Aus dem Forschungs- und Technologiezentrum Westküste
der Christian-Albrechts-Universität zu Kiel

Characterisation of harbour porpoise (*Phocoena phocoena*) habitat in German waters

Dissertation

zur Erlangung des Doktorgrades
der Mathematisch-Naturwissenschaftlichen Fakultät
der Christian-Albrechts-Universität zu Kiel

vorgelegt von

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Kiel, Dezember 2008

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Tag der mündlichen Prüfung: 03.02.2009

Zum Druck genehmigt:

Kiel, den

Der Dekan

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CHAPTERS

Summary

The harbour porpoise (*Phocoena phocoena*) is an important top predator and as such an indicator species for its environment. Before the beginning of the 21st century, little data existed on distribution and abundance of harbour porpoises in German waters of North and Baltic Sea. As a consequence, virtually nothing was known about important habitats, seasonal differences in distribution and environmental variables determining its distribution. Studies of habitat characteristics of harbour porpoises have been driven both by the need to support conservation and management actions and the increasing availability of suitable tools (e.g. GIS, remote sensing, regression modelling techniques). This thesis aimed to characterise the habitat of harbour porpoises in German waters by estimating abundance, examining spatial and seasonal patterns in distribution, deriving habitat prediction models and investigating the feeding ecology of porpoises in order to infer on predator-prey dynamics. A comprehensive database was set up based on results of aerial surveys conducted year-round in the course of five consecutive years (2002-2006), following standard line transect methodology. Robust abundance estimates for different surveys, that accounted for animals missed on the transect lines, could be derived for the Baltic and the North Sea. In the Baltic Sea, these estimates are especially important to evaluate the effect of bycatch that was found to be a major threat to porpoises throughout the western Baltic Sea. In the North Sea, presented abundance estimates will serve as a baseline for management decisions with respect to the projected construction of large offshore wind farms and its possible impacts on porpoises. Important habitats were detected in offshore waters of the German North Sea: in spring, the two hot spots 'Borkum Reef Ground' and 'Sylt Outer Reef' (SOR) were identified as key foraging areas for harbour porpoises. In summer, the large hot spot SOR persisted, causing a strong north-south density gradient. In autumn, porpoises were more evenly distributed and density was lower than during spring and summer. Differences in these seasonal hot spots were investigated in relation to several static (e.g. depth, slope) and dynamic (e.g. sea surface temperature, chlorophyll) predictors by applying generalised additive models (GAM) and mixed models (GAMM). The key habitat descriptors as selected by the models varied between seasons. Predictors explaining most of the variance were the hydrographical parameter 'residual currents' and proxies for primary production and fronts (chlorophyll and nutrients) as well as the interaction 'distance to coast/water depth'. In order to address possible seasonal dietary shifts, two methods, the traditional method of stomach content analysis and the new method of quantitative fatty acid signature analysis (QFASA) were applied to elucidate the feeding ecology of harbour porpoises in German waters. A multivariate analysis revealed significant seasonal and between-year fluctuations in the relative importance of prey species: in spring, mainly sandeel, goby and herring contributed with high masses whereas cod was most important in summer. Cod seemed to be an important prey item throughout the study period. Goby and flatfish species appeared to be more important before 2001, whereas in the period 2002-2006 sandeel, herring and sprat contributed more to the diet.

In conclusion, this thesis discovered important temporal and spatial patterns of habitat use and elucidated its underlying causes as harbour porpoise density were set in relation to the German Bight environment. This thesis could fill addressed gaps in knowledge and improved our understanding of harbour porpoise ecology in German waters and possibly beyond.

