SPATIAL AND TEMPORAL DISTRIBUTION OF HARBOUR PORPOISES IN RELATION TO THEIR PREY

PhD thesis
Signe Sveegaard

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Abstract: The population status of harbour porpoises has been of concern for several years due to anthropogenic influences, especially incidental bycatch in gillnet fisheries. Proper management of a wide-ranging species such as the harbour porpoise requires reliable information on distribution, migrations, status of biological populations, and habitat preferences. This PhD thesis examines these issues. Harbour porpoise distribution is examined by means of satellite tracking (Paper II) and acoustic surveys, along with the agreement in results between these two very different methods (Paper III). The data from satellite tracking are also used to identify the boundaries of a genetically distinct harbour porpoise population and new abundance estimates are calculated for this population (Paper IV). Next, the underlying causes governing harbour porpoise distribution are explored by reviewing available information on harbour porpoise diet (Paper V) and correlating the distribution of satellite tracked porpoises with distribution of a main prey species, herring (Paper VI). Finally, the seasonal variations in distribution of harbour porpoises observed in a Danish strait, the Sound, are explored by examining the stomach content of porpoises from the area. Overall, this PhD thesis introduces several new applications for satellite telemetry data that – in combination with acoustic surveys – has significantly contributed to the current knowledge of harbour porpoise distribution. Furthermore, the thesis provides evidence of a porpoise-prey relationship which is important information in the conservation of the species, due to its influence on harbour porpoise distribution.

Keywords: Harbour porpoise, *Phocoena phocoena*, satellite tracking, acoustic surveys, distribution, prey, diet, herring, cod, Kattegat, Skagerrak, Belt Sea, the Sound

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PREFACE & ACKNOWLEDGEMENTS

This thesis is the result of a three year PhD project, conducted at the National Environmental Research Institute (NERI), Aarhus University.

The work has concentrated on abundance and distribution of harbour porpoises, the validity of methods used for studying this distribution and the underlying causes determining the movements and distribution of porpoises. These topics are currently of great scientific and political interest, due to the implementation of the EC Habitat Directive in Europe, scheduled to be concluded in 2012.

The thesis consists of seven manuscripts of which two are accepted for publication in peer reviewed journals (II & III), one has been submitted (VI), two are nearly ready for submission (IV & VII), one awaits further data in order to be completed (V) and the last manuscript (I) represents an introduction to the thesis in form of a review paper.

This thesis was supervised by Jonas Teilmann and Kim N. Mouritsen and I owe them both great thanks. Jonas; from I met you in 2004 you have impressed me with your knowledge, capability of handling stressful situations and your good humour. Thank you for believing in me, for including me in your work and for all your help throughout this PhD. Kim; your statistical skills, ecological knowledge and cool Jutlandic mind has made a great contribution to this PhD. I thank both my supervisors for always taking the time to discuss different projects with me, in spite of your busy schedules.

Numerous other people have contributed to this PhD. I wish to thank all my colleagues at the Department of Arctic Environment (NERI), which has provided an inspiring and pleasant atmosphere during this PhD. A special thanks to Jacob Nabe-Nielsen for introducing me to the wonders of modelling, and to Rune Dietz, Frank Riget, Jakob Tougaard and Susi Edrén for all their incredible help and fruitful discussions. My warmest thanks to Line A. Kyhn for your interesting and critical mind as well as your invaluable friendship, which has made a tremendous contribution to my life during this PhD as well as the last twelve years.

Several projects in this PhD have involved cooperation with people at other institutes which also deserves thanks. Roland Lick, Hilde Aarefjord, Carl Kinze, Patrik Börjesson, and Per Berggren are thanked for providing data for the prey analysis and for fruitful discussions on the best practice for prey analysis. Douglas Gillespie, Andreas Nygren andthe crew on RV Skagerak are is thanked for scientific advice and help in the field during the acoustic surveys. Furthermore, I thank all my partners at DTU Aqua for valuable and fruitful collaboration.

During the lay-out phase of this PhD, I came into contact with National Geographic photographer, Bill Curtsinger, and underwater photographer, Lars Laursen, who kindly donated their amazing photos to be used in this thesis. Thank you.

I wish to thank my family and friends for their support and encouragement throughout this study. And, finally, I owe my deepest thanks to Morten for all the help and support you have given throughout this PhD and for being so incredibly cool about my many hours away from home during field work and conferences.

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DANSK RESUMÉ

Marsvinets populations status har givet årsag til bekymring i gennem længere tid pga. negativ menneskelig påvirkning især i form af utilsigtet bifangst i garnfiskeri. Forsvarlig forvaltning af marsvin kræver pålidelig viden om udbredelse, migration, status af biologiske populationer og habitat præferencer. Denne afhandling omhandler disse emner.

Paper I giver en oversigt over den nuværende viden om marsvineudbredelse, metoder til at studere denne udbredelse og de underliggende økologiske faktorer, så som byttedyr og havmiljø, der potentielt kan have indflydelse på udbredelsen. Endvidere gennemgås, hvordan denne viden er blevet benyttet i forvaltningen af marsvin i Danmark og perspektiver og anbefalinger for fremtidig forskning diskuteres.

Det resterende af afhandlingen er fordelt på to emner: I første del, undersøges marsvins udbredelse og brugen af og overensstemmelser mellem metoder til at studere denne udbredelse og i anden del, undersøges sammenhængen mellem marsvins bevægelser og de underliggende økologiske forhold, der influerer marsvinets udbredelse.

I **Paper II** undersøges bevægelser fra 64 satellitmærkede marsvin, for at bestemme dyrenes udbredelse og identificere højtæt-hedsområder i den østlige Nordsø, Østersøen og farvandet imellem. Resultaterne viser, at marsvin har en klumpet fordeling med ni højtæthedsområder i disse farvande. Tætheden af marsvin i flere af højtæthedsområderne varierer over året. **Paper III** anvender akustiske surveys, som en uafhængig metode til at teste den tidsmæssige og rumlige stabilitet af udbredelsen fundet med satellit telemetri i Paper II. Sammenligningen af de to metoder viser en god overensstemmelse, hvilket bekræfter tilstedeværelsen og stabiliteten af områder med høj marsvinetæthed og derudover validere brugen af de to metoder i studier af marsvineudbredelse.

I **Paper IV**, benyttes data fra de satellitmærkede marsvin til at definere populationsgrænser for en genetisk adskilt population af marsvin, der residerer i Kattegat, Bælthavet, Øresund og den vestlige Østersø. Denne population er vigtig i forvaltningssammenhænge, da den udgør det eneste mulige input af nye gener til den truede bestand af marsvin i Østersøen. Medbrug af de nye populationsgrænser, udregnes bestandsestimater baseret på to større visuelle surveys i 1994 og 2005 til at være 27.767 (CV=0.45) i 1994 og 10.865 (CV=0.32) i 2005. Selvom denne nedgang ikke er statistisk signifikant, giver den dog anledning til bekymring.

Hovedmotivationen for marsvins bevægelser er formodet at være bytte-relateret. I anden del af afhandlingen, undersøges dette nærmere. Paper V giver et overblik over al eksisterende viden om marsvineføde baseret på analyser af marsvinemaveindhold for den genetiske population omtalt i Paper IV. Endvidere udregnes sæsonvariation i præferencer af byttedyr, for to studier med tilgængelige data. Resultaterne viser, at torsk, sild, kutling og hvilling i de vigtigste byttearter, selv om den relative betydning af hver art kan variere både mellem sæsoner og geografisk. Disse resultater er herefter sammenlignet med tilgængelig viden om udbredelsen af disse byttearter og den temporale og rumlige sammenhæng mellem marsvineudbredelse og deres bytte bliver gennemgået. Ikke desto mindre forårsager manglen på information om byttearternes udbredelse at detaljerede analyser af den rumlige sammenhæng mellem rovdyr og bytte ikke kan foretages. Paper VI sammenligner udbredelsen af satellitmærkede marsvin med udbredelsen af sild, fundet ved årlige akustiske silde surveys. Tæthed af makrel, der ikke er marsvinebytte men som prædaterer på sild, og dybde er også inkluderet i analyserne for at undersøge om interaktioner mellem sild, makrel og dybde influere på marsvineudbredelse. Resultaterne viser, at tæthed af marsvin og makrel er korreleret med sild, der så er korreleret med dybde. Paper VII bygger videre på denne viden, og undersøger hvorfor sæsonvariation i marsvinetæthed i Øresund, ikke korrelere med kendt udbredelse og tæthed af fisk, især sild. Ved at undersøge maveindholdet af marsvin fra Øresund, vises det at marsvin i højtæthedsperioden (april-oktober) spiser mere varieret bytte, gennemsnitligt indtager mere bytte og at forekomsten af byttearter er højere end i lavtæthedsperioden (november-marts). Endvidere vises, at torsk er den vigtigste bytteart i højtætsperioden mens sild er den vigtigste i lavtæthedsperioden. Det foreslås, at forekomsten af hydrografiske fronter om foråret i den nordlige del af Øresund, medfører større fø-

detilgængelighed i denne sæson og at dette sammen med manglende adgang til området med høj vinter-sildetæthed forårsaget af intens trafik, er hovedårsagerne bag den lave tæthed af marsvin observeret om vinteren.

Denne PhD afhandling introducerer flere nye metoder til brug af satellit telemetri data, der – sammen med akustiske surveys – har bidraget signifikant til vores viden om marsvins udbredelse. Endvidere, giver denne afhandling bevis for en rovdyr-byttedyr relation, der er vigtig information at medtage i forvaltning af arten, pga. dens indflydelse på marsvins udbredelse.

ENGLISH SUMMARY

The population status of harbour porpoises has been of concern for several years due to anthropogenic influences, especially incidental bycatch in gillnet fisheries. Proper management of a wide-ranging species such as the harbour porpoise requires reliable information on distribution, migrations, status of biological populations, and habitat preferences. This PhD thesis discusses these issues.

Paper I provides an overview of the present knowledge on harbour porpoise distribution, the methods of examining this distribution, and the underlying ecology of prey and marine environment potentially affecting harbour porpoise distribution. Furthermore, the use of this information in the protection and management of harbour porpoises in Denmark is discussed, as well as future perspectives for this research to aid the protection of harbour porpoises.

The remaining parts of the PhD thesis are divided into two: one examining the harbour porpoise distribution and the usage of, and agreement between, methods for studying this distribution. The second part explores the underlying ecological causes governing harbour porpoise movements.

In part one, Paper II examines the movements and area preferences of 64 satellite tagged harbour porpoises, in order to determine the distribution and identify high density areas in the eastern North Sea, the western Baltic, and the waters in between. Results show an uneven harbour porpoise distribution, with concentrated occurrences in nine high density areas within the study area. Several of these areas are subject to significant seasonal variation. Paper III applies acoustic vessel surveys as an independent method to test the temporal and spatial stability of the distribution found by satellite telemetry in Paper II. The comparison of the two methods reveals a strong spatial agreement between them, which confirm the presence and stability of areas of high porpoise density, and, furthermore, validates the applicability of the two methods as tools for studying the distribution of harbour porpoises. In Paper IV, data from satellite tracked harbour porpoises are used to define the population boundaries of the genetically distinct population inhabiting Kattegat, Belt Sea, the Sound and the western Baltic Sea. This population is of particular importance in conservation efforts since it represents the only possible new gene flow into the endangered population in the Baltic Sea. Using the new identified boundaries, abundance estimates for the population were calculated based on two large-scale visual surveys in 1994 and 2005, to be 27,767 (CV=0.45) in 1994 and 10,865 (CV=0.32) in 2005. Although not statistically significantly different in a statistical sense, the declining trend gives reason for concern.

The main drivers governing harbour porpoise movements are hypothesised to be prey-related. In the second part of the PhD thesis, this hypothesis is tested. Paper V reviews all available studies on harbour porpoise prey preferences based on analysis of stomach content for the genetically distinct harbour porpoise population discussed in Paper IV. Furthermore, the seasonal prey preferences are recalculated using accessible data from two of the reviewed studies. Cod, herring, gobies, and whiting are identified to be the primary prey species, although the relative importance of each species varies across seasons. These results are subsequently compared to available knowledge on the distribution of these fish species and the spatial and temporal correlation between porpoise and their prey is assessed. However, a serious lack of information on prey species distribution prevents any detailed analysis of temporal or spatial correlations between predator and prey. Paper VI compares the distribution of satellite tracked harbour porpoises with distribution of a main prey species, herring, obtained through annual acoustic surveys. Depth and density of a non-prey species, mackerel, are also included in the analysis to examine if the interactions between density of herring, mackerel (which preys on herring) and depth affect the distribution of harbour porpoises. It is found that densities of porpoises and mackerel are positively correlated with herring densities, which in turn is correlated with depth. Paper VII builds onto this analysis, and examines why the seasonal variation in harbour porpoise occurrence in a Danish strait does not correspond with the seasonal distribution of fish abundance (especially herring). By examining the harbour porpoise stomach content, it is found that in the high porpoise density season (April-October), mean prey weight per stomach is larger and the frequency of occurrence as well as

the diversity of prey species is higher than in the low density season (November-March). Furthermore, cod is found to be the main prey species, in terms of weight in the high season, and herring in the low season. The development of frontal zones in the spring in the northern part of the Sound is suggested to aid the porpoises in locating their prey, and unavailability of the overwintering herring due to heavy boat traffic is suggested to be the cause of the low winter abundance.

In conclusion, this PhD thesis introduces several new applications for satellite telemetry data that - in combination with acoustic surveys - has significantly contributed to the current knowledge of harbour porpoise distribution. Furthermore, the thesis provides evidence of a porpoise-prey relationship which is important information in the conservation of the species, due to its influence on harbour porpoise distribution.

PAPER 1

Harbour porpoise distribution: Methods, ecology and movement in Danish and adjacent waters – a review

Signe Sveegaard

Harbour porpoise distribution: Methods, ecology and movement in Danish and adjacent waters – a review

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ABSTRACT

The population status of harbour porpoises has been of concern for several years, and the establishment of Marine Protected Areas (MPAs) is being implemented in the EU as a method to protect this species. In order to designate MPAs, high-density areas for the species must be identified. In this paper, I review and discuss the present knowledge on harbour porpoise distribution, the methods for examining this distribution and the underlying ecology of prey and marine environment potentially affecting harbour porpoise distribution. Several methods for studying harbour porpoise distribution exists and of these, I recommend that local monitoring of MPAs use aerial or boat-based visual surveys, acoustic surveys with towed hydrophones or passive acoustic monitoring (PAM) using dataloggers and that monitoring of the entire population should use aerial or boat-based visual surveys. Satellite tracking may be used to identify high density areas and for monitoring movement and distribution, but cannot inform on trends in abundance. Distribution of porpoises is well studied in most Danish waters. Harbour porpoises have been found to gather in several high density areas, primary located in the narrow straits of Little Belt, Great Belt, the Sound and Fehmarn Belt as well as in the turbulent waters between Kattegat and Skagerrak and in the southern Danish North Sea. Distribution of harbour porpoise were found in different studies to correlate with distribution of main prey species and prey diversity as well as frontal zones, depth and other environmental variables, and the management of fish stocks could therefore be included in management of porpoises. Conclusively, I describe how this knowledge has been utilized in the designation of MPAs in Denmark, and discuss future perspectives and best approaches to protect and monitor harbour porpoises within this geographical area.

1 INTRODUCTION

Over the last decades the need to protect small cetaceans in order to maintain sustainable populations has become increasingly apparent. Small cetaceans, such as the harbor porpoise (*Phocoena phocoena*, Linneaus 1758) face threats of incidental by-catch in fishing gear (e.g., Vinther and Larsen 2004), pollution, habitat destruction, food depletion (Reijnders 1992) and other anthropogenic disturbances such as underwater noise, shipping, oil and gas exploration, as well as marine constructions including bridges and wind farms (Carstensen et al. 2006).

The establishment of Marine Protected Areas (MPAs) has been suggested as a method for protecting small cetaceans (e.g., Hoyt 2005). Indeed, according to the EC Habitat Directive (92/43/EEC), all relevant EU member states are legally obliged to protect the harbor porpoise in its entire range as well as by designating MPAs, referred to as Special Areas of Conservation (SAC).

In order to design a proper management plan for cetaceans, information on distribution, seasonal movements, abundance, reproduction, and diet must be available, as well as an understanding of how anthropogenic effects such as incidental by-catch, marine constructions, pollution and traffic influence these factors. However, due to the difficulties of studying these animals, this information is rarely accessible. For a wide ranging species such as the harbour porpoise, knowledge is generally obtained from visual and acoustic detections as well as examination of stranded or bycaught individuals. Furthermore, the development of novel methods such as satellite tags and acoustic tags has significantly added to our understanding of harbour porpoises. In order to effectively study and protect the species, it is essential that the correct use and limitations of these methods are understood. Moreover, consistency and agreement between applied methods is critical. Furthermore, in order to understand the temporal and spatial fluctuations in porpoise distribution, we need a solid knowledge of the drivers that influence porpoise movements and, consequently, the distribution. Is it distribution of prey, seasonal social interactions such as reproduction, avoidance of heavy vessel traffic, or a mix of these?

In this paper, I review and discuss the present knowledge on harbour porpoise distribution, the methods for examining this distribution and the underlying ecology of prey and marine environment potentially affecting harbour porpoise distribution. Furthermore, I will describe how this knowledge has been utilized in the designation of Natura2000 areas in an EU country (Denmark), and discuss future perspectives and best approaches to protect and monitor harbour porpoises within this geographical area.

2 METHODS FOR STUDYING DISTRIBUTION

Methods for studying harbour porpoise distribution fall into the following categories: 1) Satellite telemetry tracking of individual animals, 2) Visual observations, which may be dedicated surveys from ship, aircraft or land, incidental sightings or 'platforms of opportunity', 3) Acoustic monitoring using either a towed array from a boat or static acoustic monitoring with porpoise click detectors, and 4) Strandings. Each method has different benefits and limitations that must be carefully considered before implementation. Furthermore, monitoring of cetaceans is generally defined as the examination of abundance and/or distribution, and Berggren et al. (2006) suggest that monitoring of small cetaceans may be addressed at two spatial scales: (1) Regional monitoring where the requirement is to monitor the use of a specified area by a particular species, e.g. national waters, marine protected areas or construction sites, and (2) Population-level monitoring where the objective is to monitor the status of a whole population. The aim in both cases is to detect if relative abundance changes by more than a certain percentage over a certain time period. The usability of each method in relation to regional and population monitoring will be included in the discussion of methods.

To date, two extensive reviews of monitoring methods have been published (Evans and Hammond 2004, Berggren et al. 2008b). These aim at describing monitoring methods for all small cetaceans in European waters. In this section, I will describe and discuss these methods, but focus on the methods employed for harbour porpoises in Danish waters and the developments since the publication of previous reviews.

2.1 Satellite tracking

Harbour porpoises have been tagged with satellite transmitters since 1994 (Read and Westgate 1997). However, due to the difficulties in catching the porpoises unharmed, few scientific institutions have employed this method. In fact, all taggings has been conducted in either the Bay of Fundy, Canada (Read and Westgate 1997, Johnston et al. 2005) or in Danish waters (Teilmann et al. 2007, Sveegaard et al. In press, Paper II). In these areas, national fishing methods (herring weir in Canada and pound nets in Denmark) permit capture of the porpoise in bowl-shaped nets that allow the porpoise to breathe. Furthermore, the mask size of these nets is too small for the porpoises to get entangled.

Satellite tracking of harbour porpoises can provide information on the individual porpoise e.g. provide detailed movement patterns (Read and Westgate 1997), diving behaviour (Otani et al. 1998, Teilmann et al. 2007), seasonal movements, home range, distribution (Sveegaard et al. In press, Paper II). Recently, it has also been used for identifying high-density areas (Sveegaard et al. In press, Paper II) and suitable habitats (Edrén et al. 2010) as well as defining population boundaries (Teilmann et al. In prep., Paper IV). The disadvantages of the method include difficulties in catching porpoises and costly tagging equipment. The sample size of tagged porpoises is therefore often limited. To date, the highest number of a single cetacean species tagged within a single study is 82 harbour porpoises, 1997-2010, tagged in Danish waters (64 porpoises, 1997-2007, Sveegaard et al. In press, Paper II; 18 porpoises, 2008-2010, J. Teilmann, unpubl. data). The tracking locations of 64 of these porpoises were actually used to examine the distribution of the entire population (Sveegaard et al. In press, Paper II), see section on Distribution below.

The accuracy of locations from satellite tracked marine mammals may vary according to species, behaviour, and transmission settings of the tag. This is especially a problem for marine mammals that are submerged for the majority of the time, prohibiting uninterrupted transmission of locations, and the raw data may therefore include a high proportion of low accuracy locations. Consequently, the locations have to be filtered before use. Freitas et al. (2008) and Sveegaard et al. (In press, Paper II) provide comprehensive details and discussion of this filtering. Both studies agreed that a filter including swimming speed as well as distance and angle between positions modified according to each species, yielded the most reliable results.

The appropriate choice of analysis for satellite tracking locations may vary according to the aim of the study: When examining behaviour and movement on a small spatial scale, e.g., in relation to foraging behaviour, the entire time series of locations may be of interest, while for large scale studies, e.g. examinations of distribution, locations should be standardised to one location per porpoise per day (Sveegaard et al. In press, Paper II). The spatial density of locations may be calculated using Kernel density estimates (Worton 1989) as done in Johnston et al. (2005) and Sveegaard et al. (In press, Paper II). However, the Kernel results are significantly influenced by the choice of settings in the Kernel density estimation program (Beyer 2004, Sveegaard et al. In press, Paper II) and thus, reporting of all relevant settings used and the reason for these choices, should be included in all studies.

The tags may be attached by either suction cup (Hanson and Baird 1998) or by perforation of the dorsal fin (Read and Westgate 1997, Sveegaard et al. In press, Paper II). Suction cups are less invasive but only remain on the animal for a maximum of a few days. Tags attached by piercing of the fin have stayed on the porpoise for op to 17 month, but the procedure of perforating the fin is likely to be instantly stressful for the animal (Eskesen et al. 2009). Several types of tags have been deployed on porpoises in the wild. These include Time-Depth Recorders (Otani et al. 1998, Teilmann et al. 2007) and acoustic tags (A-tags), that are able to record the echolocation clicks of the porpoise, as well as log information on diving behaviour (Akamatsu et al. 2007). This data can provide essential information of foraging behaviour, and diurnal rhythm unparalleled by any other method or tag. The size of the A-tag is generally much larger than the satellite tag, and can potentially disturb the hydrodynamics of the porpoise. Consequently, it is only deployed for a short period of time (few weeks at most). The A-tag requires retrieval of the tag to access the recorded information, and it is therefore often equipped with a time release mechanism. Nevertheless, tags are often lost, and the method may consequently be very expensive.

In summary, satellite tracking may provide high resolution spatial information on movement and behaviour for up to a year and a half that can not be obtained with any other method. Furthermore, it may contribute to the knowledge of large scale distribution, when a sufficient number of animals are tagged. Whether the number of tagged animals is adequate may be tested with the use of other methods, e.g. surveys. Satellite tagging has the disadvantages of potential stress inflicted on the animal during tagging, costly equipment and difficulties in catching the porpoises.

2.2 Visual observations

Visual observation of cetaceans is the most widely used method for examining the distribution and abundance of harbour porpoises in both large scale population studies and small scale regional studies. The visual methods range from simple recordings of incidental sightings from 'platforms of opportunity' to the devoted mark-recapture line transects survey methodology. However, common to all visual surveys is that they are strongly dependent on weather, e.g. for a small cetacean like the harbour porpoise surveying is only recommended during daylight hours and in very calm weather (Teilmann 2003, SCANS II 2008). Furthermore, visual surveys are influenced by observer skills and experience. To produce reliable and comparable results (especially required in line transect surveys), training of observers prior to the survey as well as tests of inter-observer comparability is therefore necessary (Berggren et al. 2008b). This section will review the different visual observation methods for studying distribution of harbour porpoises.

2.2.1 Dedicated surveys

A widely used method for examining distribution of harbour porpoises and other small cetaceans is by visual line transect surveys from boat or plane (Heide-Jørgensen et al. 1992, Heide-Jørgensen et al. 1993, Hammond et al. 2002, Scheidat et al. 2004, SCANS II 2008). Surveys can provide an instant view of the distribution and, if repeated, also reveal seasonal or yearly variations in distribution. At present, observations from surveys are the only method that facilitates calculations of population size (Hammond et al. 2002, SCANS II 2008), although static acoustic monitoring may soon become an alternative (Kyhn 2010). As such, visual surveys may be appropriate for both regional and population studies.

Visual surveys of small cetaceans by vessel or aircraft generally apply the method of line transect sampling (Buckland et al. 2001). Here, a survey region is sampled by placing a number of lines at random location in the region or, more commonly, a series of systematically spaced parallel lines (Thomas et al. 2010). The observer travels along these pre-determined transect lines, recording all animals along the path as well as the distance to the transect line. For methods on measuring the distance from the animal to the transect line, see Berggren et al. (2006). In standard line transect methods it is assumed that all animals on the transect line is detected), and that the probability of detection declines with distance to the line (Fig. 1). The measured distance between the line and the animal are used to determine a detection function (g(x)). Once the detection function is found, an estimate of the effective strip width (ESW) (the distance from the ship at which animals missed inside ESW = animals observed outside ESW) can be calculated (Fig. 1).

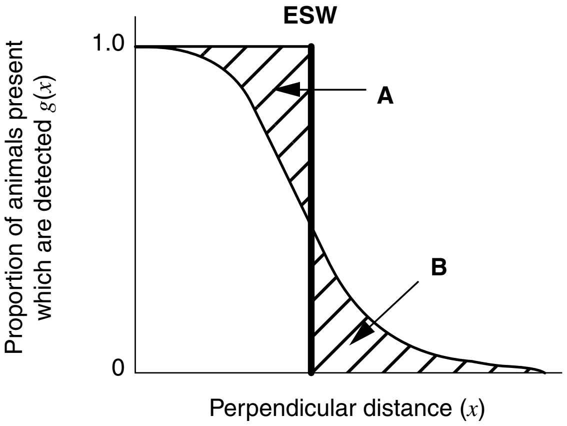

Figure 1. Curve of distance between harbour porpoise observation and the transect line in line transect distance sampling. **A)** represents the animals inside the ESW that are not detected and **B)** represents the animals outside the ESW that are detected. Modified from Buckland et al. 2001.

For transect surveys of cetaceans, however, this is not the case, since cetaceans may be out of sight when they are diving or avoiding the ship (availability bias) or simply missed by the observers (perception bias) (Buckland et al. 2001). In such cases, g(0) will always be less than 1, and it is therefore necessary to assess how large the bias is. On shipboard surveys, perception bias may be estimated by having two observer platforms collecting data simultaneously (Laake and Borchers 2004). The two observers search independently of each other, and the difference between their observations can subsequently be used to calculate the proportion of detected schools for each platform (Berggren et al. 2008b). This is termed mark-recapture distance sampling and was employed during the SCANS (Small Cetaceans in the European Atlantic and North Sea) surveys (SCANS II 2008). Once the detection function is calculated, the abundance measurements may be conducted using the 'Distance' software package (Thomas et al. 2010).

'Distance' provides methods for estimating detection functions, density and abundance, as well as survey design. Since the first version was released, the program has undergone several improvements and the latest version, Distance 6.0, can conduct mark-recapture distance sampling (with double observer platforms) (as used in Sveegaard et al. In press, Paper III) as well as Density Surface Modelling (DSM) (as used in SCANS II 2008). DSM includes environmental variables, e.g. depth, to explain and predict the distribution of animals in the abundance estimates, which may be useful in areas of sparse coverage (Thomas et al. 2010).

In summary, dedicated visual vessel or aircraft surveys have the advantage of allowing estimation of absolute and relative abundance. The technique can be used in both regional and population studies and thereby provide information on changes in spatial and temporal distribution. The disadvantages are added equipment cost for double platforms and high sensitivity to weather conditions.

2.2.2 Incidental observations

In areas where little or no previous information is available, the collection of incidental sightings from the public, ferry personnel or others can provide the first indications of spatial distribution. In Denmark, a large scale collection of incidental sightings in 2000-2002 was conducted (called 'Lookout for whales, dolphins and porpoises', Kinze et al. 2003). Here, about 4000 sightings were reported and 13 species identified, one of which had not previously been observed in Denmark. However, in studies like this, effort, which is not likely to be evenly distributed across the year, has strong influence on the results. The distribution of sightings will, therefore, reflect the distribution of vessels and observers more than it will represent true animal distribution. However, in spite of these short-comings, collected incidental sightings can be a useful and inexpensive method for identifying focus areas where other methods can then be applied (Berggren et al. 2008b).

2.2.3 Fixed land based surveys

Fixed-point land-based watching may be used to identify coastal areas with high abundance of cetaceans and to determine fluctuations in densities within these inshore areas both seasonally and over longer terms (Berggren et al. 2008b). This method has not been used in Denmark to examine cetacean distributions, perhaps due to the fact, that land-based surveys often are conducted from highly elevated lookout points on headlands or coastal rocks, of which Denmark has few. A major disadvantage of this method is that it only provides information on changes in occurrence of animals in a relatively limited area (up to of a few kilometres), and can therefore mainly be used to examine the small scale regional distribution.

2.2.4 Platform of opportunity

Data for monitoring cetacean populations can be collected in conjunction with other research projects, making use of so-called 'platforms of opportunity'. These platforms may be oceanographic or fisheries research vessels, ferries, cruise liners or whale watching boats that can be used to collect sightings or acoustic data by placing equipment or observers on board (Evans and Hammond 2004, Berggren et al. 2008b). A disadvantage is that often very little or no control of survey area or time is possible. However, like records of incidental sightings this is an inexpensive way of collecting data and it may provide useful information for planning and employing other more structured methods.

2.3 Acoustic monitoring

Like all odontocetes, the harbour porpoise uses echolocation for the detection and ranging of acoustic targets, e.g. prey, predators or conspecifics. The unique echolocation clicks of porpoises are very short (50-150 microseconds), narrowband and of high frequency, mainly 120-150 kHz centred around 130 kHz (Kastelein et al. 2002, Villadsgaard et al. 2007). Due to these properties, the echolocation clicks from harbour porpoises are easily separated from other marine sounds, e.g. low frequency noise from boats, or other odontocetes inhabiting Danish waters such as the white-beaked dolphin (*Lagenorhynchus albirostris*) (Rasmussen et al. 2002). This makes harbour porpoise clicks highly suitable for acoustic monitoring.

Acoustic monitoring of cetaceans has several advantages over visual methods for example that they can be automated, does not require daylight, is independent of human observers and less sensitive to weather conditions (Berggren et al. 2008b). The disadvantages are that these methods rely on the animals to emit sounds regularly, and the occurence of harbour porpoise sound emission is not well known. Acoustic monitoring may be conducted by ship-based surveys or stationary acoustic loggers. These methods will be discussed in this section.

2.3.1 Acoustic Surveys

The acoustic system using towed hydrophones in European waters was developed by the International Fund for Animal Welfare (IFAW) team. The system has undergone several technical developments since its invention in 1994, e.g. analogue filtering has been replaced with digital real-time signal processing (Gillespie and Chappell 2002, Sveegaard et al. In press, Paper III). The current system consists of a tow cable with two to three high frequency omnidirectional hydrophones placed near the end of the cable. The hydrophones are towed astern the survey vessel and have a maximum detection range of 500 m (Sveegaard et al. In press, Paper III). The hydrophones are connected through a buffer box to a computer with a high speed data acquisition system sampling output from each hydrophone at 500 kHz. The data are logged using an automated detection system developed for SCANS-II (SCANS II 2008).

Surveys using towed hydrophones have been conducted in Danish waters in 1994 (SCANS, Hammond et al. 1995), 2001-2002 (Gillespie et al. 2005), 2005 (SCANS II 2008) and 2007 (Sveegaard et al. In press, Paper III), all with the aim of measuring the distribution of harbour porpoises and, for the SCANS surveys, also of other small cetaceans. Acoustic surveys have the advantage of large spatial coverage, which is clearly illustrated by the spatial magnitude of the SCANS surveys. However, unless repeated, the method has a low temporal coverage.

It is essential that the vessel towing the hydrophones is relatively quiet for the porpoise signals to be detected and for the porpoises not to be scared off (SCANS II 2008). This was clearly illustrated in 2009 when I attempted to examine the abundance of fish and porpoises simultaneously during the annual ICES acoustic herring survey (Simmonds 2003) in Kattegat and Skagerrak. The herring survey was conducted by DTU Aqua on the Research Vessel Dana. Dana is a 70 m long trawling vessel, has a draft of 6.5 m and two large main engines as well as three auxiliary engines. Furthermore, for the acoustic assessment of herring, echo sounders of 18 kHz, 38 kHz and 120 kHz (all Simrad EK60) were used contentiously through out the survey. Whether it was the large engine or the echo sounder signals of 120 kHz (directly in the main hearing range of harbour porpoises (Kastelein et al. 2002) is unknown, but although passing through several areas of known high porpoise density with functional equipment, no detections were recorded.

Data from towed hydrophones are generally analysed as number of porpoise detections per sampling unit. The sampling unit may vary in different studies e.g. 1 km (Sveegaard et al. In press, Paper III) or 100 km (Gillespie et al. 2005), resulting in a click density estimate that can be compared between areas and seasons. However, direct comparisons between different surveys can only be made if all technical equipment and handling of data such as type of ship, background noise level and the person analysing data are identical. To mitigate this following SCANS-II, the IFAW team developed a method for correcting relative density estimates between the different research vessels (SCANS II 2008).

To date, it is not possible to calculate absolute abundance based on data from towed hydrophones. This is due to several difficulties, e.g. the fact that the quantity of harbour porpoise vocalisation is unknown and that the porpoises may react to the survey vessel or the hydrophones by either being attracted to or repelled from the ship. Both of these factors will significantly influence the results of abundance estimates based on acoustics. However, for relative measures of abundance, this is of less consequence as long as the behaviour of porpoises is uniform throughout the survey area. Another necessity before calculating total abundance is the establishment of a link between numbers of recorded clicks to the number of recorded porpoises.

In summary, towed hydrophones have the advantages of high spatial resolution and may be a valuable tool in both regional and population studies, although currently total abundance can not be calculated. Another benefit is that the method is relatively independent of daylight and weather conditions. Performance is, however, dependent on the noise level of the vessel.

2.3.2 Static acoustic loggers

Static acoustic dataloggers can be used for monitoring sonar activity of harbour porpoises and thereby assess relative porpoise abundance in a given location. In most studies, the Time-Porpoise Detector (T-POD, developed by Nick Tregenza, http://www.chelonia.demon.co.uk) has been used (Carstensen et al. 2006, Verfuss et al. 2007, Kyhn et al. 2008). The T-POD has undergone several improvements since its first generation and five different versions presently exist. The newest, the C-POD, is the first digital version, and it allows for detection of broader-band clicks and collects a wider range of data to advance species identification (www.chelonia.demon.co.uk). In 2011-2012, 300 C-PODs will be deployed throughout the Baltic Sea in order to assess the population status of harbour porpoises (http://www.sambah.org/) in these waters. By using a method of distance sampling termed point sampling, where observations/ detections are collected from points (the PODs) rather than lines, estimates of the total abundance of harbour porpoises in the Baltic will be made. However, since no studies using the C-POD have been published yet, this review will focus on the T-POD.

The T-POD is a small self-contained data-logger that logs echolocation clicks from harbour porpoises. It consists of a hydrophone, an amplifier, two band-pass filters and a built-in memory. By applying user defined settings, it detects clicks using filter parameters such as bandwidth and frequency of porpoise echolocation sounds (For specifications of parameters, see Berggren et al. (2006)). Software analyses the data using an algorithm for detecting click train characteristic of the species. The detec-

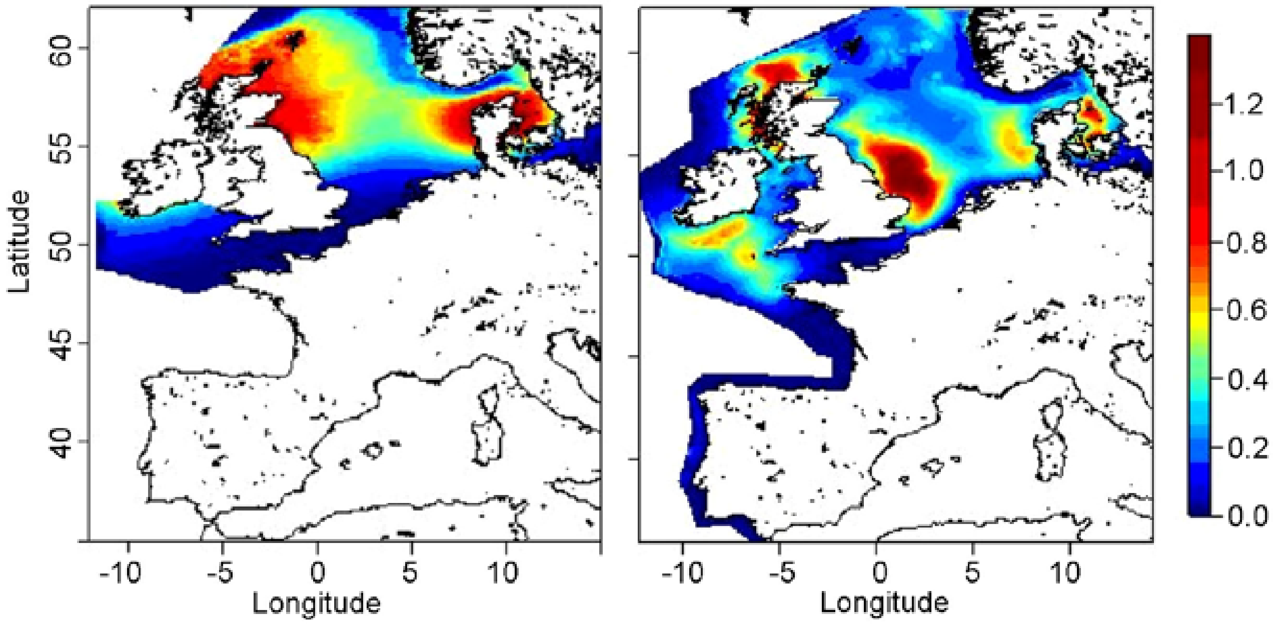

Figure 2. Estimated harbour porpoise density surface (animals per km^2) in 1994 (left panel) and 2005 (right panel). (Modified from SCANS II 2008).

tion range of the T-POD has been examined in the field and these results show a maximum detection range of 300-400 m from the T-POD, with a detection function of 81% from 0-100 m from the T-POD and 31% from 100-200 m (Tougaard et al. 2005). However, the detection function is strictly dependent on the detection threshold of the individual T-POD (Kyhn 2010), which means that the now six different versions of PODs are difficult to compare without calibrations and individually assessed detection functions.

The data obtained from T-POD detections can be analysed in several ways depending on the purpose of the study. However, some commonly calculated variables are porpoise positive minutes (PPM; number of minutes with detections of porpoise clicks), inter click interval (ICI; time between detected porpoise clicks), and encounter frequency (Enc/day; number of encounters recorded per day). An encounter is defined as series of clicks separated by silent periods of ten minutes or longer (Carstensen et al. 2006). These variables may subsequently be compared over any temporal scale. For further analysis, statistical models have been developed to treat T-POD data quantitatively when studying the effects of wind farm construction in a BACI (Before-After-Control-Impact) design (Carstensen et al. 2006).

In Danish waters, static acoustic detections of harbour porpoise echolocation clicks have mainly been carried out in small scale studies, e.g. in monitoring the impact of large marine constructions such as wind farms (Brasseur et al. 2004, Tougaard et al. 2006). In the German Baltic, however, T-PODs were used together with aerial surveys to examine the entire harbour porpoise population in the area and identify important porpoise habitats to be designated as marine protected areas according to the EC Habitat Directive (92/43/EEC, Verfuss et al. 2007). As such, the method may be appropriate for both regional and population studies if a sufficient number of acoustic loggers are deployed. The method has the advantages of being only moderately affected by weather, able to provide data with high temporal resolution, inexpensive, usable with little manpower and yield data that may be used to estimate relative abundance. The disadvantage is that the loggers have low spatial resolution (range < 400 m), which means that a high number of loggers must be deployed to obtain detailed coverage.

2.4 Strandings

The distribution and seasonal variation of stranded porpoises may be the first step towards the development of a species list and produce a rough measure of seasonal variation in distribution (Evans and Hammond 2004, Siebert et al. 2006). However, the findings and reports of stranded animals are highly related to the effort of beach patrolling, and since this effort is unlikely to be evenly distributed, the results are biased towards areas of higher beach patrolling. However, physical examination of stranded porpoises can supply valuable information on genetic differences in populations (Andersen 2003, Wiemann et al. 2010), gender and seasonal parameters (e.g., sexual maturity, mating season and time of parturition) (Lockyer 2003b, Siebert et al. 2006), as well as prey preferences (Benke et al. 1998, Börjesson et al. 2003, Sveegaard et al. In prep., Paper V). This information may be of great value in the monitoring of harbour porpoises if it, for instance, becomes apparent that it is necessary to strengthen protection in the breeding season, or if the local stock of an important prey is declining in a protected area.

3 DISTRIBUTION

The harbour porpoise has a northern circumpolar distribution (Gaskin 1984). It is the most common cetacean in Danish waters and the only cetacean known to breed here besides the occasional occurrence of the white-beaked dolphin (*Lagenorhynchus albirostris*) (Kinze 2007). The harbour porpoise is divided in several populations throughout its range (Andersen 2003, Lockyer 2003a). In Danish waters, studies on satellite telemetry, genetics and morphological studies have identified at least three populations; one in the northern North Sea including Skagerrak and the northern part of Kattegat, one in the Inner Danish Waters (southern Kattegat, Belt Seas, the Sound and western Baltic), and a third in the Baltic Sea (Andersen et al. 1997, Wiemann et al. 2010, Galatius et al. 2010). Information on population boundaries as well as the potential migration between populations is essential to include in management of the species in order to assess the success of protective conservation measures, e.g. restrictions of gillnet fishery.

In this section, I will review and discuss the current knowledge on harbour porpoise abundance and distribution in Danish and adjacent waters. A similar review was conducted in 2008 with the aim of identifying key habitats of harbour porpoises to be designated as Natura 2000 marine protected areas (Teilmann et al. 2008) under the Habitat Directive (92/43/EEC 1992). Therefore, this review aims to summarize the most important results presented in Teilmann et al. 2008, as well as new findings.

3.1 Abundance

In Danish and adjacent waters, several studies have estimated densities in smaller areas based on different methods (Heide-Jørgensen et al. 1993, Gillespie et al. 2005, Kyhn 2010). However, estimates of total harbour porpoise abundance have only been conducted based on internationally coordinated large scale visual surveys in northern European waters; SCANS in 1994 (Hammond et al. 2002) and SCANS-II in 2005 (SCANS II 2008). These estimates were based on distance sampling (Thomas et al. 2010), and the abundance of harbour porpoises inhabiting the western Baltic, the North Sea, the English Channel and the Celtic Sea was

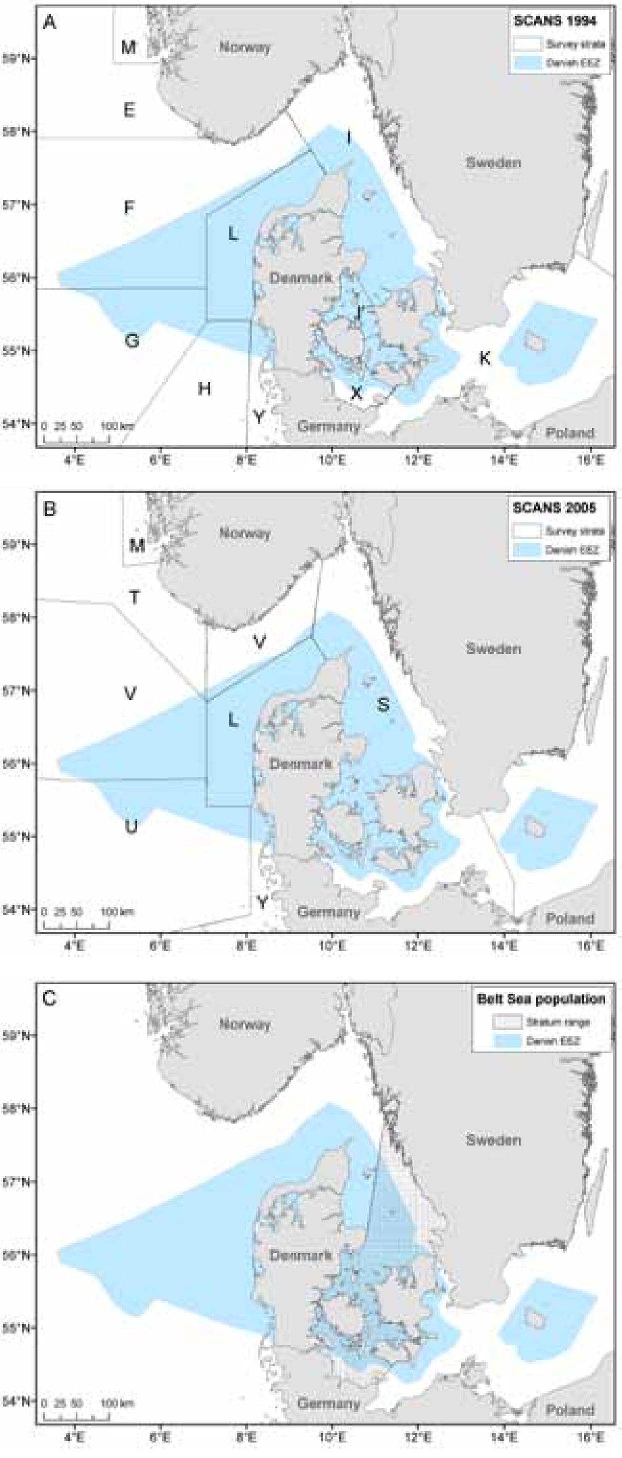

Figure 3. Survey strata from (A) SCANS I (1994), (B) SCANS II (2005) and (C) the extent of the Belt Sea population of harbour porpoises.

