the presented work, as described under the declaration on Funding. We sincerely thank the Dutch stranding network volunteers and organisations for their help with reporting and retrieving stranded specimens. We would like to thank Kristine Meise and Soledad Luna for helpful comments made on an earlier version of this paper. We would also like to thank the three anonymous reviewers for their valuable comments and suggestions.

Funding In Denmark, porpoise tracking data were collected as part of the DEPONS project funded by the offshore wind developers Vattenfall, Forewind, ENECO Luchterduinen, Ørsted and Scottish Power Renewables (www.depons.au.dk). The Danish National Contingency Plan concerning strandings of marine mammals is funded by the Danish government and is run jointly by the Danish Environmental Protection Agency; Danish Nature Agency; the Fisheries and Maritime Museum; the Natural History Museum of Denmark; the Department of Ecoscience, Aarhus University and the Department of Veterinary and Animal Sciences, University of Copenhagen (previously, the Center for Diagnostic DTU and Department of Chemistry and Bioscience, Aalborg University, were also involved). In Germany, funding is provided by the German Federal Ministry for the Environment, Nature Conservation and Nuclear Safety, Federal Agency for Nature Conservation and Federal Ministry of Food and Agriculture. In Schleswig–Holstein, health monitoring is funded by the Ministry for Energy Transition, Climate Protection, Environment and Nature (MEKUN), POD-Monitoring by the National Park Administration, LKN.SH. In the Netherlands, funding for aerial surveys is provided by the Ministry of Agriculture, Nature and Food Quality. Post-mortem examinations are conducted at the Faculty of Veterinary Medicine of Utrecht University, also commissioned by the Ministry of Agriculture, Nature and Food Quality, and since 2016 embedded under the Statutory Research Tasks Unit for Nature and the Environment of Wageningen UR (project reference numbers WOT-04–009-045).

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Handling and instrumentation of porpoises were conducted under permission issued to Jonas Teilmann from the Environmental Protection Agency (Ministry of Environment and Food of Denmark, NST-3446–0016) and the Animal Experiments Inspectorate (Ministry of Environment and Food of Denmark, 2015–15-0201–00549).

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities. The study is compliant with CBD and Nagoya protocols.

Data availability Different datasets were generated and/or analysed during the current study. In the following, we provide an overview of their availability:

The combined dataset of aerial survey data from Danish, German and Dutch waters is not publicly available but requests regarding this data can be directed to Anita Gilles (Anita.Gilles@tiho-hannover.de) or Signe Sveegaard (ssv@ecos.au.dk).
The combined dataset of Danish, German and Dutch strandings is available as supplementary material with IJsseldijk et al. (2020).
The Dutch database on strandings is public and can be accessed at www.walvisstrandingen.nl until early 2024, after which it will be available on www.stranding.nl. Data requests can be directed to Guido Keijl (guido.keijl@naturalis.nl).
The German dataset of passive acoustic monitoring is not publicly available, but Ursula Siebert (Ursula.Siebert@tiho-hannover.de) and Britta Diederichs (Britta.Diederichs@lkn.landsh.de) can be contacted regarding availability.
The telemetry data are not publicly available, but requests regarding this data can be directed to Jonas Teilmann (jte@ecos.au.dk).

Author contribution All authors contributed to the conception of the work. Data collection was done by JB, CBT, RD, SCVG, AG, LLIJ, GOK, JN-N, AR, MS, JS, US, SS and JT. All authors contributed to data analysis and interpretation; maps were created by JV and SS. All authors contributed on the drafting of the work and/or the critical revision of it. All authors read and approved the final manuscript to be published.

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