Zusammenfassung

Der Schweinswal (*Phocoena phocoena*) ist ein wichtiger Top-Prädator und als solcher eine Indikatorart für seinen Lebensraum. Vor Beginn des 21. Jhs. standen nur wenige Daten zur Verteilung und Abundanz von Schweinswalen in deutschen Gewässern der Nord- und Ostsee zur Verfügung. Demzufolge existierten große Wissenslücken über wichtige Habitate, Unterschiede in saisonalen Verteilungsmustern sowie zu Umwelteigenschaften für die Erklärung der raum-zeitlichen Verteilung. Sowohl die Notwendigkeit, Schutz- und Managementmaßnahmen zu unterstützen, als auch eine zunehmende Verfügbarkeit geeigneter Visualisierungs- und Statistikmethoden (z.B. GIS, Fernerkundung, Regressionsmodelle), förderten die Erarbeitung wissenschaftlicher Studien zur Habitatcharakterisierung des Schweinswals. Ziel und Hauptaugenmerk der vorliegenden Studie ist die Charakterisierung des Habitats des Schweinswals in deutschen Gewässern: Hierzu wurden Bestände abgeschätzt, raum-zeitliche Verteilungsmuster untersucht, Habitatmodelle erstellt und, um Rückschlüsse auf die Dynamik der Prädator-Beute-Beziehung ziehen zu können, die Nahrungsökologie der Schweinswale erforscht. Basierend auf Erfassungen von Schweinswalen mittels Flugzählungen, die im Verlauf von fünf Jahren (2002-2006) nach der Linientransekt-Methode durchgeführt wurden, ließ sich eine umfassende Datenbank aufbauen. Es konnten belastbare Bestandsschätzungen für Nord- und Ostsee ermittelt werden, wobei die nicht erfassten Tiere auf den Transektlinien berücksichtigt wurden. Für die Ostsee sind diese Schätzungen besonders wertvoll, um den Effekt von Beifang zu bewerten, der – wie gezeigt wird – eine große Bedrohung für Schweinswale in der westlichen Ostsee darstellt. In der Nordsee dienen die ermittelten Bestandsgrößen als Basislinie, um den möglichen Effekt der geplanten Konstruktion der Offshore-Windkraftanlagen auf Schweinswale abzuschätzen. Im Verlauf der Studie konnten wichtige Habitate für Schweinswale im Offshore-Bereich der Nordsee bestimmt werden: So scheinen im Frühling v.a. die Bereiche um den Borkum Riffgrund und das Sylter Außenriff eine Schlüsselrolle als Nahrungsgründe einzunehmen. Im Sommer stellte sich ein ausgeprägter Nord-Süd Dichtegradient ein, der besonders durch eine sehr hohe Dichte im Sylter Außenriff bedingt wurde. Im Gegensatz dazu war die Verteilung im Herbst wesentlich gleichmäßiger und die Dichte im Vergleich zu Frühling und Sommer am geringsten. Diese jahreszeitlichen Unterschiede in der Schweinswaldichte wurden weitergehend untersucht und durch die

Anwendung von verallgemeinerten additiven Modellen (*generalised additive models* GAM) und gemischten Modellen (*mixed models* GAMM) zu statischen und dynamischen Habitatvariablen (e.g. Wassertiefe, Meeresoberflächentemperatur) in Beziehung gesetzt. Die von den Modellen selektierten Variablen variierten zwischen den Jahreszeiten. Der Großteil der Varianz wird durch die hydrographischen Parameter "Restströmung", die *proxies* für Primärproduktion und Fronten (Chlorophyll und Nährstoffe) sowie durch die Interaktion "Abstand zur Küste/Wassertiefe" erklärt. Um mögliche saisonal bedingte Unterschiede in der Nahrungswahl zu untersuchen, wurden die folgenden Methoden angewandt: zum einen die traditionelle Methode der Mageninhaltsanalyse und zum anderen die (relativ) neue Methode der quantitativen Fettsäureanalyse. Eine multivariate Analyse wies auf signifikante jahreszeitliche sowie inter-annuelle Unterschiede bei der relativen Wichtigkeit der Beutearten hin: waren dies im Frühling vor allem Sandaal, Grundel und Hering, so stellte im Sommer der Dorsch die wichtigste Beuteart. In allen untersuchten Jahren erscheint Dorsch als wichtige Nahrungsart zu fungieren. Grundel und Plattfische erschienen hingegen verstärkt vor 2001 in der Nahrung der Schweinswale, die Zeit von 2002 bis 2006 wurde zunehmend von Sandaal, Hering und Sprotte bestimmt.