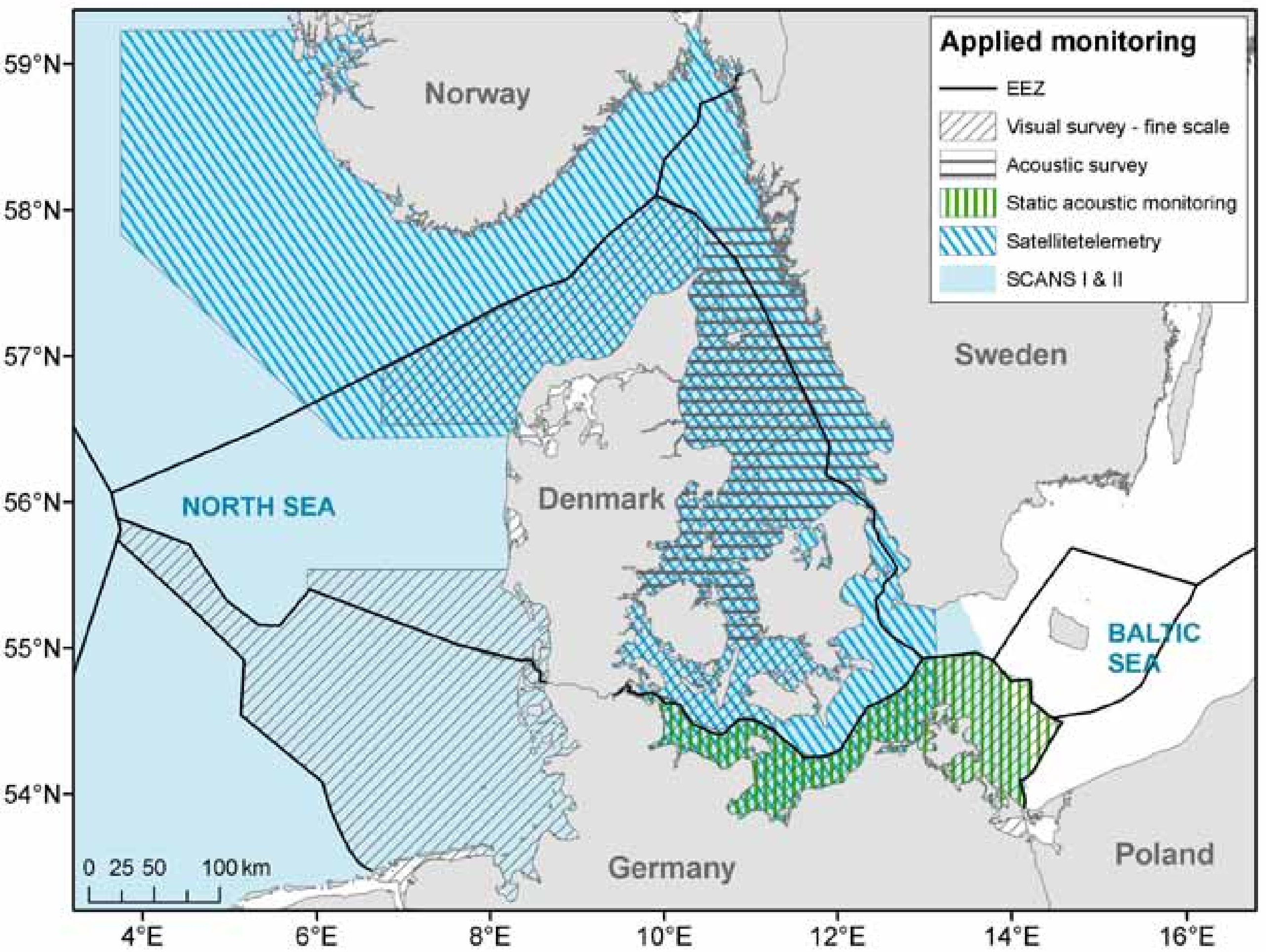

Figure 4. Overview of the methods employed in Danish and adjacent waters. SCANS I & II refer to two broad-scale dedicated visual and acoustic surveys conducted in 1994 and 2005. For satellite tracking, only the area covered sufficiently to identify high density areas is included.

calculated using density surface modelling (DSM) and determined to be 345,132 (Coefficient of Variation (CV) = 0.16) in 1994 and 315,027 (CV = 0.17) in 2005 (SCANS II 2008). Model variables included in the DSM to predict porpoise presence were latitude, longitude and depth in both surveys, and in 2005, distance to coast was incorporated as well. The relatively small difference in total abundance between the two surveys was not statistically significant and was interpreted as no overall change during the ten years. However, the relative distribution of porpoises had shifted from the northern part of the study area (Northern North Sea) to the southern part (English Channel) (Fig. 2). During the surveys, the area was divided into several large blocks (strata) and surveyed visually from either boat or plane. The shape and extent of the majority of these survey blocks was not identical in SCANS and SCANS-II, making comparison on a smaller scale, i.e. for a single population or within national boundaries non-feasible. As an example, Danish waters were covered by eight different strata in 1994 and six different strata in 2005 (Fig. 3A-B). The unequal division of strata is impractical for monitoring plans on smaller scales, e.g. for biological populations or within national borders in local management plans. The harbour porpoises inhabiting Kattegat, the Belt Seas, the Sound and the Western Baltic are believed to constitute a genetically distinct population (Andersen 2003, Wiemann et al. 2010), hereafter called the Belt Sea population. This population is particularly important in management issues, since it represents the only possible source for new gene flow into the small and endangered population of harbour porpoises in the Baltic Sea (Hiby and Lovell 1996, Koschinski 2002, Berggren et al. 2004). Indeed, in 2008, the Baltic Sea population of porpoises was categorized as 'Critically Endangered' on the IUCN red list (www.iucnredlist.org). The majority of the Belt Sea population resides in Danish territory and since the management plans for this population are about to developed, information on population range and abundance are or high importance (see later section on Protection below). Consequently, we conducted separate estimates for the Belt Sea

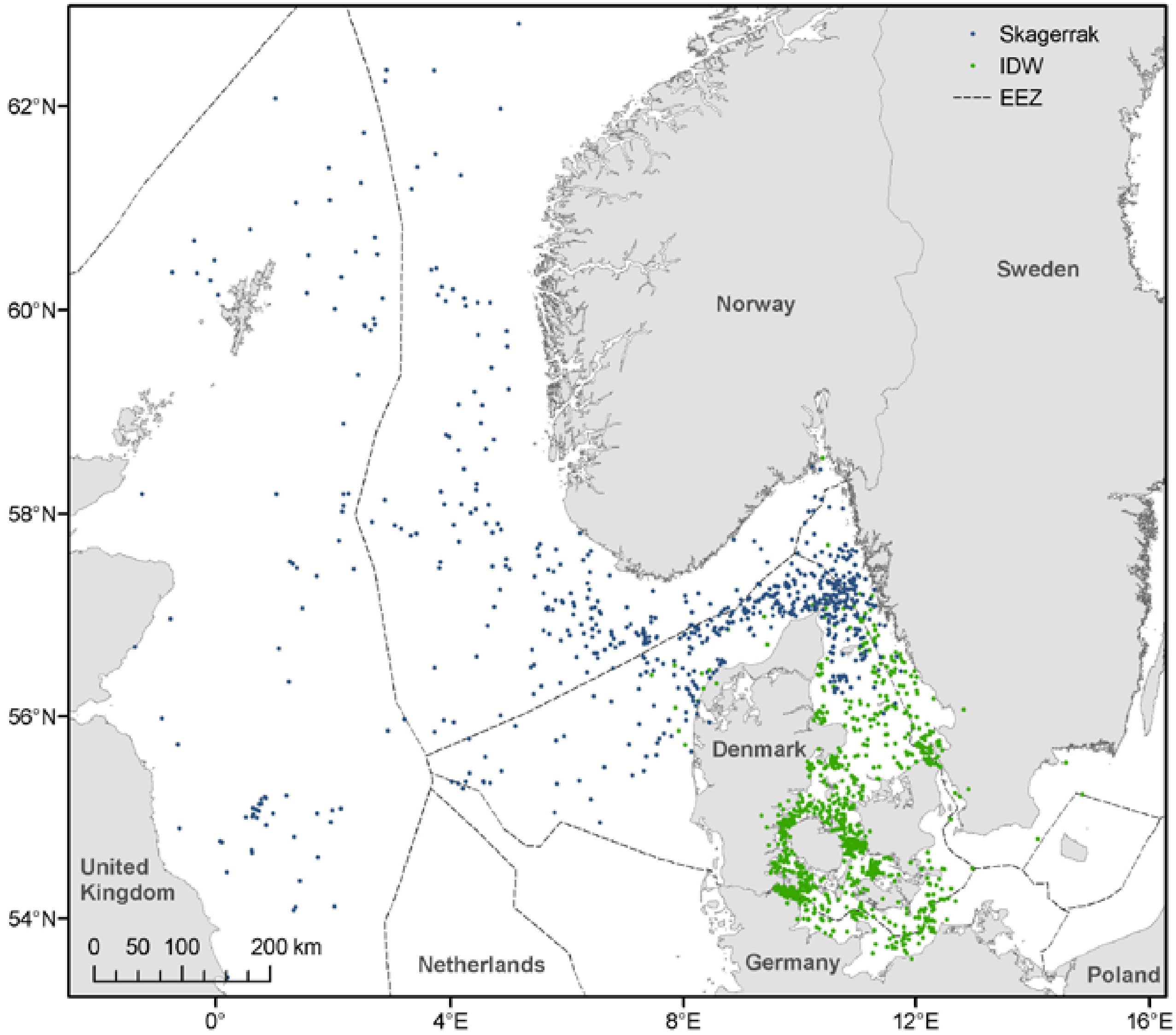

Figure 5. Locations (one per every fourth day per porpoise) of the 64 harbour porpoises, *Phocoena phocoena*, tracked between 1997 and 2007. Locations from porpoises in the Inner Danish waters (IDW) are green (N = 38 porpoises, n = 933 locations) and locations from porpoises tagged in Skagerrak are blue (N = 26 porpoises, n = 665 locations) (from Sveegaard et al. In press, Paper II).

population based on the data from the two SCANS surveys (Teilmann et al. In prep., Paper IV). This required the designation of a precisely determined border between the Skagerrak/North Sea population and the Belt Sea population, although satellite tracking data has shown that the border represents a wider area, a transition zone, between 56°30′N and 57°30′N. However, based on satellite tracking data from each of the two populations, we calculated a diagonal boundary from Djursland in Denmark to Lysekil in Sweden (Fig. 3C). The boundary between the Belt Sea population and the Baltic Sea population is defined by the underwater ridges, Drogden Sill in the Sound and Darss Sill in the Kadet Channel (Wiemann et al. 2010). However, for the abundance estimates, the population area was limited by the possibilities of comparing the two SCANS surveys, and since the K-strata in 1994 had too few observations for an abundance to be estimated, the boundary were defined as the northern Sound and Fehmarn Belt (Fig. 3C). We did not use DSM estimates, but instead Line Transect (LT) estimates, since the bathymetry in the Belt Sea has very little variation (max. depth <80 m) and no biologically meaningful variable could therefore be included in the modelling. The population size was calculated to be 27,767 (CV = 0.45, 95% confidence interval (CI) = 11,946-64,549) in 1994 and 10,865 (CV=0.32, 95% CI = 5,840-20,214) in 2005. Due to the large variations caused by the relatively small survey area with relatively few transect lines this difference is not statistically significant. Nevertheless, we recommend that further studies are conducted to examine if the observed trend in fact represents a decrease in the Belt Sea population during the last decade.

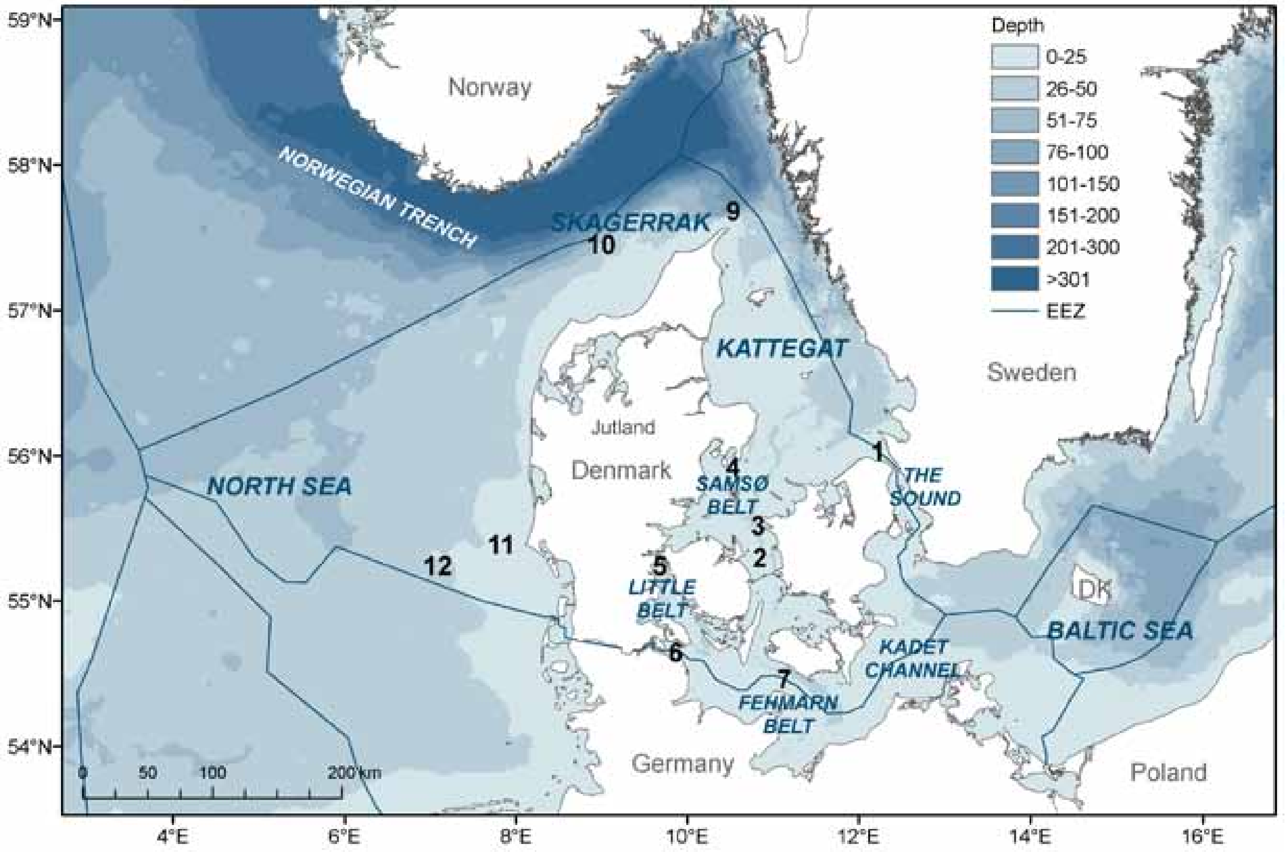

Figure 6. Map of Denmark and the Danish EEZ with numbers indicating the high-density areas for porpoises: Northern Sound (1), Great Belt (2), Kalundborg Fjord (3), northern Samsø Belt (4), Little Belt (5), Smålandsfarvandet (6), Flensborg Fjord (7), Fehmarn Belt (8), Tip of Jutland (9), Norwegian trench (10), Horns Reef (11), Southern North Sea (12). The numbers are arbitrary.

3.2 Distribution in Danish and adjacent waters

During the last twenty years, the distribution of harbour porpoises in Danish and adjacent waters has been examined by means of visual surveys from boat and plane (Heide-Jørgensen et al. 1992, Heide-Jørgensen et al. 1993, Hammond et al. 2002, SCANS II 2008), detections of incidental sightings and strandings (Kinze et al. 2003, Siebert et al. 2006), passive acoustic monitoring (Verfuss et al. 2007), acoustic surveys (SCANS II 2008, Sveegaard et al. In press, Paper III) and satellite tracking (Teilmann et al. 2007, Sveegaard et al., In press, Paper II). The effort has, however, not been distributed evenly across the different waters. For instance, Kattegat and the Belt Seas have been examined with all of the mentioned methods while only a few visual survey transects have been conducted in the Danish part of the Central North Sea (Fig. 4).

Data from satellite tracked harbour porpoises cover a large part of the Danish marine territory and has been the primary source of information for the identification of the high-density areas to be designated as SACs (Teilmann et al. 2008). Sveegaard et al. (In press, Paper II) tagged 64 porpoises (24 porpoise near Skagen and 40 porpoises along the eastern coast of Jutland, in the Belt Sea and in the Danish part of the western Baltic) from 1997-2007. The tracked porpoises were not distributed evenly, but gathered in certain high-density areas (Fig. 5). These are presumably key habitats, defined as the parts of a species' range essential for day-to-day survival, as well as for maintaining a healthy population growth rate. Areas that are regularly used for feeding, breeding, raising calves, and migration are all part of key habitats (Hoyt 2005). Based on the satellite tracking data, the following key habitats were identified within the range of the Belt Sea population: northern Sound, Great Belt, Kalundborg Fjord, northern Samsø Belt, Little Belt, Smålandsfarvandet, Flensburg Fjord, and Fehmarn Belt.

For the Skagerrak population, a large area at the border between northern Kattegat and the south-eastern Skagerrak, called the Tip of Jutland, as well as three smaller areas along the Norwegian trench were recognized (Fig. 6). The harbour porpoises were tagged in an area believed to contain two distinct populations (the Belt Sea population and the Skagerrak/North Sea population) and an approximate abundance of 44,000 individuals (estimated during SCANS-II, abundance summarized for area S, V and L, see sections on Visual surveys and Abundance) (SCANS II 2008). The obtained satellite tracking data were used to examine the distribution of these populations. Whether the distribution of the 82 tagged animals represents a population of this size must be tested, which was done in Sveegaard et al. (In press, Paper II). Here, we compared the overall and seasonal distribution of 64 of the tagged harbour porpoises, 1997-2007, to the relative distribution of harbour porpoises found during six acoustic surveys (one every second month) in 2007 using a towed hydrophone in Kattegat, the northern part of the Belt Sea and the Sound. We found a good accordance between the two methods with significantly more acoustic detections in the high-density areas already identified by satellite tracking. We concluded that the results from satellite tracking indeed were representative for the overall distribution of the harbour porpoise population in the area.

The existence and stability of the high-density areas were further supported and confirmed by aerial surveys and static acoustic monitoring in the Western Baltic (Gillespie et al. 2005, Siebert et al. 2006, Verfuss et al. 2007), and by aerial surveys in Skagerrak (Teilmann et al. 2008).

In the North Sea, less information is available on harbour porpoise distribution, especially in the central part that is only covered by the two SCANS surveys (Fig. 4). In both surveys, however, porpoises were observed in the area (Area L-F in 1994 and L-V in 2005). Further studies are needed if presence or actual high-density areas are to be identified.

In the southern part of the Danish North Sea, at least 40 aerial surveys have been conducted from 1999 to 2007. High-density areas were primarily found along Horns Reef (11) and along the German border (12) about 50-100 km offshore (Fig. 6) (Teilmann et al. 2008). This last area continues on the German side of the EEZ identified by German aerial surveys (Gilles et al. 2009). During these 40 surveys, high concentrations of porpoises were also found at Dogger Bank along the Danish border, and it is likely that this high density continues also onto Danish territory.

3.2.1 Seasonal distribution

The distribution of harbour porpoises and the location of high-density areas have been found to change seasonally in Skagerrak, Kattegat and the Belt Seas: The Skagerrak/North Sea population moves west in the winter and the Belt Sea population moves south (Sveegaard et al. In press, Paper II, Sveegaard et al. In press, Paper III). This change is not a coordinated migration but a gradual net movement of the population resulting in very low winter abundance in some of the summer high-density areas, e.g. the Sound.

Seasonal changes in distribution could potentially be related to reproduction, but so far no specific breeding areas have been localized in Danish waters. However, during the first SCANS survey, the highest ratios of calves to adult porpoises were observed in the Belt Seas (Hammond et al. 1995) and since the Belt Sea population inhabiting these waters is rather stationary it is likely that both birth (mainly in June and July) and conception (July-August) also occurs in these waters (Sørensen and Kinze 1994). The calves are nursed for 8-10 months (Lockyer and Kinze 2003), and may be particularly vulnerable in the period after weaning, when they are on their own for the first time: Inexperience can lead to increased susceptibility to bycatch. This is supported by the fact that bycatches are dominated by physically immature porpoises (Lockyer and Kinze 2003). In Danish waters, the pregnancy rate has been found to be between 0.61 and 0.73 calves per year (Sørensen and Kinze 1994).

4 PORPOISES AND PREY

The environmental or biological factors governing harbour porpoise distribution are not well understood. The harbour porpoise is a small whale with limited body fat inhabiting a cold environment, and must consequently feed daily to maintain the necessary energy requirements (Koopman 1998, Lockyer et al. 2003, Lockyer 2007). The distribution of harbour porpoises is therefore believed to follow the distribution of its main prey species (Koopman 1998, Santos et al. 2004).

The harbour porpoise consumes a wide range of prey species and does not rely on a single, narrow range of prey sizes (MacLeod et al. 2006). In the waters between the eastern North Sea and the western Baltic Sea, the major prey species during the last 25 years, were found to be herring (*Clupea harengus*), sprat

(*Sprattus sprattus*), cod (*Gadus morhua*), whiting (*Merlangius merlangus*), gobies (Gobiidae) and sandells (Ammodytidae) (Aarefjord et al. 1995, Benke et al. 1998, Börjesson et al. 2003). The relative importance of these species as harbour porpoise prey varies between regions (Benke et al. 1998, Santos and Pierce 2003). For example, Aarefjord et al. (1995) found that the most dominant prey species (in terms of weight) in Kattegat and Skagerrak was herring, followed by cod, and poorcod (*Trisopterus minutus*), but in the adjacent eastern part of the North Sea, prey were dominated by whiting, followed by cod and long rough dab (*Hippoglossoides platessoides*). The relative importance of each prey species may also vary over time, but little is known about changes in prey preferences on a finer temporal scale. However, Sveegaard et al. (In prep., Paper V) gathered and compared all available data on harbour porpoise diet for the Belt Sea population in Danish waters (see Abundance section) on a seasonal basis and found that while cod were an important prey throughout the year, herring was predominantly consumed in the first and second quarter of the year, gobies mainly in the second quarter and whiting in the third quarter. Consequently, the significance of each prey species may change both spatially and temporally according to the availability of prey.

The question of how prey distributions reflect the movements of harbour porpoises has been examined indirectly by modelling porpoise presence with selected environmental variables which potentially could represent distribution of prey. In European waters, the detections of harbour porpoises from visual and acoustic surveys as well as from satellite tracking of porpoises have been correlated with depth, seabed slope, sediment type, salinity, distance to coast, tidal state and temperature. Of these, depth, distance to coast and tidal state were found to be significant predictors of porpoise distribution in more than one study (MacLeod et al. 2007, Marubini et al. 2009, Bailey and Thompson 2009, Edrén et al. 2010), while sediment type (Bailey and Thompson 2009), temperature (MacLeod et al. 2007) and salinity (Edrén et al. 2010) were found significant in one study each. Although Edrén et al. (2010) advocate that the included variables are selected to serve as proxies for prey distribution, none of the studies attempted to explain the ecological causal relationship between depth, distance to coast or porpoise distribution. Marubini et al. (2009) and Embling et al. (2010) suggested that the discovered association between harbour porpoises and tidal state is likely to reflect changes in prey distribution. Tidal state has previously been found to correlate with porpoise movements in areas containing local frontal zones: Johnston et al. (2005) found that density of porpoises was positively correlated with the presence of an island wake. The wake caused a local front during ebb tide, leading to aggregation of prey. Johnston et al. (2005) also found that porpoise density was significantly greater during flood than ebb tide phases in this focal region. Skov and Thomsen (2008) found a similar result at Horns Reef in the North Sea. Here, small-scale fronts and upwelling created by interactions between the semidiurnal tidal currents and the steep seabed topography was found to be the main driver of the occurrence of harbour porpoises. This study was, however, criticized for the handling of variables in their model, lack of model validation and the use of data collected during the pile-driving phase of a wind farm at Horns Reef (Tougaard and Wisz 2010). In a rebuttal, Skov and Thomsen (2010) comment on the issues raised by Tougaard and Wisz (2010) and reject the critique. Regardless of critique the overall conclusion of Skov and Thomsen (2008) seems plausible, since several other studies find frontal zones to be important habitat drivers. For instance, in two separate studies examining the direct correlation between harbour porpoise presence and their prey on different spatial scales, it was suggested that the development of frontal zones were the potential drivers for the observed porpoise distribution (Sveegaard et al. In prep., Paper VII, Sveegaard et al. In review, Paper VI).

In Sveegaard et al. (In review, Paper VI), we compared the distribution of satellite tracked harbour porpoises in Kattegat and Skagerrak with the distribution of herring and found that densities of porpoises were strongly positively correlated with herring densities, which in turn was correlated with depth. Furthermore, the high densities of herring and porpoises were mainly found in frontal zones, namely along the Norwegian Trench and the turbulent transition between Kattegat and Skagerrak. Although no significant correlation of depth to porpoise distribution was found in this study, the fact that porpoise prey are correlated to depth, may explain why other modelling studies (e.g., Marubini et al. 2009, Bailey and Thompson 2009) at other locations and spatial scales have found porpoise presence to correlate with depth. In Sveegaard et al. (In prep., Paper VII), we examined whether the difference in seasonal porpoise distribution found by satellite tracking and acoustic surveys in a Danish strait, the Sound, were reflected in the choice of consumed prey examined by harbour porpoise stomach content. We found that the season of high density of harbour porpoises was associated with higher diversity of fish, higher availability of a primary prey species (cod), and larger average mass of the individual prey. Furthermore, we suggested that development of frontal zones in the northern part of the Sound in the spring is an important driver for porpoise abundance since it may aid the porpoises in locating their prey.

In conclusion, our current knowledge of drivers for habitat selection by harbour porpoises is incomplete. Recent knowledge indicate that distribution of main prey species, prey diversity, frontal zones, depth and other environmental variables play an important role. However, the level of influence of these different variables seems to vary between areas and possibly seasons. Consequently, I suggest that if availability of prey is to be included in the management of porpoises, e.g. in Natura2000 sites, the correlation between porpoise distribution and biological and environmental variables must be studied within each area.

5 PROTECTION AND MANAGEMENT

The harbour porpoise is listed in annex II and IV of the Habitats Directive (92/43/EEC). This implies that all EU member states are legally obliged to protect harbour porpoises in its entire range, as well as designate Marine Protected Areas (SACs). Together with Special Protected Areas (SPA) designated according to the Birds Directive (79/409/EEC), SACs will form a coherent European network of protected areas namely the Natura2000 network. The Natura2000 network includes both marine and terrestrial areas and is scheduled to be completed by 2012 (European Commission 2007).

The process of designating SACs is divided into two stages described in the article 4 of the Habitat Directive. First, all member states must identify important sites for each species, called Sites of Community Importance (SCI). These sites must be classified according to a list of criteria assessing the relative importance of each area for each of the protected species and habitats, as well as the combined community importance on a national and global level. When these classifications are carried out and approved in the EU, the site will be designated as a SAC. All member states are then legally obliged to take the necessary conservation measures to protect the species and habitats within each SAC and maintain their status as 'favourable'. In Denmark this monitoring will be systematised in the NOVANA-program (www.blst.dk). All member states must report to the EU commission every 6th year on the conservation state of protected species and habitats in the designated SACs. The conservation status for a species will be taken as 'favourable' when three conditions are met: 1) the population is sustainable, 2) its natural range is stable, and 3) the habitat is sufficiently large to maintain the population on a long term basis.

In Denmark, the designation of SACs for harbour porpoises is in progress and currently all areas have the status of SCI. The designation process has been complicated: the Habitat Directive states that: *'for aquatic species which range over wide areas, SACs will be proposed only where there is a clearly identifiable area representing the physical and biological factors essential to their life and reproduction'*. However, as demonstrated in this review, the currently available information is insufficient to identify '*the physical and biological factors essential to life and reproduction*' of harbour porpoises. Consequently, it was decided in the EU, that SACs for porpoises should be selected on the basis of (1) the continuous or regular presence of the species (although subject to seasonal variations), (2) good population density (in relation to neighbouring areas) and (3) high ratio of young to adults during certain periods of the year. Therefore, we examined all existing knowledge of harbour porpoise distribution in Danish and adjacent waters and conducted new acoustic surveys (Teilmann et al. 2008, Sveegaard et al. In press, Paper III). The designation of SCI was then based on knowledge gained from these studies.

The location and spatial extent of selected SCI as well as the location of the identified high-density areas (see section on Distribution) are shown in Fig. 6. Except for area 4 (Northern Samsø Belt) and area 11 (Horns Reef) all the identified high-density areas have been designated as SCIs although the spatial extent of some of the designated areas deviate somewhat from the original extent of the identified high-density areas, e.g. in Great Belt (area 2), where the biological range of the high-density area was larger and at the tip of Jutland (area 9) where the high-density area extended towards the south in Kattegat (Fig. 5) (Sveegaard et al. In press, Paper II).

The monitoring plans for Danish harbour porpoises in its entire range as well as in the identified SACs have not yet been completed. The choice of regulations, e.g. restrictions on fisheries within the protected areas will naturally have a large impact on the efficiency of the SACs and limit the potential threats within the areas. However, at present the implementation of the Habitat Directive has already improved and constricted the regulations on environment and nature conservation within

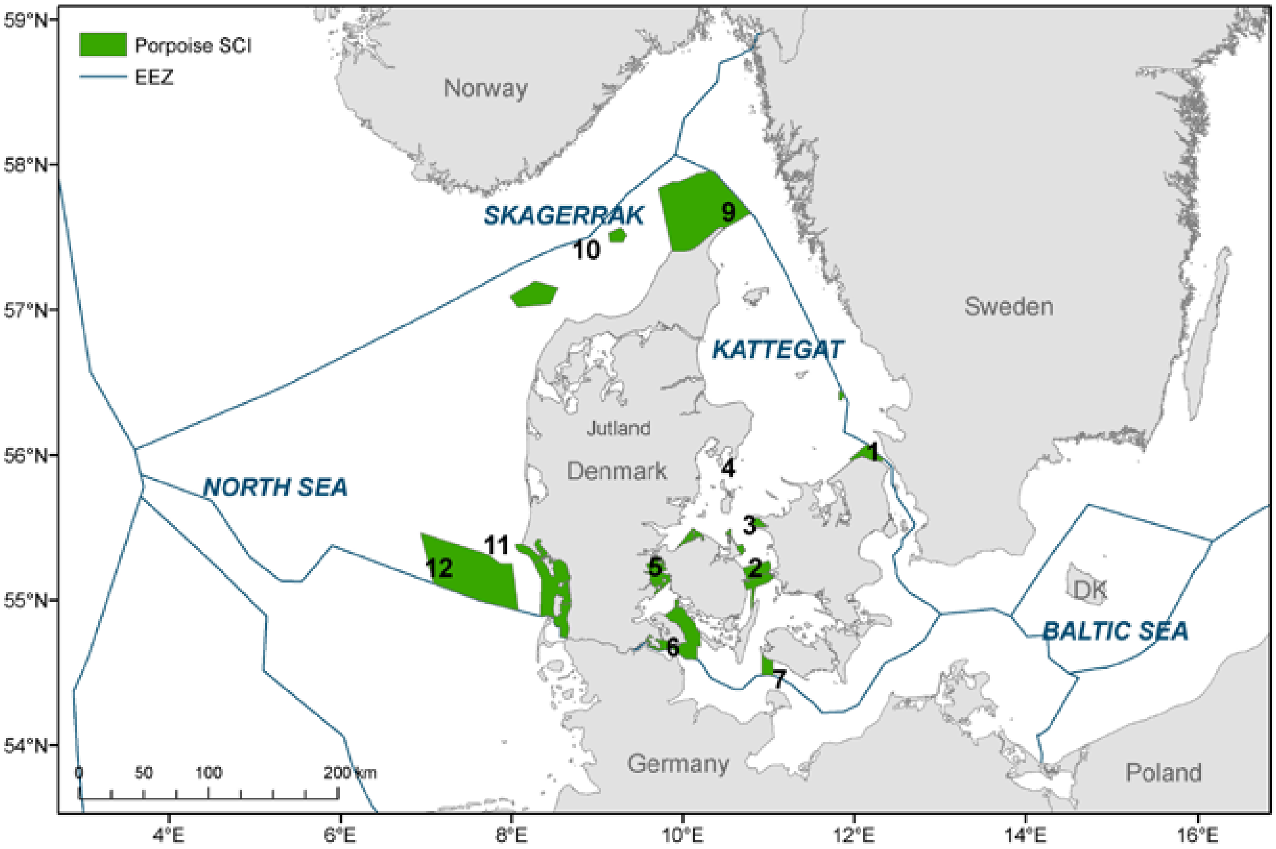

Figure 7. Special Areas of Protection in Danish waters. Numbers illustrate the location of identified high-density areas in Teilmann et al. (2008): northern Sound (1), Great Belt (2), Kalundborg Fjord (3), northern Samsø Belt (4), Little Belt (5), Smålandsfarvandet (6), Flensborg Fjord (7), Fehmarn Belt (8), Tip of Jutland (9), Norwegian trench (10), Horns Reef (11), Southern North Sea (12).

the assigned protected areas. For instance, the designation of a SAC automatically causes a number of restrictions for new anthropogenic influences in the area to come into existence. For example, comprehensive Environmental Impact Assessments (EIA) are required if new developments, e.g. wind farms or bridges are to be approved within or adjacent to a SAC. In order for the development to be approved, the conclusion of the EIA must be that the new development is not detrimental to the population within the SAC.

In later years, much attention has been given to the designation of SACs and the consequential regulations within them. However, since the sizes of SACs merely include a relatively small percentage of the harbour porpoise's range, I reccommend, that further protection beyond the boundaries of the SACs should be implemented. This should focus on mitigation of bycatch as this is currently the biggest threat to the sustainability of Danish porpoise populations (Vinther and Larsen 2004, Larsen et al. 2007).

Management plans must ensure that the abundance of porpoises within each SAC is stable or increasing and further, that the total abundance of harbour porpoises in Danish territory is not declining. Monitoring of each SAC encompass detection of trends in relative density on a regional level. According to the review of methods above, the best methods for this are aerial or boat-based visual surveys, acoustic surveys with towed hydrophones or passive acoustic monitoring (PAM) using data loggers e.g. T-PODs. For the monitoring of changes in total abundance of harbour porpoises, PAM and acoustic surveys are currently not able to provide abundance estimates and thus only aerial or boat-based visual surveys can currently be used for this purpose. Satellite tracking is ideal for monitoring movement (including migrations) and distribution, but not trends in abundance (Berggren et al. 2008a).

Measuring the success of management plans is essential. It is thus important to define clear measurable objectives in both the regional monitoring of SACs and in the monitoring of the entire population. Furthermore, the chosen monitoring methods should be kept consistent to reduce method-related variation and increase power in trend analysis (Berggren et al. 2008a).

Many issues regarding the monitoring of harbour porpoises still need to be addressed. For instance, the SCANS surveys showed that the population in the North Sea had moved from north to south during the ten years between surveys (SCANS II 2008). The cause of this the shift is unknown but declining fish stocks, shifts in prey distribution or anthropogenic disturbances have all been shown to cause changes in distribution of porpoises (Reijnders 1992, Carstensen et al. 2006). How are such shifts to be implemented in national management plans? Should designated SACs, which no longer contains a high density of porpoises, still be subject to expensive monitoring? According to the NOVANA program, the extent of the identified SACs should be evaluated every 6th year and modified according to current research. However, even small spatial changes in the SAC boundaries will have to go through a comprehensive bureaucracy of hearings and approvals, and it is my concern that this will limit the flexibility of the system and consequently the efficiency of the protection scheme. However, the twenty years of harbour porpoise studies in Kattegat, the Belt Seas, the Sound and the western Baltic, discussed in this review, indicate that the harbour porpoise distribution in these waters is relatively stable. This should be tested in future monitoring programmes, e.g. by a time-trend study based on regular acoustic surveys throughout the year and the deployment of acoustic dataloggers in and adjacent to the designated areas. Nevertheless, focussing management effort and economy on protecting the harbour porpoise in its entire range by the mitigation of bycatch, will decrease the problem of potential reallocation of harbour porpoises, and will in my opinion be the best way to ensure the sustainability of harbour porpoise populations.

6 PERSPECTIVES AND RECOMMENDATIONS

Our knowledge of harbour porpoise distribution has increased significantly in the last decade due to developments and deployment of several new techniques. We have been able to identify relatively permanent high-density areas using mainly satellite tracking and acoustic surveys, and we now know more about which factors may act as drivers for harbour porpoise movement. Nevertheless, several issues related to harbour porpoise conservation deserve additional scientific attention.

Clearly, more information on harbour porpoise distribution and abundance in the central North Sea is needed (Fig. 4). Satellite tracked porpoises tagged near Skagen (57°N, 10°E) swam as far west as the UK (1°W) and as far north as 62°N, but did not swim south of 55°N along the west coast of Jutland in Danish territory (Fig. 5) (Sveegaard et al. In press, Paper II) although this area has been found in both Danish and German studies to contain high densities of porpoises, e.g. at Horns Reef (Teilmann et al. 2008, Gilles 2009). This indicates that the porpoises in the south-eastern North Sea may constitute a separate population, and the range of this population could potentially extend north into the central part of the North Sea. The distribution of harbour porpoises in the central North Sea requires more attention and could be examined either by visual or acoustic surveys or possibly by satellite tracking of porpoises caught along the Danish west coast. If high-density areas are located, these should be designated as SACs and included in the Natura2000 network.

A similar lack of knowledge on porpoise distribution and abundance exists in the Baltic Sea. Here, however, as previously mentioned (see section on passive acoustic monitoring), a large scale international project, SAMBAH (www.samhah.org) aims to examine this in 2010-2012 by the methods of PAM. In areas of low density, PAM may be the best monitoring option, since it can be used continuously for months, and the likelihood of porpoise detection increases per hour of monitoring.

In the last few years, the number of studies examining drivers for harbour porpoise habitat selection has increased. Results indicate that porpoises may be influenced by distribution of main prey species, prey diversity, frontal zones, depth and other environmental variables, although the influence of each factor seems to vary between areas. If availability of prey is to be included in the management of porpoises, e.g. in SACs, the correlation between the spatial and temporal distribution of harbour porpoises and biological and environmental variables should be studied more closely. This could be done in several ways. For instance, acoustic surveys detecting both fish and harbour porpoises simultaneously, e.g. using active sonar outside of the porpoise hearing range for fish detection and towed hydrophones for harbour porpoise detection may provide new insight on the correlation of predator and prey. Furthermore, the newest available methods for fish detection such as the 900 kHz multibeam sonar (BlueView Technologies) and the 330 kHz side scan sonar (Imagenex Sportscan) may provide single target resolution of size and wide coverage, yielding an even more detailed image of the prey preferences of porpoises. Based on previous experience, such a survey must be conducted using a relatively silent boat. Furthermore, the spatial fish distribution may change over time and it is thus important to survey both day and night and to cover several seasons to understand diurnal and seasonal variation in the correlation between porpoises and fish.

Another recently developed method for exploring the foraging behaviour of harbour porpoises is the deployment of archival acoustic tags (e.g., A-tags or D-tags) (Akamatsu et al. 2005, Tyack et al. 2006, DeRuiter et al. 2009) onto the animals. Such tags can record the quantity and timing of echolocation clicks as well as diving behaviour and body movements of the porpoise and may thus provide information on the detailed utilisation of the surrounding habitat by each individual harbour porpoise. Echolocation behaviour leading up to and following prey capture can be recognized due to fast-repetition-rate clicks (DeRuiter et al. 2009) and archival tag recordings combined with satellite tags may thus provide information on the location of specific foraging areas, as well as the daily rate and timing of foraging. Furthermore, more knowledge on variation in click repetition rates in relation to area, time of day, depth, diving behaviour or habitat will greatly complement the data obtained from PAM and acoustic surveys.

Finally, the anthropogenic influence and usage of marine areas are constantly increasing. The need for sustainable energy sources has lead to a strong increase in the construction of offshore wind farms. Other marine installations such as underwater parks of turbines to extract ocean current energy are presently being developed. Furthermore, other offshore constructions, such as bridges and tunnels, the extraction of natural resources, overfishing of preferred prey species, and unsustainable bycatch will negatively influence marine mammal populations if not controlled and mitigated. Consequently, it is of major importance that monitoring of marine mammal populations is maintained, both locally in relation to new marine constructions and in the designated SACs, and also on a population level, where the cumulative effects of anthropogenic use of the sea, may appear.

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PAPER II

High-density areas for harbour porpoises (*Phocoena phocoena*) identified by satellite tracking

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High-density areas for harbor porpoises (*Phocoena phocoena*) identified by satellite tracking

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ABSTRACT

The population status of harbor porpoises has been of concern for several years, and the establishment of Marine Protected Areas (MPAs) has been suggested as a method to protect the harbor porpoise (*Phocoena phocoena*, Linneaus 1758) and other small cetaceans. In order to designate MPAs, high-density areas for the species must be identified. Spatial distribution of small cetaceans is usually assessed from ship or aerial surveys. As a potentially more accurate alternative, this study examined the movements and area preferences of 64 harbor porpoises, satellite tagged between 1997 and 2007, in order to determine the distribution in the North Sea, the western Baltic, and the waters in between. Results show that harbor porpoises are not evenly distributed, but congregate in nine high-density areas within the study area. Several of these areas are subject to significant seasonal variation. The study found no differences in the home range size of males and females, but immature harbor porpoises have larger home ranges than mature porpoises. The use of satellite telemetry for identifying areas of high harbor porpoise density can be of key importance when designating MPAs.

Key words: harbor porpoise, *Phocoena phocoena*, small cetacean, conservation, kernel density estimation, key habitat, Marine Protected Area.

In the last few decades, the need to protect small cetaceans in order to maintain sustainable populations has become increasingly apparent. Small cetaceans, such as the harbor porpoise (*Phocoena phocoena*, Linneaus 1758) face threats of incidental bycatch in fishing gear (*e.g.*, Vinther and Larsen 2004), pollution, food depletion (Reijnders 1992), and other anthropogenic disturbances such as underwater noise, shipping, oil and gas exploration, as well as construction at sea including bridges and offshore wind farms (*e.g.*, Carstensen *et al.* 2006).

The establishment of Marine Protected Areas (MPAs) has been suggested as a method to protect small cetaceans (*e.g.*, Hoyt 2005). In the EU, all relevant member states are legally obliged to protect the harbor porpoise by designating MPAs, referred to as Special Areas of Conservation (SAC) according to the EC Habitat Directive (92/43/EEC 1992). The designation of marine SAC in the EU is scheduled to be completed by 2012 (European Commission 2007).

A first step toward designation of MPAs for cetaceans is to identify the key habitats of the target species. Key habitats refer to those parts of a species' range that are essential for day-to-day survival, as well as for maintaining a healthy population growth rate (92/43/EEC 1992). Areas that are regularly used for feeding, breeding, raising calves, and migration are all part of the key habitats (*sensu* Hoyt 2005). For the harbor porpoise, knowledge of the physical and biological factors defining key habitats is currently insufficient. It may, however, be assumed that the areas with the highest porpoise densities are also the areas where factors essential to life and reproduction are best fulfilled (European Commission 2007). Hence, the designation of MPAs may be based on the density of harbor porpoises.

Until recently, distribution of small cetaceans has mostly been estimated visually by ship and aerial surveys (Heide-Jørgensen *et al.* 1992, 1993, Hammond *et al.* 2002, Scheidat *et al.* 2004). However, visual surveys can only be conducted in daylight under calm weather conditions, which generally limits large-scale surveys to the summer months (Hammond *et al.* 2002, Teilmann 2003). In the last decade, acoustic surveys, in which an array of hydrophones is towed behind a vessel, have been applied (Gillespie *et al.* 2005). The hydrophones record the echolocation clicks emitted by the porpoises and can thereby provide a relative measure of abundance also under less favorable weather conditions. In Germany, aerial surveys intended to identify MPAs for harbor porpoises were successfully supplemented in areas of low density by stationary acoustic data loggers (T-PODs) (Verfuss *et al.* 2007).

In the North Sea, the western Baltic, and the waters in between, two large-scale studies of porpoise distribution have been conducted, namely the two Small Cetacean Abundance in the North Sea (SCANS) surveys in 1994 and 2005 (Hammond *et al.* 2002, Anonymous 2006). These were, however, not detailed enough for small-scale identifications of high-density areas, but intended for large-scale abundance estimation of porpoises in European waters. In the last decade, satellite tagging has been conducted in order to investigate harbor porpoise movement, behavior, and presence in relation to environmental factors (Teilmann *et al.* 2007, Edrén *et al.*, in press). Satellite tracking can provide detailed information on individual movements for up to a year and has the advantage of combining temporal and spatial information on a broader scale.

This study uses satellite telemetry data collected from 64 individual porpoises over a 10-yr period to identify key habitat use from the North Sea through Skagerrak, Kattegat, and Belt seas to the western Baltic.

MATERIALS AND METHODS

Study Area

The study area was divided into two areas based on tagging locations and lack of porpoise movements between the two areas: (1) the southern Kattegat, Belt Sea, and western Baltic (defined as the Inner Danish Waters, hereafter IDW) and (2) northern Kattegat, Skagerrak, and northeastern North Sea (defined as the waters north of Læsø, hereafter Skagerrak) (Fig. 1). The main part of the IDW is between 10 and 40 m deep and due to the many islands the only passage from the Baltic proper to Kattegat is through the narrow straits of Little Belt (<2 km wide), Great Belt (18 km wide), and Øresund (<7 km). The North Sea and Skagerrak includes deeper waters, in particular, the Norwegian Trench that runs along the Norwegian/Danish border and represents a sudden drop in depth from 100 to 700 m.

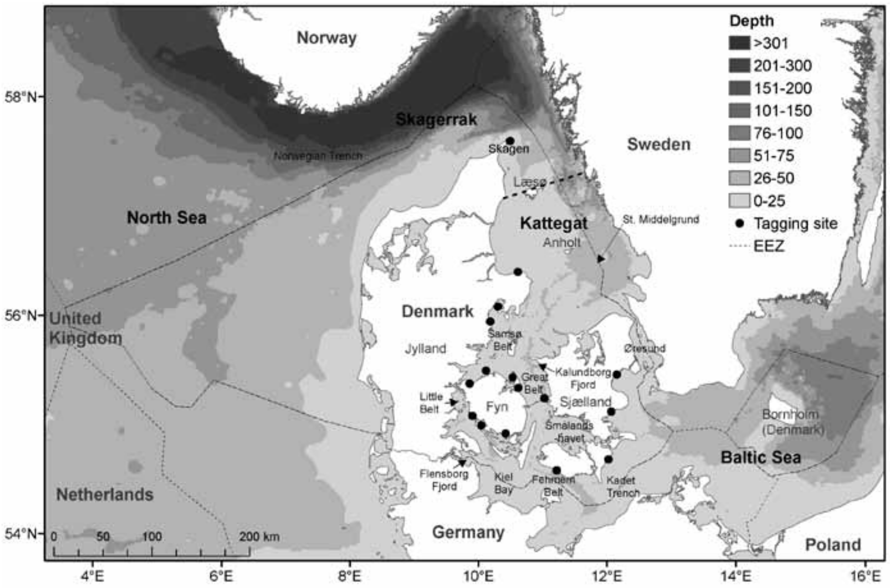

Figure 1. Map of the study area with names mentioned in the text indicated. The locations of the pound nets where the harbor porpoises, *Phocoena phocoena*, were caught and tagged are indicated with black dots. The bold dashed line indicates the division of Skagerrak and the Inner Danish waters. Thin dashed line indicates international Exclusive Economic Zones (EEZ). Map projection universal transverse Mercator, Zone 32N, WGS84.

Satellite Tagging of Harbor Porpoises

Twenty-four harbor porpoises were tagged at Skagen on the northern tip of Jylland between May 2000 and September 2003 and 40 harbor porpoises were tagged in IDW from April 1997 to October 2007 (Fig. 1). The porpoises were either assigned to the IDW group or the Skagerrak group depending on where the majority of the tracking period was spent. This assignment was performed to objectively categorize the porpoises tagged in Kattegat near the border between the two groups (Fig. 1).

Porpoises were caught incidentally in pound nets. A pound net is a Danish type of trap fishery consisting of a long net of up to 1 km leading the fish such as herring (*Clupea harengus*), mackerel (*Scomber scombrus*), garfish (*Belone belone*), and eel (*Anguilla anguilla*) from shore toward the main net. The main net consists of several compartments each leading the fish or porpoise further into the net. The last of the main nets is constructed in the shape of a pot allowing the trapped porpoise to breathe at the surface.

Harbor porpoises were usually tagged within 24 h of being discovered by the fisherman. Six different types of transmitters were used: Telonics ST-10 and ST-18; Wildlife Computers SDR-T10, SDR-T16, and SPOT2; and Sirtrack Kiwi 101, taking advantage of technical developments over the 10-yr study period so the smallest and most hydrodynamic tags were always used. All transmitters used the Argos system. Tags were duty cycled to transmit every 1, 2, 3, or 4 d and programmed to give 50–1,000 transmissions per duty day (Teilmann *et al.* 2008). The transmitters weighed 105–240 g in air. Prior to attachment, the dorsal fin was anaesthetized with 5% lidocaine salve. Each transmitter was attached by perforating the fin using a 6-mm cork borer and subsequently fastening the transmitter using 2–3 polyoxymethylen 5-mm pins covered with silicone tubes. The pins were attached to the transmitter on one side of the dorsal fin and secured with a backing plate and iron nuts on the opposite side to allow the transmitter to detach after about 1 yr. The animal was released after about 30 min (for more details on tagging procedure and effects of tagging, see Geertsen *et al.* 2004, Teilmann *et al.* 2007, and Eskesen *et al.* 2009).

Contact with the porpoises was not evenly distributed throughout the year because the majority of animals were tagged in spring (March–May), which is the main season for the pound net fishery (Table 1).

Data Analysis

The locations of the tagged animals were determined by the ARGOS system maintained by Service Argos. Locations are classified by the Argos system into one of six location classes (LC) according to level of accuracy (3, 2, 1, 0, A, B) measured in kilometers of uncertainty for latitude and longitude, respectively. Studies have shown that there can be significant error in all LCs (up to several kilometers), but that even the low-accuracy locations may provide useful and valid information if they are appropriately filtered (*e.g.*, Vincent *et al.* 2002). Thus, all LCs were used in this study after being filtered by an SAS-routine, Argos-Filter v7.03 (Douglas 2006). The filter is a Distance-Angle-Rate (DAR) filter and applies user-defined settings for distance between successive locations, turning angles and maximum swim speed to filter out the most unlikely locations. The filter is comparable to the R-based Speed, Distance, Angle (SDA) filter tested by Freitas *et al.* (2008). They found that this type of filter was very efficient at removing unrealistic low-accuracy locations (0, A, and B as defined by Argos), but preserved a significantly higher percentage of high-accuracy

Table 1. Monthly distribution of numbers of active transmitters on harbor porpoises (HP) divided by age and sex in the Inner Danish waters (IDW) and Skagerrak between 1997 and 2007. Mature females are defined as length ≥143 cm and mature males as length ≥135 cm (Lockyer and Kinze 2003).

Group	Age group	Total HP	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
IDW	Mature F	5	0	0	0	3	5	4	2	2	1	1	1	0
	Mature M	7	0	0	0	4	5	5	4	1	1	2	3	1
	Immature F	11	3	3	2	8	10	9	7	5	1	1	3	3
	Immature M	15	3	2	2	4	7	7	7	7	6	8	8	4
	Total	38	6	5	4	19	27	25	20	15	9	12	15	8
Skagerrak	Mature F	1	1	1	1	1	1	0	0	0	0	0	1	1
	Mature M	5	2	1	1	1	1	0	0	3	2	1	2	2
	Immature F	6	1	1	1	0	2	4	4	4	4	2	2	1
	Immature M	14	5	3	3	3	6	7	4	6	10	9	9	8
	Total	26	9	6	6	5	10	11	8	13	16	12	14	12
Both groups	Total	64	15	11	10	24	37	36	28	28	25	24	29	20

locations (1, 2, and 3) than filters only based on swimming speed, such as the filter used by Vincent *et al*. (2002). Filter test of our data gave similar results and it was concluded that the DAR filter was appropriate for the analysis in this study. For an example of the DAR filtering method, see Appendix 1 in the online supplementary material. The filter settings for this study were: maxredun = 5 (distance between locations in kilometers. If two locations are within close distance of each other, here <5 km, they are both retained, because the likelihood of both being wrong is small), minrate = 10 (maximum swim speed, kilometer/hour. Locations leading to swim rates >10 km/h are excluded), ratecoef = 10 (angle between vector lines to previous and following location, that is, if this angle is <10° the location is excluded). The minrate value was selected based on velocity measurements of a wild harbor porpoise where average speed was 5.3 km/h and close to 95% of all recordings were less than 10 km/h (Teilmann 2000). The value of 10 km/h was chosen to avoid overestimation of high swimming speed. All other settings were set as default. Locations from all six LCs were filtered and the most accurate location was selected for each day resulting in a total number of 4,583 locations. Daily locations were selected automatically from the filtered dataset by the Argos Filter routine based on LC level and number of uplinks per transmission.

Wildlife telemetry data are inherently spatially and temporally nonindependent because sequentially collected telemetry locations are serially correlated and animals may display individual behavior. Thus, pooling all data is only justifiable when behavior do not differ between individuals (Aebischer *et al.* 1993), which can not be ruled out in this study. Consequently, this study applied two techniques: (1) by weighing each animal equally in the analysis (Fieberg 2007) the porpoise becomes the sampling unit instead of the telemetry location, and pooling of data across individuals is avoided (Aebischer *et al.* 1993. For further information on weighing, see Appendix 2 in the online supplementary material) and (2) the data sets were subsampled according to calculated time to independence, that is, the minimum time it takes for an animal to cross its entire range (Rooney *et al.* 1998). In this study, porpoises were recorded traveling up to 100 km/d in a straight line. The distance from Skagen to Kiel Bay, that is, the home range of the IDW group is approximately 380 km. Thus, only locations from every fourth day for each individual were used in the analysis.

Furthermore, to avoid overrepresentation of the area of the tagging site, the average daily distance from the deployment site were plotted for all individuals. A tree-regression analysis (Crawley 2002) showed that days 0–4 deviated significantly from day 5 and onward. Consequently, all locations from days 0–4 were removed from the analysis.

The telemetry data were imported into ArcGIS 9.3 (ESRI) and the locations mapped with the Zone 32 (N) Universal Transverse Mercator projection, using the WGS 1984 datum.

To identify key habitats for harbor porpoises, kernel density estimation grids were produced in ArcMap V9.3 using the fixed kernel density estimator (Worton 1989) by means of Hawth's Analysis Tool V3.27 (Beyer 2004). Smoothing factor (bandwidth) was set to 20,000 and output cell size to 1 km^2. This was based on thorough inspection of kernel contours during tests of alternate band-width as recommended by Beyer, the creator of Hawth's Analysis Tools. For further explanation of the chosen smoothing factor, see Appendix 3 in the online supplementary material.

The kernel density estimate is a nonparametric estimation that calculates the density distribution from a random sample of Argos locations, for example, from one or more satellite tagged porpoises. By determining the smallest possible area containing user-specified percentages of the locations, the kernel grid was divided into percentage volume contours from 10% to 90% in 10% intervals. For instance, the 10% volume contour consists of the smallest possible area containing 10% of the locations used to generate the original kernel density estimation grid. This means that the area within the 10% contour represents areas with highest density and the 90% contour almost the entire range of the porpoises.

The kernel density estimation tool unfortunately does not give the possibility of excluding land during the analysis. Thus, the kernel contours (especially the larger ones) will extend onto land areas and thereby mask the coastline making the distribution maps difficult to read. In order to avoid this, the kernel contours are placed underneath the land layer on all maps. As a measure for comparing porpoise distribution, a high-density area was arbitrarily defined as kernel percent volume contours of $\leq$30%. The outer contour lines of the 30% polygons are highlighted on maps for illustration purposes. Area size of all kernel polygons and the proportion extending on to land were calculated.

The relative size and form of the kernel density estimation grid is dependant on the total number of locations and their distribution, that is, adding more porpoise locations to the analysis may alter the shape of the high-density areas. To challenge the validity of the high-density areas determined by the kernel density estimator, results were compared to results obtained for the same data using a grid-based method, which takes into account the inaccuracy of each Argos location and where each grid cell is independent of other grid cells and the total number of locations (Tougaard *et al.* 2008). Both methods identified the same high-density areas. For further explanation of the comparison, see Appendix 4 in the online supplementary material.

Variation in the distribution of porpoises was analyzed by seasons, defined as winter (December–February), spring (March–May), summer (June-August), and autumn (September–November). The unit of analysis was the individual porpoises' median latitudinal and longitudinal location, analyzed according to season in SPSS using one-way ANOVA followed by Fisher's least significant difference *post hoc* tests (*i.e.,* mean median location by season). To meet assumptions of normal distribution of data and homogeneity of variance, median locations were rank transformed prior to analysis. Data from the IDW and Skagerrak groups were analyzed separately. A single porpoise from IDW displayed a different movement pattern than the rest of the group and was excluded from the analysis of seasonal movements.

Area sizes for kernel density polygons (10%–90%) were calculated by age-class (immature and mature) and sex for the IDW group and the Skagerrak group, respectively.

RESULTS

Satellite Telemetry

The period of transmission from the tagged porpoises varied between 14 and 349 d (median = 98 d) and the average number of transmissions per porpoise per active transmission day was 1.87 ± 0.84. The 64 porpoises were grouped according to the area in which they spend the majority of their time. The 24 porpoises tagged at Skagen (the Skagerrak group) never moved south of Anholt (Fig. 1). Of the 40 porpoises tagged in IDW, two porpoises, tagged in the northern part of the IDW, swam immediately after tagging north into Skagerrak and the North Sea and stayed

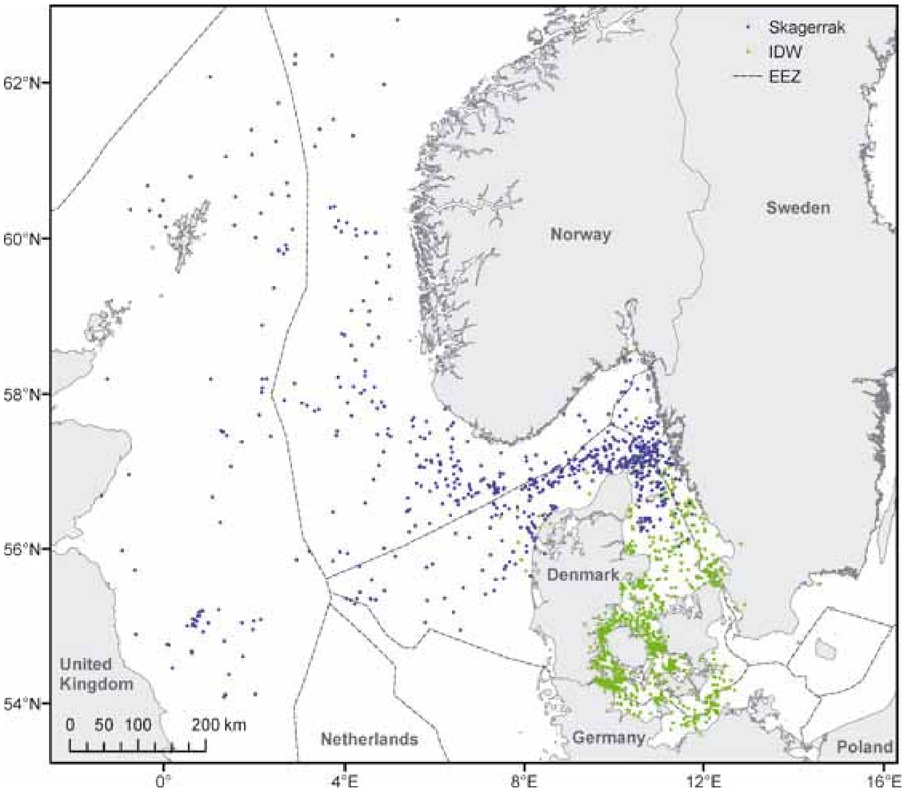

Figure 2. Locations (one per fourth day per porpoise) of the 64 harbor porpoises, *Phocoena phocoena*, tracked between 1997 and 2007. Locations from porpoises in the Inner Danish waters (IDW) group are green ($N = 38$ porpoises, $n = 933$ locations) and locations from porpoises tagged in the Skagerrak group are blue ($N = 26$ porpoises, $n = 665$ locations). Map projection universal transverse Mercator, Zone 32N, WGS84. Dashed line indicates international Exclusive Economic Zones (EEZ).

there for the entire contact period. Consequently, they were considered belonging to the Skagerrak group. There was little overlap between tracks from the IDW group ($n = 38$) and the Skagerrak group ($n = 26$) (Fig. 2). Furthermore, the Skagerrak group displayed a significantly faster average swim rate (0.85 km/h) than the IDW group (0.64 km/h) (Student's t-test, $P < 0.05$). We found no significant difference in average swim rate between mature (0.73 km/h) and immature porpoises (0.79 km/h).

To avoid autocorrelation, only locations from every fourth day for each individual were used in the analysis. This reduced the data set by 67%, but did not alter the resulting high-density areas.

Distribution

The kernel density percent volume contours of the 38 IDW porpoises and the 26 Skagerrak porpoises demonstrate that the North Sea and western Baltic is not utilized evenly by the tagged harbor porpoises (Fig. 3). The high-density areas for the entire

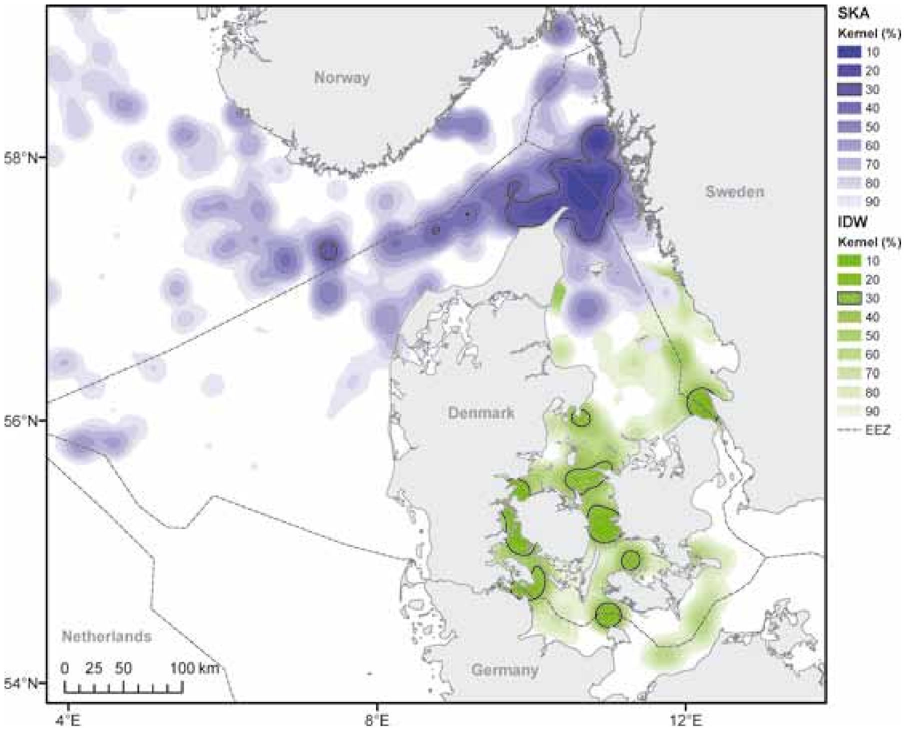

Figure 3. All year distribution of harbor porpoises *Phocoena phocoena* tagged between 1997 and 2007 displayed by fixed kernel density based on one location every four days from each other. The Inner Danish waters (IDW) group are shown in green ($N = 38$ porpoises, $n = 950$ locations) and the Skagerrak group (SKA) are shown in blue ($N = 26$ porpoises, $n = 665$ locations). Black line indicates high-density areas defined as the 30% kernel contour. Projections as in Figure 2. Dashed line indicates international Exclusive Economic Zones (EEZ). Kernel layers are placed below the land layer.

year, defined as kernel density contours ≤30%, were found to be northern Øresund, northern Samsø Belt, Kalundborg Fjord, Little Belt, Great Belt, Smålandshavet, Flensborg Fjord, and Fehmarn Belt for the IDW group and a large area at the border between northern Kattegat and the southeastern Skagerrak (hereafter called the tip of Jylland) as well as three smaller areas along the Norwegian trench for the Skagerrak group (see Fig. 1, 3).

Proportion of land for each kernel percentage contour within the Skagerrak and the IDW group were similar but varied greatly between the two groups. In the IDW group, the percentage of land within each kernel was 22%–30% and for the Skagerrak group 1%–3% (see Fig. 4). This difference is due to the morphology of the IDW with many island and belts *vs.* Skagerrak and the North Sea with much larger open oceans.

In spring and summer (the reproductive period), the Skagerrak porpoises stay close to the tip of Jylland while the IDW animals spread out in the entire range of their distribution (Fig. 5). The high-density areas for the spring and summer are the tip of Jylland, Store Middelgrund, northern Øresund, southern Samsø Belt, Smålandshavet,

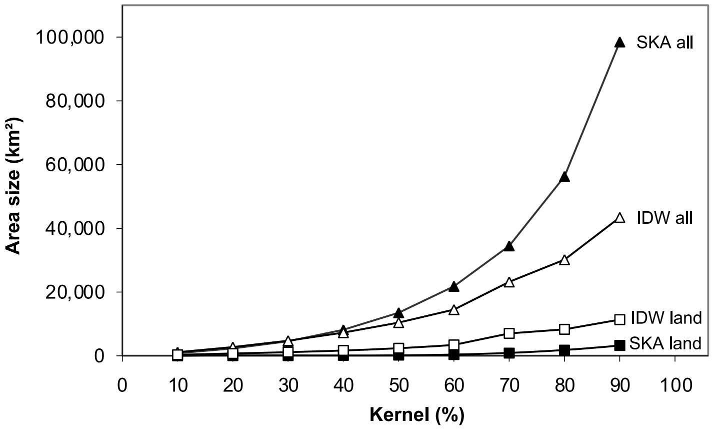

Figure 4. Area size of each kernel density contour and the area comprising land within each kernel for Inner Danish Waters (IDW) ($N = 38$ porpoises) and the Skagerrak group (SKA) ($N = 26$ porpoises).

Little Belt, Flensborg Fjord, Great Belt, and Fehmarn Belt (Fig. 1). In autumn and winter the distribution is somewhat different, with the Skagerrak porpoises moving further west into the northeastern North Sea (although high porpoise density still remains in Skagerrak) and the IDW porpoises moving south avoiding the Kattegat area. The main high-density areas for autumn and winter are the tip of Jylland, an area along the slope to the deep Norwegian Trench, the southern Little Belt, Flensborg Fjord, Great Belt, Kalundborg Fjord, Fehmarn Belt, and the Cadet Trench.

Based on median location as the unit of analysis, the central tendency (mean of medians) in these locations differed significantly between seasons. Whereas the IDW population shows no seasonal variation in longitudinal locations (one-way ANOVA, $F_{3,75} = 0.07$, $P = 0.98$), the southward movements from spring to winter is significant (one-way ANOVA, $F_{3,75} = 2.85$, $P = 0.043$; significant *post hoc* tests: spring–autumn and spring–winter, $P = 0.030$) (Fig. 6). In contrast, the Skagerrak (SKA) shows no overall latitudinal movements during the course of the year (one-way ANOVA, $F_{3,57} = 0.15$, $P = 0.93$), whereas the longitudinal westward movements into the North Sea from spring to winter is statistically significant (one-way ANOVA, $F_{3,57} = 3.42$, $P = 0.023$; significant *post hoc* tests: spring–winter and summer–winter, $P \leq 0.026$) (Fig. 6).

The combined home range, that is, the kernel density percentage contours (10%–90%), of the immature porpoises for the IDW and the Skagerrak group, was larger than the mature porpoises (Fig. 7) with immature home range being up to four times larger than the mature home ranges for the Skagerrak group and up to two times larger for the IDW group. Males and females within the IDW group showed no difference in home range size, but males in the Skagerrak group had larger home ranges than females. This may be attributed to the low number of female porpoises tagged in Skagerrak in comparison to males.

DISCUSSION

Our data provide new insight to the distribution patterns of harbor porpoises from the North Sea to the western Baltic Sea and intermediate waters. High-density

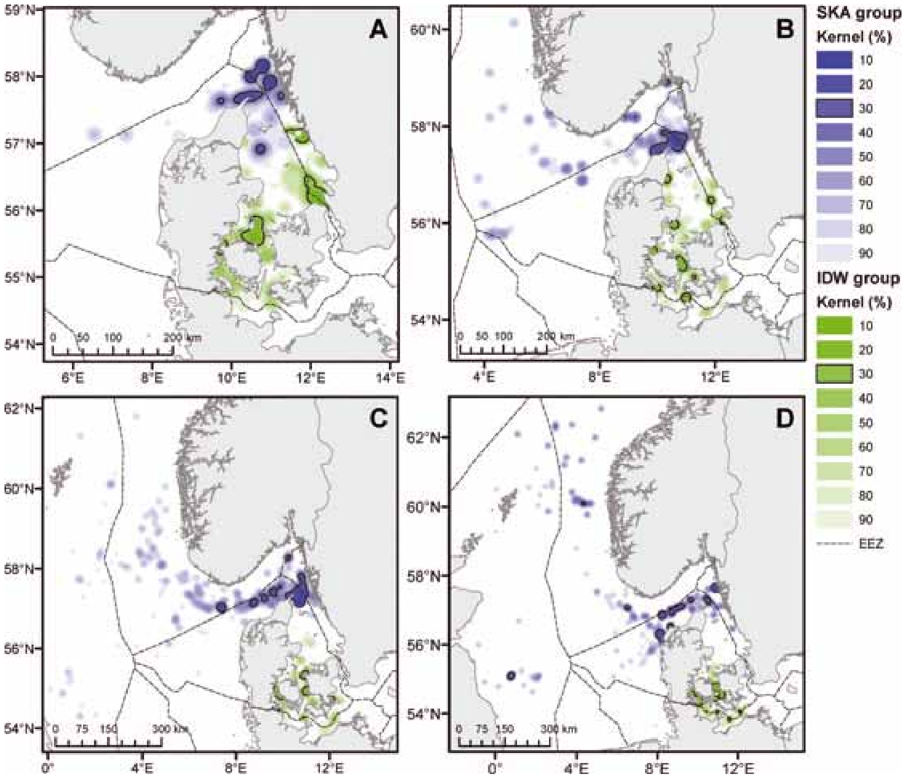

Figure 5. Seasonal distribution for harbor porpoises *Phocoena phocoena* tagged in the Inner Danish Waters (IDW) population (green) and in Skagerrak (blue) displayed by fixed kernel density estimations based on one location every four days from each other. Black line indicates high-density areas defined as the 30% kernel contour. (A) spring (IDW: $N = 29$, $n = 268$; Skagerrak: $N = 12$, $n = 103$), (B) summer (IDW: $N = 27$, $n = 353$; Skagerrak: $N = 18$, $n = 155$), (C) autumn (IDW: $N = 17$, $n = 210$; Skagerrak: $N = 19$, $n = 250$) and (D) winter (IDW: $N = 8$, $n = 119$; Skagerrak: $N = 12$, $n = 157$). Projections as in Figure 2. Dashed line indicates international Exclusive Economic Zones (EEZ). Kernel layers are placed below the land layer.

areas were clearly identified and thus, harbor porpoises do not distribute evenly, but aggregate in certain areas, that is, key habitats. The 64 individual tracks were used to identify nine high-density areas for harbor porpoises using weighted kernel density estimation. The two porpoise groups showed very little overlap in distribution and may belong to each of the two porpoise populations (one in the Kattegat, Belt Sea, and the western Baltic and one in Skagerrak and the North Sea) indicated previously by genetic methods (Andersen *et al.* 2001).

Four of the high-density areas found by satellite tracking are supported by previous studies using other methods. For instance, Heide-Jørgensen *et al*. (1993) conducted aerial surveys in the waters north of Fyn, Great Belt, and the Kiel Bay and found that the density in Great Belt was more than twice that of the other areas. The highest density of harbor porpoises ever reported in Europe was also found in the Great Belt

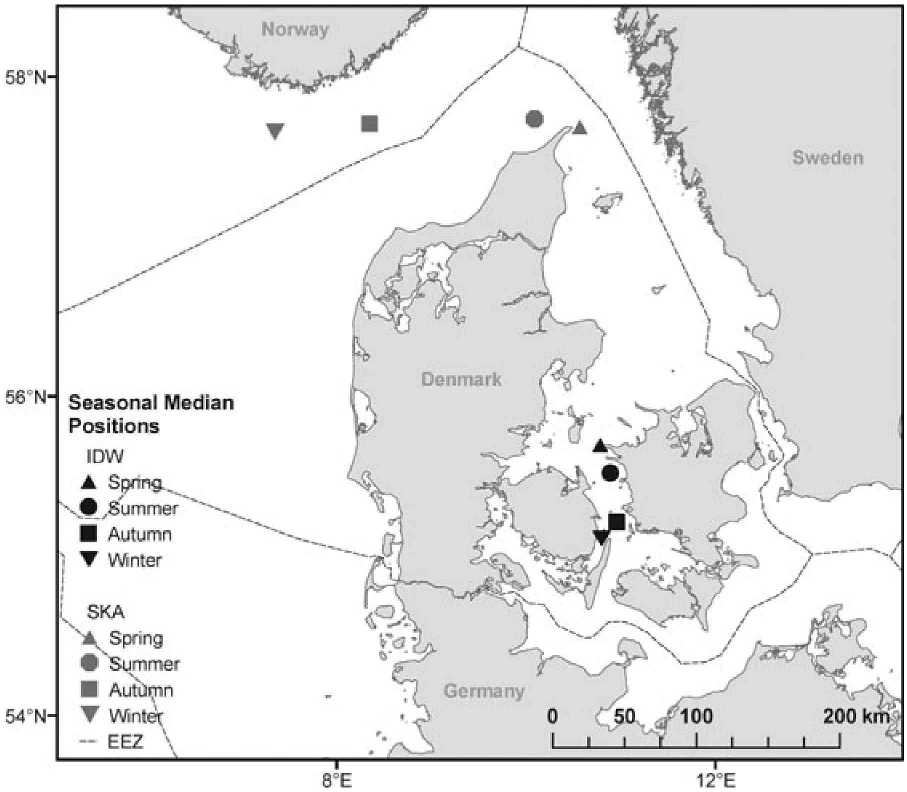

Figure 6. Mean locations of median seasonal distribution of harbor porpoises *Phocoena phocoena* (spring, summer, autumn, winter) for porpoises tagged in the Inner Danish Waters (IDW) (black) and in Skagerrak (SKA) (light gray). Spring (IDW: $N = 29$ porpoises; Skagerrak: $N = 12$ porpoises), summer (IDW: $N = 27$; Skagerrak: $N = 18$), autumn (IDW: $N = 17$; Skagerrak: $N = 19$) and winter (IDW: $N = 8$; Skagerrak: $N = 12$). Dashed line indicates international Exclusive Economic Zones (EEZ).

during spring from a ship survey (Teilmann 2003). Visual and acoustic surveys in the western Baltic indicated an increase in porpoises from east to west with particularly high porpoise density in Flensborg Fjord and in Little Belt and almost no porpoises in the Baltic proper (Gillespie *et al.* 2005). Verfuss *et al*. (2007) deployed acoustic data loggers (T-PODs) along the German Baltic coastline and found Fehmarn Belt to have the highest intensity of porpoise echolocation. Thus, entirely different methods have confirmed the presence of half of the high-density areas identified by satellite tracking in our study. Therefore, we find that kernel- and grid-based analysis of satellite tracking are valid methods for identifying high density areas for harbor porpoises.

Our study suggests a seasonal change in importance of some of the high-density areas. From spring/summer to autumn/winter, the porpoises in IDW and Skagerrak moved south and west, respectively. This shift does not seem to be a coordinated migration, but rather a gradual overall movement over a longer period. Our findings correlate with the results of Read and Westgate (1997), who satellite tracked nine harbor porpoises in the Bay of Fundy and Gulf of Maine, Canada, and found seasonal

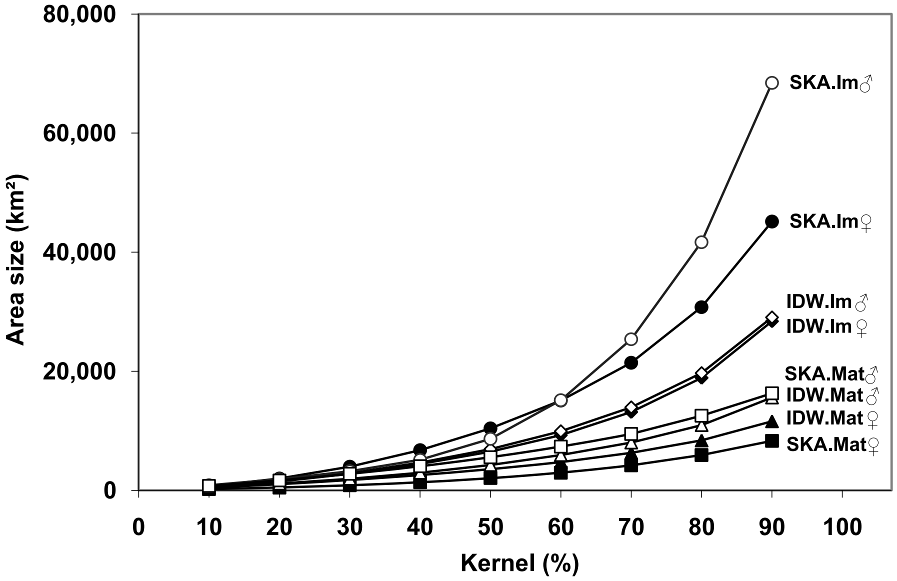

Figure 7. Area size of each kernel density contour divided by into groups by sex [females (♀), males (♂)], and age-class [immature (Im), mature (Mat)] for the two harbor porpoise groups; Inner Danish waters (IDW) and Skagerrak (SKA). Number of porpoises in each category in IDW were: mature F = 5, mature M = 7, immature F = 11, immature M = 15 and in Skagerrak (mature F = 1, mature M = 5, immature F = 6, immature M = 14).

changes in distribution to exist, but they were individually discrete and gradual. Seasonal changes in density patterns of small cetaceans have also been observed in other cetaceans, for example, bottlenose dolphins (*Tursiops truncates*) in the Moray Firth, Scotland (Wilson *et al.* 1997). The seasonal movements may be linked to changes in distribution of prey (Gaskin 1982). Our study is the first to identify a specific seasonal trend for harbor porpoises on a large scale. In fact, very little other information is available to describe the harbor porpoise distribution in the study area during the winter season, because visual surveys are difficult to conduct due to poor weather conditions and reduced number of daylight hours.

Home range size of immature porpoises was found to be considerably larger than the mature porpoises for both the IDW and the Skagerrak group. The home range of mature porpoises is comparable in both groups, but the immature porpoises in the Skagerrak group are almost twice the size of the immature porpoises in the IDW group. The difference is clearly illustrated by the fact that none of the mature porpoises moved further west than 6°E, and so only immature porpoises move north along the coast of Norway and west to the coast of the United Kingdom (3°W). This may indicate that immature and thus inexperienced porpoises have to move larger distances in order to locate prey than mature individuals or that they are less settled to a specific area. The Skagerrak porpoises move approximately 30% faster than the IDW group, which may be needed to swim the longer distances. However, it may be a consequence of the larger home ranges, which causes the distance between two satellite-logged locations to be further apart, incorrectly indicating a higher swim rate, that is, if the IDW animals swim just as fast but in circling movements, the speed measured between two locations will be slower.

No difference was found in home range size in relation to sex within the two maturity groups for the IDW group. For the Skagerrak group, both the immature and the mature males appear to have larger home range than the immature and the mature females, respectively, but this may be the result of unbalanced sample size.

The results in this study are based on the assumption that the 64 tagged harbor porpoises are representative for the general behavior of porpoises in the study area. Although the presence of high-density areas is confirmed by other methods, animals should preferably be tagged randomly throughout the study area and represent a natural distribution of sex and age classes. This is rarely possible and in this study tagging sites were restricted to the coastal regions where the pound net fishery is carried out. The age structure for wild-living harbor porpoises is unknown. Information derives from stranded or bycaught porpoises that may be biased. Strandings may contain a high proportion of naturally dead animals and bycaught individuals may represent lack of experience leading to higher probability of capture. However, except for only having tagged a single mature female in the Skagerrak group, the sex and age distribution in this study is comparable to findings in studies on bycaught (Read and Hohn 1995) and stranded harbor porpoises (Benke *et al.* 1998, Siebert *et al.* 2006, Jung *et al.* 2009).

Satellite telemetry provides presence-only data, that is, we do not know whether further tagging of porpoises would reveal new key habitats. Still, the study represents the most comprehensive satellite tagging program for any cetacean within the same region. Satellite tracking combines temporal and spatial information on a broader scale and provides unique continuous information on individual behavior as well as on a general population level unlike any other method.

The harbor porpoise is a wide-ranging species with a large home range (Read and Westgate 1997), and thus has the ability to occupy/exploit any site within the study area. Hence, the fact that (1) some areas are preferred to others, (2) that some of these areas (*e.g.*, northern Øresund) are relatively far away from the tagging sites, and (3) that porpoises often spend time in several of the identified key habitats, suggest that the presently identified key areas are relatively independent of tagging site within the range of each population.

An important prerequisite for fixed MPAs is that the key habitats do not vary greatly from year to year. This study was conducted over a 10-yr period required to catch and tag the presented number of porpoises. Compiling data over several years may hide temporal trends in spatial distribution, but inspection of the individual tracks does not suggest this to be the case. A time-trend study based on, for example, regular acoustic surveys throughout the year and the deployment of T-PODs in and adjacent to the identified key habitats, could further examine such seasonal and year-to-year changes.

Finally, this study provides information on high-density areas, which were not previously known, and the areas are identified with a resolution in time and space appropriate for use in area protection and other management. In the EU, all relevant member states are legally obliged to protect the harbor porpoise by designating SAC according to the EC Habitat Directive (92/43/EEC 1992). It is clear from this study, that international cooperation is essential in the designation of these protected areas. The harbor porpoise is a wide-ranging species and the tagged individuals utilized Danish, Norwegian, Swedish, German, and British waters and several high-density areas are divided between countries. During the process of identifying SAC for harbor porpoises in Denmark, the Danish authorities have based their selection of protected areas mainly on the data presented in this paper. Two of these areas, Flensborg Fjord and Fehmern Belt, adjoin German designated SAC for harbor porpoises. The

EC Habitat Directive thus provides a legal forum for designating large coherent protected areas across national borders in Europe, which is required in order to protect the harbor porpoise in their key habitats.

This study arbitrarily defined high-density areas as $\leq$30% kernel polygons for illustrative purposes and it should be noted that this exact limit is not scientifically supported to be used for management purposes.

ACKNOWLEDGMENTS

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SUPPORTING INFORMATION

The following supporting information is available for this article online:

Appendix S1: Filtering of Argos locations.

Appendix S2: Weighing number of locations by porpoise.

Appendix S3: Choice of smoothing factor (band-width).

Appendix S4: Global *vs*. local estimates of density.

Figure S1: Track of two harbor porpoises before (left panels) and after applying Distance-Angle-Rate filter to the original Argos data.

Figure S2: Kernel distribution of porpoises tagged in the Danish waters between 1997 and 2007 for all year round ($N = 64$ porpoises, $n = 4{,}309$ locations).

Figure S3: Comparison of smoothing factor used in Kernel density estimation of utilization distribution.

Figure S4: Distribution of porpoises tagged in Danish waters between 1997 and 2007 ($N = 64$ porpoises, $n = 4{,}309$ locations).

Figure S5: Correlation between the kernel density estimation and the grid analysis.

Table S1: Number of Argos locations of various location classes in the harbor porpoise dataset (64 porpoises) and the percentage of locations removed from the dataset by the Distance-Angle-Rate filter: (1) including all locations that passed the filtering algorithm and (2) one location per day.

THIS DOCUMENT CONTAINS SUPPORTING INFORMATION FOR:

Sveegaard, S., J. Teilmann, J. Tougaard, R. Dietz, K. N. Mouritsen, G. Desportes and U. Siebert. 2010. High-density areas for harbor porpoises (*Phocoena phocoena*) identified by satellite tracking. Marine Mammal Science.

APPENDIX 1. FILTERING OF ARGOS LOCATIONS

To remove unrealistic Argos locations, the locations were filtered by a SAS-routine, Argos Filter v7.03 (Douglas 2006). This so called DAR (Distance-Angle-Rate) filter attempts to identify implausible locations based on the fact that most suspicious Argos locations cause an animal to incorrectly move a substantial distance and then return, resulting in a tracking-path that goes 'out-and-back' (and/or further validated by unrealistic movement rates, depending on the temporal frequency of the locations). The entire DAR filtering strategy is iterated 3 times, each successive iteration using only locations that passed the previous iteration. It is necessary to iterate the DAR strategy multiple times because filtering a location during one iteration may create implausible rates of movements or suspicious angles that need to be reevaluated by a subsequent iteration.

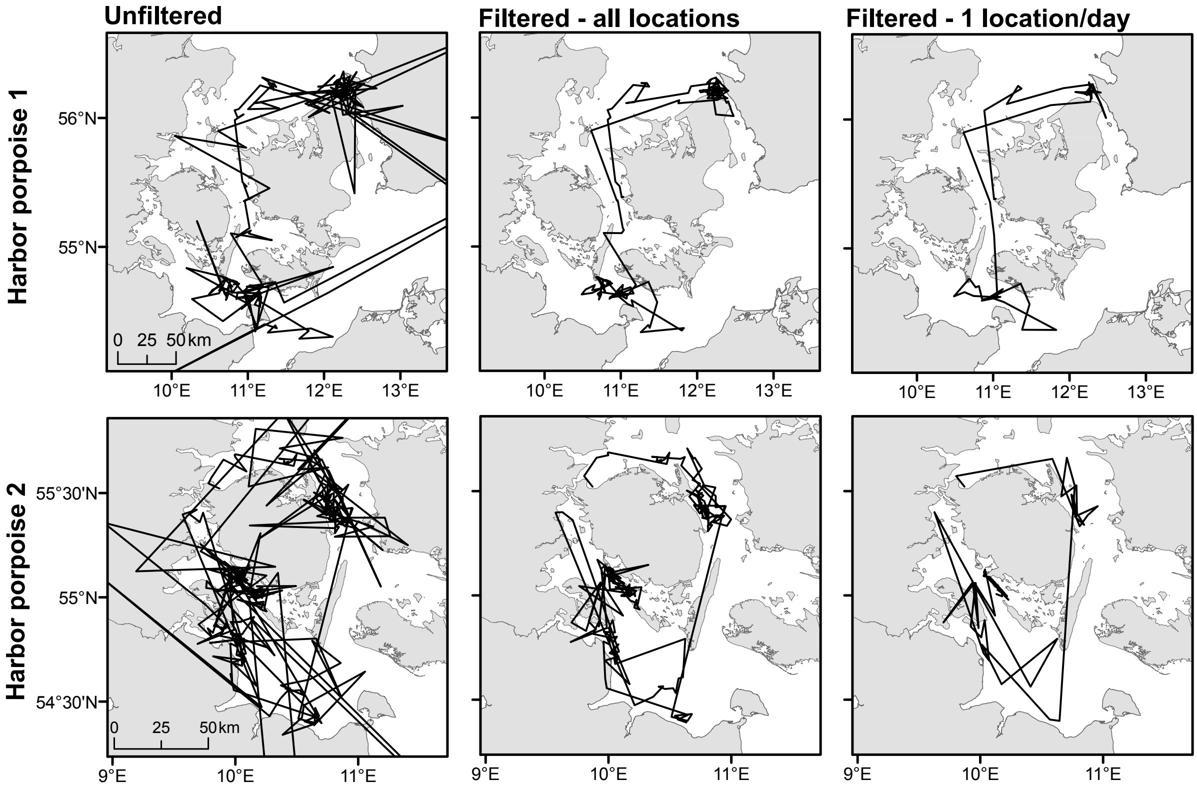

Figure s1. Track of two harbor porpoises before (left panels) and after applying DAR-filter to the original Argos data. All Argos locations that passed the DAR-filter are shown in the centre panels and the best Argos location per porpoise per day that passed the DAR-filter in the right panels. Map projection universal transverse Mercator, Zone 32N, WGS84.