Insgesamt konnte die Studie sowohl wichtige raum-zeitliche Muster in der Habitatnutzung der Schweinswale aufdecken als auch die zugrundeliegenden Faktoren beleuchten, indem die Schweinswaldichte in Beziehung zu Umweltfaktoren der Deutschen Bucht gesetzt wurde. Zudem ließen sich nicht nur die erwähnten Wissenslücken füllen, sondern insgesamt das Verständnis der Schweinswalökologie in deutschen Gewässern verbessern.

General Introduction

Describing patterns in the distribution and abundance of species is a fundamental element in ecology and must be understood in order to be able to conserve populations (Evans & Hammond 2004). Marine mammal distributions are affected by demographic, evolutionary, ecological, habitat-related and anthropogenic factors (Forcada 2002). Demographic factors include the abundance, age and sex structure of populations as well as the life cycle of individuals (e.g. Lockyer 2007). Evolutionary factors include morphological, physiological and behavioural aspects of the species' adaptations (e.g. Koopman & Zahorodny 2008). Ecological factors include biological production and use of prey, distribution of prey and predators, and competition (e.g. DeMaster et al. 2001, Bowen et al. 2002). Habitat-related factors are e.g. water temperature, salinity and the bathymetry (e.g. Macleod et al. 2004, Johnston et al. 2005). Anthropogenic factors are the human effects that alter the distribution of marine mammals including pollutants, human-induced sounds, and incidental and direct kills (Weilgart 2007). Distribution has to be regarded as a composite of all these factors.

Studies of habitat characteristics of cetaceans have been driven both by the need to support management actions (e.g. to identify candidate marine protected areas or to evaluate areas planned to be impacted by human activities) and the increasing availability of suitable tools. Geographic Information Systems (GIS) have functions for integrating and overlaying spatially referenced data sets for different habitat-related factors, potentially revealing hidden patterns and relationships. Powerful statistical tools such as generalised additive models (GAM), which are applied in species distribution, allow modelling of non-linear relationships and address challenges associated with field survey data (e.g. Guisan et al. 2002).

This thesis aims to characterise the habitat of the harbour porpoise (*Phocoena phocoena*, Linnaeus 1758) in German waters. Therefore, the objectives in this study were fourfold: (1) to estimate total abundance, (2) to examine spatial and seasonal patterns in distribution, (3) to derive quantitative spatial predictions of the density of individuals throughout the study area by using the relationships between harbour porpoise and certain physical and biological components of their environment (habitat modelling) and (4) to investigate the feeding ecology of harbour porpoises in order to infer on predator-prey dynamics.

SCIENTIFIC BACKGROUND

Status of harbour porpoises in the North Atlantic

The harbour porpoise is a small odontocete inhabiting temperate to cold waters throughout the northern hemisphere (Gaskin 1984). It is distributed in coastal waters of northern Africa, Europe and North America (Donovan & Bjørge 1995) and occurs in a thermal zone that ranges from the polar front (ca. 0.5°C) southwards to a 20 to 24°C thermocline (Tolley & Rosel 2006).

Two major surveys, the SCANS[1] and SCANSII surveys from July 1994 and July 2005, estimated abundance of small cetaceans in the North Sea and adjacent waters (Hammond et al. 2002, SCANSII 2008). In 1994, harbour porpoise abundance was estimated to be 341,366 animals (95% CI: 260,000-449,000) in an area of 1 mio. km^2. Eleven years later, SCANS II resulted in an estimate of 385,617 animals (95% CI: 261,266-569,153) which is higher than in 1994 but from a larger survey area (1.4 mio. km^2) (SCANSII 2008). When comparing estimates for the identical area covered in 1994 and 2005, no significant difference could be detected (SCANSII 2008).