Figure S1 shows tracks of two harbor porpoises tracked in this study before and after applying the DAR-filter to the original Argos data. The DAR filter removes the improbable locations and creates a plausible track with few locations on land. The DAR filter removed 34 % of the original Argos locations when including all locations that passed the DAR-filtering algorithm and 77 % when only including the best (most precise) location for each porpoise per day (Table S1). The 34 % is comparable to the findings of Freitas *et al.* (2008). They tested on 67 tracks from 9 different marine mammal species and found that their SDA-filter (Speed-Distance-Angle) removed 26-50 % of all locations. They did not test for one location per day. However, Figure S1 clearly shows that when only selecting the best location per day of the locations that passed the DAR-filter, the track becomes very plausible with only few or no locations on land.

Table S1. Number of Argos locations of various location classes in the harbor porpoise dataset (64 porpoises) and the percentage of locations removed from the dataset by the DAR filter 1) including all locations that passed the filtering algorithm and 2) one location per day.

Location Class	No filter	1. DAR-filter all locations	% removed using 1.	2. DAR-filter 1 location/day	% removed using 2.
3	307	307	0	281	8
2	894	791	12	555	38
1	2419	2009	17	1055	56
0	4175	2684	36	1081	74
A	4729	3111	34	858	82
B	7179	4132	42	651	91
Total	19703	13034	34	4481	77

APPENDIX 2. WEIGHING NUMBER OF LOCATIONS BY PORPOISE

To account for the variation in transmission longevity among porpoises, kernel density estimation with equal weight on each porpoise was used in all analysis in the paper. The weight of each location was thus calculated as:

Weight of each location (Porpoise X) = 1/total number of transmission days for porpoise X

This weighting introduces a bias towards animals with short transmitter lifetime. In order to evaluate the magnitude of the bias it was compared to an alternative kernel density estimation with equal weight on each location. This will bias the analysis towards animals with longer transmitter life.

To compare the two methods of weighting data, the study area was divided into grid cells of 4x4 km. Each cell was assigned the value of the underlying kernel density surface sampled at the centre of the cell. The two grids of weighted locations and weighted animals, respectively, can be seen in Fig. S2.

The satellite transmitters on the 64 porpoises had variable lifetime (from 14 to 349 days) and as a consequence the two different method of weighing data could produce significantly different distribution maps. However, we find that the high density areas are selected in both distribution maps although the shapes are somewhat different. A high correlation coefficient ($R^2 = 0.84$) was found when correlating the two methods cell by cell. The dataset therefore seem robust to transmitter longevity and weighting for the purpose of identifying high density areas.

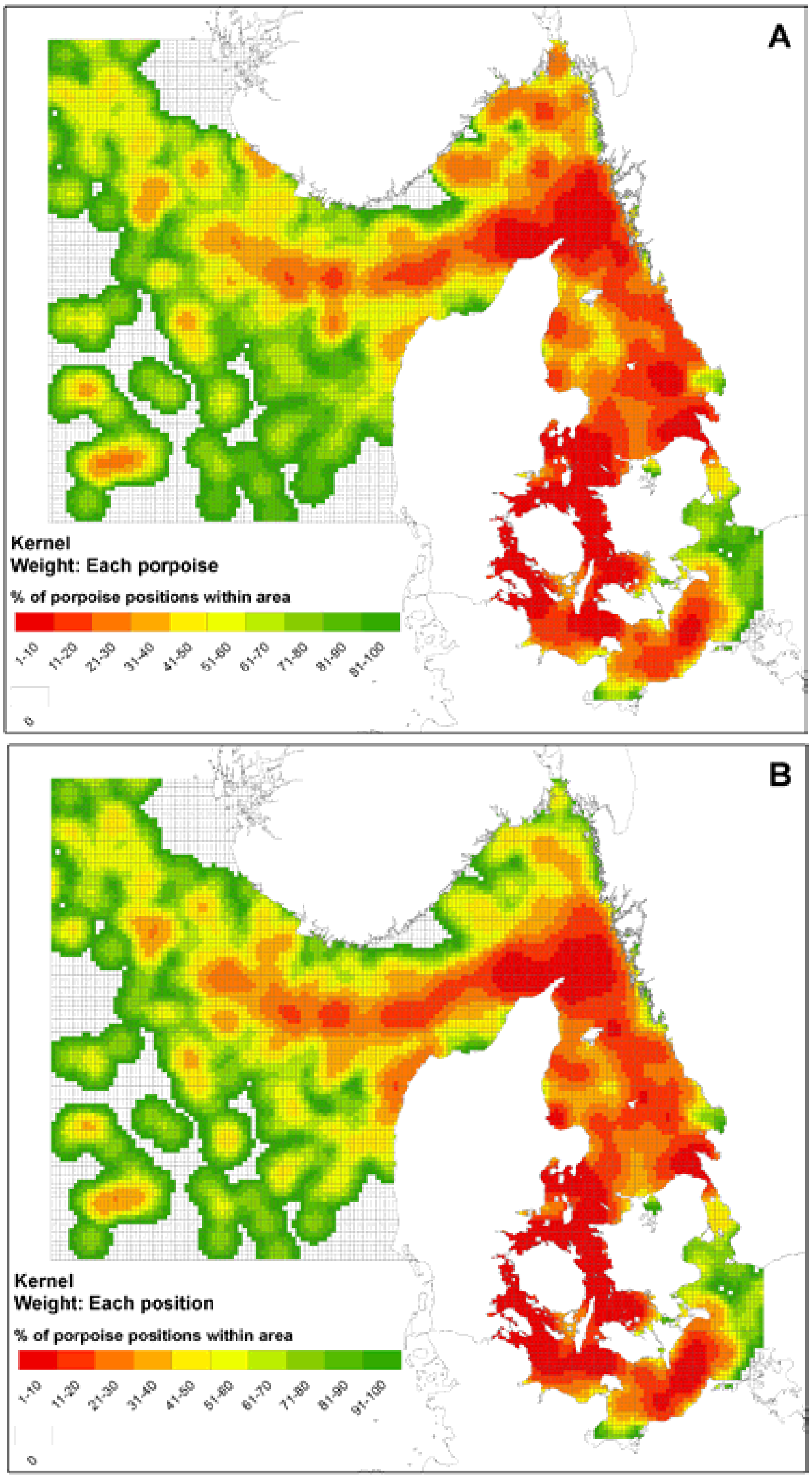

Figure S2. Kernel distribution of porpoises tagged in the Danish waters between 1997 and 2007 for all year round (N = 64 porpoises, n = 4309 locations). Comparison of methods of weighting kernel data: A) weight on each porpoise and B) weight on each location. Map projection universal transverse Mercator, Zone 32N.

APPENDIX 3. CHOISE OF SMOOTHING FACTOR (BAND WIDTH)

The impact of smoothing factor on the results of the kernel density estimations have been widely studied, although no congruence of best practice has been established (Worton 1989, Blundell *et al.* 2001). We evaluated the effects of smoothing on kernel estimates for harbor porpoises in this study by calculating the Kernel density estimates for the IDW group (38 harbor porpoises) using three different band widths: 10,000, 20,000 and 30,000 (Fig. S3). While 10,000 turned out to be too fragmented, the use of smoothing factor 20,000 and 30,000 both appeared suitable in regard to our knowledge of harbor porpoise habitats i.e. the kernel areas are relatively large and coherent (Fig.S3c and Fig.S3d). We decided on smoothing factor 20,000, which includes less land areas and did not seem to smooth out small high density area e.g. Store Middelgrund and Northern Samsø Belt.

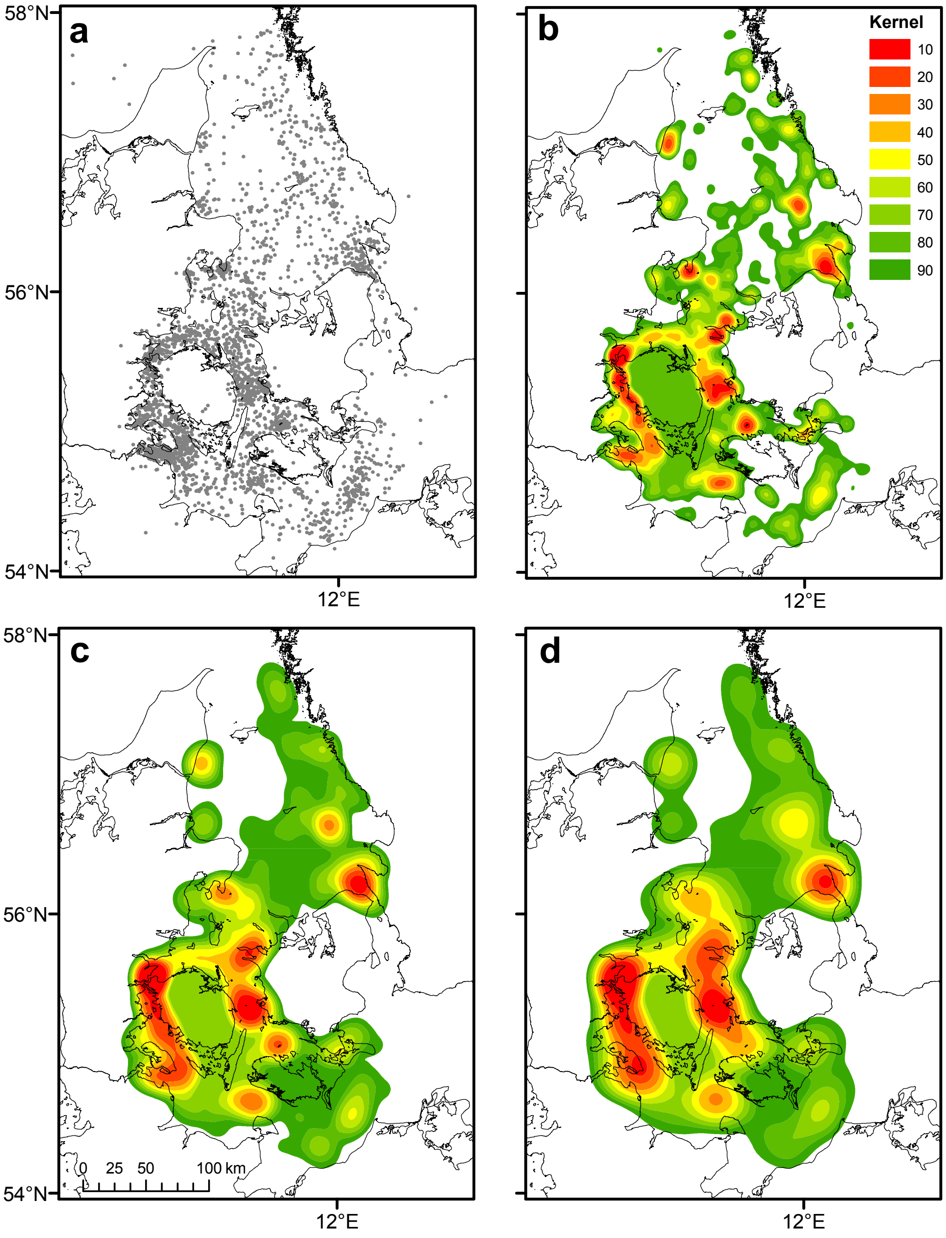

Figure S3. Comparison of smoothing factor used in Kernel density estimation of utilization distribution. a) Argos locations from tagged harbor porpoises 1997-2007, b) Kernel density estimate using smoothing factor 10,000, c) Kernel density estimate using smoothing factor 20,000, and d) Kernel density estimate using smoothing factor 30,000.

APPENDIX 4. GLOBAL VERSUS LOCAL ESTIMATES OF DENSITY

The relative size and form of the kernel density estimation grid is dependant on the total number of locations and their distribution. For instance, if individual porpoises are removed or added to the analy-sis, the size and shape of the kernel density surface will change in all areas because the kernel density estimator includes all locations in the calculations.

To challenge the validity of the high density areas determined by the kernel density estimator, re-sults were compared to results obtained for the same data using a grid-based method, which takes into account the inaccuracy on each Argos location and where each grid cell is independent of other grid cells and the total number of locations (Tougaard et al. 2008). This grid analysis divided the study area into 4x4 km squares and calculated the most likely number of true locations inside each square by weighting each location according to the accuracy of the associated location class. The method has two advantages over the kernel density analysis:

1. Each estimate is a local estimate, whose value depends only on locations within the grid cell and immediately neighboring cells. Thus, in contrast to kernel methods, where the whole dataset is in-cluded in the calculations, and data geographically far apart influence each other, the grid method produces results independent of other cells. The grid method was applied using weight on each porpoise (Fig. S4).
2. The grid method includes the inaccuracy in Argos location classes as found by (Vincent et al. 2002), in the Grid analysis. For each Argos location within a 4x4 km square grid cell the likelihood that the porpoise was actually within that cell is calculated and the value added to the cell. Likewise, the likelihood that it was actually in one of the

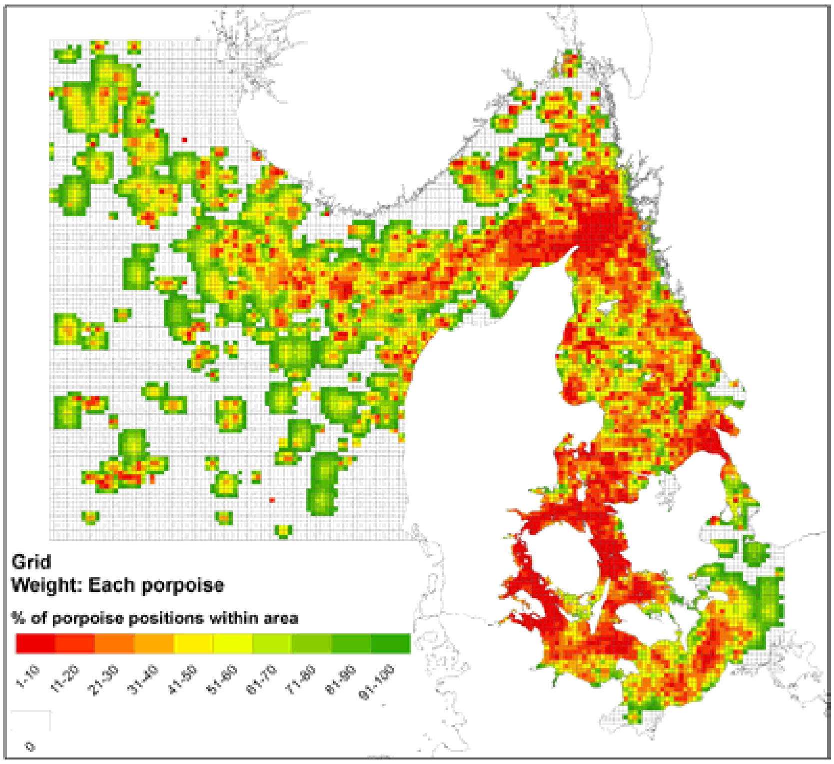

Figure S4. Distribution of porpoises tagged in Danish waters between 1997 and 2007 (N = 64 porpoises, n = 4309 locations). Grid analysis weighted by individual porpoise. Map projection universal transverse Mercator, Zone 32N, WGS84.

neighboring cells is calculated and that value added to those cells. When all values are added up a grid including the Argos inaccuracy is produced (Fig. S4).

When comparing the maps of the kernel (Fig.S2) and the grid (Fig.S3) analysis, a good overall corre-spondence with respect to high and low density areas is found. Furthermore, when examining the cor-relation further and including the entire study area (12,316 cells) a correlation of R2 = 0.54 is found, Fig S5. The residual variation from the regression line in Fig S5 is caused by the spatial smoothing by the kernel density estimation procedure. This smoothing is desired for the purpose of this study when des-ignating larger and spatially more contiguous areas as MPA candidates. Thus we choose to use kernel estimation grid with weight to each porpoise for presenting high density areas.

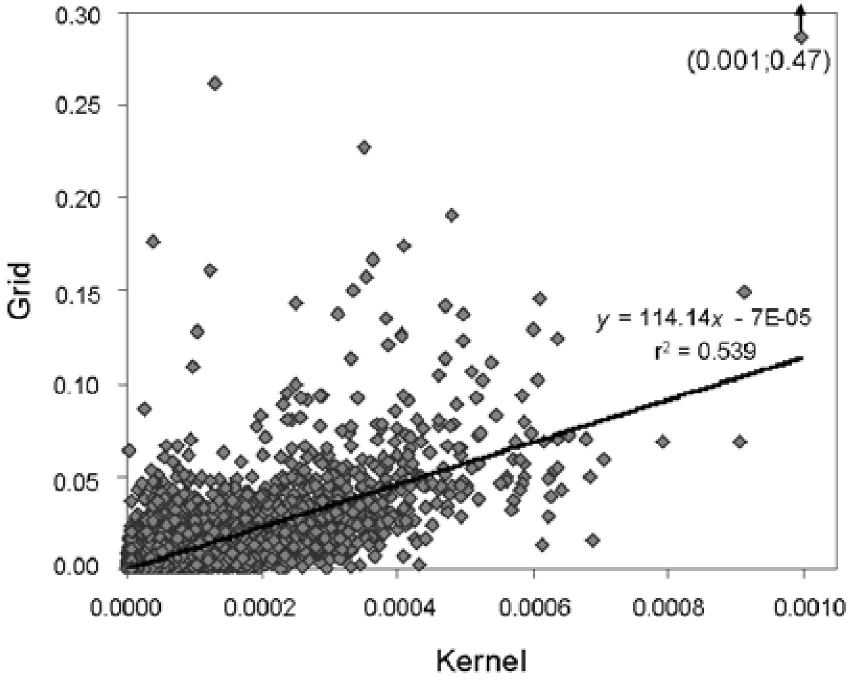

Figure S5. Correlation between the kernel density estimation and the grid analysis. Trend line, equation and R-square is shown (R2 = 0.54).

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PAPER III

Acoustic surveys confirm high density areas of harbour porpoises found by satellite tracking

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Acoustic surveys confirm high density areas of harbour porpoises found by satellite tracking

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ABSTRACT

The population status of the harbour porpoise (*Phocoena phocoena*) has long been of concern in European waters. Consequently, the European Commission (EC) Habitats Directive obligates all EC member states to designate marine protected areas (MPAs) for harbour porpoises before 2012. MPAs will be designated in the areas identified to have the highest density of porpoises. However, little is known about comparability between monitoring methods used for examining porpoise distribution and density, and conflicting results may potentially arise, especially when considering the varying sample size and temporal and spatial scales of the methods used. This study uses acoustic vessel surveys as an independent method to test the temporal and spatial permanency of previously identified areas of high harbour porpoise density from satellite tracked porpoises in inner Danish waters. Based on six acoustic surveys during 2007, we found a strong spatial concordance between the number of acoustic detections of harbour porpoise and their density distribution obtained by ten years of satellite tracking. The results confirm the presence and permanency of areas of high porpoise density, and furthermore, validate the two methods for identifying and monitoring future MPAs for harbour porpoises.

Key words: Cetacean, conservation, monitoring, kernel home range, detection rate, MPA, SAC, Habitat Directive, *Phocoena phocoena.*

INTRODUCTION

The harbour porpoise (*Phocoena phocoena*, L.) has a northern hemisphere circumpolar distribution (Gaskin and Watson 1985) divided into several spatially separated populations. Three populations have been genetically recognized from the North Sea to the Baltic Sea, with putative borders in the Kattegat, and western Baltic Sea (Andersen et al. 2001, Teilmann et al. 2004, Wiemann et al. 2010). The population status of the harbour porpoise has long been of concern due to anthropogenic influences, the main threat being incidental by-catch in fisheries (e.g., Lowry and Teilmann 1994, Tregenza et al. 1997, Berggren et al. 2002, Vinther and Larsen 2004). Thus, the designation of Marine Protected Areas (MPAs) is being implemented e.g. in the EU (92/43/EEC), as a mean to protect the species. According to the Habitat Directive, MPAs (in the Habitat Directive named Special Areas of Conservation or SACs) for each species should 'be proposed only where there is a clearly identifiable area representing the physical and biological factors essential to their life and reproduction', and that these areas should be 'identifiable on the basis of the continuous or regular presence of the species (although subject to seasonal variations), good population density (in relation to neighbouring areas) and high ratio of young to adults during certain periods of the year' (European Commission 2007). Thus, prior to the designation of MPAs, the distribution of harbour porpoises must be thoroughly examined in order to establish the existence and stability of areas of high harbour porpoise density.

In Danish waters, identification of high density areas for harbour porpoises has been conducted by analysing the tracks from 64 harbour porpoises tagged with satellite transmitters between 1997 and 2007 (Sveegaard et al. In press, Paper II). The results by Sveegaard et al. (In press, Paper II) showed that the harbour porpoises did not distribute evenly but congregated in certain high density areas. In Kattegat and the Belt Seas, nine high density areas were identified: (1) the northern part of the Sound (North of 56°N), (2) Southern Samsø Belt and Kalundborg Fjord (3) northern Samsø Belt, (4) Little Belt, (5) Great Belt, (6) Flensburg Fjord, (7) Fehmarn Belt, (8) Smålandsfarvandet and (9) the waters around the northernmost tip of Jutland (Fig. 1). The high density areas of porpoises identified by satellite telemetry in Little Belt, Great Belt, Flensburg Fjord and Fehmarn Belt were supported by previous studies using aerial and boat based visual and acoustic surveys (Heide-Jørgensen et al. 1993, Teilmann 2003, Gillespie et al. 2005) and by static passive acoustic monitoring using T-PODs (Verfuss et al. 2007). The remaining high density areas (1, 2, 3, and 6) had not previously been identified.

While the method of using satellite tracking of porpoises to identify high density areas has the advantage of combining temporal and spatial information on a broader scale, it can be criticized for extrapolating data from relatively few animals to the distribution of the entire population as well as being biased towards the locations at which animals were captured and tagged. Hence, the aim of this study was to evaluate the validity of the satellite based density models presented in Sveegaard et al. (In press, Paper II) using an alternative method.

Harbour porpoises make distinctive narrow band echolocation click sounds to navigate and search for prey. The dominant frequency of the click is around 130 kHz (Villadsgaard et al. 2007). Such high frequency clicks can be readily discriminated from other ocean sounds using a hydrophone and automatic detection software tuned to the frequency of porpoise clicks. Acoustic detection systems are less affected by sea state, weather and light, which may prevent visual surveys. Furthermore, they are believed to be more predictable and consistent in their performance than human visual observers and have proved to have a higher detection probability than visual observation in all but the calmest weather conditions (Gillespie et al. 2005, Kimura et al. 2009). However, acoustic surveys are dependent on the level of ambient noise and the vocal behaviour of the porpoises (Gillespie et al. 2005). Due to uncertainties in acoustic estimates of group size and the probability of detecting an animal close to the survey trackline, it is currently not possible to estimate absolute porpoise abundance from towed array surveys. However, if conditions are kept constant (such as ship, tow speed, array sensitivity and software settings) relative abundance between areas can be estimated and used to identify areas of high and low density.

By applying acoustic surveys as an independent method covering a large area, we here test the temporal and spatial robustness of high and low density areas previously identified by satellite tracking of harbour porpoises.

METHODS

Survey design

Six acoustic ship surveys were carried out every second month in 2007 from January to November. The survey transects were designed to pass through both low and high density areas identified by satellite tracking of porpoises in Skagerrak, Kattegat and the Danish straits (i.e. Little Belt, Great Belt and the Sound) (Fig. 1). The total survey track length was planned to be 1220 km for each survey. However, due to poor weather (surveys were only carried out in wind speed ≤15 m/s) and occasional high levels of ambient noise, the usable realized effort varied from 937 km to 1208 km between individual surveys (Table 1).

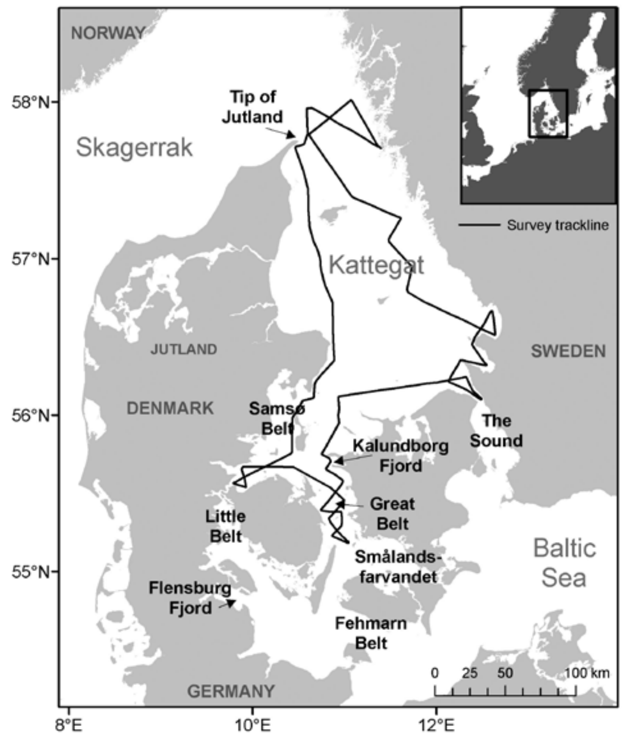

Figure 1. Map of study area emphasizing identified high density areas for harbour porpoise. The trackline for the acoustic surveys in 2007 is displayed as a black line. Map projection universal transverse Mercator, Zone 32N, WGS84.

Data collection

All surveys were conducted from the Swedish research vessel 'Skagerak'. The ship is 38 m long, 9 m wide and has a draught of 3.8 m. It was operated under engine power and maintained a speed of approximately ten knots throughout the surveys. It is essential that the vessel towing the acoustic hydrophones is relatively quiet so the porpoise signals can be detected. 'Skagerak' was used during the second 'Small Cetaceans in the European Atlantic and North Sea' (SCANS-II) survey and proved to be sufficiently quiet to detect porpoise echolocation (SCANS II 2008).

The hydrophones were connected through a buffer box to a computer with a high speed data acquisition system (National Instruments PCI 6250) which sampled signals from each hydrophone at 500 kHz, 16 bit. Time and GPS-position locations (obtained from the ship) were logged by the computer every 10 seconds.

Data were logged using an automated detection system developed for SCANS-II (SCANS II 2008). The system was based on the method described by Gillespie and Chappel (2002) but modified with digital real-time signal processing rather than analogue filters (SCANS II 2008). Harbour porpoise clicks were automatically detected in real time by the software RainbowClick (www.ifaw.org), which identifies clicks based on four criteria: (1) peak frequency (50% of the total energy should be between 110 and 150 kHz), (2) band width (measured peak width should be less than 55 kHz), (3) energy ratio between the porpoise band (100-150 kHz) and a control band (40-90 kHz) (minimum energy difference between the two bands should be 4dB), and (4) click length (the length or duration of the waveform containing 50% of the total energy should be less than 2 us). For further details, see SCANS II (2008).

The towed array consisted of a 200 m tow cable with two high frequency hydrophones (25 cm apart) with build-in preamplifiers and a depth gauge at the end. The hydrophones were towed at 5-6 m depth. Hydrophones were calibrated in a test tank during this study and were found to have a mean sensitivity of –165 dB re.1 V/uPa at 130 kHz and were omnidirectional in the plane perpendicular to the tow cable within ±6 dB. By playback of a series of artificial porpoise clicks (13 cycles of 130 kHz sine wave, raised cosine envelope) in a calibration tank while reducing the amplitude, the detection threshold of the hydrophone array under low-noise conditions was determined to be 120 dB re.1 uPa peak-peak. Assuming a source level of porpoise clicks of 190 dB re.1 uPa peak-peak, this translates into a maximal detection distance of 500 m, assuming spherical spreading and an absorption coefficient of 35 dB km^{-1}.

Table 1. Survey period, survey effort and acoustic detections of harbour porpoise (*Phocoena phocoena*) for each of the six acoustic surveys in 2007. Number of satellite positions refers to the number of positions received from all tagged porpoises from 1997 to 2007 in the two months listed in the first column (one position porpoise^{-1} day^{-1}).

Surveys	Dates	Survey effort (km)	No. of acoustic detections	Detections km^{-1}	No. of satellite positions
Jan-Feb	30 Jan – 02 Feb 2007	1037	75	0.072	332
Mar-Apr	27 Mar – 30 Mar 2007	1208	155	0.128	432
May-Jun	29 May – 31 May 2007	937	138	0.147	1210
Jul-Aug	13 Aug – 15 Aug 2007	1168	152	0.130	840
Sep-Oct	01 Sep – 04 Sep 2007	1061	200	0.189	785
Nov-Dec	19 Nov – 22 Nov 2007	1134	176	0.155	692

Acoustic survey data analysis

The porpoise signals automatically detected in real time were evaluated visually to ensure that the frequency spectrum and click intervals matched the criteria of porpoises used during SCANS mentioned above. The visual inspection of data involved detailed examination of each click (length, amplitude, waveform and spectra). If the survey ship passes either a sin gle porpoise or a school of echolocating porpoises, it appears in the software as a track of porpoise clicks showing a consistent bearing. When a number of porpoise-like clicks were identified, they were categorized as either, an 'event', a 'single track' or a 'multiple tracks', as defined during SCANS-II (Fig. 2).

An event consisted of a group of porpoise clicks without any clear bearing. A single track was a line of clicks clearly passing the hydrophone and multiple tracks were similar to single tracks but several lines of clicks appeared. The tracks were given the value 1 (event or single track) or 2 (multiple tracks) porpoise encounters in the following analysis. This is a conservative approach since even large groups of porpoises, will count for only two individuals if they pass the hydrophones simultaneously. However, harbour porpoises rarely move in large groups and in 2005, the mean group size in the study area was estimated to be 1.57 (Area S, SCANS II 2008). Furthermore, an underestimation of group size will affect the correlation between the two methods, acoustic surveys vs. satellite telemetry, negatively, thereby underestimating their agreement. This is because multiple tracks are more likely to occur in areas with many porpoises, leading to an underestimation of density in these areas.

Occasional single porpoise clicks not related to or near any track or event were excluded.

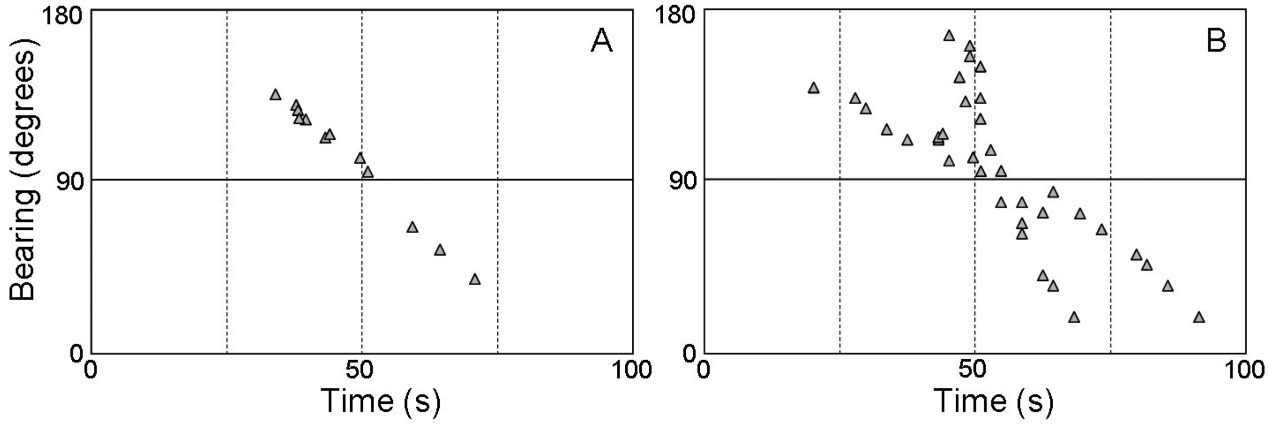

Figure 2. Examples of bearing-time plot showing click detections from harbour porpoises passing the towed hydrophones behind the survey vessel. A) A single harbour porpoise, defined as a 'single track' and B) two harbour porpoises, defined as 'multiple tracks'. A click at a bearing of 180° is directly ahead of the array, a click at 0° astern and one at 90° abeam to one side or the other.

All data were entered into ArcGIS 9.3. The trackline was divided into 1 km transects and the average detection rate per km transect (porpoises km^{-1}) was calculated. A transect leg of 1 km was chosen in order to avoid that transect legs crossed several kernel categories as would often be the case with longer leg lengths. The transect legs of 1 km may be considered temporally independent, as it is unlikely that the same porpoise will follow the survey ship and thus be detected more than once (max. range of detection 500 m). The number of detections within and between the 1 km transect legs may be spatially autocorrelated, because areas of high harbour porpoise density all are larger than 1 km^2. However, because we compare the validity of two monitoring methods, including their ability to detect the spatial structure of the population, presence of autocorrelation is not believed to invalidate our conclusions. The comparison is thus not performed on a continuous spatial scale (one segment with the next adjacent segment), but one segment of the survey data with one grid cell of the kernels derived from satellite telemetry.

The diurnal variation in acoustic detections across all six surveys, i.e. periods of night and day, was calculated and compared using a Kruskal-Wallis test.

Satellite tracking data analysis

Kernel density analyses based on the locations from the satellite tracked porpoises were conducted in ArcMap v9.3 using the fixed kernel density estimator (Worton 1989) in Hawth's Analysis Tools V3.27 (Beyer 2004). To compare satellite tracking with the individual acoustic surveys, satellite kernel densities were calculated based on the locations from the two months adjoining each survey.

For instance, kernel densities estimations for the survey at the end of January were based on locations from January-February 1997-2007. The number of satellite tracked porpoises were not evenly distributed across the year (Table 1) and consequently, the kernel density estimation grids for the 6 surveys (each consisting of positions from all tracked porpoises for two adjacent months) are based on different numbers of positions with January-February being the lowest (332 positions) and May-June being the highest (1210 positions) (Table 1).

The kernel density analysis were performed according to the method and settings described by Sveegaard et al. (In press, Paper II) with the exception that the kernel analysis in the present study used one location per transmission day instead of one location every fourth day. Sveegaard et al. (In press, Paper II) chose to use every fourth day to avoid autocorrelation, and concluded that the reduction of data did not alter the identified high density areas significantly. However, for this study we included one location per transmission day to optimise the number of locations in the two month kernel analysis. Further, while Sveegaard et al. (In press, Paper II) divided kernel density grids in ten percent volume contours (PVC), it was decided that this spatial scale was too fine for the relatively limited number of acoustic detection in this study and thus the kernel volume contours were calculated for four PVC namely 30% (highest density, containing 30% of all locations within the smallest possible area), 60%, and 90%. To avoid spatial autocorrelation the polygons were subtracted from each other resulting in: PVC 30% still containing 30% of all locations on the smallest possible area. PVC 60% now containing 31-60% of the porpoise locations and has the shape of a ring around the 30% contour and 90% containing 61-90% of the porpoise locations. This procedure does not completely exclude spatial autocorrelation, but it reduces it substantially.

Comparison of methods

Acoustic porpoise detections per 1 km trackline were calculated within each kernel PVC category i.e. within 30%, 60% and 90% and for the trackline outside the kernel PVC as well, hereafter denoted '$\mathrm{PVC}_{\mathrm{out}}$' (~outside PVC range). The non-parametric Kruskal-Wallis test was then used to test whether or not acoustic detections were evenly distributed across kernel categories for each of the six surveys separately. If this was not the case, the Kruskal-Wallis test was followed by pair-wise contrasts of kernel categories using a post hoc test correcting for multiple comparisons in order to establish which categories differing significantly from each other regarding acoustic detections. Although the statistical analyses were carried out on ranked data, mean values and associated standard errors are given in all graphical presentations to facilitate visual comparisons.

The distribution of acoustic detections across kernel categories was also tested for all six surveys combined. Contrary to the analyses of individual surveys, requirements for the application of parametric statistics were met and one-way ANOVA was used followed by Bonferroni post hoc tests.

RESULTS

Acoustic surveys

The six surveys were carried out with an effort of 937-1208 km with average number of acoustic detections per km ranging from 0.072 in January-February to 0.189 in September-October (Table 1).

The harbour porpoise detections were not distributed evenly along the trackline but showed higher densities on all surveys in certain areas, especially in the southern areas such as the Great Belt (Fig. 3).

A seasonal change in distribution was found in the northern part of the Sound with high porpoise density from May to October and low densities during winter and early spring (November to March). The Great Belt was the only area in which high densities of porpoises were detected throughout the year. In other areas, very few porpoises were detected at any time, for instance the central Kattegat (Fig. 3).

Kernel density estimation

Kernel density estimation grids were produced for each of the six surveys (Fig. 3). Only two high density areas (30%) were identified in all six survey periods, namely the northern tip of Jutland and the Great Belt. The northern part of the Sound, northern Samsø Belt and northern Little Belt all had high porpoise density from May to August, while Southern Samsø Belt/Kalundborg Fjord supported high densities in November and December. In general, the central Kattegat had very low harbour porpoise density throughout the year except during March-April when three high density areas were identified along the Swedish coast.

No significant difference was found in the number of porpoise detections per km transect during night (mean=0.13 detections km^{-1}) and day (mean=0.11 detections km^{-1}) across the six surveys (Kruskal-Wallis test, $\chi^2_{23} = 17.63$, P = 0.777).

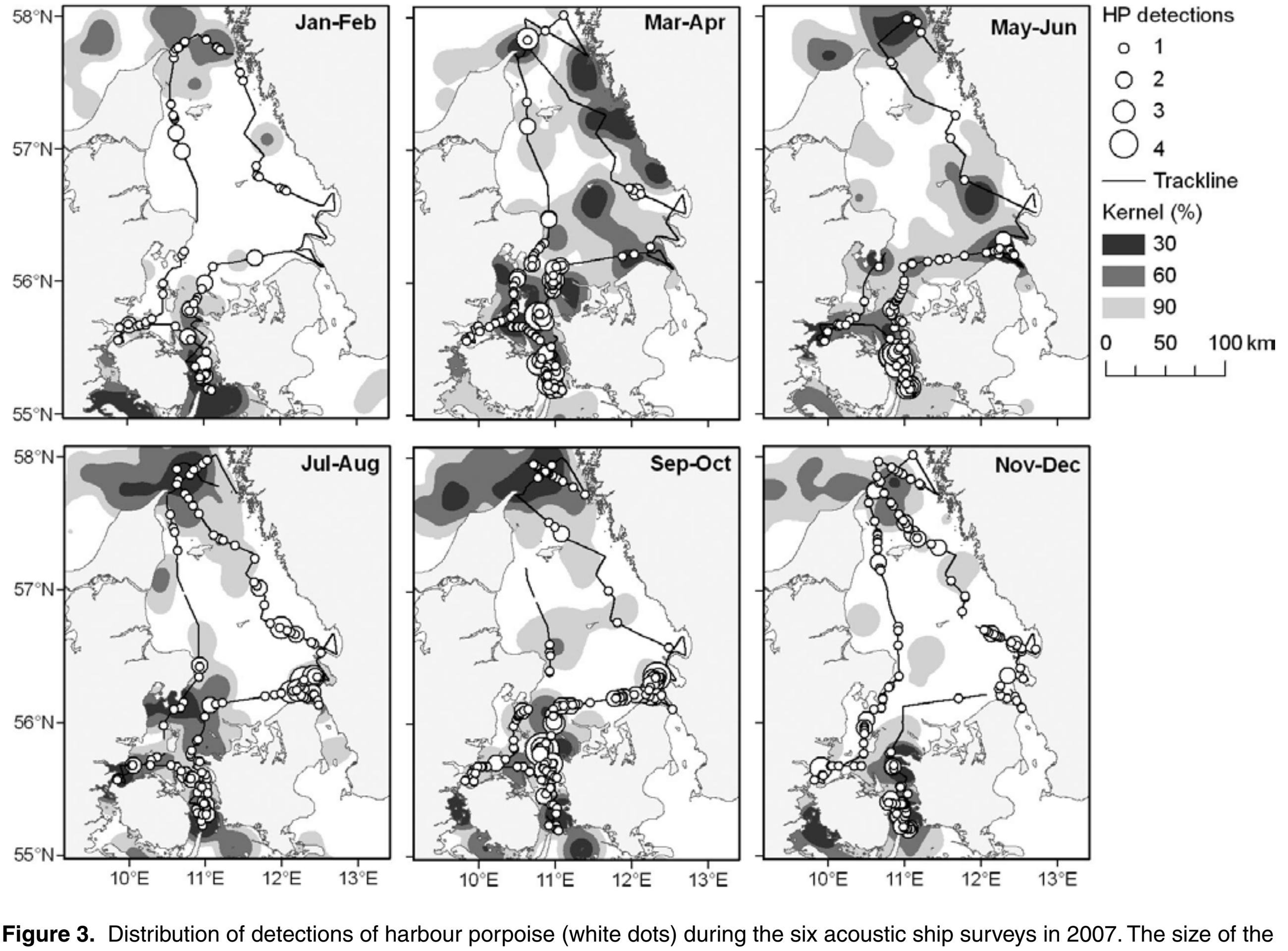

Figure 3. Distribution of detections of harbour porpoise (white dots) during the six acoustic ship surveys in 2007. The size of the dots corresponds to the number of detections per km. The survey trackline is displayed in black. The underlying kernel density percentage volume contours are generated from satellite tracked porpoises during 1997-2007: high density areas (30%) are displayed in dark grey and the lower densities (60 and 90%) in increasingly light grey. Map projection universal transverse Mercator, Zone 32N, WGS84.

Comparison of methods

In all six surveys, acoustic detections of porpoises were not evenly distributed across kernel categories (Kruskal-Wallis test, Jan-Feb: χ^2=11.930, P=0.008; Mar-Apr: χ^2=28.658, P<0.005; May-Jun: χ^2=18.945, P<0.005; Jul-Aug: χ^2=9.206, P= 0.027, Sept-Oct: χ^2= 12.287, P=0.007; Nov-Dec: χ^2=29.558, P=0.005) (Fig. 4). Post hoc testing showed that in three surveys (Mar-Apr, May-Jun and Nov-Dec) the number of porpoise detections per km were significantly higher in the 30% kernel than in PVC_{out} (outside the kernel range), and in four surveys (Mar-Apr, May-Jun, Jul-Aug and Sep-Oct) the number of detections were significantly higher in the 60% than in the PVC_{out} (Fig. 4). The seemingly lower level of acoustic detections in the 30% than in the 60% kernel category during the Jul-Aug and Sep-Oct survey were not statistically significant (Fig. 4). A more clear pattern is obtained when the average of all six surveys are compared (Fig. 5), and together these results suggest an overall declining trend in acoustic porpoise detection with increasing kernel percentage, in turn demonstrating that results obtained by the two methods are correlated.

DISCUSSION

This study demonstrates that the identified high density areas are relatively stable over a 10 year period and also verifies the use of acoustic surveys and satellite tracking as two powerful methods for monitoring porpoise density.

All six acoustic surveys resulted in an overall significant difference in number of detections between the four PVC's categories, and while not all pair-wise comparisons of kernel categories produced significant differences in post hoc tests, the individual surveys all indicated a general positive relationship between the two methods. Considering the very different nature of data obtained from short-term acoustic detections and long-term satellite tracking in addition to potential year to year variation in porpoise distribution, the level of concordance between the two methods strongly support the identified high density areas.

Seasonal movement of harbour porpoises has been recognized prior to this study in other geographical areas, and has been described as a gradual

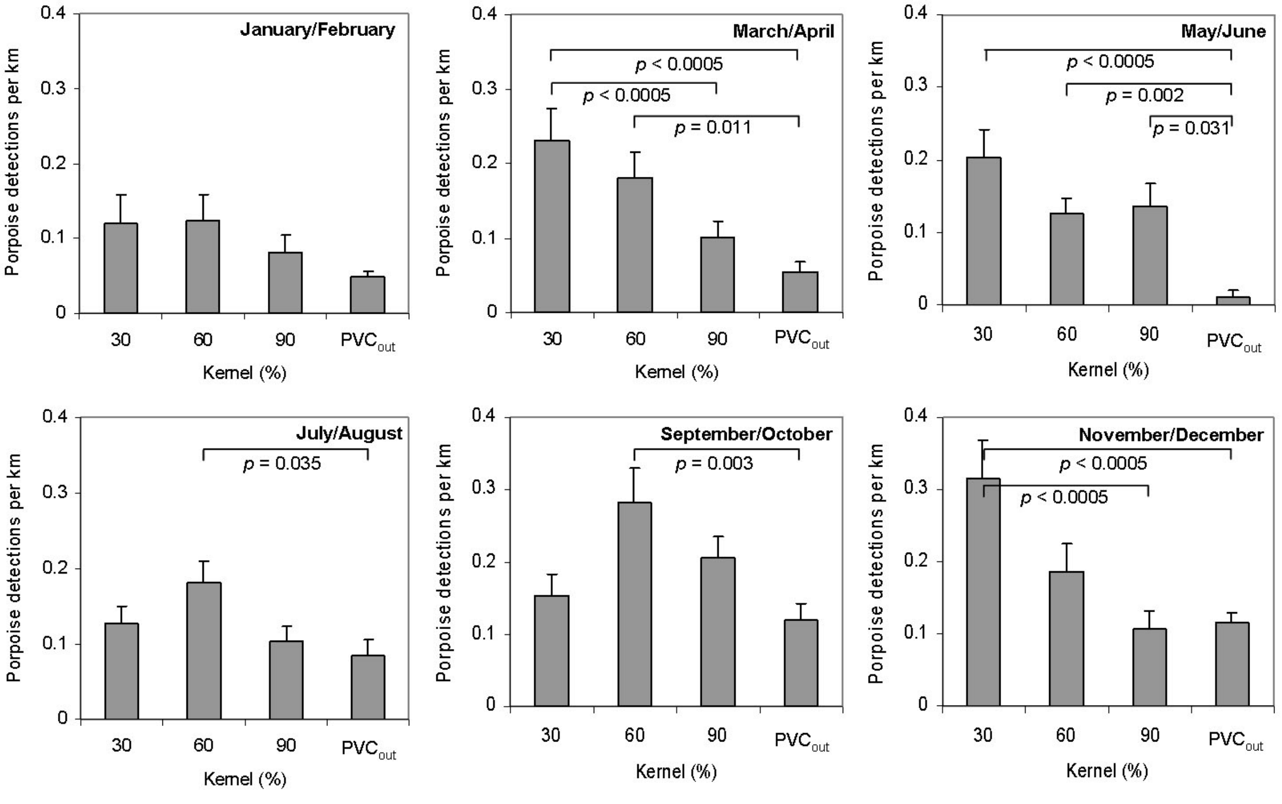

Figure 4. The relationship between densities of harbour porpoise (*Phocoena phocoena*) found by acoustic detections during six ship surveys in 2007 (mean porpoise detections km^{-1} and SE) and by satellite telemetry during 1997-2007 (kernel %). PVCout denotes the number of acoustic detections outside the range of the kernel Polygon Volume Contours. Each graph represents one survey (see Table 1) as well as all positions from the satellite tagged porpoises from each two months period. Post-hoc tests: horizontal lines above bars show the significant differences between kernel categories.

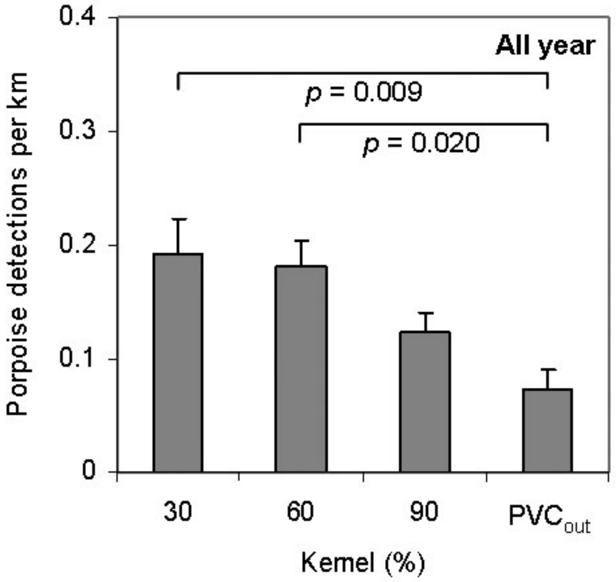

Figure 5. The relationship between densities of harbour porpoises (*Phocoena phocoena*) found from mean of all acoustic ship surveys during 2007 (porpoise detections km^{-1}, mean of six surveys and SE) and satellite telemetry during 1997-2007 (kernel %). PVCout denotes the number of acoustic detections outside the range of the kernel Polygon Volume Contours. Acoustic detections were not evenly distributed across kernel categories (One-way ANOVA, $F_3 = 5.826$, $P = 0.005$). Post-hoc tests: horizontal lines above bars show the significant differences between kernel categories.

net movement rather than coordinated migration (Read and Westgate 1997, Verfuss et al. 2007). This pattern was confirmed by Sveegaard et al. (In press, Paper II) who found seasonal changes in the distributional patterns of satellite tracked porpoises: porpoises tagged in the inner Danish waters moved south in the winter whereas porpoises tagged in Skagerrak moved west towards the North Sea. It was proposed that the major movements occur during August-September and March-April although summer and winter habitats overlap to some extent. The present study found seasonal changes in the distribution of high density areas of porpoises in the northern Sound corresponding to the change in distribution found by Sveegaard et al. (In press, Paper II).

The use of acoustic surveys as a mean of examining the distribution of porpoises and other cetaceans has become increasingly applied (Gillespie et al. 2005, Boisseau et al. 2007, SCANS II 2008, Li et al. 2009). Since this survey method is relatively unaffected by weather, observer variability and available man power, it often constitutes a reliable and cost effective alternative to other methods such as visual surveys from boat or plane. Nevertheless, several aspects of critical importance are yet to be clarified. For instance, if porpoises are either attracted or deterred, this will affect density estimates. Palka & Hammond (2001) demonstrated that harbour porpoises did display avoidance to the survey vessel in up to 1 km distances from the ship. This may be a significant bias during visual surveys if this is not correct for. For acoustic surveys, however, the bias is less important because as long as vessel avoidance behaviour is similar between individuals or constant within the geographical area surveyed, the relative density estimates will not be influenced.

Another potential bias is whether porpoise echolocation activity has a constant diurnal and seasonal pattern. Teilmann et al. (2007) found that harbour porpoises tagged with time-depth recorders displayed higher dive rates during October-November than during the summer month. They suggested that this may be caused by an increased foraging activity during the autumn period, compensating for higher energy requirements as the water temperature decreases during autumn. A general higher foraging activity is likely linked to higher echolocation activity, and because hydrophones of the towed array are positioned only a few meters below the water surface, a higher frequency of deep dives by feeding porpoises likely reduces acoustic detection rates. How these aspects affect the detection rates during acoustic surveys is unknown, but the present study found a marked seasonal difference in detection rates with lower detection rates in January-February and higher rates in September-October.

Diurnal variation in echolocation activity may also influence detectability. Porpoises may be relatively silent during periods of resting and perform increased echolocation activity during foraging. Harbour porpoise dive rates have been found to vary diurnally, with porpoise displaying higher dive rates during daylight hours (Teilmann et al. 2007) and making fewer, but deeper dives at night (Westgate et al. 1995). The differences are believed to be caused by diurnal changes in prey distribution. However, in the present study we did not find a significant difference in detections between day and night. This may be due to porpoises responding to the ship by echolocating either towards the ship or investigating the hydrophone array no matter what time of day this occurs.

Spatial distribution data from satellite tracking is potentially biased towards the area of tagging i.e. if the harbour porpoise has a small home range it may stay near the tagging position throughout the period of tracking. Consequently, the results will not be representative for the distribution of the whole porpoise population. This potential problem was rejected by Sveegaard et al. (In press, Paper II), where porpoise distribution was not particularly connected to the tagging sites.

Acoustic surveys represent many possibilities in future research. The aim of this study was to evaluate the distribution and densities of porpoises found by satellite tracking of porpoises. Consequently, the survey trackline was constructed to cover areas of both high and low porpoise density. However, acoustic surveys may in the future be used for estimating porpoise abundance e.g. using distance sampling and it is thus important that tracklines are laid out in a random design (Thomas et al. 2010) and not fixed as in the present study.

This study is of high relevance to the conservation of harbour porpoises. Protection of small cetaceans are often directed toward their key habitats by designation of MPAs, for instance by the implementation of EU's Habitat Directive (92/43/EEC). In 2010 the results of the present study along with the results of Sveegaard et al. (In press, Paper II) were the main scientific basis for designation of Special Areas of Conservation (SAC) for harbour porpoises in Denmark. Thus, a verification of both the spatial and temporal stability of such key habitats are of great importance. If the areas of high porpoise density change from year to year, they will not benefit the porpoises and it would be very cost inefficient to designate MPAs. The areas identified in this study are however relatively stable between years with some seasonal variations. When implementing a management plan for such areas, it is essential to know when an area is used by the animal and when not, especially in relation to fishery where the presented results can contribute to the protection of the species.

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PAPER IV

Status of a harbour population – evidence for population separation and declining abundance

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Status of a harbour porpoise population - evidence of population separation and declining abundance

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ABSTRACT

Three separate harbour porpoise populations has been identified in the waters between the North Sea and the Baltic Sea, namely (1) North Sea and Skagerrak, (2) Kattegat, Belt Sea, the Sound and Western Baltic and (3) the inner Baltic. Proper management of harbour porpoises require reliable information on population status and range. In this study, we use satellite tracking data from harbour porpoises to define population boundaries between these populations and based on these new population boundaries, abundance estimates for the population inhabiting Kattegat, Belt Sea, the Sound and Western Baltic was calculated based on two visual surveys (SCANS) in 1994 and 2005. The population size in was calculated to be 27,767 (CV=0.45, 95% CI=11,946-64,549) in 1994 and 10,865 (CV=0.32, 95% CI=5,840-20,214) in 2005. Although these estimates are not significantly different on the 5% level, we advocate that the declining trend is taken seriously, that conservation actions are taken to ensure that favourable conservation status is established for the Belt Sea harbour porpoise population.

INTRODUCTION

Proper management of a species require reliable information on population status. This requires knowledge of movements, migrations, habitat preferences, identification of population boundaries, and regularly repeated abundance estimates. This information is seldom available for cetacean populations due to the difficulties in studying animals in the continuum of the oceans where animals may move between areas with neighbouring populations. In the last decades, harbour porpoises in European waters have been studied intensely to identify separate populations and monitor the status of the species (e.g., Siebert et al. 2006, Wiemann et al. 2010). The main driver for this effort has been the fact that several thousands of harbour porpoises are bycaught in gillnet fisheries (Tregenza et al. 1997, Vinther and Larsen 2004). Despite a reduced fishing effort due to depleted fish stocks and the use of pingers on gillnets to avoid bycatch, the status of the harbour porpoises in Europe still remain unclear (Siebert et al. 2006).

The harbour porpoise is the smallest and also the most numerous cetacean in Europe (Hammond et al. 2002). It has a wide continuous but uneven distribution throughout European waters. The distribution is presumably linked to the distribution of prey (Koopman 1998, Santos and Pierce 2003), which in turn is linked to environmental parameters such as hydrography and bathymetry (e.g., Bailey and Thompson 2009, Edrén et al. 2010, Embling et al. 2010), but so far only few studies have studies the direct relationship between porpoises and their prey, and many issues in this regard remains unclear (Sveegaard et al. In prep., Paper VII, Sveegaard et al. In review, Paper VI) Abundance estimates for smaller areas have been conducted (e.g., Heide-Jørgensen et al. 1993, Gillespie et al. 2005), but large scale surveys have only been carried out in 1994 (SCANS I, (Small Cetaceans in the European Atlantic and North Sea)) and 2005 (SCANS II). For the Northeast Atlantic continental shelf waters the total number of harbour porpoises was estimated in 1994 to be 341,366 animals (CV = 14.0; Hammond et al. 2002) and in the equivalent area in 2005 to be 334,948 (CV = 0.16; SCANS II 2008). No abundance estimates for subareas representing biological populations are available.

Studies using various methods have tried to understand the population structure of harbour porpoises in the North East Atlantic and in particular the transition zone between the North Sea and the Baltic Sea. This transition zone consists of waters from the Skagerrak in the north through the Kattegat, the Danish Belt Seas, the Sound and the western Baltic Sea to the inner Baltic Sea (Fig. 1). Studies on skull differences, contaminant levels, stable isotopes and genetics have tried to elucidate the population structure in this area. The results are somewhat inconsistent, possibly due to small sample sizes differences in area definition and methods. However, more comprehensive molecular and morphological studies have recently confirmed the existence of several harbour porpoise populations in the study area (Wiemann et al. 2010, Galatius et al. 2010).

Kinze (1985) used non-metric characters to divide porpoises from the Kattegat/Belt Sea and the Dutch North Sea coast into two groups. Börjesson and Berggren (1997) compared harbour porpoise skull measurements between the Swedish south and east coast (inner Baltic Sea) to the Swedish west coast (Kattegat and Skagerrak) and found significant differences between females but not males. Huggenberger et al. (2002) analysed metric and non-metric characters in porpoise skulls and found differences between the North Sea, the Skagerrak/Kattegat/Belt Seas/western Baltic and the inner Baltic east of the Darss and Limhamn

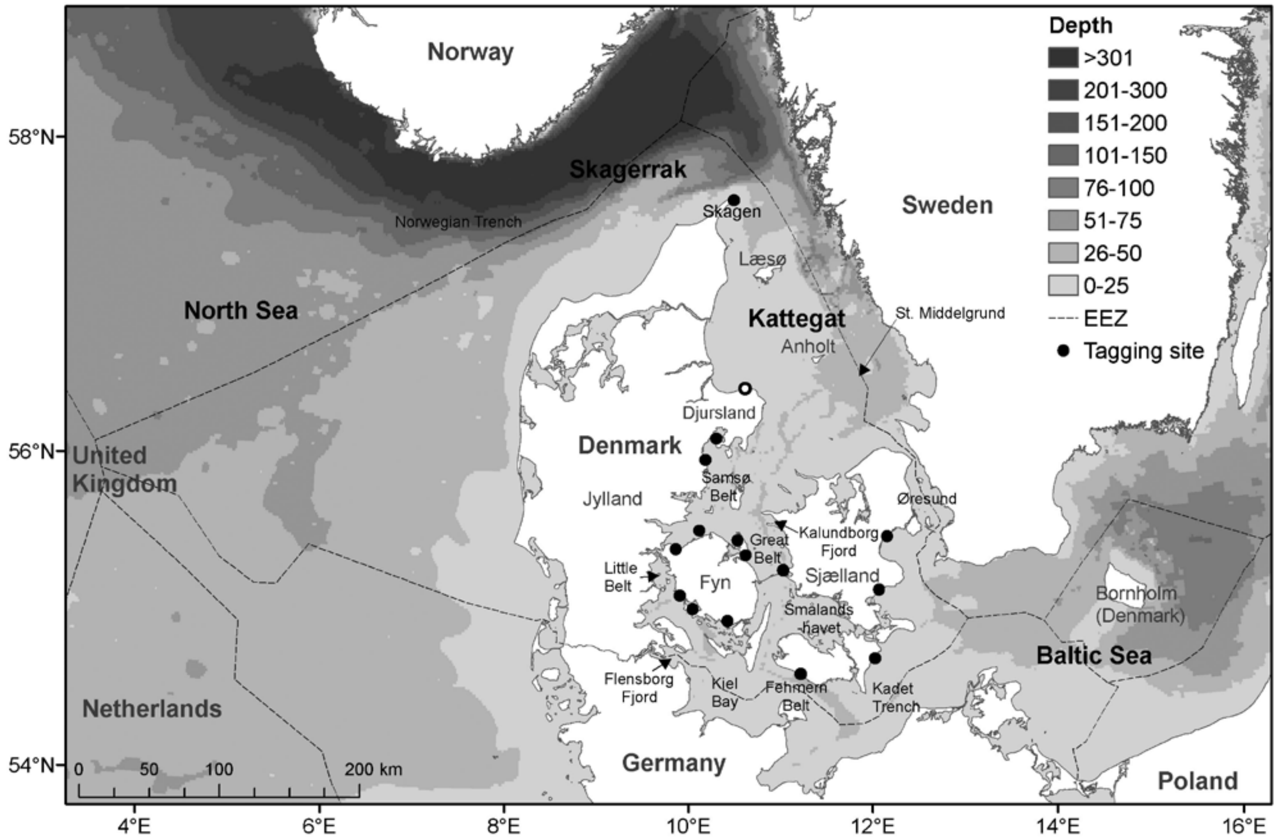

Figure 1. Map of the study area with names mentioned in the text. The locations of the pound nets where the harbor porpoises were live caught and tagged are indicated with black dots. The tagging location on Djursland (open circle) was excluded in the population border calculation to avoid erroneous assignments of locations. The thin dashed line indicates the international Exclusive Economic Zones (EEZ). Map projection universal transverse Mercator, Zone 32N, WGS84.

underwater ridges (Fig. 1). Galatius et al. (2010) used the new geometric morphometric technique with higher power to detect differences and found significant differences in skull shape between 1) North Sea and Skagerrak, 2) Kattegat, Belt sea, the Sound and Western Baltic, 3) the inner Baltic. Three different boundaries between area 2 and 3 were tested. All three turned out to give significant results showing little power to determine an exact border, should there be any. In addition, no linear trend in skull shape was found through the waters from the North Sea to the inner Baltic, indicating population structure based on morphological specialization to a geographical region rather than isolation by distance. Bruhn et al. (1999) found differences in PCB loads between the North Sea and Baltic Sea, while Bergreen et al. (1999) found differences in PCB levels between the Swedish inner Baltic coast and the Swedish Kattegat/Skagerrak coast. Analyses of stable isotopes, can determine differences in diet, but did not show any significant results along the Swedish coastline (Angerbjörn et al. 2006). By analysing mitochondrial DNA restriction fragments, Wang & Bergreen (1997) showed significant differences between the Swedish Baltic coast and the Swedish Kattegat/Skagerrak coast. Tiedemann et al. (1996) tested differences in mitochondrial DNA sequence patterns and found significant differences between the North Sea and the German/Polish Baltic coast. Andersen et al. (1997) used microsatellite markers and isozymes from the nuclear genome to detect differences between the Kattegat/Belt Sea/western Baltic and the North Sea, although fairly high gene flow was suggested. Andersen et al. (2001) used 12 microsatellite markers to test population structure in the northeast Atlantic. They found that the Skagerrak porpoises clustered with the North Sea animals and that this population was different from Kattegat/Belt Sea/Sound/Western Baltic. Furthermore, no difference was found between samples from the Swedish south coast (inner Baltic) and the Kattegat/Belt Sea/Sound/Western Baltic. Wiemann et al. (2010) used both mitochondrial and microsatellite DNA from the largest sample size tested so far (n=497) covering all areas from the North Sea to the inner Baltic Sea. Evidence was found for separation between populations in the northern Kattegat, at the Darss underwater ridge and in the northern part of the Sound. To summarize, three separate populations has been identified in the transition zone between the North Sea and the Baltic Sea, namely (1) North Sea and Skagerrak, (2) Kattegat, Belt Sea, the Sound and Western Baltic (from now on called the Belt Sea population), and (3) the inner Baltic.

The porpoises in the inner Baltic have long been of concern and was in 2008, assigned the status of 'Critically Endangered' on the IUCN red list (www.iucnredlist.org). Little is known about the distribution and status of this population, but until the first half of the 20th century, porpoises were abundant in the inner Baltic Sea. However, a dramatic decline has been observed during the past 50-100 years (Skora et al. 1988; Koschinski 2002; Andersen et al. 2001). Based on two separate surveys, estimated population sizes of 599 (CI=200-3300) animals in 1995 (Hiby and Lovell 1996) and 93 (95% CI=10-460) in 2002 (Berggren et al. 2004). Due to very few observations these estimates have great uncertainties. Management plans to protect porpoises in the Baltic Sea as well as the Belt Sea population that represents the only possible source of new gene flow into the Baltic Sea is therefore highly needed.

Based on the identified population structure found in the studies mentioned above, we will use satellite tracking data from harbour porpoises to define population boundaries between these populations. The boundaries will be defined as the line between populations showing the least overlap in movements of satellite tagged harbour porpoises from the North Sea/Skagerrak population and the Belt Sea populations. Based on these new population boundaries, new abundance estimates will be calculated based on the 1994 and 2005 surveys to reveal the status of this population.

MATERIALS & METHODS

Determining population borders

To monitor the status of a population, it is essential to determine the exact borders of the area from which the abundance can be estimated. In species like the harbour porpoise where populations are often overlapping, it is difficult to establish such borders. In this study, we use locations from satellite tracked porpoises from separate populations to calculate the border that creates the minimum overlap, i.e. the smallest number of locations on the 'wrong' side of the border.

Twenty-four harbour porpoises were tagged at Skagen on the northern tip of Jylland between May 2000 and September 2003 and 58 harbour porpoises were tagged in the Belt Sea from April 1997 to June 2010 (Fig. 1). Porpoises were caught alive incidentally in pound nets. Harbour porpoises were usually tagged within 24 h of being discovered by the fisherman. An Argos satellite transmitter was attached to the dorsal fin of the porpoises using 2–3 polyoxymethylen 5-mm pins covered with silicone tubes (Geertsen et al. 2004, Teilmann et al. 2007, for more details on tagging procedure, transmitters and effects of tagging, see Eskesen et al. 2009, Sveegaard et al. In press, Paper II). Satellite contact remained for up to seventeen month (mean transmission time: 106 days). The locations of the tagged animals were determined by the ARGOS system. Locations were filtered by a SAS-routine, Argos-Filter v7.03 (for details on location error and the filtering process, see Douglas 2006, Sveegaard et al. In press, Paper VII). The most accurate location was selected for each day resulting in a total number of 5,855 locations. The locations were imported into ArcGIS 9.3 (ESRI) and the mapped with the Zone 32 (N) Universal Transverse Mercator projection, using the WGS 1984 datum.

To determine the border between populations in the Kattegat, each tagged animal was assigned to either the North Sea/Skagerrak population or the Belt Sea population based on tagging site. Thirteen porpoises tagged in the middle of the transition zone (on Djursland in the central Kattegat, Fig. 1) were excluded from the analysis, since the population affiliation of these animals are uncertain and we wanted to avoid assignments to a wrong population. Furthermore, only the locations within the area of the transition zone were included in the analysis. This meant exclusion of locations west of 10˚E and south of 56˚25’N (Fig. 3). To obtain equal contribution from animals from the two populations, the dataset was normalised to one location per animal per day. This was done by multiplying (weighting) each location by the duty cycle (days between transmissions) of each tag, i.e. if a tag was set to transmit every second day, each location from that tag would weigh double in the analysis. The number of animals was also normalised by multiplying the proportion of animal between the two populations to all locations. This only applied weight to the locations from the porpoises tagged in the Skagerrak/North Sea population.

The optimal method for defining the population border would be to focus on the distribution of mature harbour porpoises in the reproduction period, which may potentially exchange genes between populations. In this area, length of harbour porpoise at sexual maturity has been defined females >143 cm and males >135 cm corresponding to an age of 3-4 years (Lockyer and Kinze 2003). However, since porpoises grow 5-10 cm in length per year at this age, and since several of the porpoise transmitted for a long period and thus reached maturity within the time of transmission, we defined sexual maturity as females >140 cm and males >130 cm at the time of tagging. Nevertheless, only 2 mature porpoises from the Belt Sea population and 6 from the Skagerrak/North Sea population swam into the transition zone in the reproductive period (May-August), and consequently, we decided to include the distribution of (1) all porpoise locations all year, (2) mature porpoises in the reproductive season and (3) immature porpoises in the reproductive season in the analysis. The border was calculated as an east-west line between Denmark and Sweden with fewest possible porpoise locations from the Belt Sea population north of the line and fewest possible porpoise locations south of the line from the Skagerrak/North Sea population. Furthermore, the number of locations on the ‘wrong’ side of the line should be equal for both populations. A standard linear equation (y=a*x+b) was used and the performance of the slope (a) was tested in 0.5 degree steps (i.e. for every 1˚E the slope was set to 0.5˚N, 1.0, 1.5, etc). For each of these steps the line that divided the overlapping

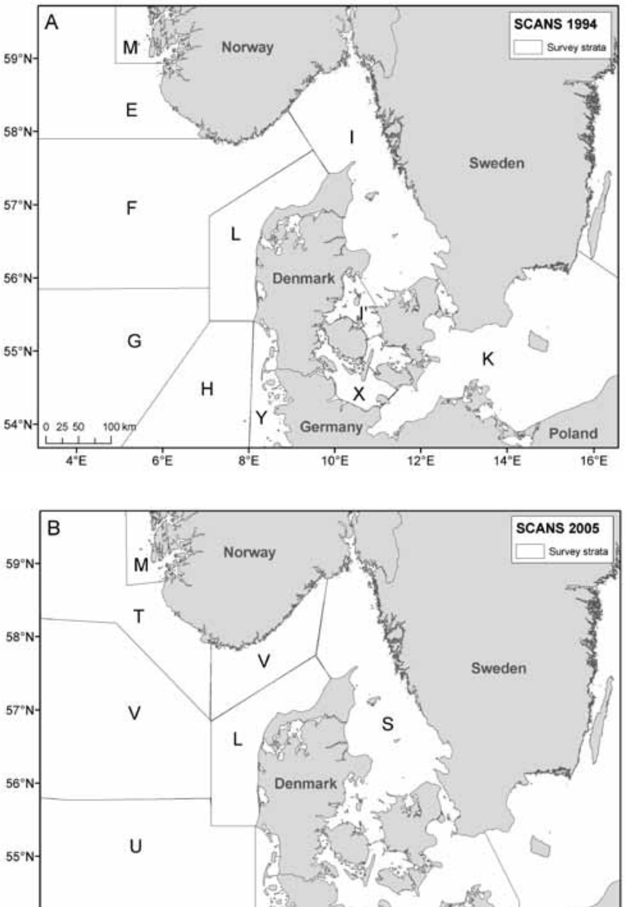

Figure 2. Survey strata used in **A)** the SCANS I survey in 1994 and **B)** survey strata used in SCANS II in 2005 (Modified from SCANS II 2008).

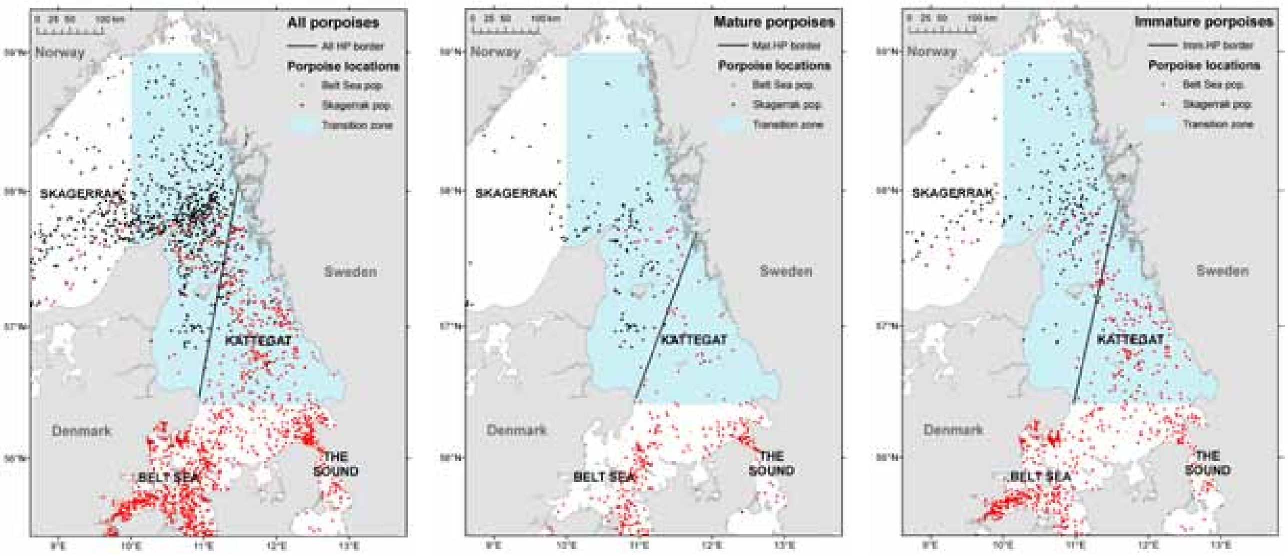

Figure 3. Locations from satellite tracked harbour porpoises from 1997-2010 (1 porpoise^{-1} day^{-1}). The area used for calculating borders between the Belt Sea and the Skagerrak/North Sea populations are indicated with a blue square, while the resulting border is shown with a black line. Left panel: all harbour porpoises all month (Skagerrak = 24 porpoises, Belt Sea = 22 porpoises), centre panel: mature harbour porpoises in the reproductive season from May to August (Skagerrak=6, Belt Sea=2) and right panel: immature harbour porpoises in the reproductive season (Skagerrak=9, Belt Sea=6).

locations equally was found by manually adjusting 'b' in the equation. When all the lines with the best fit for each step were found, the one with the lowest equal number of overlapping locations was chosen.

Since no porpoises were tagged in the inner Baltic Sea this approach could not be used to find the border between the Belt Sea population and the population in the inner Baltic Sea. Instead morphometric and genetic evidence supported by satellite locations were be used to set this border.

Abundance estimation

For the abundance estimation, the population area was limited by the possibilities of comparing the two SCANS surveys. Since the strata east of Fehmarn Belt in 1994 (Strata 'K', see Fig. 2) had too few observations for an abundance to be estimated, this area could not be included in the analysis. Instead, the boundary was defined as the narrowest part of the northern Sound and Fehmarn Belt (Fig. 2). To the north, the boundary was defined by the satellite locations as described above.

Shipbased double platform line transect surveys, were conducted in the study area from late June to mid July in both 1994 and 2005, in addition part of the Belt Sea and western Baltic was covered by a double aerial survey in 1994 (SCANS II 2008). Since the strata for the two surveys did not cover identical areas new calculations was made for shipbased surveys (strata I in 1994 and S in 2005). For 1994 the aerial survey for strata X was added to the shipbased survey (Fig. 2A). The abundance estimates from area X and part of area I in 1994, was summarised and a new coefficients of variance (CV) and confidence intervals (CI) was calculated using the method described in Buckland et al. (2001), i.e. the combined standard error (SE) was found by applying the formula:

$$SE_{BeltSeaPop}=\sqrt{(SE_{StrataI}^2+SE_{StrataX}^2)}$$

and the new CV by dividing $SE_{BeltSeaPop}$ by the combined abundance estimate. Observers on two platforms were used to correct for animals missed on the transect line and also for the effects of movement of animals in response to the ship (Laake and Borchers 2004). Survey effort was only conducted in sea state 0–2 in order to be able to calculate a reliable detection function (Teilmann 2003). The calculations followed exactly those given in SCANS II (2008) and provide an unbiased estimate of the total abundance of harbour porpoises.

RESULTS

The calculated borders between the Belt Sea population and the Skagerrak/North Sea population for all porpoises, mature porpoises and immature porpoises are shown in figure 3. Due to the little

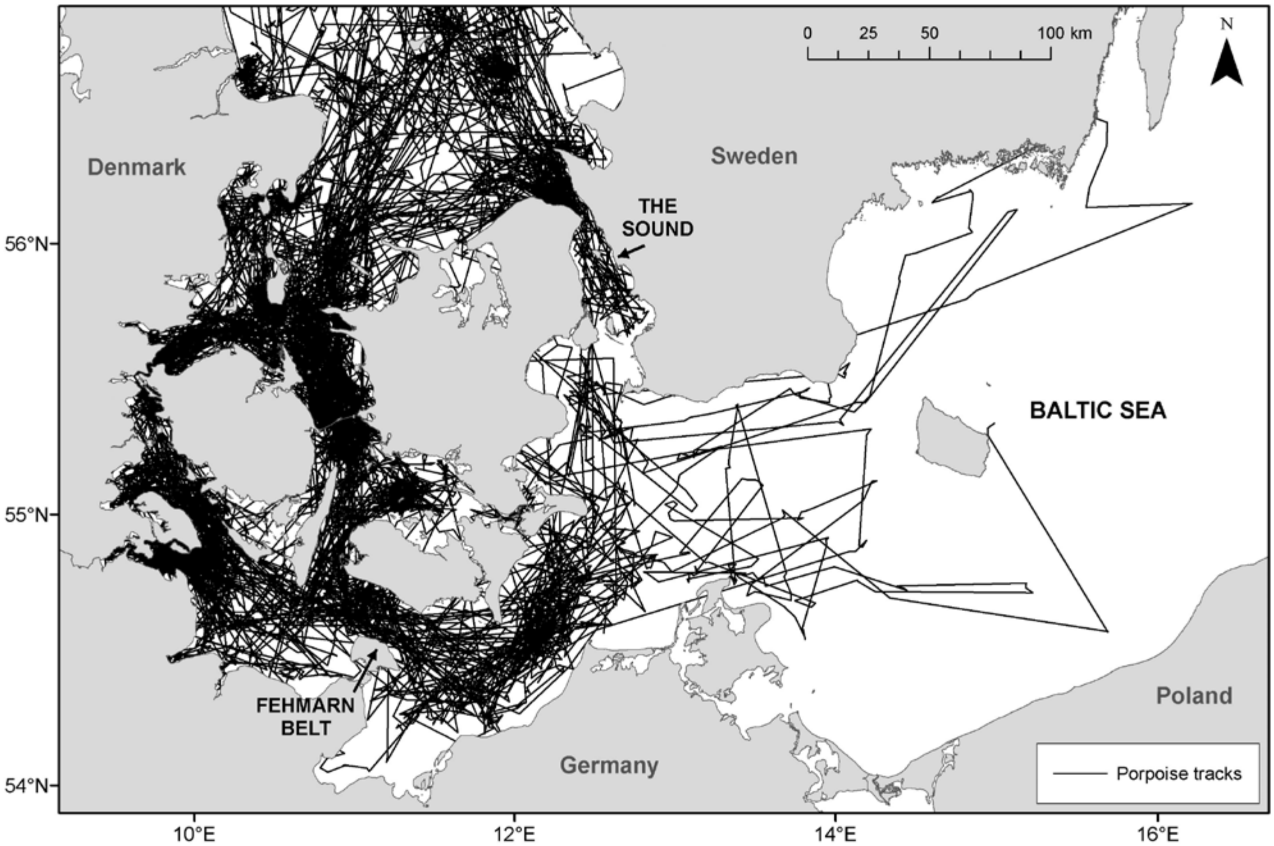

Figure 4. Tracks from 58 satellite tracked harbour porpoises from the Belt Sea population, showing the extent of movements into the inner Baltic.

variation between the lines and the low number of locations from the mature harbour porpoises, we chose to set the population border based on 'All porpoises' (Fig. 3A). The best fit for all population borders in the Kattegat resulted in a diagonal line (y=3x+23.55) from the eastern point of Djursland (10°55′15″E, 56°28′37″N) in Denmark to the Swedish coast (11°27′54″E, 58°03′28″N) (Fig. 3). For this line, 3.7 % of the locations belonging to one population were found on the opposite side of the line. Based on the available data, this line provides a fixed border between the two populations that will be used to divide the populations in the abundance estimations below.

For the southern border, Galatius et al. (2010) found that Fehmarn Belt was an equally good border to separate the population in the inner Baltic as the two alternatives; the Darss underwater ridge and a line from the south-eastern point of Sweden to the German/Polish border. Wiemann et al. (2010) and other previous studies found a separation at the Darss underwater ridge. Porpoise were not tagged in the inner Baltic Sea and we therefore only know that the animals from the Belt Sea population swim into the inner Baltic but not how far porpoises from the inner Baltic move westward (Fig. 4). Given the few porpoises that swim east of 13°E, the border based on satellite tracking will probably lie west of this line. This is still within the population boundary estimated by Galatius et al. (2010), but about 50 km east of the Darss underwater ridge. However, since the SCANS I survey in 1994 was limited to west of Fehmarn Belt, this border was chosen to

Table 1. On track survey effort, total number of observations of individual harbour porpoises, *Phocoena phocoena* (N), estimates mean group size, harbour porpoise density, harbour porpoise abundance and upper and lower 95% confidence intervals (CI). CVs are given in parentheses.

Survey	Year	Area (km^2)	Survey effort (km)	N	Mean group size	Porpoise density (CV)	Porpoise abundance (CV)	Lower CI	Upper CI
SCANS	1994	30,254	595	160	1.46	1.16 (0.46)	27,769 (0.45)	11,946	64,549
SCANS-II	2005	30,254	639	122	1.66	0.36 (0.32)	10,865 (0.32)	5,840	20,214

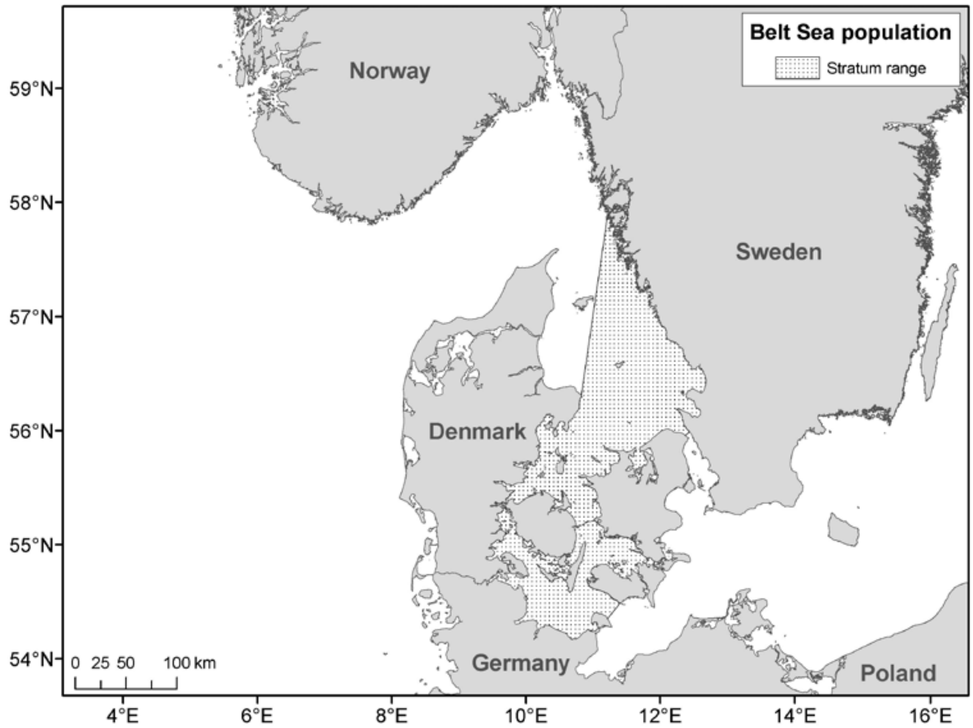

Figure 5. The scattered area illustrates the extent of the Belt Sea harbour porpoise population and the area used for abundance estimations in the present paper.

estimate abundance for the Belt Sea population. This resulted in 14% of the locations for the satellite tagged Belt Sea porpoises to be outside (East of) of the population boundary.

Abundance estimation

The Belt Sea population size was calculated to be 27,767 (CV=0.45, 95% CI=11,946-64,549) in 1994 and 10,865 (CV=0.32, 95% CI=5,840-20,214) in 2005 (See table 1). Although this equals a decrease in density from 1.16 porpoises/km^2 in 1994 to 0.36 porpoises/km^2 in 2005, the high variations of the estimates does not provide statistically significant results on 5% level ($p > 0.05$).

DISCUSSION

Movements of harbour porpoises are complex, and although limited seasonal movements have been found, no organised seasonal migration pattern have been found and consequently most animals utilise the same area year round (Sveegaard et al. In press, Paper VII). No difference in home range have been found between the sexes, but immature porpoises have twice the home range size compared to adults in the Belt Sea population area, suggesting some exploratory behaviour of young animals (Sveegaard et al. In press, Paper VII). The northern border of the Belt Sea population was determined with only 3.7% of locations outside the population boundary and the south-eastern border with 14% locations outside. The latter could indicate that the actual population border between the Belt Sea population and the Baltic Sea population may be located further east. However, in this study we did not have the option of moving it for the abundance analysis, due to limitations in survey data.

Nevertheless, the based on the results of this study, and the supporting evidence from genetics and morphometrics (Wiemann et al. 2010, Galatius et al. 2010), we are quite confident that the Belt Sea population can be defined by an area with fixed borders year round.

The establishment of an exact boundary is important, if a monitoring program of the population and their habitats should be established as required by the EU Habitats Directive, stating that all member states shall take action to maintain or restore a favourable conservation status of harbour porpoises (92/43/EEC). Member States are required to report every six years on whether their conservation status is favourable and on the implementation of measures taken to ensure this. Conservation status is defined in the Habitats Directive as ‘the sum of the influences acting on the species that may affect the long-term distribution and abundance of its populations’ and can be considered as ‘favourable’, if the species is maintaining itself as a viable component of its natural habitats and if abundance and range are maintained. This only makes sense, if the population structure is known as smaller populations may disappear unnoticed if only abundance of porpoises on a European level is assessed. This may have been the case for the two SCANS surveys, where the overall abundance between the SCANS surveys in 1994 and 2005 revealed no overall change in abundance. The distribution had, however, changed significantly from the northern North Sea to the southern North Sea. Whether this is a result of changing fish stocks, or declines in local populations is unknown (SCANS II 2008).

Satellite tagging of porpoises in the Belt Sea region has taken place between 1997 and 2010, covering most of the period between the two SCANS surveys, and no emigration have been observed that coincide with the overall SCANS results (Sveegaard et al. In press, Paper VII). The declining abundance estimates from 27,767 in 1994 to 10,865 in 2005 is therefore unlikely due to emigration into the southern North Sea or to the inner Baltic. Although the abundance estimates have large confidence intervals, this should give reasons for great concern and until further abundance estimates are available, the population should be considered as having an unfavourable conservation status. Bycatch of porpoises in gillnets are believed to be a major threat to porpoises throughout their range (Read et al. 2006), but no estimate of bycatch in the Kattegat, Belt Sea, Sound or the Baltic exists. Siebert et al. (2006) reported that a significantly higher proportion of the stranded harbour porpoises on the German Baltic coast compared to the German North Sea coast could be determined as bycatches and that fishermen reported higher bycatch rates in the Germen Baltic than in the German North Sea. This is further supported by the fact that bycatch was found to be the primary cause of death for harbour porpoises in the Baltic Sea while infectious diseases and perinatal death predominated in the North Sea (Wünschmann et al. 2001, Siebert et al. 2001).

Although the abundance estimates have overlapping confidence intervals, the Belt Sea population may be close to extinction before new abundance estimates are available and significant results are obtained. In conclusion, we therefore recommend that actions are taken to ensure that favourable conservation status is re-established for the Belt Sea harbour porpoise population. The main pressure seem to be the bycatch in gillnet fishery, however, the influence of other threats from construction work, seabed exploitation, contaminants, and diseases should also be investigated and considered.

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PAPER V

Prey availability and preferences of harbour porpoises in Kattegat and adjacent waters – a review

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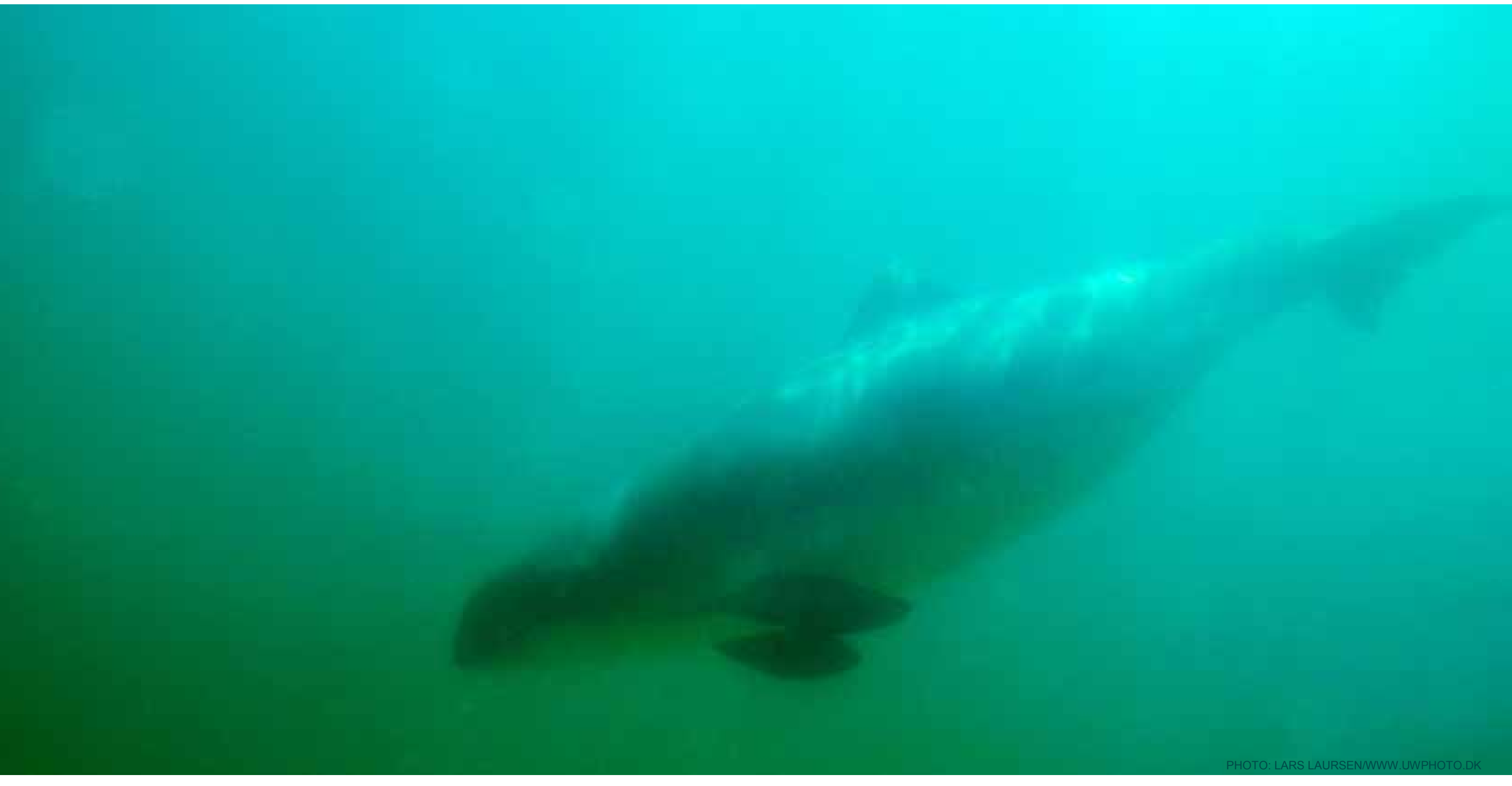
Jacob Nabe-Nielsen & Jonas Teilmann

In prep., not ready for publication due current data unavailability



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Prey availability and preferences of harbour porpoises in Kattegat and adjacent waters – a review

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ABSTRACT

Harbour porpoises are opportunistic feeders with constant high energy requirement. The distribution of harbour porpoises is therefore likely to be correlated with distribution of their main prey species. This study reviewed all available studies on porpoise stomach analysis for a genetically distinct harbour porpoise population inhabiting Kattegat, the Belt seas, the Sound and the Western Baltic. Cod, herring, gobies and whiting were identified to be the primary prey species. The seasonal changes in prey preferences were subsequently compared with available knowledge on the distribution of these fish species in order to assess how porpoise behaviour and distribution is related to the distribution of their prey. It was found that the prey species were indeed present within the study area, and the spatial seasonal changes in harbour porpoise prey preferences corresponded well for spatial distribution of cod, whiting and gobies, but less so for herring. This study is the first to relate porpoise prey preferences to information on prey distribution in order to explain variations in porpoise movements and distribution.

INTRODUCTION

The harbour porpoise has been observed in most parts of the Kattegat and adjacent waters (e.g., Hammond et al. 2002, Kinze et al. 2003), but it is not evenly distributed within its range (Siebert et al. 2006, Sveegaard et al. In press, Paper II). In Kattegat, the Belt seas (the Sound, Great Belt and Little Belt) and the western Baltic, harbour porpoises are known to gather in several high density areas, especially in the narrow straits of Little Belt, Great Belt, Fehmarn Belt and the Sound (Verfuss et al. 2007, SCANS II 2008, Scheidat et al. 2008, Sveegaard et al. 2011). The importance of some of the high density areas vary over the year (Sveegaard et al. In press, Paper II).

Due to its small size, limited body fats and high energy expenditure, the harbour porpoise requires a constant high energy input (Koopman 1998) and eats about 3.5–5.5 kg per day (Lockyer et al. 1999). The distribution of harbour porpoises is therefore presumably linked to distribution of prey. The most important prey species in the North Sea, the western Baltic and the waters in between are herring, sprat, cod, whiting, sandeels and gobies (Aarefjord et al. 1995, Börjesson et al. 2003, Santos et al. 2004). This implies that the harbour porpoise distribution can be expected to be positively correlated with the distribution of these species (Koopman 1998, Santos et al. 2004). The correlation has mainly been tested indirectly by modelling porpoise distribution based on environmental variables as proxies for prey. Salinity, depth, tidal state and sediment type have been found to have a significant influence on porpoise distribution in Danish and Scottish waters (MacLeod et al. 2007, Marubini et al. 2009, Bailey and Thompson 2009, Edrén et al. 2010, Embling et al. 2010).

This study aims to identify preferred prey species for the genetically distinct harbour porpoise population inhabiting Kattegat, the Belt seas and the Western Baltic (Wiemann et al. 2010) by comparing available data from porpoise stomach analysis in the area and re-analysing this data to gain insights into the seasonal changes in prey selection. The seasonal changes in prey preferences will be compared with available knowledge on the distribution of these fish species in order to assess how harbour porpoise distribution are correlated to and possibly can be predicted from distribution of their prey.

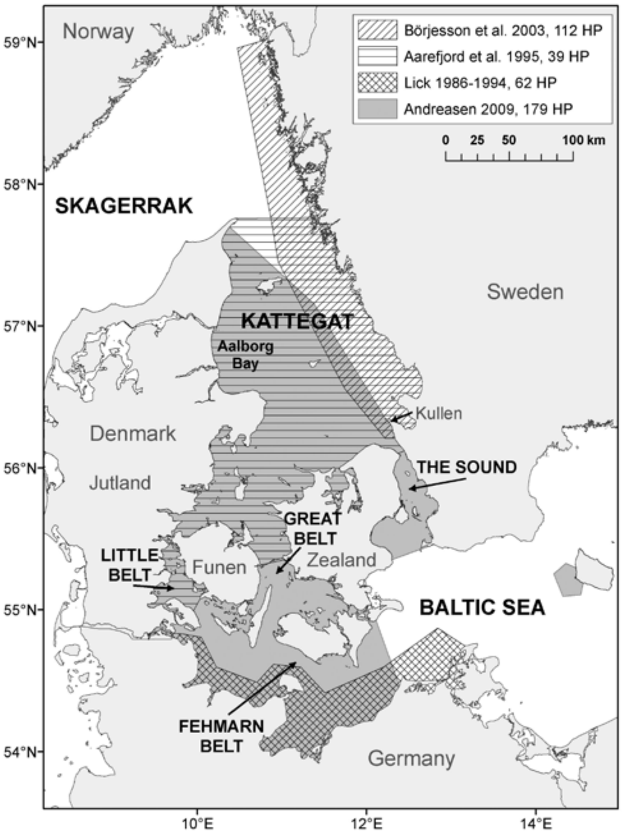

Figure 1. Map of the study area with the estimated coverage of each the four studies indicated.

METHODS

Study area

Kattegat, the Belt seas and the German Baltic Sea are relatively shallow areas with average depths of 23 m and a maximum depth of about 100 m. The area constitutes a mixing zone for the highly saline bottom water flowing in from the North Sea and the brackish surface water flowing out of the Baltic.

Harbour porpoise prey selection

Several studies on prey selection in porpoises have been conducted during the last twenty-five years in Kattegat, the Belt seas and the German Baltic (Figure 1). Aarefjord et al. (1995) analysed porpoise stomach contents from Kattegat collected in Danish and Swedish waters. Some of the Swedish data were also included in the study of Börjesson et al. (2003). Lick collected and analysed 62 stomachs from 1986–1994 (FTZ, University of Kiel). The results have been published partly in Lick's PhD thesis (data from 1986–1990) (Lick 1991) and partly in German reports and a peer reviewed paper (data from 1991–1994) (Lick 1994, Lick 1995, Benke et al. 1998). However, in this study, all data collected by Lick were combined, and will be referred to as Lick (1986–1994). Andreasen (2009) published data from 179 porpoise stomachs in her master thesis from the University of Copenhagen. The stomach samples were collected from 1985–2006. Stomachs from 1985–1992 were collected by C. C. Kinze, Zoological Museum. The Danish Institute for Fisheries Research collected 77 stomachs samples from 1996 to 2002 under the projects of ByCare and Epic. The remaining samples were collected along the German and Danish Baltic Coast by FTZ in1994–2006 (Gilles et al. 2008, Gilles 2009).

Each study examined the stomach content from 39 to 179 bycaught or stranded harbour porpoises (Table 1). Aarefjord et al. (1995) and Börjesson et al. (2003) collected stomach samples in the northern half of the study area and the results from Börjesson et al. (2003) extend beyond Kattegat and into Skagerrak. Lick collected stomach samples in the southern part and Andreasen (2009) in the entire area, although 90% of her samples are from the southern part (Belt Sea and western Baltic). The number of years that stomach samples was collect-

Table 1. Studies on harbour porpoise prey preferences in the Great Belt and adjacent waters. The studies of Lick 1991, 1995 and Benke et al. 1998 are referred to as Lick (1986-1994).

Author	Year	No. porpoises	Area
Andreasen 2009	1985 -2006	179	Kattegat, Danish straits, Western Baltic
Lick 1991	1986-1990	36	Danish straits, Western Baltic
Lick 1994; 1995 & Benke et al. 1998	1991-1994	26	Danish straits, Western Baltic
Börjesson et al. 2003	1988 -1996	112	Western Kattegat and western Skagerrak
Aarefjord et al. 1995	1985 -1990	39	Kattegat

ed varies among the four studies with Aarefjord et al. (1995), Börjesson et al. (2003) and Lick (1986–1994) collecting for 5, 8 and 9 years, respectively, and Andreasen (2009) collecting for 21 years. All four studies had an almost equal distribution of the sexes and 48% of all porpoises were females and 52% were males.

The methods used for analysing the stomach content were comparable among the four studies and is described in details in Börjesson et al. (2003). In short, the fore stomach and the lower part of the oesophagus were rinsed with running water and the content separated through a net of sieves with mesh sizes of 2 mm, 1 mm and 0.5 mm, respectively. The remains in the sieves, such as whole or partly digested prey items, fish bones and otoliths were counted, identified and measured.

When examining prey preferences it is particularly interesting to look at (1) the frequency of occurrence, %O (the number of stomachs found to contain a particular prey species divided by the total number of stomachs with identifiable remains, multiplied by 100), (2) the frequency of numerical occurrence, %N (the number of individuals of the particular prey species divided by the total number of prey individuals found, multiplied by 100) and (3) the frequency of estimated weight of each species, %W (the total weight of the particular prey species divided by the total weight of all prey species, multiplied by 100). All three variables were either available in the published data or calculated for the four studies for all years. %O and %W were also calculated for the four quarters of a year for Lick (1986–2006) and Andreasen (2009)[1]. The results for each study were weighed according to total number of stomachs examined for %O, according to total number of otoliths for %N and according to the total mass of prey for %W. The results of frequency of occurrence (%O) by Andreasen (2009) was, for example, based on the analyses of 179 porpoise stomachs, equivalent to 45.7% of the total number of stomachs in the four studies. Consequently, all Andreasens (2009) results were multiplied by 0.457. Aarefjord et al. (1995) does not provide the total mass for the study. The total weight was estimated based on average weight of prey (from Andreasen et al. 2009). The weighting values are listed in Table 2.

The lengths and weights of the consumed fish were calculated using otolith size regression (allometric equations) for fish in the North Sea and Skagerrak. Estimated lengths and weights were calculated using the equations from Leopold (2001) for Lick (1986–1994) and for Andreasen (2009) and from Härkönen (1986) for Aarefjord et al. (1998) and Börjesson et al. (2003). In cases where it was not possible to measure the otolith length, the weight and length of the fish was calculated based on the average otolith length from the remaining samples.

Distribution of prey species

The majority of current knowledge on fish species derives from fishery research, monitoring of commercial fisheries as well as data from landings. To gather information on the abundance, ecology and distribution of herring, cod, whiting, and gobies in the study area, an extensive literature search in Web of Science, Science Direct and Google Scholar was conducted. Furthermore, ICES (International Council for the Exploration of the Sea) provides available electronic data for examining fish landings namely (1) Online distribution maps, 'ICES FishMaps', of commercial fish species in Kattegat based on Catch Per Unit Effort (CPUE) and (2) the DATRAS survey database, which provides data for further analysis on average CPUE for certain fish species in the Belt seas and the Western Baltic. For this study only cod is relevant, as the other species caught are not part of the porpoise diet. Data for (1) also derives from the DATRAS survey database, which is maintained by the ICES secretariat in Copenhagen. The surveys in Kattegat are primarily conducted by DTU Aqua and in the southern

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[1] Seasonal calculations of prey data from Aarefjord et al. 1995 and Börjesson et al. 2003 will be included before publication.

Table 2. Percent numerical occurrence (%N), percent occurrence (%O) and percent weight (%W) of harbour porpoise prey species, derived from stomach analyses from four studies. Weight factor refers to the fraction of the total number of fish, occurrence or weight constituted by the fish in each study* The total weight was estimated based on average weight of prey (from Andreasen et al. 2009).

Study		Cod	Whiting	Gadidae spp.	Saithe	Norway pout	Herring	Sprat	Sandeels spp.	Goby spp.	Eel	Eelpout	Pearlsides	Hagfish	Fish <5%	Weight factor
Lick (1986-1994)	%N	1.7	0.1				1.8	0.8	0.0	91.8		0.1			1.5	30.3
	%O	43.5	8.1				43.5	6.5	4.8	40.3		4.8			25.8	15.8
	%W	50.5	0.5				15.9	2.7	0.1	28.9		0.1			0.1	12.1
Andreasen (2009)	%N	6.6	3.2	1.0		1.0	2.5	0.8	3.2	78.3	0.2	1.6			2.7	48.4
	%O	50.0	20.0	19.0		5.0	21.0	9.0	12.0	49.0	5.0	6.0			18.0	45.7
	%W	52.6	14.3	5.5		0.4	7.9	0.5	1.9	6.5	0.9	6.2			3.7	49.0
Börjesson et al. (2003)	%N	0.6	17.4	9.0	2.0	8.2	8.3	8.6	5.6	19.0			8.9	7.8	14.8	15.7
	%O	8.0	17.9	31.2	13.4	27.7	62.5	18.8	10.7	40.2			9.8	25.9	0.0	28.6
	%W	5.5	5.4	6.8	5.0	4.1	56.2	9.0	1.8	0.8			0.4	1.4	12.7	35.7
Aarefjord et al. (1995)	%N	0.7	1.0	1.0			7.0	1.0	0.1	83.0			2.0		3.2	5.6
	%O	8.0	21.0	21.0			54.0	15.0	21.0	36.0			8.0		0.0	9.9
	%W*	10.6	8.2	11.1			42.1	1.1	0.1	13.1			2.2		11.5	3.2

part by Institute of Sea Fisheries (ISH) and Institute of Fishing Technology and Fishery Economics (IFF) in Hamburg. The surveys are conducted with large trawlers that require a certain depth to operate. Consequently, areas with shallow water such as the Bay of Aalborg in Kattegat and the entire coastal zone are not included in these surveys. The minimum spatial scale in the ICES FishMaps is a 9th ICES square (approx. 400 km^2). The user of ICES FishMaps may optionally divide the fish distribution maps in quarters of a year and by length or age group. However, data for many species are only available in one or two quarters, namely the quarters in which the dedicated survey is conducted. ICES FishMaps were visually examined for herring and whiting. Based on downloaded data from DATRAS, average CPUE were calculated for the most important porpoise prey species for the ICES area 21, 22, 23 and 24, respectively.

RESULTS

Harbour porpoise prey selection

Up to 24 different fish species were identified in each of the four studies. In this review, however, only the species that occurred in more than five percent of the stomachs in at least one of the original unweighted analysis was included (Table 2). In terms of %O (Figure 2A), gobies (Gobiidae) were found in 45% of the harbour porpoises stomachs, herring (*Clupea harengus*) in 40%, cod (*Gadus morhua*) in 33% and whiting (*Merlangius merlangus*), sprat (*Sprattus sprattus*) and sandeel (*Ammodytidae*) were found in 18%, 12% and 11%, respectively. The majority of herring was reported by Börjesson et al. (2003). Gadidae spp. that represent unspecified species of the cod family, here pre-sumably mainly cod and whiting, were found in 20% of the stomachs. The other species; saithe (*Pollachius virens*), Norway pout (*Trisopterus esmarkii*), eel (*Anguilla anguilla*), eelpout (*Zoarces viviparous*), pearlsides (*Maurolicus muelleri*) and Atlantic hag fish (*Myxine glutinosa*) were found in one or two of the original studies, but occurred in less than 10% of the stomachs and constituted less than 3% of the total prey weight and are, thus, not believed to be of high importance (Table 2).

Gobies were the most numerous family in the stomachs and constituted 72% of the individuals (Figure 2B). The majority of gobies were observed by Lick (1986–1994). It is difficult to distinguish goby species based on otoliths. They are very similar and deteriorate fast in the stomach of a porpoise. An identification has never the less been attempted in two of the four studies, namely Andreasen (2009) and Lick (1986–1994). Andreasen (2009) found that sand goby (*Pomatoschistus minutus*) and black goby (*Gobius niger*) to be present in the sample, but it only constituted 0.2% and 1.2% of the total number of goby otoliths. The remaining 98.6% of the goby otoliths were too small and similar for visual separation. Similarly, Lick (1986-1994) found black gobies to constitute 1% of the total goby otolith sample size. Consequently, sand goby and black goby were pooled with the other goby species in the analysis.

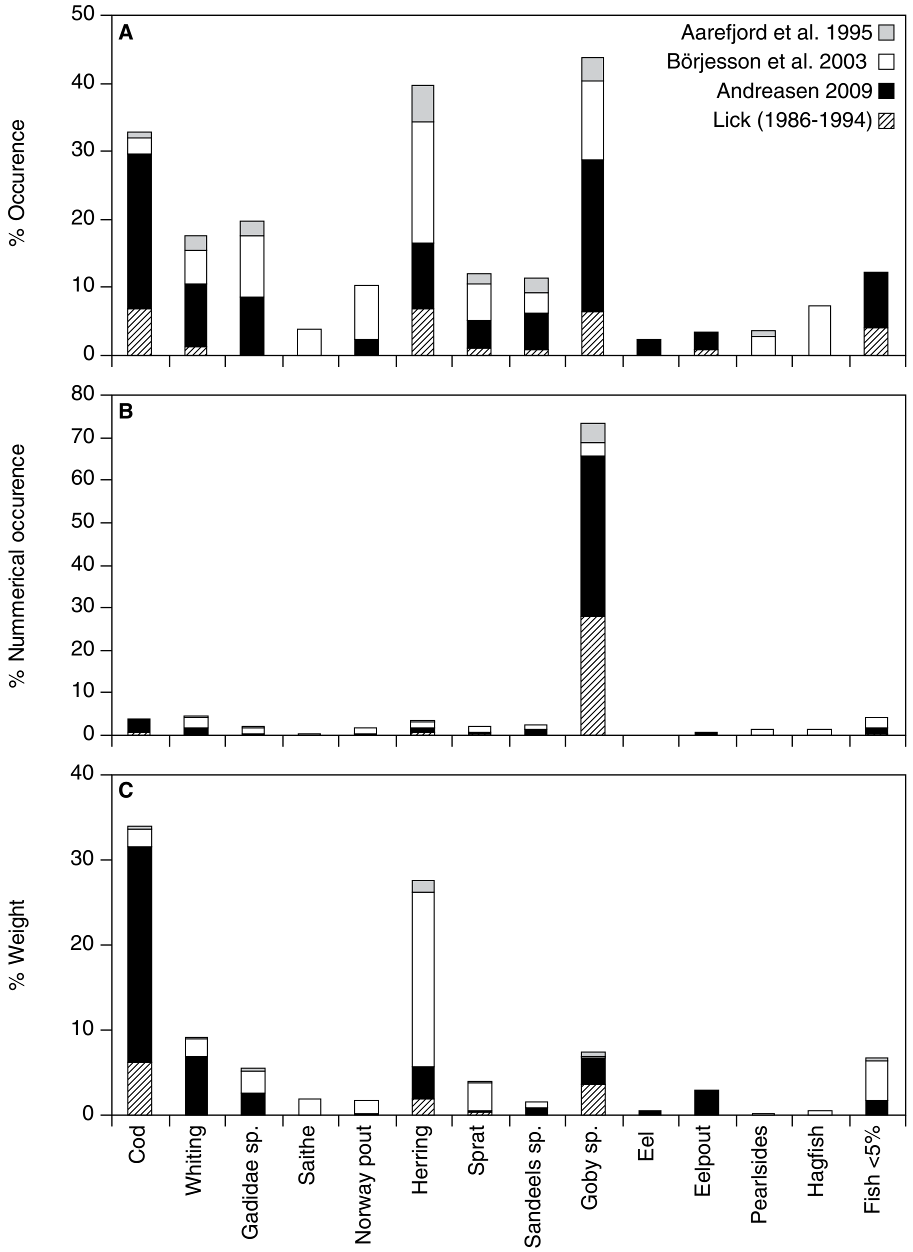

Figure 2. A) Frequency of occurrence (top panel), **B)** Numerical occurrences (%N) (centre panel), and **C)** Percentage by weight of fish species in stomachs of harbour porpoises. 'Gadidae spp.' refers to unidentified cod species. Data are weighted according to the number of porpoise stomachs in each study (Modified from Lick (1986-1994), Aarefjord et al. 1995, Börjesson et al. 2003, Andreasen 2009).

Cod and herring were the most important prey species in terms of weight (Figure 2C). They constituted 34% and 28% of the total ingested mass, respectively. The majority of cod were found in Andreasen (2009) and Lick (1986–1994) and the majority of herring were found in Börjesson et al. (2003). Whiting and gobies constitutes 9% and 7%, but the remaining species constituted less than 5% of the total mass.

Andreasen (2009) provided information on seasonal changes (i.e. quarters of the year) in prey preferences based on occurrence and weight of each species and corresponding values were calculated for the 62 stomach samples of Lick (1986–1994). Cod, herring and gobies were the most important in all quarters in terms of percentage occurrence (O%) (Figure 3). Gobies occurred in 53–58% of the stomach samples in the first, second and the fourth quarter. Cod occurred in most stomachs in the third quarter (58%), but was also important in the second and the fourth quarter. Herring occurred in 22–30% in all quarters. Of other species, sandeels only occurred in the second quarter and whiting was highest in the second quarter (22%) and occurred in 14–16% of the stomachs in the three other quarters of the year.

Cod contributed 38–56% of the total consumed mass in any season and was the most important species in terms of weight in the first, third and fourth quarter (Figure 4). Gobies comprised the largest proportion of the total mass in the second quarter (22%) and her-ring in the first quarter (18%). Whiting varied but were most important in the first (8%) and the third quarter (19%).

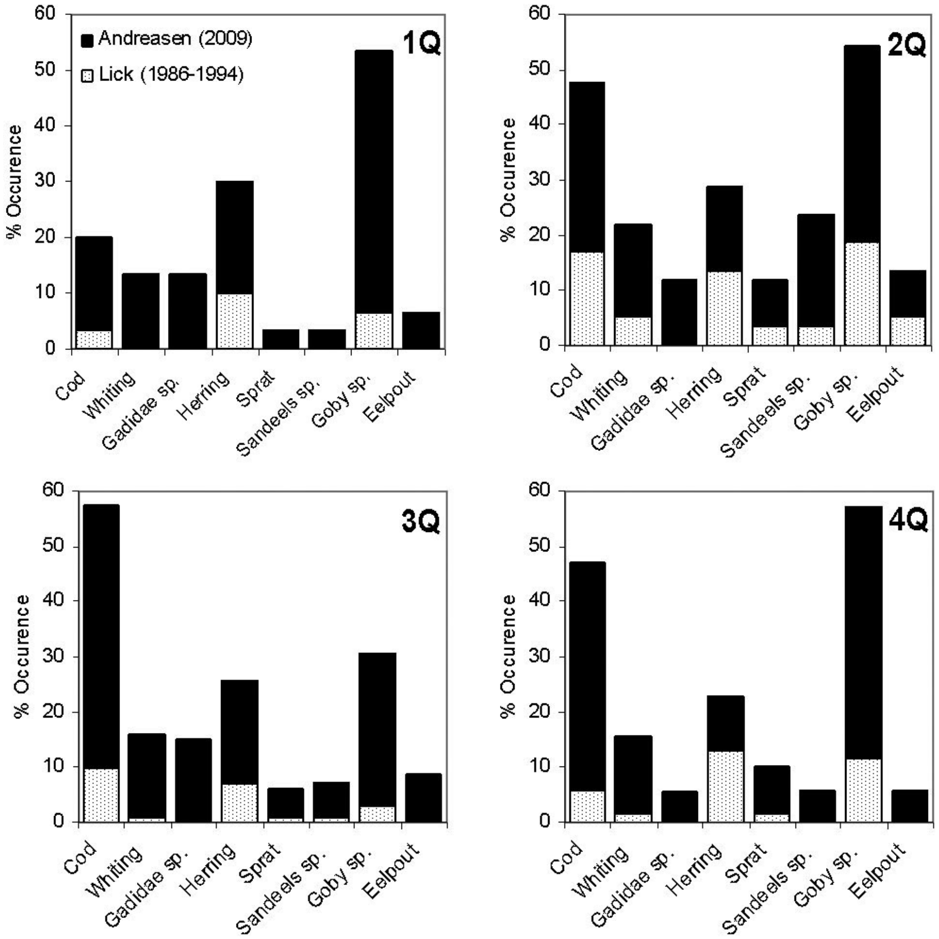

Figure 3. Percentage by occurrence (%O) of fish species found in the stomachs of harbour porpoises by Lick (1986–1994) and Andreasen (2009). Data were divided in the four quarters of the year: 1Q) January-March (N_{Lick}=5, $N_{Andreasen}$=25), 2Q) April-June (N_{Lick}=22, $N_{Andreasen}$=37), 3Q) July-September (N_{Lick}=15, $N_{Andreasen}$=65), and 4Q) October-December (N_{Lick}=18, $N_{Andreasen}$=52). Results for %O are weighted according to the number of porpoise stomachs in the two studies for each season.

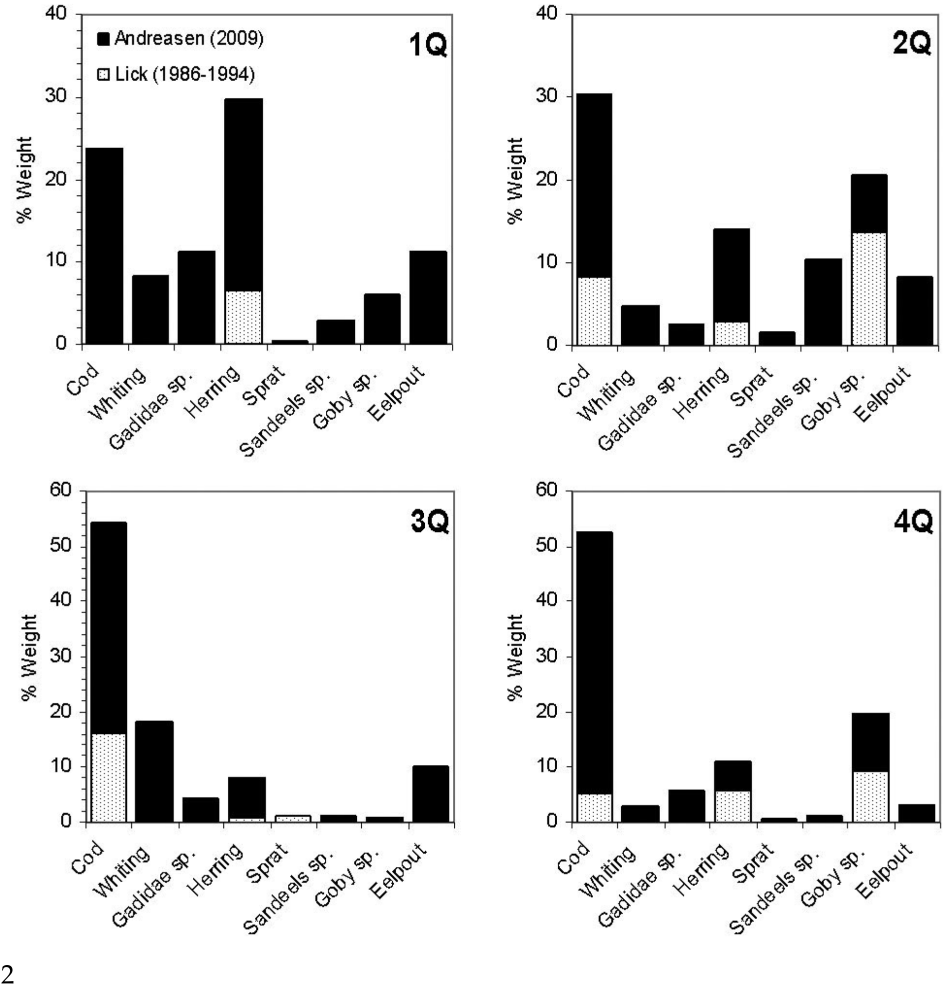

Figure 4. Percentage by weight (%W) of fish species found in the stomachs of harbour porpoises by Lick (1986–1994) and Andreasen (2009). Data is divided in the four quarters of the year: 1Q) January-March (N_{Lick}=5, $N_{Andreasen}$=25), 2Q) April-June (N_{Lick}=22, $N_{Andreasen}$=37), 3Q) July-September (N_{Lick}=15, $N_{Andreasen}$=65), and 3Q) October-December (N_{Lick}=18, $N_{Andreasen}$=52). Results for %W are weighted according to the total mass of prey for each quarter.

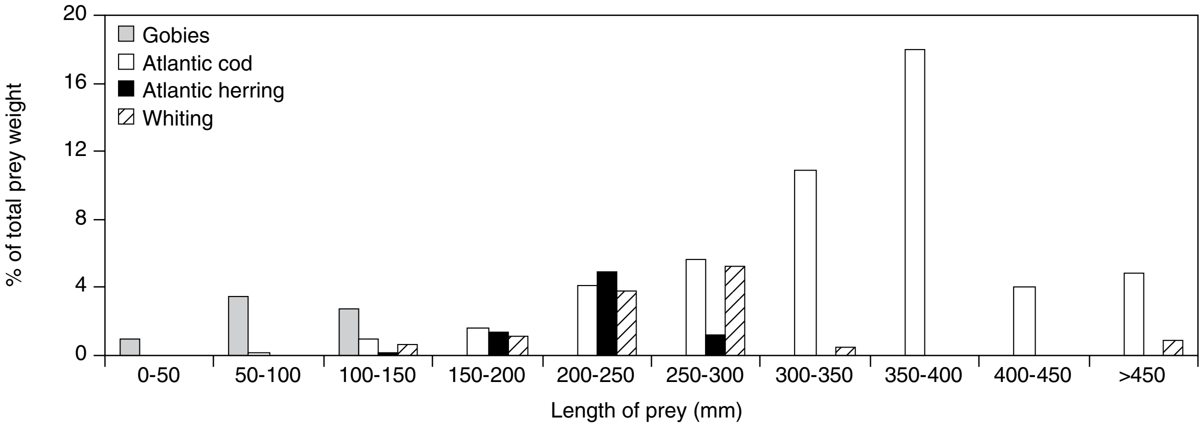

Figure 5. Length distributions of the four most important prey species in harbour porpoise stomach content. Length estimated from measured otoliths using equations by Leopold (2001) (modified from Andreasen 2009).

When combining the results from the four studies a clear pattern emerged with herring and cod being the most important species in terms of occurrence and weight, followed by gobies and whiting. Consequently, this review of the biology and distribution of porpoise prey species will focus on these four species.

Porpoises swallow their prey whole, so there is a natural limit to the size of the prey they can consume. Aarefjord et al. (1995) found that the largest fish eaten was 49 cm, but that 74% of the prey had a length of 25 cm or smaller. This is consistent with Börjesson et al. (2003), who found that the average length of prey is 26 cm for herring, 28 cm for cod, 19 cm for whiting and 4.5 cm for gobies. Andreasen (2009) provided detailed length distribution for the four species (Figure 5) and found that 94% of prey was smaller than 45 cm. Porpoises are therefore able to eat all sizes of herrings and gobies, while adult cod and whiting reach sizes that cannot be consumed (approx. 100 cm and 70 cm, respectively).

Biology and distribution of the four most important prey species

Herring (*Clupea harengus*)

Herring has a maximum length of 40 cm, but most adult fish are in the range of 20–30 cm (ICES 2010b). They feed on a variety of plank-tonic organisms. The Danish herring stock constitutes of several races that are mixed during most of the year but that are reproductively separated by having distinct spawning grounds and spawning seasons, namely Baltic Sea spring spawners (BSSS) and North Sea autumn spawners (NSAS) (Nielsen et al. 2001; Stæhr 2008). Worsøe et al. (2002) found that according to the Danish fishery, many smaller spawning areas exists for the BSSS along the coastline of Zealand and Funen and along the east coast of Jutland. In the study area, the NSAS only spawns along the north coast of Zealand and around Kullen in Sweden.

Herring move great distances during the year. The BSSS spawn in the spring in the shallow waters near the island of Rügen in the western Baltic where they deposit their sticky eggs on coarse sand, gravel, small stones and rock. After spawning, they migrate north to the deep waters of Skagerrak and the Eastern North Sea. In autumn, they migrate south and spend the winter in the Sound and Great Belt (Nielsen et al. 2001). During their first year, herring grow to ca. 12 cm and stay in shallow waters until they are about 20 cm (Muus et al. 1998).

The minimum landing size in commercial fishery is 20 cm (ICES 2010b), which overlaps with the porpoise diet, which ranges from 10 to 30 cm.

The average annual catch rates displayed on ICES Fish maps show that herring is caught throughout Kattegat with highest densities from January to March and lowest from October to December (ICES fish map).

The correlation between the herring distribution and environmental factors has been examined and the key determinants of herring distribution were found to be zooplankton abundance and the nature of the seabed substrate. The preference of bottom substrate may vary according to life cycle stage. In the spawning season, for example, herring prefer gravel and coarse sand for spawning (Reid & Maravelias 2000; Maravelias 2001). Corten (2002) suggested that herring migrations are subject to conservatism, i.e. that migration routes are regulated by habits developed in the juvenile stage rather than by environmental factors. This would mean that abiotic factors are poor predictors of herring distribution.

Gobies (Gobiidae)

Gobies are one of the largest fish families with about 1900 species. They are all relatively stationary. About ten species of gobies are found in Danish waters, but the relative abundance is unknown. They all live in the benthic zone, but the different species have adapted to different habitats (Muus et al. 1998). The largest species, the black goby, length <18 cm, and the sand goby, length <11 cm, live on coarse sand or gravel from the low shore to depths of approximately 50 m. Costello (1992) found that black goby was the most abundant of the large gobies in Irish waters (0.35 m^{-2}), but found no correlation between their distribution and bottom substrate. *Lesueurigobius friesi*, length <13 cm, is found from 10 to 130 m depth and lives in holes (Muus et al. 1998) while the spot-ted goby (*Gobiusculus flavescens*), length <6 cm, lives in schools in sea weed at depth on less than 5 m (Costello 1992). Gobies are relatively sessile and stay in close range of hiding places such as stones, coarse gravel or sea weed and will thus rarely be found in areas with fine sand bottom substrate (Muus et al. 1998). The difference in habitat selection is suggested to be caused by inter-specific com-petition which forces the smaller species into more open habitat (Wiederholm 1987). In a comparative study in south-western Ireland, the densities of the smaller species of gobies such as the spotted goby were much higher (1.83 m^{-2}) than densities of larger gobies (Costello 1992).

Gobies have a strong diurnal rhythm. Costello (1992) found a significantly higher number of spotted and black gobies during daytime than in night surveys. Furthermore, the black goby was noted to be unusually inactive, only moving when disturbed, and some spotted goby were found lying on the algae and could actually be picked up from the algae, before ‘waking up’ and swimming away. This may indicate that some species of go-bies are very exposed to predation at night.

Gobies are not caught commercially in North European waters and consequently very little information is available on their distribution and abundance. There are no quantitative studies on goby abundance in Danish waters, but they are probably distributed throughout the study area (Assistant Professor Peter Rask Møller, University of Copenhagen; pers. comm. April 2010). Further, gobies are very poorly represented in trawl survey catches since their slender bodies easily pass through even a small-meshed trawl and they are usually found in shallow inshore waters, beyond the reach of the vessels used (www.ICES.dk).

Cod (*Gadus morhua*)

Cod can grow to a maximum size of 150 cm and 40 kg, but in recent years the majority of the cod in Skagerrak and Kattegat have been 1–2 years old (10–40 cm) (ICES 2010a). The cod primarily inhabit the demersal zone in waters from 0–200 m depth (Muus et al. 1998), but may also be found in pelagic waters and in depth of up to 500 m (Bergstad 1991).

Cod spend their first 3–5 month pelagically, but when reaching a length of 3–6 cm, cod adopt a demersal lifestyle. Juveniles of the oceanic stocks move to relatively deep water while coastal cod inhabit shallow waters (Muus et al. 1998). Growth hereafter depends on availability and type of prey. In the North Sea, a cod of 45 cm is about 2 years old (Daan 1974).

Cod is divided in different stocks. Some of these stocks are resident coastal cod, which are believed to live their entire life close to the coast, undertaking only relatively short migrations to feed or spawn. Other stocks, called oceanic cod, migrate great distances every year (Bergstad and Hoines 1998). The inner Danish waters are inhabited by a mix of the two Atlantic stocks, and two endemic stocks, known as the Belt Sea stock (Müller 2002) residing in the Belt seas and the western Baltic and the Kattegat stock residing in Kattegat (Vitale et al. 2008). Most stocks spawn in the first quarter of the year. Spawning areas have been found in the most of the areas inhabited by the Baltic cod stock (Aro 2000) and in the south eastern Kattegat along the Swedish coast (Vitale et al. 2008).

Cod is an important commercial species in the Danish fishery and the minimum landing size is 30 cm in Kattegat and Skagerrak (www.ICES.dk).

Cod is distributed throughout the study area, although the Kattegat stock has been subjected to a prolonged period of high fishing intensity, resulting in severe depletion (Cardinale and Svedang 2004). However, Vitale et al. (2008) examined average catch per unit effort (CPUE) in the first quarter of the year and found that the deeper waters in east Kattegat near the spawning areas had the highest densities. ICES Fish maps allowed us to examine

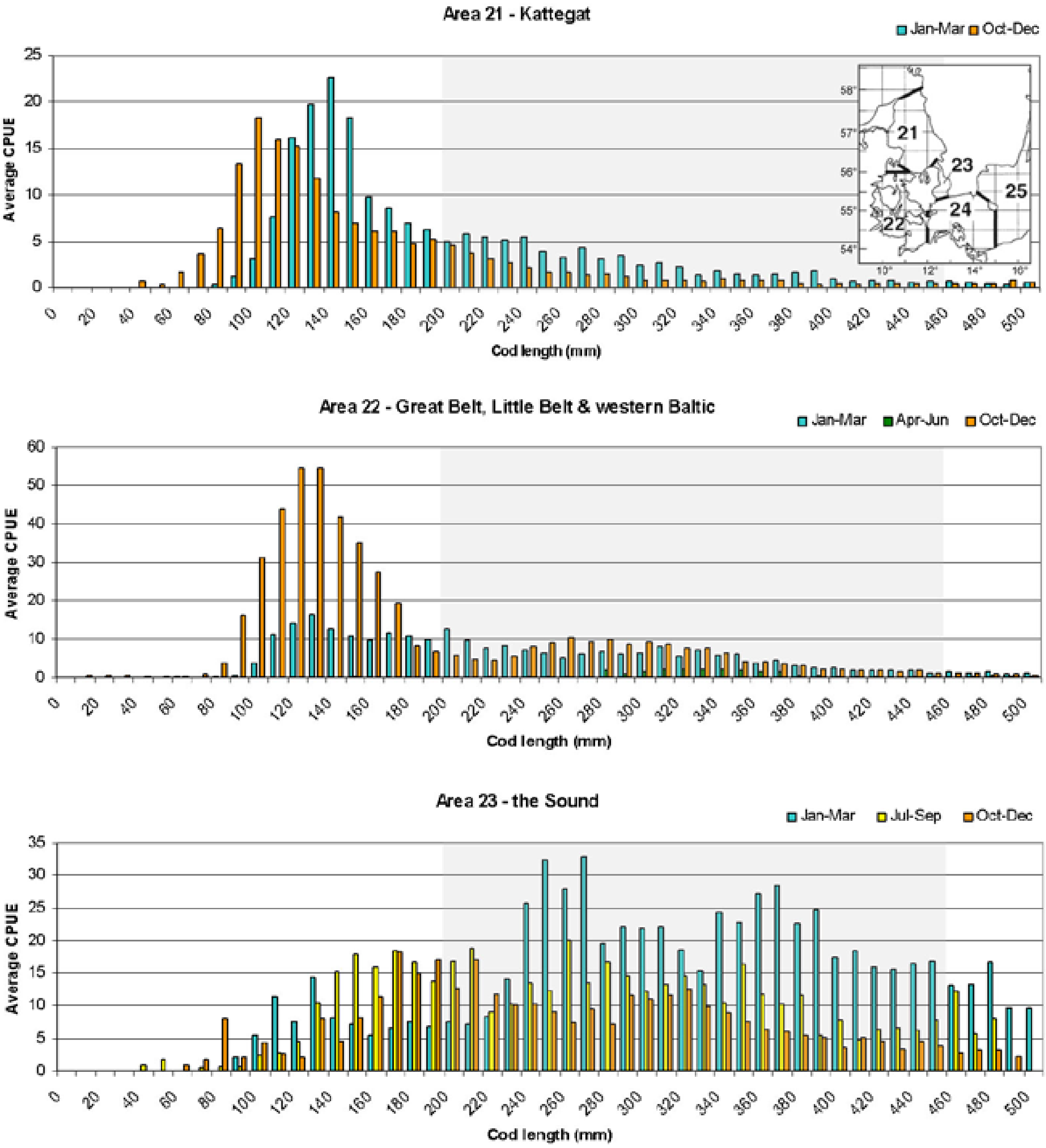

Figure 6. Average Catch per unit effort (CPUE) per season with effort for different length of cod (Gadus morhua) in the ICES subdivision areas 21, 22 and 23. Data are average from 1991-2010. Map of ICES subdivisons are displayed in top panel (modified from www.helcom.fi). Data are from DATRAS database at www.ices.dk containing catch information and statistics from the Baltic International Trawl Survey (BITS). Shaded areas illustrate the preferred cod prey size of porpoises.

the distribution of small cod (<45 cm, potential prey for porpoises). Small cod are primarily found in the southern Kattegat in January-June and in the northern Kattegat in July-December, indicating that they migrate between areas in the different seasons.

CPUE per season was downloaded for cod from DATRAS database (www.ices.dk) for the ICES subdivision areas 21, 22 and 23 (Figure 8). The data derive from the Baltic International Trawl Survey (BITS) and are divided on differ-ent length of cod. In ICES area 21 (Kattegat) and 22 (The Belt Sea and the western Baltic), the majority of cod caught are smaller than 20 cm and thus, probably juveniles spawned the previous winter. Catch rates are similar in area 21 (the Sound) for the first and fourth quarter, but the size of the juvenile cod is generally a few cm larger in the first quarter, indicating growth between the seasons. In area 22, the catch rates are significantly higher in the first quarter than in the fourth, but the distributions of cod length are similar. The distribution of cod catch rates in the Sound (area 23) are very different from area 21 and 22 with the majority of cods being between 10 and 45cm.

The distribution of cod may be correlated with bottom substrate. Wieland et al. (2009) examined catch rates of cod in the eastern North Sea and Skagerrak and found significantly higher rates in the summer on bottom substrates consisting of gravel or stone than on sand. They suggested that this could be related to prey species e.g. sandeel on inhabiting this substrate. The correlation was not significant in the winter, which suggests that bottom type preference may change with season. Finally, Bergstad & Hoines (1998) found that cod migration from a Norwegian fjord to the open ocean of the North Sea was enhanced by high herring presence. This corresponds well with both species being present in high densities in the Sound from August to February (Figure 5, Nielsen et al. 2001).

Whiting (*Merlangius merlangus*)

Whiting spawn in the pelagic zone and the eggs and juvenile stay there for 3–6 months, before moving to shallower coastal areas. At about one year of age, they move back into the deeper waters and primarily inhabit the demersal zone (Worsøe et al. 2002). They may, however, move into the pelagic zone in search of prey (ICES 2010c). Whiting grow slower than other gadoids and there is great individual variation in growth rates correlated with availability of prey (Hislop et al. 1991).

Whiting may be found throughout the study area. In Kattegat, ICES FishMap show an even distribution of average annual catch rates throughout the year of small whiting (<45 cm), with a tendency to slightly higher rates in the first quarter of the year. Furthermore, while 1 and 2+ year old whiting are found in equal amounts in the North Sea, Kattegat is dominated by 1 year old whiting with an average length of 18 cm (ICES 2010c). The minimum landing size in commercial fisheries in Skagerrak and Kattegat is 23 cm.

The spatial distribution of mature whiting has been linked to depth (whiting prefer 100–200 m deep water) and to patterns in sea surface temperature in the winter in the North Sea, where whiting prefer warmer waters (Zheng et al. 2001, Zheng et al. 2002). The immature whiting (younger than 2 year) prefer shallower waters, indicating an age-related shift in distribution (Zheng et al. 2001).

DISCUSSION

From the current study, it is evident that the harbour porpoise is an opportunistic feeder, preying on a number of different species of fish in the study area. The most frequently occurring species in the diet are gobies followed by herring, cod and whiting. Gobies are also the most abundant in terms of number of fish (%N). Numerical occurrence of fish species is, however, a relatively poor estimate of a species' importance as prey for harbour porpoises, since a few larger fish may easily weigh more than a large number of smaller fish and thus be of much greater nutritional value. We found that cod constitutes the largest proportion of the total mass, followed by herring, gobies and whiting.

The prey preferences of harbour porpoises change over the year. Table 3 summarizes the relative importance of the prey species in different season as well as the availability of prey.

Table 3. Choice and availability of preferred prey species of harbour porpoises in the Inner Danish Waters. The seasons are defined as quarters of the year: Winter (Jan-Mar), Spring (Apr-Jun), Summer (Jul-Sep) and Autumn (Oct-Dec).

	Spring (2Q)	Summer (3Q)	Autumn (4Q)	Winter (1Q)
Porpoise prey	Cod, and to a small extent herring and gobies	Cod, whiting, herring	Cod, gobies	Cod, whiting
Herring	High densities in western Baltic	Low density	High densities in the Sound and the Great Belt	High densities in the Sound, the Great Belt and Kattegat
Gobies	Probably available all year			
Cod	Few data, but ICES Fish map indicate presence in kattegat	High densities in the Sound	High densities in the sound (size 10-50cm) and in Kattegat (10-20 cm)	High densities in the sound (size 10-50 cm), and in the western Baltic, the Belt Seas and Kattegat (10-20cm)
Whiting	Few data, but ICES Fish map indicate presence in Kattegat			Few data, but ICES Fish map suggest that the highest densities are found in Kattegat

Andreasen (2009) and Lick (1986-1994) found cod to be the species that occurred in the diet of most porpoises, whereas Börjesson et al. (2003) found herring to occur most frequently in the porpoise stomach content. This indicates a geographical change in prey preferences with the porpoises in Kattegat and Skagerrak consuming mainly herring and porpoise in the Belt Seas and the western Baltic consuming mainly cod. However, a possible bias to this conclusion is that Börjesson et al. (2003) only sampled by-caught animals (thus very fresh and in good condition and often killed while actually feeding), while Andreases (2009) and Lick (1986-1994) also analysed stranded specimens, which may have died due to old age or sickness and their diet thus not representative of an healthy animal. However, in Germany it was found that of the stranded porpoise that was still fresh enough to determine cause of cause, 71–74% of the stranded porpoises in 2007–2008 was expected to be by-caught animals.

The seasonal distribution of herring does not correlate well with the prey preferences found in this study. Due to the stock of Baltic Sea Spring Spawners, the western Baltic and the Belt seas have the highest density of herring in autumn and winter. Herring is, however, not the preferred prey of porpoises in these two seasons, although herring may be overrepresented in the winter due to low sample size of harbour porpoise stomachs. However, analysis may be biased in favour of species with large and robust hard parts (e.g. cod) since small, fragile otoliths break early in the digestion process and, thus, cannot be recovered or are completely digested. The distribution of popoises in Skagerrak and Kattegat has been positively correlated with herring distribution (Sveegaard et al. In review, Paper VI). Consequently, the large proportion of herring in our analysis may derive from porpoises caught in Skagerrak and the Northern Kattegat outside the range of the Belt Sea population as included in Börjesson et al. (2003). Alternatively, the porpoises may catch herring from local coastal populations, of which less is known.

A high occurrence of cod in porpoise stomachs was found throughout the year. This corresponds well with the fact that in study area four different stocks of cod occur; two migrating stocks from the Atlantic and two residential endemic stocks. The average size of cod in the majority of the study area is 10–20 cm, which overlaps with the size that harbour porpoises consume. The Sound contains larger specimens (20–45 cm), which have been shown to constitute the majority of consumed cod. Furthermore, cod primarily inhabit the demersal zone in waters <200 m depth, which corresponds with the geographical distribution of harbour porpoises (Sveegaard et al. In press, Paper II).

Whiting did not constitute a large proportion of ingested prey, but the higher density of whiting found in the first quarter of the year in ICES FishMaps corresponds well with the higher percentage of consumed whiting in that season. Thus, whiting may be preferred prey, but perhaps due to the low densities within the study area, whiting does not constitute a large proportion of the ingested prey, nor does it occur particularly frequently.

Gobies constitute a major prey item in terms of occurrence and number of individual fish. If the results for gobies could be divided on species level, distribution maps may be specified by the difference in choice of bottom substrate by the different goby species. However, the many different species of gobies inhabiting different depths and bottom substrates may cause gobies to be available in all parts of the study area. Also, due to their inactivity at night, they may constitute very easy prey during night time. The broad availability of gobies combined with the high frequency of occurrence but the rather low frequency in weight in the porpoise diet may indicate that gobies constitute a form of 'back up' prey, when larger more energy efficient prey species are not available.

The energy density (kJ g^{-1} wet weight) of the prey species is different and varies with size of the fish. Herring has the highest energy density ranging from 4.6 to 8.4 kJ g^{-1} for length of fish between 8 and 30 cm, whiting range from 4.1-5.0 kJ g^{-1} for fish with length of 10-30 cm (Pedersen and Hislop 2001), cod of 20 cm has an energy content of 4.2 kJ g^{-1} (Lawson et al. 1998) and for gobies, Temming & Herrmann (2003) measured energy content of 4.62 kJ g^{-1} for fish of 3–13 cm. Thus, to optimize energy intake, the harbour porpoise would benefit from prioritising herring to other species, which may also seem to be the case especially in the first quarter of the year. Furthermore, it will probably require less energy for the porpoise to catch a few large fish such as cod or herring in comparison to many small fish such as gobies or sandeel, unless these species were available in significantly larger densities, making the effort per fish caught relatively small.

Overall, the predominant four prey species are of very different size, have different life cycles and inhabit different zones in the water column. Furthermore, some are stationary and confined to certain bottom substrates (gobies) while others migrate long distances every year (cod and herring). This indicates that harbour porpoises are able to switch between several different foraging behaviour and strategies throughout the year: from bottom or dermersal feeding on gobies, cod and whiting to pelagic feeding on herring. Teilmann et al. (2007) studied dive behaviour in 14 harbour porpoises tagged with Time-Depth-Recorders in the Baltic Sea. The porpoises were found to alter dive behaviour over seasons from an average of 29 dives h^{-1} in the spring and summer to 43 dives h^{-1} in autumn. The higher dive rates in au-tumn were suggested to reflect an increased foraging activity in autumn, compensating for higher energy requirements as the water temperature decreases.

To date, the knowledge of fish distribution is too limited and broad scale to predict harbour porpoise distribution within the studied area. Clearly, more knowledge of the spatial and temporal distribution of prey species is needed. The relationship between fish species and marine environmental factors would need to be further studied to act as reliable and predictive proxies for prey species in harbour porpoise distribution modelling. A finer spatial resolution in the prey preferences of harbour porpoises could reveal finer geographical differences in prey species. This would probably require a larger samples size, since a minimum of 71 samples within each geographical region have been proposed in order to provide a 95% confidence that all taxa at species level with relative frequencies >5% are found (Börjesson et al. 2003). Furthermore, annual or decadal changes in harbour porpoise diet may result in an even poorer correlation between ingested prey items pooled across decades and average prey availability per area. We recommend that future studies aim to determine the direct correlation between harbour porpoise density and fish density e.g. by simultaneous acoustic surveys for both fish and porpoises in areas with known prey preferences.

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PAPER VI

Spatial aggregation of harbour porpoises determined by herring distribution

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Spatial aggregation of harbour porpoises determined by herring distribution

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ABSTRACT

Our knowledge of harbour porpoise (*Phocoena phocoena*) distribution on a fine spatial scale has significantly improved in the last decade due to the development of new monitoring methods including satellite tracking, acoustic surveying and passive acoustic monitoring. Evidently, porpoise densities vary both seasonally and diurnally, and although the exact cause of their movements is unknown, harbour porpoise distributions are presumably related to distribution of prey. This hypothesis has been tested indirectly by using environmental factors such as water temperature, salinity and depth as proxies for prey distribution, but the direct correlation between prey and predator distribution has not previously been studied. Here, we establish such a relationship between the distribution of porpoises and their prey by comparing the relative densities of porpoises in Kattegat, Skagerrak and the eastern North Sea based on satellite tracking data for 35 individuals from 1998 to 2009 with the distribution of herring (*Clupea harengus*) obtained through annual acoustic surveys from 2000 to 2009. Studies of stomach contents has shown that herring is one of the most important prey items in these waters. Depth and density of a non-prey species, mackerel (*Scomber scombrus*), was also included in the model to examine how the interactions between density of herring, mackerel (preys on herring) and depth could potentially affect the distribution of harbour porpoises. The comparison was conducted on quarter ICES squares level using satellite tracking data from June-August, surrounding the annual acoustic fish surveys in July. Mantel tests, partial Mantel tests and Hurdle models were used for the analysis, as these tests are efficient in including and adjusting for spatial autocorrelation in the data set. We found that densities of porpoises and mackerel were strongly positively correlated with herring densities, which is in turn was correlated with depth. Around 95% of the herrings in the study area were of the sizes preferred by porpoises. Our results give the first evidence of porpoise-prey relationships which is important information in management of the species and identification of key habitats.

Key words: Satellite tracking, acoustic survey, ICES, cetacean, Mantel test, Hurdle model, *Phocoena phocoena*, fish, marine mammals

INTRODUCTION

Our knowledge of harbour porpoise (*Phocoena phocoena*) distribution on a fine spatial scale has significantly improved in the last decade due to development of new monitoring methods. In Scandinavian waters, from the eastern North Sea, the western Baltic and the waters in between, harbour porpoise distribution has been examined using visual surveys from boats and plane (Heide-Jørgensen et al. 1993, Hammond et al. 2002), acoustic surveys from boats (SCANS II 2006, Sveegaard et al. In press, Paper III), passive acoustic monitoring (PAM) (Carstensen et al. 2006, Kyhn et al. 2008) and satellite tracking (Teilmann et al. 2007, Sveegaard et al. In press, Paper II). The conclusion of these studies is that although porpoises may be detected throughout the area, the distribution is not even but patchy with porpoises congregating in high densities in certain areas e.g. in the Great Belt, the northern Sound, around the northern tip of Jutland and along the southern slope of the Norwegian Trench.

The distribution of porpoises in the high-density areas varies across seasons (Sveegaard et al. In press, Paper III, Sveegaard et al. In press, Paper II), which is not the result of a coordinated migration but rather due to a gradual shift in their distribution. The underlying explanation for this movement is not understood, but harbour porpoise distribution has been suggested to be related to the distribution of prey species (Read & Westgate 1997, Koopman 1998) or perhaps the distribution of breeding habitat (Northridge et al. 1995). In recent years, this hypothesis has been tested indirectly by modelling different environmental factors as proxies for prey distribution in Scottish (MacLeod et al. 2007, Marubini et al. 2009, Bailey & Thompson 2009, Embling et al. 2010) and Danish waters (Edrén et al. 2010). Overall, these studies found depth (MacLeod et al. 2007, Marubini et al. 2009, Bailey & Thompson 2009), distance to coast (MacLeod et al. 2007, Marubini et al. 2009, Bailey & Thompson 2009, Edrén et al. 2010) and tidal current (Marubini et al. 2009, Embling et al. 2010) to have significant influence on porpoise distribution and in two studies, sediment type (with porpoises preferring sandy bottom, Bailey & Thompson 2009) and temperature (MacLeod et al. 2007) had significant explanatory power in the models. The direct correlation between prey and predator distribution, however, has to our knowledge not previously been studied for porpoises. This is primarily due to lack of information on prey abundance and distribution on a sufficiently fine spatial and temporal scale to be relevant (Santos & Pierce 2003).

The choice of prey species has been found to vary both spatially and temporally (Benke et al. 1998). In Kattegat and Skagerrak, prey preferences of harbour porpoises are primarily clupeids, gadoids, gobies and sandeels (Aarefjord et al. 1995, Börjesson et al. 2003). Herring (*Clupea harengus*) of 15–30 cm is, however, the single most important prey species, occurring in 54–70% of porpoise stomachs and contributing 46–55% of the total ingested mass (Aarefjord et al. 1995, Börjesson et al. 2003, Andreasen 2009). The harbour porpoise requires a constant high energy intake due to its small size, limited body fat reserves and high energy expenditure (Koopman 1998).

Distribution and abundance of herring is examined annually during the ICES coordinated acoustic herring survey (see Methods). These surveys aim at pelagic species and are thus not representative for other of the major harbour porpoise prey species. It is, however, able to provide a relative assessment of mackerel (*Scomber scombrus*). Mackerel is an interesting species because it preys on small herring (<10 cm) in the study area as well as on zooplankton (Dahl & Kirkegaard 1986), but is rarely consumed by porpoises. Therefore, mackerel may both predate on herring and compete with herring for food. Herring density has been found to be correlated with depth (Maravelias et al. 2000) and consequently, interactions between herring density, mackerel density and depth could potentially affect the distribution of harbour porpoises.

This study aims to examine the relationship between the distribution of harbour porpoises and herring by comparing the density of locations from satellite tracked porpoises with herring densities found by annual acoustic surveys in Kattegat and Skagerrak. To further examine the spatial distribution and potential influence of other variables on porpoise distribution, depth and distribution of a non-prey species, mackerel, will be included in the analysis. We hypothesise that harbour porpoises and mackerel are correlated with herring densities, but that harbour porpoises and mackerel are not correlated due to their different prey size preferences.

METHODS

Study area

The study area is limited to the area with available data on harbour porpoise and herring densities. The acoustic herring surveys cover an area north of 56°N and east of 5°E (the eastern North Sea, Skagerrak and Kattegat) (Fig. 1). The availability of harbour porpoise tracking data within that region cover all of Kattegat and Skagerrak, but does not extend south of 57°N in the North Sea. Consequently, the area in the North Sea from 56°N to 57°N was excluded from the analysis. The study area was divided into grid cells of 0.25°N × 0.5°E (~870 km^2, equivalent to a quarter of a ICES square). This size was estimated to be the smallest possible size, when the acoustic surveys are required to pass through each one of them.

The study area stretches over a varied bathymetry with relatively shallow water (<50 m) in Kattegat and the southern Skagerrak, and deeper waters (~700 m) in the Norwegian Trench in the Northern Skagerrak.

Fish density

Herring and mackerel densities were calculated based on the annual ICES coordinated acoustic herring survey in July. In Skagerrak and Kattegat (east of 6°E and north of 56°N), the surveys are conducted on the research vessel (RV) Dana by DTU Aqua at the National Institute of Aquatic resources (DTU Aqua). Ten annual surveys in the two first weeks of July from 2000 to 2009 are included in this study.

The survey track lines alters slightly among years but are approx. 1950 nautical miles (nmi) and designed to enter all ICES squares within the study area (Fig. 1). The speed of the vessel during acoustic sampling was 9–11 knots.

The acoustic data were collected using mainly a Simrad EK60 38 kHz echosounder with the transducer (Type ES 38 7×7 degrees main lobe) in a towed body. The towed body runs at approx. 3 m depth in strong current and down to about 6–7 m in low current. Data from Simrad EK60 echosounders running at 18 kHz and 120 kHz were also collected, but were not directly used for the survey estimate but as an aid in species identification. Acoustic data were recorded as

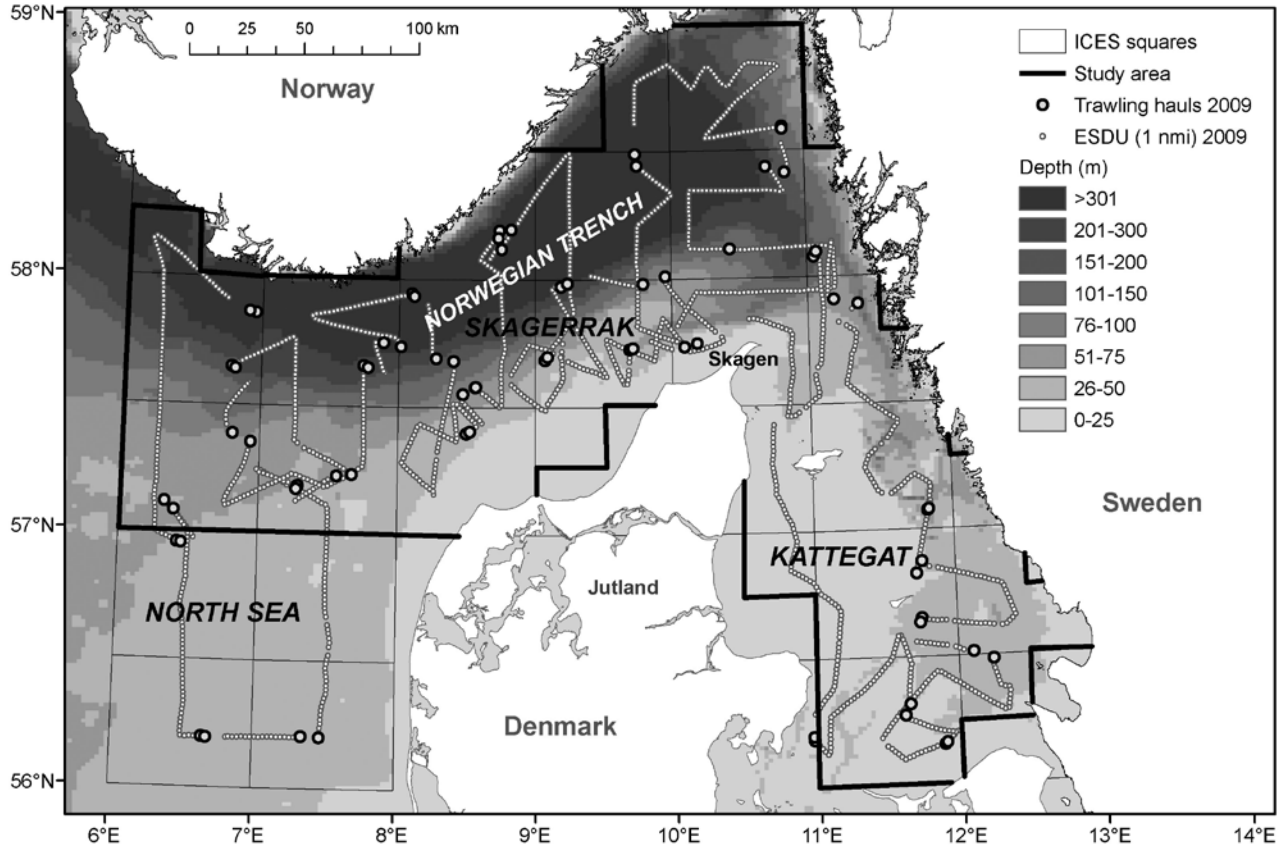

Figure 1. Study area in Skagerrak and Kattegat. The bold line encompasses the area with data for herring, mackerel and harbour porpoise. ICES squares are indicated as well as an example of the acoustic herring survey transects (ESDU: Elementary Sampling Distance Unit = 1 nmi) and trawl hauls in July 2009.

raw data on a hard disk 24 hours a day, also during trawl operations, but data recorded during trawling was excluded from the biomass estimate. The sampling unit was one nautical mile (nmi). During trawl hauls the towed body is taken aboard and the EK60 38 kHz echosounder run on the hull transducer. Echosounders were calibrated prior to each survey.

Trawl hauls were carried out during the survey for species identification. Pelagic hauls were carried out using a FOTÖ trawl (16 mm in the codend), while demersal hauls were carried out using an EXPO trawl (16 mm in the codend). Trawling was carried out in the time intervals 10:00 to 15:00 and 20:30 to 03:00 UTC, usually two day-hauls (mostly demersal) and two night-hauls (mostly pelagic). The strategy was to cover the largest possible number of depth zones within each geographical stratum. In the deeper areas, midwater-hauls were made to help identify the largest depth at which herring would be expected. One-hour hauls were used as a standard during the survey, but sometimes shortened if the catch indicators indicated very large catches.

The fish caught were sorted into species groups and length groups within each species. Number of individuals and weight for each length group for each species was recorded with emphasis on pelagic species. The clupeid fish were measured to the nearest 0.5 cm total length, other fish to 1 cm, and the weight to the nearest 0.1 g wet weight.

The number of fish per species in the survey area is assumed to be in proportion to the contribution of the given species in the trawl hauls. Therefore, the relative density of a given species is estimated by subarea using the species composition in near-by trawl hauls. The nearest trawl hauls are allocated to subareas with uniform depth strata. Details on calculations of fish density are given in ICES (2002) and ICES (2009).

Average number of herring and mackerel per sampling units (nmi) within each grid cell were calculated. In order to study the mackerel-herring relationship, the average length distribution (in 2006–2009) of herring and mackerel on the acoustic surveys were calculated.

Harbour porpoise density

From 1997–2009, 75 harbour porpoises were tagged with satellite transmitters in Danish waters. Twentyfour of these were tagged near Skagen on the northern tip of Jutland and 51 were tagged in Kattegat, the Belt Sea or the Western Baltic (For more information on tagging procedure, satellite tags and settings, see Geertsen et al. 2004, Teilmann et al. 2007, Eskesen et al. 2009, Sveegaard et al. In press, Paper II).

All transmitters used the Argos system (www.argos-system.org) where locations are classified into six classes depending on the level of accuracy. This study included all location classes, but filtered all locations by a SAS-routine, Argos-Filter v7.3 (Douglas 2006). This is a Distance-Angle-Rate filter that removes unlikely locations based on maximum distance and swim rate between locations and minimum angle between three consecutive locations (for further details on filtering, see Sveegaard et al. In press, Paper II).

In order to optimize sample size, we decided to include all porpoise locations from June to August. Furthermore, previous analysis has shown that by removing locations from the first four days after tagging from the analysis, over representation of the tagging site is avoided (Sveegaard et al. In press, Paper III, Sveegaard et al. In press, Paper II). This led to a total number of 508 locations (one location porpoise^{-1} day^{-1}) transmitted by 34 harbour porpoises from June to August. The remaining 48 harbour porpoises did not enter the study area during the acoustic herring survey.

Of the 34 porpoises, seventeen were tagged near Skagen and seventeen were tagged along the eastern coast of Jutland and around the Danish islands south of the study area.

The telemetry data were imported into ArcGIS 9.3 (ESRI) and the locations mapped with the Zone 32 (N) Universal Transverse Mercator projection, using the WGS 1984 datum. Number of locations per grid cell was calculated.

Environmental variables

Modelling of porpoise distribution based on environmental variables have shown that depth, distance to coast and tidal state, may predict habitat preferences of porpoises (MacLeod et al. 2007, Marubini et al. 2009, Bailey & Thompson 2009, Edrén et al. 2010, Embling et al. 2010). The rather large grid cell size used in our study makes distance to coast a spurious variable, and thus we only included depth as a variable. The changes in tidal state are very low in these waters (maximum amplitude <30 cm) compared to changes in the north-western North Sea (amplitude >100 cm) (Massmann et al. 2010), where this parameter was found to be significant (Marubini et al. 2009, Embling et al. 2010) and were consequently not included. Average depth per grid cell was calculated in ArcGIS (Depth grid source: ETOPO2v2 2010).

Data analysis

Two statistical analysis methods were applied; Mantel tests (Mantel 1967) and Hurdle analysis (Zeileis et al. 2008). Each method has advantages and disadvantages e.g. Mantel tests includes the spatial structure and geographical distances between observations to estimate and adjust for autocorrelation in the data set, but cannot be used for assessing the relative importance of different predictor variables using Akaike Information Criterion (AIC; Burnham & Anderson 2004), since it does not produce a log-likelyhood estimate. Hurdle models can produce full models and include all interaction terms, but does not allow for a direct investigation of the effect of the spatial structure in the dataset. Instead, a nearest neighbour is included to adjust for autocorrelation in the Hurdle models.

Biological distribution data, such as the ones used in this study, are often spatially dependant, which needs to be included in the choice of statistical analysis (Legendre 1993, Dormann et al. 2007). To test our data for autocorrelation, we used Mantel tests (using the vegan library v1.17 for R2.11.1). Mantel tests are useful for exploring and dealing with spatial autocorrelation in the data set and have previously been used in several ecological studies of cetaceans (e.g., Spitz et al. 2006, Torres et al. 2008). The Mantel test is a permutation test that measures the correlation between two matrices. One of these matrices is in our case a matrix containing the geographical distances between the sample points (i.e. the centers of the squares). The other matrix contains the numeric differences between observed densities of herring, mackerel or porpoises in the same locations (here the entire square is used), or alternatively the difference in depth. In a Mantel test the rows and columns in one of the two matrices are permuted at random. The significance level of the observed correlation is calculated as the proportion of the permutations that lead to a higher correlation coefficient. We produced five matrices: Four difference matrices calculated as the difference between pairs of grid cells for each of the variables: porpoise density, herring density, mackerel density and average depth in each grid cell and a fifth distance matrix. The geographical distances were calculated as the shortest possible swimming distance between grid cell centre points for the marine species i.e. they could not swim over land. All data were log-transformed to reduce the effect of outliers. The four difference matrices were tested one by one against the distance matrix to test for autocorrelation in the data sets.

Partial Mantel tests were used to test for correlation between two variables while adjusting for spatial autocorrelation (Legendre 2000). We tested the correlation between the following variables while taking autocorrelation into account: porpoise/herring, mackerel/herring, porpoise/mackerel, porpoise/depth, herring/depth and mackerel/depth.

Relative importance of explanatory variables was tested using the Hurdle analysis. We investigated the distribution of porpoise locations within each grid cell in relation to herring, mackerel and depth. A nearest-neighbour variable (average number of harbour porpoises in neighbouring grid cells, maximum eight cells) was included to compensate for spatial autocorrelation among the grid cells (Donnelly 1978, Perry et al. 2002). Prior to analysis, data for herring, mackerel, and depth were log-transformed. In order to have comparable grid cells of equal size, the number of porpoises per grid cell were scaled up in costal grid cells with area size <870 km^2. For instance, in a grid cell of 435 km^2, the number of porpoise locations would be multiplied by two.

Two types of models were applied and compared based on the lowest AIC: generalized linear models for Poisson distributed data (GLM; Dobson 2002) and Hurdle models (using the 'pscl' library v1.03.5 for R2.11.1). Our data are overdispersed and Poisson distributed, and these models are appropriate to handle such data. The Hurdle analysis (AIC = 419.6) yielded a better fit than the GLM poisson fit (AIC = 526.4) with the same regressors and consequently, the Hurdle model was chosen for the following model reduction.

Hurdle count models are two-component models with a truncated count component for positive counts and a hurdle (binary) component that models the zero counts (Zeileis et al. 2008). The model was initiated with the following variables to describe number of porpoise locations: Nearest neighbour, herring density, mackerel density and average depth, as well as the interaction variables herring:depth and herring:mackerel. The interaction mackerel:depth did not seem biologically rele-vant for describing porpoise movement

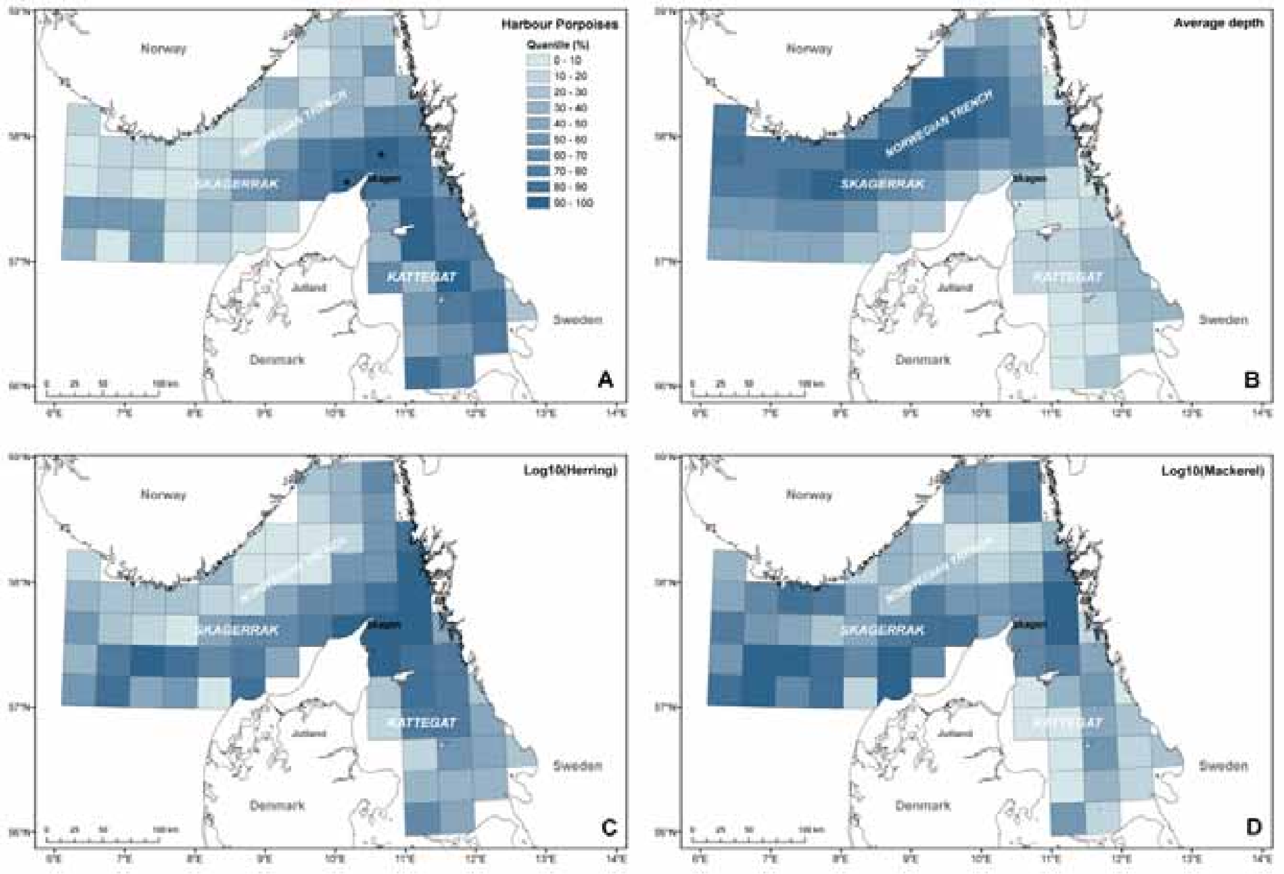

Figure 2. Hurdle model variables. **A:** Number of harbour porpoise (*Phocoena phocoena*) observations within each grid cell in June–August in 1997-2009, **B:** Average depth in study area, **C:** Log_{10}(herring density) (*Clupea harengus*) based on acoustic surveys and trawl from 2000-2009, and **D:** Log_{10}(mackerel density) (*Scomber scombrus*) based on acoustic surveys and trawl from 2000-2009. The grid cells indicated with stars in A have the highest densities and refer to two columns in Fig. 3.

and was not included. The order of reductions in the Hurdle model began with the binomial zero hurdle part and removed the least significant terms first. Non-significant main terms were only removed if they were not part of an interaction. After removing all non-significant terms in the binomial part, the same procedure was followed for the count model until the most parsimonious model with the lowest possible AIC was obtained.

RESULTS

Analyses including geographical distance

We found significant spatial autocorrelation in the porpoise distribution (Mantel test, Z=0.141, p=0.0062), in average depth (Mantel test, Z=0.3050, p=0.0001) and in the mackerel distribution (Mantel test, Z=0.0978, p=0.0253) but no evidence for spatial autocorrelation in the herring distribution (Mantel test, Z=–0.0956, p=0.995) on the spatial scale used here. Autocorrelation indicates that observations are non-independent, which must be dealt with in further analysis.

Significant correlations were found, while adjusting for the autocorrelation, between porpoises and herring (Partial Mantel, Z=0.2536, p<0.0001), mackerel and herring (Partial Mantel, Z=0.1895, p=0.0017) and herring and depth (Partial Mantel, Z=0.1868, p=0.0002). This means that both number of porpoise locations and mackerel density are strongly correlated with the herring densities after taking into account that data recorded in areas close to each other are similar merely because they are close together. Furthermore, herring densities are strongly correlated with bathymetry when the effect of spatial dependency in measurements is adjusted for. We found no correlation between porpoise and mackerel (Partial Mantel, Z=–0.1270, p=0.9962), porpoises and depth (Partial Mantel, Z=0.02406, p=0.3046) and mackerel and depth (Partial Mantel, Z=–0.02871, p=0.7147).

Relative importance of explanatory variable

The model simplification left only the nearest neighbour variable in the binary part of the Hurdle model. However, after removing the mackerel:herring interaction from the poisson-part of the model, the remaining models gave AIC values with differences (Δ_i) ≤2. Delta AIC (Δ_i) indicates 'strength of evidence' of the model simplification and according to Burnham & Anderson (2004) all models with $\Delta_i \leq 2$ have substantial support and are equally parsimonious. Consequently, Akaike weights (w_i) were calculated for the models (only the four remaining models are displayed, Table 1). Akaike weights are useful as 'weight of evidence' for each model and are interpreted as the probability that each model is the best model for the data (Burnham and Anderson 2004). While Hurdle models 2–4 have similar w_i, the value for model 1 is clearly lower and the model is therefore not considered. Hurdle models 2–4 are equally parsimonious and are all accepted as valid models. However, the only significant variable in model 2 is nearest neighbour, which basically describes the autocorrelation in porpoise distribution already identified in the Mantel tests. In model 3 and 4, herring density is significant in describing porpoise distribution as well as the nearest neighbour variables and depth is included in model 3 although not significant. This confirms the results from the Mantel test, namely that among all variables in the model, only the herring density is correlated with the density of porpoise locations when adjusting for spatial dependency of data.

The calculated variables of porpoise locations, $\log_{10}$(herring density) and $\log_{10}$(mackerel density) within in the 77 grid cells are illustrated in (Fig. 2). All species have high densities around Skagen, but while porpoise (2A) and herring (2C) show high densities in Kattegat and along the Norwegian Trench, mackerel (2D) has low density in Kattegat and the highest densities in the western Skagerrak.

In order to visually examine the correlation between porpoise density, herring density and depth, a 3D plot of the 77 grid cells excluding the cells with no porpoise locations, was created (Fig. 3). The 3D plot shows that porpoise density increases with herring density and both species are generally found in water depth less than 150 m. The two highest columns (with $\log_{10}$(Porpoise locations) $>4\times10^{-3}$) represents the two grid cells near Skagen that are indicated with stars in Fig.2A.

Examination of length distribution found in the acoustic surveys (including trawl samples) showed an average length of herring of 20.5±0.55 cm and that the majority of herring are 15–25 cm (83%). The average length of mackerel is 28.6±0.58 cm and the majority of mackerel are 20–30 cm (89%) (Fig. 4).

DISCUSSION

The high daily energy requirements of small cetaceans like the harbour porpoise and the numerous herring population in the study area, led us to hypothesize that harbour porpoise distribution would be positively correlated with abundance of its main prey. Our findings in this study support this theory. In fact, the hurdle model found herring to be the only significant variable, of those tested, to describe harbour porpoise distribution. Similarly, in the partial Mantel test, we found a strong significant correlation between distribution of porpoises and herring while including and adjusting for spatial autocorrelation. The result is further supported by the fact that 95% of the herring found in the study area during the acoustic surveys has the prey length preferred by porpoises (20-30cm).

This is the first study to demonstrate a direct correlation between harbour porpoises and a specific prey species, but not the first time that porpoise presence has been found to correlate with aggregations of fish. Johnston et al. (2005) examined the

Table 1. Summary of Hurdle models. Δi = AIC differences, wi = Akaike weights. Model variables are harbour porpoise density (POR), Nearest neighbour (NN), Herring density (HER), Mackerel density (MAC) and average depth (DEP). Bin = binary part of data. Stars indicates the level of significance: *(P<0.05), **(P<0.01), ***(P<0.001).

Hurdle ID	Model variables	AIC	Δi	wi
1	POR~NN***+HER+DEP+MAC+HER:DEP+BinNN*	410.016	1.541	0.131
2	POR~NN***+HER+DEP+HER:DEP+BinNN*	408.475	0.000	0.284
3	POR~NN***+HER**+DEP+BinNN*	408.838	0.364	0.237
4	POR~NN***+HER**+BinNN*	408.674	0.199	0.257

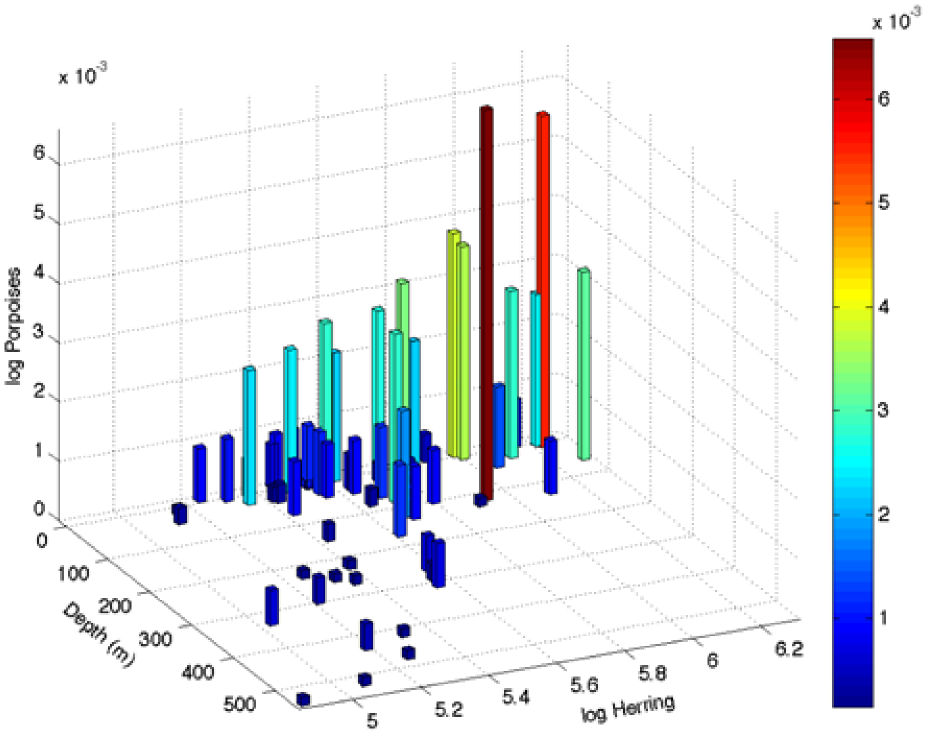

Figure 3. 3-dimensional plot of harbour porpoise (*Phocoena phocoena*) density (= Log_{10}(porpoise locations per square)) as a function of herring (*Clupea harengus*) density and depth.

movement of six satellite tagged harbour porpoises in the Bay of Fundy, and found that regions with stronger currents, such as islands and headland wakes, aggregate prey and represent foraging habitat for harbour porpoises. Vorticity or turbulence in marine areas is often correlated with hydrographical fronts e.g. caused by differences in temperature, current or bathymetry (Wolanski & Hamner 1988). These frontal zones are in turn correlated with enhanced primary production due to upwelling of nutrients (Pingree et al. 1975), making an area attractive for fish species and consequently, for larger marine predators like the harbour porpoise. Skov & Thomsen (2008) found that small-scale changes in local currents caused by tidal currents in an area with steep changes in bathymetry were the main factors affecting porpoise presence. They further suggested that feeding at predictable frontal structures with enhanced availability of prey may be a beneficial foraging strategy, by reducing the size of the area in which the porpoise searches for prey.

Our study area holds two major upwelling zones: The Northern Kattegat front, that separates Kattegat surface water (26 PSU) and Skagerrak water (34 PSU), and the Norwegian Trench, representing a steep drop from about 100 m to 700 m depth (Jakobsen 1997, Danielssen et al. 1997). Both areas are biologically productive zones and all species examined in this study appear to be attracted to these areas, confirming that frontal zones may represent important foraging areas for fish as well as for harbour porpoises.

Herring density was found to be correlated with depth in the partial Mantel test and like harbour porpoises they seem to prefer the waters south of the Norwegian Trench with depth <100m and the area around Skagen. Herring has previously been found to show a preference for zooplankton-rich waters with depths between 100 and 150m in the north-western North Sea and to aggregate in areas characterised by a seabed of sand and gravel (Maravelias et al. 2000). This is in line with previous harbour porpoise modelling studies that found depth and sandy seabed substrate to correlate with porpoise distribution (MacLeod et al. 2007, Marubini et al. 2009, Bailey & Thompson 2009).

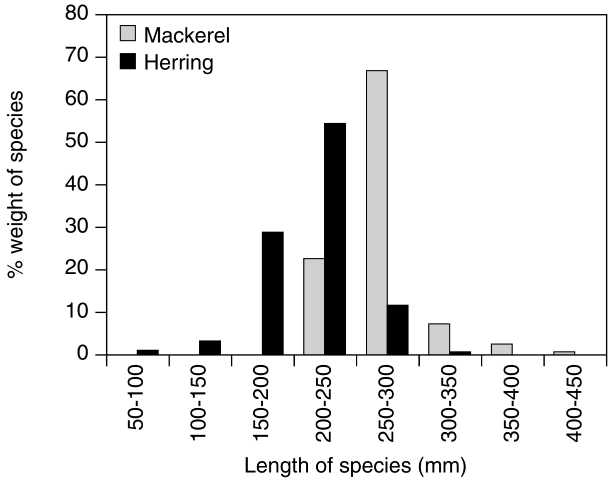

Figure 4. Length distributions of mackerel (*Scomber scombrus*) and herring (*Clupea harengus*) found in the acoustic surveys.

We also found that harbour porpoise densities do not significantly correlate with mackerel distribution and bathymetry. Mackerel is not a preferred prey species of harbour porpoises (Aarefjord et al. 1995, Börjesson et al. 2003), which indicates that harbour porpoises do not follow any fish species, but rather specific prey species. This could explain why not all studies find harbour porpoise presence to be correlated with environmental variables, supposed to predict nutrient rich regions with enhanced prey availability as proxies for general fish.

We found mackerel and herring densities to be correlated. The majority of mackerel (89%) in the acoustic surveys were medium-sized fish of 20–30 cm. Mackerel of this size are 0–2 years old and herring has been found to constitute 50–60% of their prey while the remaining prey were crustaceans (primarily the copepod, *Calanus finmarchicus* (Mehl & Westgård 1983, Dahl & Kirkegaard 1986). However, *C. finmarchicus* is also a primary prey of herring (Corten 2001), and the correlation found may thus be a result of mackerel predating directly on herring, competing with herring for copepods or a mix of the two. Analyses of length distribution of herring, obtained from the acoustic surveys, showed that only 1% of the herring are less than 10 cm and thus potential prey for mackerel. Furthermore, juvenile herring generally aggregate in shallow coastal areas unlike adult herring that move to pelagic waters (Muus et al. 1998). Young herring as well may therefore be under-represented in the acoustic surveys, that generally takes place at least 15 km from the coast and has less effort in shallow areas e.g. western Kattegat. Consequently, the pelagic acoustic surveys may not be ideal for assessing juvenile herring and their predators, and we suggest that mackerel densities in these areas are correlated with herring due to mutual predation on *C. finmarchicus*. Unlike mackerel, harbour porpoises prefer herring of 15–25 cm length, and in the acoustic surveys, 83% of the herring were within this length category.

This study has taken a step in the direction of defining the relationship between harbour porpoises and their prey. However, we compared variables sampled over ten years and sample units of ca. 900 km^2, which is generally much larger than other porpoise distribution modelling studies (MacLeod et al. 2007, Marubini et al. 2009, Bailey & Thompson 2009). The choice of spatial and temporal scale may affect the results. For instance, Bailey & Thompson (2009) found that distribution of harbour porpoise detections encounters was only significantly related to the environmental variables sand, distance to coast and depth, when these were measured on a grid scale of 1×1 km and 2×2 km, but not on a 4×4 km grid scale. Consequently, spatial scale plays an important role, and when possible different scales should be tested. In this study, however, the spatial coverage of the acoustic surveys planned for large-scale estimation of fish abundance, made smaller spatial scales impossible. Temporal scale is another influential factor since variations in climate from year to year may cause temporal shift in the onset of herring migration. This study was, however, restricted by the number of harbour porpoise satellite locations, which would be inadequate for comparing shorter time intervals.

Finally, this study successfully demonstrated a positive correlation between distribution of harbour porpoises and the abundance of a primary prey species, herring. The highest porpoise densities are found around Skagen, based on satellite tagging data as well as acoustic surveys for porpoises (Sveegaard et al. In press, Paper III, Sveegaard et al. In press, Paper II), this area was designated as a ‘Natura 2000’ harbour porpoise habitat according to the EC Habitat Directive (92/43/EEC) in 2010. Consequently, our findings may be important in future management of harbour porpoises. E.g. changes in prey abundance or distribution e.g. caused by climate changes, over fishing or other disturbances, may lead to alterations in the distribution of harbour porpoises. Thus, we advocate that management of prey species are incorporated into management plans for protected areas for harbour porpoises. Clearly, more research is needed to fully understand harbour porpoise foraging strategy and this predator and prey relationship. However, these findings provide new insight into the ecological food chain of harbour porpoises and should initiate more studies exploring this subject.

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PAPER VII

Seasonal correlation identified between the distribution of harbour porpoises and their prey

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ABSTRACT

Seasonal variations in presence of harbour porpoises in the Sound, a narrow strait connecting the Baltic Sea and Kattegat, result in low densities in the winter (November-March) and high densities in the summer (April-October). Due to high energy requirements, the occurrence of porpoises is expected to correlate with prey distribution. This does however not correspond with the high abundance of overwintering herring in the Sound. By examining the stomach content of 53 porpoises from the Sound, we studied this controversy, while still hypothesizing that the prey preferences of the harbour porpoises would reflect an increase in food quantity and/or quality in the season of high density season. We found that in the high density season (April-October), mean prey weight per stomach was larger and the level of occurrence as well as the diversity of prey species was higher, than in the low density season (November-March). Furthermore, cod was found to be the main prey species in terms of weight in the high season and herring in the low season. No difference was found in the number of prey species between the two seasons, but the relative distribution of numbers was different. The development of frontal zones in the spring in the northern part of the Sound is suggested to aid the porpoises in locating their prey, and unavailability of the overwintering herring due to heavy traffic is suggested to be the reason behind the low winter abundance of harbour porpoises.

Key words: Herring, mackerel, acoustic survey, satellite tracking, *Phocoena phocoena*.

INTRODUCTION

Kattegat, Belt Seas, the Sound and the western Baltic are inhabited by a genetically distinct population of harbour porpoises *Phocoena phocoena* (Wiemann et al. 2010) (Fig.1). In the last two decades, our knowledge on the distribution of this population has greatly improved due to development and application of novel methods such as acoustic monitoring and satellite tracking (Teilmann et al. 2007, Sveegaard et al. In press, Paper III, Sveegaard et al. In press, Paper II). All or part of this population has been studied by the use of visual surveys from boat and plane (Heide-Jørgensen et al. 1992, Heide-Jørgensen et al. 1993, Hammond et al. 2002), detections of incidental sightings and strandings (Kinze et al. 2003, Siebert et al. 2006), passive acoustic monitoring (Verfuss et al. 2007, Kyhn et al. 2008), acoustic surveys (SCANS II 2008, Sveegaard et al. In press, Paper III) and satellite tracking (Teilmann et al. 2007, Sveegaard et al. In press, Paper II). These studies show that harbour porpoises within this region do not distribute evenly but aggregate in certain high density areas, mainly in the narrow straits of Little Belt, Great Belt, the Sound and Fehmarn Belt. Furthermore, the distribution has been found to change across the year with the harbour porpoises moving south in the winter. This change is not a coordinated migration but a gradual net movement of the population resulting in very low winter abundance in some of the summer high density areas, e.g. the Sound (Sveegaard et al. In press, Paper III, Sveegaard et al. In press, Paper II).

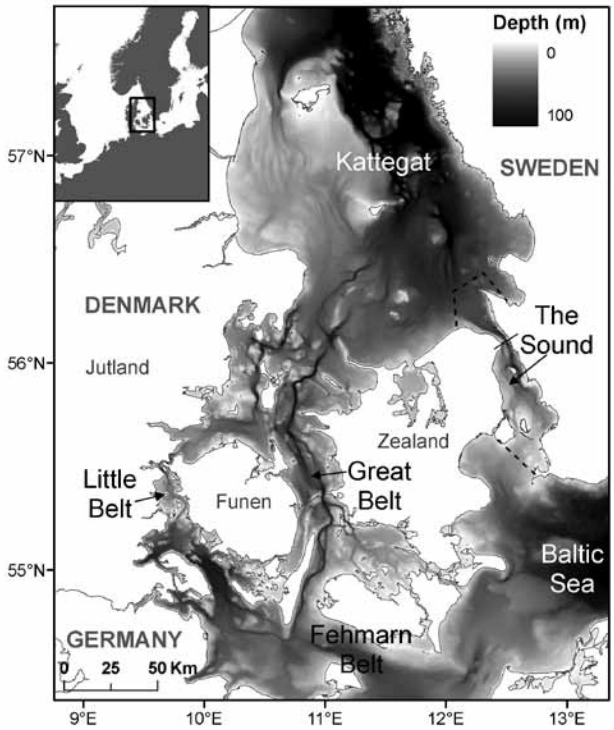

Figure 1. Map of the Sound and adjacent waters displaying bathymetry. The dashed lines indicate the area within which all harbour porpoise samples were collected. The thin black line at the narrowest part of the Sound illustrates the division of the strait in a northern and a southern part.

The environmental or biological factors governing harbour porpoise distribution is not well understood. However, the harbour porpoise is a small whale with limited body fat inhabiting a cold environment, and it must consequently feed at a high daily rate to maintain energy requirements (Koopman 1998, Lockyer et al. 2003, Lockyer 2007). The distribution of harbour porpoise is therefore expected to follow the distribution of its main prey species (Koopman 1998, Santos et al. 2004). In support of this, harbour porpoise distribution have been found to correlate with the abundance of herring (*Clupea harengus*) in Kattegat and Skagerrak (Sveegaard et al. In review, Paper VI) as well as environmental variables such as bathymetry, sediment type and temperature that are believed to affect presence of prey (Marubini et al. 2009, Bailey and Thompson 2009, Edrén et al. 2010, Embling et al. 2010).

Due to the high energy requirements, the harbour porpoise cannot afford to be too specialized and is generally believed to be an opportunistic feeder (Börjesson et al. 2003, Santos et al. 2004). In the waters between the eastern North Sea and the western Baltic Sea, major prey species include herring (*Clupea herangus*), sprat (*Sprattus sprattus*), cod (*Gadus morhua*), whiting (*Merlangius merlangus*), gobies (Gobiidae) and sandeels (Ammodytidae) (Aarefjord et al. 1995, Benke et al. 1998, Börjesson et al. 2003). The relative importance of these species to harbour porpoise varies between regions (Benke et al. 1998, Santos and Pierce 2003) and possibly over time, but little is known about changes in prey preferences on a small spatial and temporal scale such as seasonal variations in a small area like the Sound.

The Sound is subjected to heavy ship traffic, with about 59,000 vessels going through in 2008 (~70% of the traffic between Kattegat and the Baltic Sea; www.helcom.fi). Due to the high level of traffic, the use of trawl or any type of towed fishing device has been banned in the Sound since 1932 except for a small area in the centre of the strait north of Zealand (Svedang 2010). This makes the Sound unique to any other part of the adjacent seas by providing an environment of undisturbed benthic flora and fauna, which allows for rich and varied fish populations. The trawl ban also provide some protection of local stocks of herring, cod and flatfish as well as species migrating though the strait (Svedang 2010). The southern part of the Sound (as indicated on Fig. 1) constitutes an important overwintering habitat for herring from August to February, and in this period, the abundance of herring may thus be up to three times greater than in the rest of the year (Nielsen et al. 2001).

Harbour porpoise in the Sound has been found in several studies to vary seasonally, with high densities in the summer and low densities in the winter (Sveegaard et al. In press, Paper III, Sveegaard et al. In press, Paper II). However, this distribution seems counter-intuitive: Why do porpoise leave the Sound in the winter when abundance of mature herring, one of their main prey species, is high?

Here, we examine this controversy, by studying whether the seasonal differences observed in harbour porpoise distribution in the Sound, can be explained by their prey selection. We do so, by analysing the stomach content of stranded and bycaught harbour porpoises in the area across the year. Due to their constant high energy requirement, we hypothesize that the prey preferences (stomach content) of the harbour porpoises will reflect an increase in food quantity and/or quality in the season of high density season.

METHODS

Study area

The Sound (ICES Subdivision 23) is a transition area between the brackish water from the Baltic Sea and the more saline water from Skagerrak/Kattegat (Jakobsen 1980). The Sound is about 100 km long, 5-25 km wide and has a maximum depth of 40 m, and limited to the south by the Drogden sill which is approximately 7-8 m deep (Jakobsen and Castejon 1995).

Harbour porpoise distribution

From 1997 to 2010, 58 harbour porpoises were tagged with satellite transmitters along the eastern coast of Jutland and in the Belt Beas (the waters around Funen). Nineteen of these moved into the Sound during the period of transmission (For information on tagging, transmitter types, filtering of data, and more, see Sveegaard et al. In press, Paper II). Number of locations (one per day per harbour porpoise) was calculated for each month

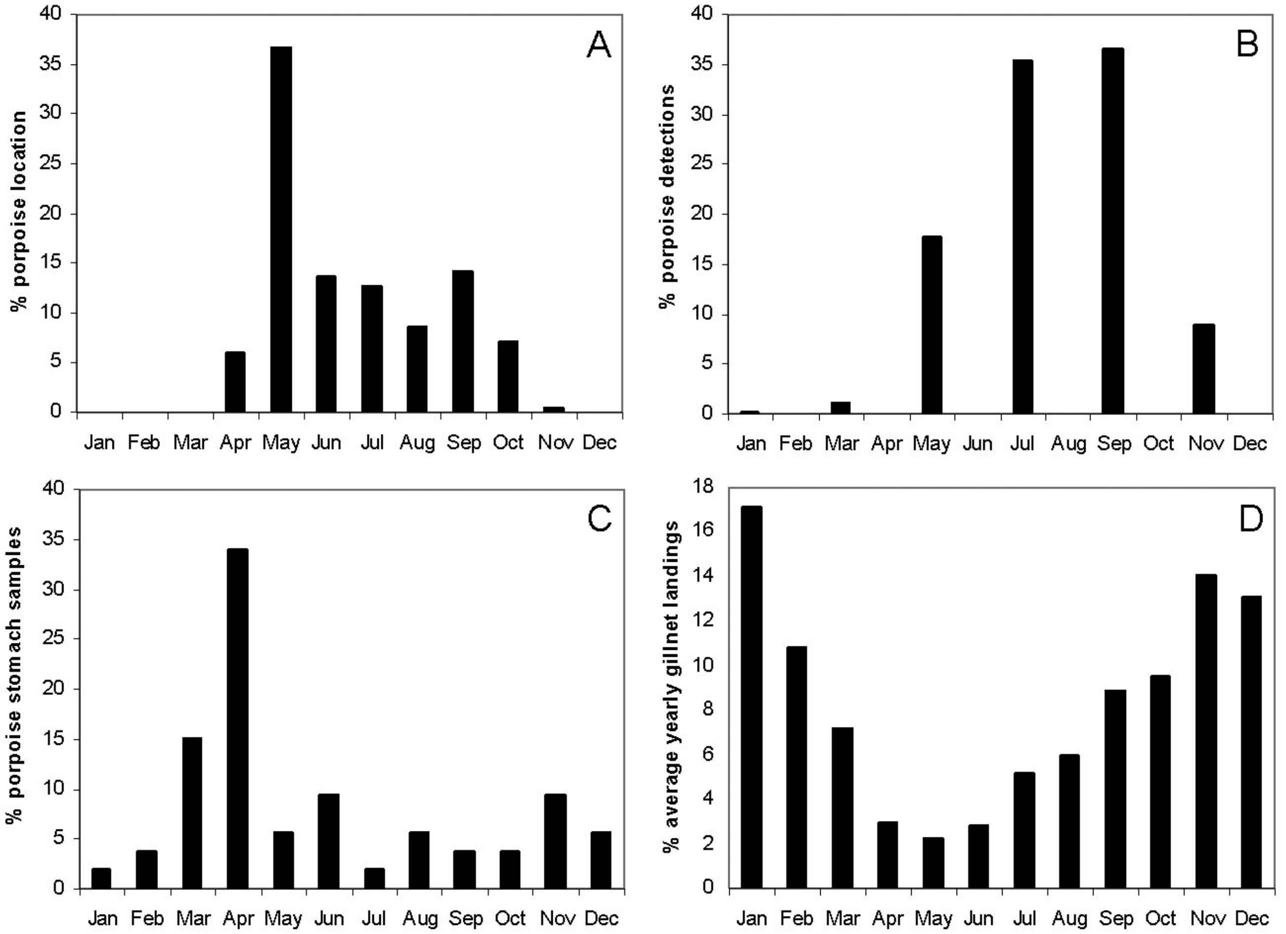

Figure 2. Monthly percentile distributions in the Sound of **A)** number of locations from satellite tracked harbour porpoises, 1997-2010, **B)** number of porpoise detections from six acoustic surveys, 2007, **C)** number of harbour porpoise stomach samples and **D)** Mean weight per year of fish landings from gillnet fisheries, 1987-2010.

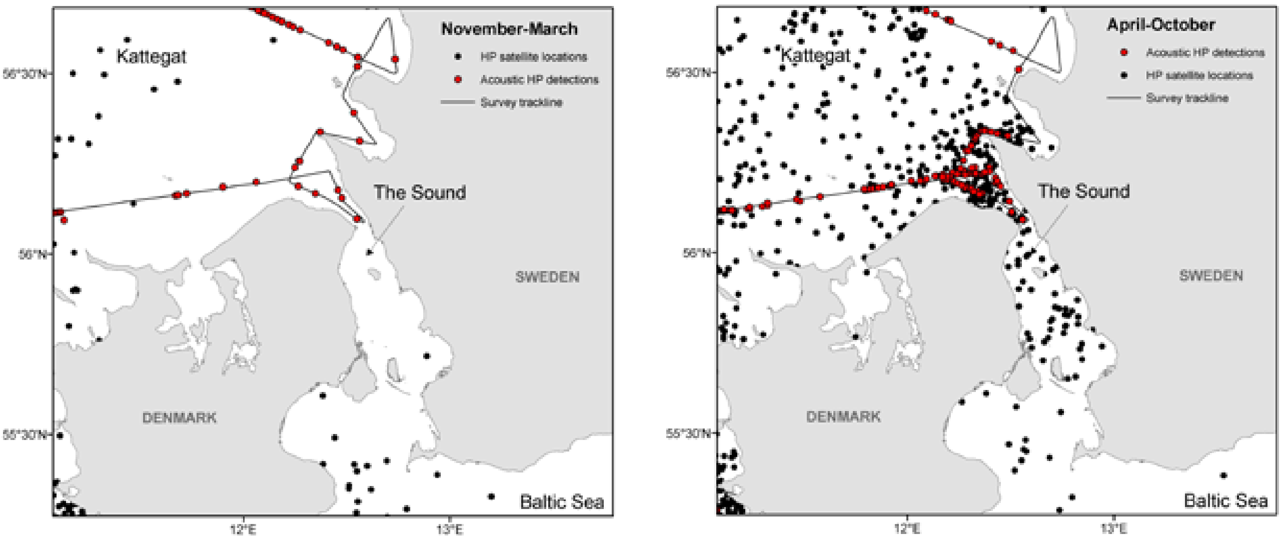

Figure 3. Distribution of harbour porpoises (latin) (HP) from satellite tracking (1997-2010) and acoustic surveys (2007) in the Sound from November through March (left panel) and from April through October (right panel).

in the Sound (Fig. 2A). To further validate this seasonal distribution, six acoustic surveys using a towed hydrophone array to detect the echolocation clicks from harbour porpoises were conducted in 2007 (for information on method and analysis, see Sveegaard et al. In press, Paper II).The porpoise detections from the surveys showed the same seasonal variation as the satellite locations with the surveys in May, July and September having significantly more detections than the surveys in January, March and November (Fig. 2B). The combined data from satellite tracking and acoustic surveys allowed us to divide the year into a low density season (November-March) and a high density season (April-October) (Fig. 3).

Assessment of prey preferences

The fifty-three harbour porpoises (22 females, 31 males; mean length: 120±16 cm, range: 91-170 cm) used in the analysis were all incidentally bycaught in fishing gear or found stranded within the Sound during 1987-2010. Eighteen were collected by I. Lindstedt (Natur-historiska Museum, Göteborg) and C.C. Kinze (Zoological Museum, Copenhagen) from 1987-1989 and stomach content were analysed by H. Aarefjord (Norwegian Institute for Nature Research, Oslo) (7 bycaught, 11 unknown), 17 were collected and analysed by H. Andreasen (DTU-Aqua) from 1989-2000 (14 bycaught, 3 stranded) and 18 were collected in 2009-2010 by J.P. Pedersen (The Øresund Aquarium) and analysed by H. Andreasen and S. Sveegaard (18 bycaught, 1 stranded).

The samples are not distributed evenly across the year, but peaks in April with 18 porpoise samples (Fig. 2C). That dead porpoises can be found during all month of the year in the Sound demonstrates that porpoises are present at all times. However, harbour porpoises are caught by gillnets which are mostly applied during the season with low porpoise density (as judged by gillnet caught fish landings in the Sound, Fig. 2D), which provides a reasonably large sample size of bycaught harbour porpoises also during the winter season where harbour porpoises are relatively rare in the region.

The method of analysis was similar for all stomachs. First, the stomach and the lower part of the oesophagus were rinsed with running water and the content separated through a stable of sieves with mesh sizes of 2 mm, 1 mm and 0.5 mm, respectively. Retained whole or partly digested prey items, fish bones and otoliths were counted, identified and measured. The number of prey consumed by each porpoise was then calculated by summing the number of intact prey items and the number of prey estimated from remains for each species. For fish, this was estimated as the number of otoliths divided by two.

Wet weight of each fish was estimated from measured length and width of otoliths according to Härkönen (1986). Although other fish size/otolith size relationships are available, Härkonen (1986) was chosen because it is based on data collected in close proximity of the Sound (Skagerrak and Kattegat). Regarding fish length estimates, however, Leopold (2001) was used rather than Härkonen (1986) because the latter provided an insufficient otolith size-range for some species.

Because small otoliths (e.g. gobies) degrades faster than larger otoliths (e.g. cod), the estimated dimensions of larger fish species may tend to be overestimated. Correction for this potential bias was not carried out because information on otolith degradation was unavailable for some samples.

Preliminary porpoise sample analysis

The analysed harbour porpoise stomachs were collected in two separate time periods, 1987-2000 (n=35) and 2009-2010 (n=18). If a shift in prey preferences of harbour porpoises have occurred between these periods it could bias the results. Consequently, the two groups of porpoises (1987-2000 and 2009-2010) were tested for differences in the number of species within each stomach, as well as total weight of prey, total number of fish and relative dominance of prey species.

Nineteen porpoise stomachs were analysed from the low density month (November-March) and 34 porpoise stomachs from the high density month (April-October). The two groups were analysed for differences in sex ratios and lengths of porpoises. Furthermore, the overall correlation between porpoise length and the maximum and mean prey consumed was tested.

Analysis of stomach content

When examining prey preferences it is particularly interesting to look at (1) the frequency of occurrence, %O (the number of stomachs found to contain a particular prey species divided by the total number of stomachs with identifiable remains, multiplied by 100), (2) the frequency of numerical occurrence, %N (the number of individuals of the particular prey species divided by the total number of prey individuals found, multiplied by 100) and (3) the frequency of estimated weight of each species, %W (the total weight of the particular prey species divided by the total weight of all prey species, multiplied by 100). These measurements were calculated for the period of high (April-October) and low (November-March) harbour porpoise density.

Some otoliths were degraded to an extent were they could not be identified on species level, but solely on family level. This was unproblematic in calculation and interpretation of %O, %N, and %W, but could potentially invalidate analyses of species diversity and richness. Consequently, fish classified as Clupeidae spp. and Gadidae spp. were assigned to species groups: fish assigned to a family group in stomachs that also contained species identified family members were assigned to the identified species according to the relative proportion of the latter. In stomachs, that solely contained family level identifications, Clupeidae spp. and Gadidae spp. were assigned to the most frequent species across all samples.

Species richness and Simpson's diversity index was calculated for each stomach and the results compared between high and low season. Simpson's diversity index is a simple mathematical measure that characterizes species diversity in a community. Diversity indices provide additional information about community composition than species richness (i.e., the number of species present within each stomach), since they also take the relative abundances of different species into account. Simpson's diversity index was calculated as the proportion of each species relative to the total number of species within each stomach. This number is squared and the proportions for all the species in the stomach are summed, and the reciprocal is taken. In this form (also named Hill's N2) the unit is 'species', interpreted as the number of equally frequent species necessary to obtain the diversity observed in the sample in focus (Krebs 1999).

Statistical analysis

For general comparison between high and low season, Student's t-test or paired t-test were used depending on the scale of the data. For comparison of agreement between season in distribution of %Occurrence, %Numerical occurrence and %Weight, we used Kendall's coefficient of concordance. This is a non-parametric statistic that does not assume normal distributed data and may be used for assessing agreement among probability distributions.

RESULTS

Preliminary porpoise sample analysis

The comparison of the two temporally separated groups of porpoises (1987-2000 and 2009-2010), showed no significant differences in the number of species within each stomach (Students t-test, t_{51}=1.466 P=0.149), total weight (Students t-test, t_{51}=1.466 P=0.340), total number of fish (Students t-test, t_{51}=0.553, P=0.590), and the relative dominance of consumed prey species/groups between periods (Related-Samples Kendall's Coefficient of Concordance, P=1.000). The two groups were consequently pooled in the following analysis.

Furthermore, for the porpoises in high (April-October) and low season (November-March) no difference was found in sex ratios (χ^2-test, P=0.570) and length (Students t-test, t_{30}=1.829, P=0.077). We found no correlation between length of the porpoise and the maximum or mean prey it had consumed ($F_{1,51}$=0.151, P=0.699). Hence, sex and size are not further considered in the analysis.

Assessment of prey preferences

In the 53 analysed stomachs, a total of 1442 individual fish from eight families and thirteen species was identified. The longest fish eaten was a European eel, *Anguilla anguilla*, of 59 cm that was found undigested in the stomach of a 138 cm long female porpoise. The mean fish length was 16.6±9.0 cm across all samples. The maximum and mean prey lengths of each consumed fish species are illustrated in Fig. 4. For all relevant species, the maximum length is longer in the high season than in the low season. A similar pattern exists for also mean fish length, eels being the only exception. In tests of individual fish species, only cod (*Gadus morhua*) was statistically significantly longer in the high density season (maximum length: Student's t-test, t_{19}=3.009, P=0.007; mean length: t_{19}=3.567, P=0.002). Similar results were also found for the wet weight of fish (data not shown). Considering all fish species together, porpoises in the high density season consumed marginally significant longer prey items than in the low season (maximum length: Student's t-test, $t_{30.6}$=1,941, P= 0.062; mean length: $t_{28.3}$=1,836, P=0.077). Furthermore, we found significant higher mean prey per stomach in the high season (mean: 1343.5±322.2 g) than in the low season (mean: 380.5±95.9) (Students t-test, $t_{38.5}$=2.865, P=0.007), but the number of prey species did not differ between seasons (Mann-Whitney U-test, U=338.5, p=0.773).

Overall, herring and cod appeared to be the most important prey species in terms of occurrence, size and weight and may therefore potentially influence the spatio-temporal distribution of harbour porpoises. Consequently, the length distribution of these prey items was further analysed for both seasons (Fig. 5). There is no apparent difference between the length distributions in the two seasons for herring, but for cod, the majority of fish eaten in the low season are less than 20 cm and in the high season they are over 30 cm.

In terms of occurrence, herring, cod and gobies dominated as prey in both high and low season (30-44%) (Fig.6A). However, no difference was found in frequency of occurrence for eel and gobies. Overall, we found a marginally significant higher occurrence in the high season compared to the low season (Paired t-test, t_{16}=2,080, P=0.054), and further, the distribution of occurrence across fish species differed between high and low season (Kendall's Coefficient of Concordance, P=0.029). The latter was due especially to contributions from sandeel, sprat and a range of gadoids.

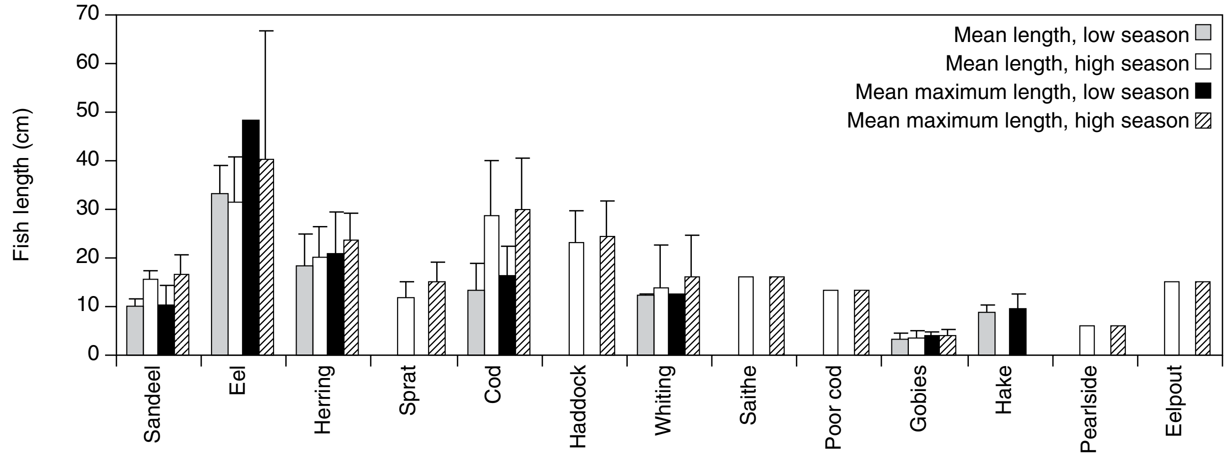

Figure 4. Mean length of individual fish species per stomach and mean maximum length of prey per stomach found in harbour porpoise (*Phoecoena phocoena*) in high (Apr-Oct, N_{fish}=458) and low (Nov-Mar, N_{fish}=984) season in the Sound. Error bars represent standard deviation of mean fish length. Species include sandeel (Ammodytidae ssp.), eel (*Anguilla anguilla*), herring (*Clupea harengus*), sprat (*Sprattus sprattus*), cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*), saithe (*Pollachius virens*), poor cod (*Trisopterus minutus*), gobies (Gobiidae spp.), hake (*Merluccius merluccius*), pearlside (*Maurolicus muelleri*), eelpout (*Zoarces viviparous*).

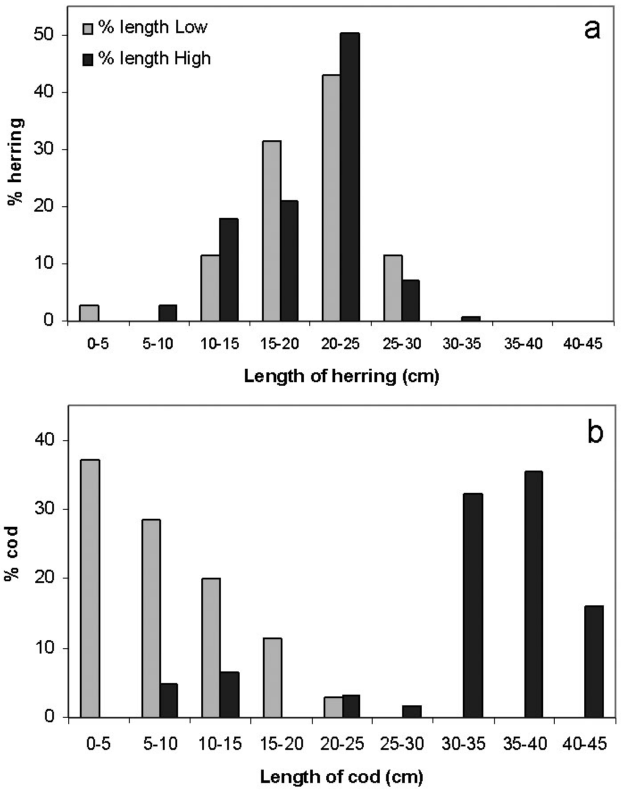

Figure 5. Length distribution of **a)** herring (*Clupea harengus*) and **b)** cod (*Gadus morhua*) consumed by harbour porpoise (across stomachs) in the Sound divided in high (Apr-Oct, $N_{herring}$=139, N_{cod}=62) and low (Nov-Mar, $N_{herring}$=35, N_{cod}=35) harbour porpoise density period.

Regarding the numerical occurrence (%N), we similarly found that the distribution across fish species differed significantly between high and low season (Kendall's Coefficient of Concordance, P=0.029) (Fig. 6B). Particularly more gobies are consumed during the low season compared to the high season, whereas sandeel, herring, sprat and gadoids (especially cod and whiting) are consumed more frequently in the high season.

For total percentage weight (%W) of consumed species, the most noticeable difference between high and low season it the high weight proportion of herring in low season and he high weight proportion of cod in high season (Fig. 6C). As opposed to occurrence and numerical occurrences, the distribution of fish weight across species did not differ significantly between high and low season (Kendall's Coefficient of Concordance, P=0.808). This suggests that it is the same prey species that contribute to the bulk of prey weight found in the porpoise stomachs in both seasons.

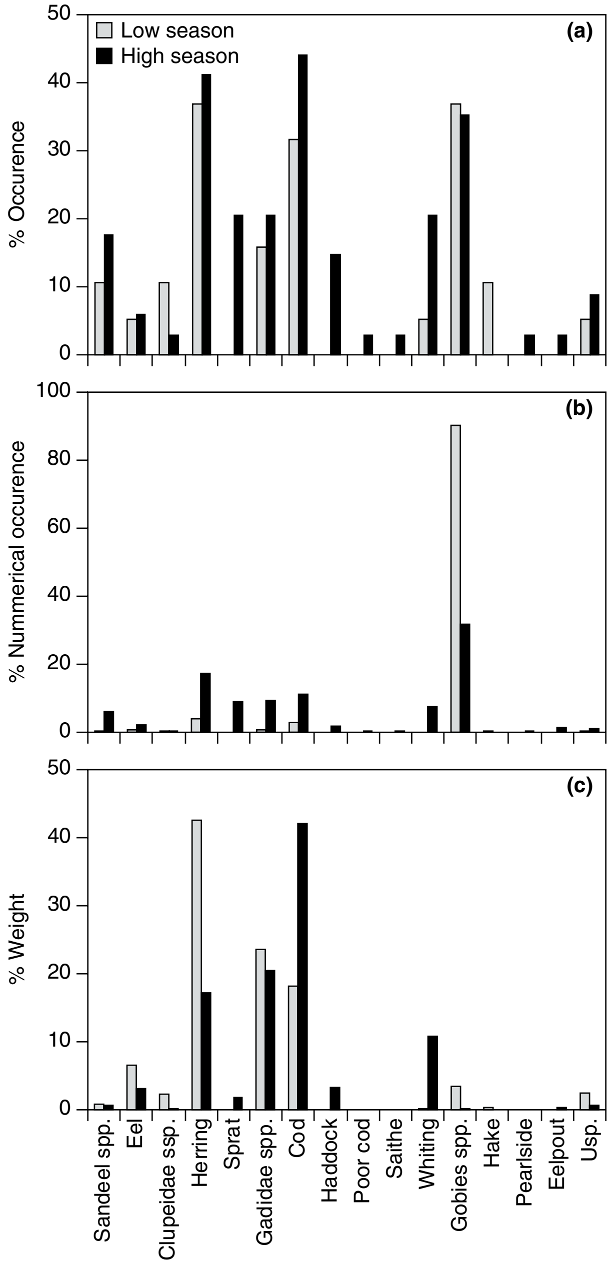

Figure 6. a) Frequency of occurrence, **b)** Percentage numerical occurrences and **c)** Frequency of summarized mass of fish species in stomachs of harbour porpoises (*Phocoena phocoena*) in high (Apr-Oct, N_{fish}=458) and low (Nov-Mar, N_{fish}=984) season, respectively. Sandeel spp., Clupeidae spp., Gadidae spp. and Gobies spp. refers to unidentified species of each family. Usp. denotes unspecified fish species. For scientific names of species, see Fig. 4.

The porpoise diet was more divers in the high season than in the low season. Of the 13 species found, twelve were present in the summer and 7 in the winter. Furthermore, in the low season, 47% of all porpoises had consumed only one prey species and the maximum number of species found in a stomach was three. In the high season, 32% had consumed one species while 35% had consumed 3-5 species. The mean Simpson's diversity index – obtained for the prey community of each porpoise stomach – was significantly higher (by 33%) in the high season (Simpsons index value=1.71±0.11) than in the low season (Simpsons index value=1.29±0.10) (Students t-test, $t_{49.1}$=2.724, P=0.009). Simpson's diversity index includes evenness (frequency of species) as well as species richness in the calculations.

Higher index values, thus, represent generally more varied food consumption and not merely that a few individuals of new species are included. We only marginally significant difference between the two seasons in species richness, (Students t-test, $t_{48.6}$=1.942, p=0.058). Consequently, the increase in Simpson diversity index in high season is mainly caused by a higher evenness in prey selection.

DISCUSSION

Satellite tracking and acoustic surveys of harbour porpoises clearly demonstrate a seasonal variation in porpoise presence in the Sound with high densities in the summer (April to October) and low densities in the winter (November to March). In accordance with our hypothesis, we found both quantitative and qualitative differences in consumed prey between seasons: In the high season, mean prey weight per stomach was larger, the level of occurrence of prey species was higher, and a higher diversity of species was found. Furthermore, cod was found to be the main prey species in terms of weight in the high season and herring, the main prey species in the low season. The mean cod weight was higher in the high season. No difference was found in the number of prey species between the two seasons, but the relative distribution of numbers was different. That the number of fish individuals did not differ between seasons, but the mean prey weight per stomach did, indicates that the quality i.e. weight of prey is enhanced in the high season.

The porpoise diet was more varied during high season than in low season. In total, we found 13 different species of which twelve were present in the high season and seven in the low season. The number of species is comparable to other studies in adjacent areas e.g. Aarefjord et al. (1995) also found thirteen species during the examination of forty porpoise stomachs in Kattegat, R. Lick found eight different species in the German Baltic (62 porpoise stomachs) (Lick 1991, Lick 1994, Lick 1995) and Börjesson et al. (2003) found twenty species in Kattegat and Skagerrak (112 porpoise stomachs), indicating a decline in species diversity from the North Sea and Skagerrak to the Baltic Sea. However, due to the absence of trawling, the Sound has been found to contain higher fish diversity due to the undisturbed benthic flora and fauna, which allows for rich and varied fish populations (Svedang 2010). In fact, while several fish species have either disappeared or been reduced to remnant populations in Kattegat, stocks of a range of demersal fish species such as cod, whiting and haddock occur in higher densities, and has larger age diversity, in the Sound by comparison (Angantyr et al. 2007). For an opportunistic feeder like the harbour porpoise, high prey species diversity may be an important factor determining habitat selection in time and space. The different prey diversity in high and low season may partly be caused by the different species lifehistory as well as seasonal variation in activity levels. For instance, sandeel are buried through out most of the winter and the adult eels either hide or swim off to spawn (Muus et al. 1998). An additional factor is that the fish become more easily available in the spring and summer due to the appearance of oceanic frontal zones. Frontal zones are the boundaries between two different water masses in the ocean and can have a major influence on the biology of pelagic organisms because they result in zones of convergence and eddies where debris and organisms accumulate (Wolanski and Hamner 1988). These frontal zones are in turn correlated with enhanced primary production due to upwelling of nutrients (Pingree et al. 1975), making an area attractive for fish species and consequently, for larger marine predators like the harbour porpoise. During outflows from the Baltic, the low saline surface water will propagate northward through the Sound creating a frontal zone in the northern part where the Baltic water (salinity ~8-10‰) meets the more saline bottom waters (salinity ~18-25‰) in Kattegat (Pedersen 1993, Gustafsson 1997, Gustafsson 2000). The flow in the Sound is statistically well correlated to the air pressure and wind field over Scandinavia: a westerly wind is related to a surface current towards the Baltic Sea, whereas an easterly wind is related to a surface current out of the Baltic Sea (Pedersen 1993, Jakobsen and Castejon 1995, Nielsen 2005). In Denmark, strong easterly wind occurs mainly in spring (Cappelen and Jørgensen 1999), increasing the likelihood of frontal zones to develop in the Sound. Vorticity or turbulence in marine areas is often correlated with hydrographical fronts e.g. caused by differences in temperature, current or bathymetry (Wolanski and Hamner 1988). Skov and Thomsen (2008) found that fronts caused by current and gradients in bathymetry were a significant habitat driver in porpoises presence at Horns Reef in the North Sea. They further suggested that feeding at predictable frontal structures with enhanced availability of prey may be a beneficial foraging strategy, by reducing the size of the area in which the porpoise searches for prey. Consequently, frontal zones developing in the Sound in the spring may be an important driver for harbour porpoise to gather there in this season.

The frontal zones may also explain why the density of porpoises does not correlate well with fishery landings peaking in the winter (Fig. 2D) and the fact that the Rügen spring spawning herring stock are known to over-winter in the Sound from autumn to late spring (Nielsen et al. 2001). In a recent study, the locations from satellite tracked porpoises were highly correlated with herring density during summer in Kattegat and Skagerrak (Sveegaard et al. In review, Paper VI). Here, it was suggested that the presence of hydrographical frontal zones leading to upwelling and high productivity between Kattegat and Skagerrak and along the Norwegian Trench, may aid the porpoises in locating the herring. In this study, we found that the porpoise present during low season prefer herring, but apparently the high concentrations of herring per se is not adequately attractive for the porpoises to gather in higher densities in the Sound during the winter.

However, the influence of heavy traffic in the Sound constitutes an alternate explanation for why porpoise does not pursue herring during winter. The majority of over-wintering herring are found in the southern part of the Sound (Nielsen et al. 2001). Edrén et al. (2010) analysed satellite telemetry data from 39 harbour porpoises (of the 58 porpoises mentioned in Methods) by spatial modelling. Based on variables such as bottom salinity and distance to coast, they predicted the Sound – especially the southern part – to have high probabilities of harbour porpoise occurrence (~high habitat suitability) across seasons. However, very few positions from satellite tracked porpoises were found in this area (Fig. 3), and so, they speculated that heavy ship traffic might limit the number of harbour porpoises in the area. If this is true, the narrowest part of the Sound separating the northern and the southern part by merely 5 km, that additionally has three ferry routes running 24 h d^{-1}, may constitute a form of barrier, precluding the majority of porpoises from entering the southern part of the Sound.

We found cod to be the most important prey species in the high season occurring in 44 percent of the porpoise stomachs and constituting 42 percent of the total prey mass. In addition, a large proportion of consumed Gadidae spp. is likely to be cod as well, further strengthening the tendency. Interestingly, we found great difference in the sizes of cod in high and low season, with 84 percent of cod being longer than 30 cm in high season and 85 percent less than 15 cm in low season (Fig. 5). Cod is an important commercial species, which has caused several stocks to the point of extinction (Cardinale and Svedang 2004). However, the Sound harbours a demographically separate cod subpopulation (Cardinale and Svedang 2004, Angantyr et al. 2007), and due to the ban on trawling, cods in the Sound are more abundant and have higher age diversity than cods in Kattegat (Svedang 2010, Sveegaard et al. In prep., Paper V). This may be an important factor in determining the presence of porpoise in the Sound. The development of fronts, may explain why cods in the Sound become more accessible to porpoises in the high season.

Gobies constitute a major prey group in terms of occurrence and number of individual fish in the analysed stomachs. The Sound has been found to hold several species of gobies in large quantities (e.g. two-spotted goby, *Coryphopterus flavescens*, and black goby, *Gobius niger*) (Angantyr et al. 2007). This broad availability of gobies combined with the high frequency of occurrence, despite their relatively low individual weight, may suggest gobies to constitute a kind of 'back up' prey, when larger more energy efficient and possibly easier accessible prey species are not available.

The combined effect of higher diversity, the presence of frontal zones, higher mean weight of prey and high availability of the primary prey, cod, are believed to cause the observed shift in porpoise abundance in the Sound. The low density of harbour porpoises in November-March that corresponds poorly with the high abundance of herring in this season, may be caused by lower availability of prey due to lack of fronts or perhaps by habitat exclusion from the southern part of the Sound caused by heavy traffic. However, other factors may also contribute to the distribution. For instance, the high density season correspond with the month for parturition (June-July) and mating (August-September) for harbour porpoises in the Danish waters (Lockyer and Kinze 2003). So far, no specific breeding areas have been identified in Danish waters and consequently the drivers for distribution in relation to this are unknown. Our result indicates that porpoise movements are influenced by a complex ecological marine system and perhaps by heavy traffic as well. Our current knowledge is still insufficient to explain all aspects of harbour porpoise distribution. , but this study has taken us a step further in understanding porpoise habitat preferences and potential drivers for their movements.

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SPATIAL AND TEMPORAL DISTRIBUTION OF HARBOUR PORPOISES IN RELATION TO THEIR PREY

The population status of harbour porpoises has been of concern for several years due to anthropogenic influences, especially incidental bycatch in gillnet fisheries. Proper management of a wide-ranging species such as the harbour porpoise requires reliable information on distribution, migrations, status of biological populations, and habitat preferences. This PhD thesis examines these issues. Harbour porpoise distribution is examined by means of satellite tracking (Paper II) and acoustic surveys, along with the agreement in results between these two very different methods (Paper III). The data from satellite tracking are also used to identify the boundaries of a genetically distinct harbour porpoise population and new abundance estimates are calculated for this population (Paper IV). Next, the underlying causes governing harbour porpoise distribution are explored by reviewing available information on harbour porpoise diet (Paper V) and correlating the distribution of satellite tracked porpoises with distribution of a main prey species, herring (Paper VI). Finally, the seasonal variations in distribution of harbour porpoises observed in a Danish strait, the Sound, are explored by examining the stomach content of porpoises from the area. Overall, this PhD thesis introduces several new applications for satellite telemetry data that – in combination with acoustic surveys – has significantly contributed to the current knowledge of harbour porpoise distribution. Furthermore, the thesis provides evidence of a porpoise-prey relationship which is important information in the conservation of the species, due to its influence on harbour porpoise distribution.

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