Thirteen putative populations in the North Atlantic were defined by the International Whaling Commission (IWC) (Donovan & Bjørge 1995, Tolley et al. 1999). However, the delineation of these putative sub-populations and exact stock boundaries is difficult and not unequivocal (IWC 2000). In the North and Baltic Seas, for instance, a number of studies on genetics, morphology and contaminant load of porpoises indicate that several subpopulations of porpoises occur in the Skagerrak-Kattegat Seas, the Belt Seas and the Baltic Proper (Kinze 1985, Andersen 1993, Tiedemann et al. 1996, Börjesson & Berggren 1997, Berggren et al. 1999, Huggenberger et al. 2002). Population-level differences have been found between porpoises from the Belt Seas and the North Sea (Kinze 1985, Andersen 1993) and between the Skagerrak-Kattegat Seas and the west coast of Norway (Wang & Berggren 1997). Further genetic differences were found between animals from the northern North Sea and central/southern North Sea as well as within the central North Sea (Walton 1997, Tolley et al. 1999, Andersen et al. 2001). These facts show that it is important to establish a conservation and management plan by region.

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[1] **S**mall **C**etacean **A**bundance in the **N**orth **S**ea and Adjacent Waters

Threats and protection measures

Because the harbour porpoise inhabits coastal waters it is affected by a variety of anthropogenic impacts (review in Kaschner 2001, Scheidat & Siebert 2003), including by-catch in fishery (Kock & Benke 1996, Vinther 1999, Lockyer & Kinze 2003, Vinther & Larsen 2004, Siebert et al. 2006, Scheidat et al. in press) and habitat degradation due to chemical pollution (Jepson et al. 1999, Siebert et al. 1999, Das et al. 2006a, b, Beineke et al. 2007) or noise pollution (Richardson et al. 1995, Koschinski et al. 2003, Lucke et al. 2008). Local populations of porpoises in the Baltic and Black Seas are seriously depleted (Donovan & Bjørge 1995, Koschinski 2002). There is evidence that abundance in the south-eastern North Sea has declined since the 1940s (Smeenk 1987, Reijnders 1992, Camphuysen & Leopold 1993). Recently, some of the local populations show a slow come-back, e.g. in Dutch coastal waters (Camphuysen 2004), what is thought to be caused by a distributional shift rather than an increase in population growth rate.

To address these threats, the protection of harbour porpoises was made the subject of several international agreements and conventions. In EU waters the species is listed in Appendix II of the Bern Convention (implemented in 1982), in Appendix II of the Convention on the Conservation of Migratory Species (CMS; implemented in 1983), in Annex II and IV of the EU Habitats and Species Directive (implemented in 1992), in Annex V of the Convention for the Protection of the Marine Environment of the Northeast Atlantic (Oslo and Paris Convention OSPAR, implemented in 1998). The Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS) was concluded in 1991 under the auspices of the CMS (or Bonn Convention) and entered into force in 1994. It is principally intended to address the problems of fishery bycatch and habitat degradation (including chemical and noise pollution) in the Baltic and North Seas. Through the recent update of the 2008 IUCN[2] Red List of Threatened Species the status of *P. Phocoena* has changed from 'vulnerable' to 'least concern' as global abundance of the harbour porpoise is at least about 700,000 individuals (Hammond et al. 2008). The status of the Baltic Sea subpopulation, however, is recognised as 'critically endangered' (Hammond et al. 2008).

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[2] International Union for the Conservation of Nature and Natural Resources

In 2000, ASCOBANS and IWC agreed that total anthropogenic removal levels (i.e. bycatch and other human related mortalities) of more than 1.7% of the estimated harbour porpoise population size must be considered unacceptable (IWC 2000). The most recent ASCOBANS resolutions explicitly state that the immediate precautionary objective is to reduce bycatch levels to 1% of the best available population estimate (ASCOBANS 2000).

Status of harbour porpoises in German waters

The harbour porpoise is the only cetacean species found regularly in both the German North and Baltic Seas (Reijnders 1992, Benke et al. 1998, Scheidat et al. 2004, Siebert et al. 2006). Density in the Baltic Sea is much lower than in the North Sea (Scheidat et al. 2004, Siebert et al. 2006). The subpopulation 'Baltic Proper' is regarded as critically endangered since density and range of porpoises are believed to be much reduced (review in Koschinski 2002). The probable causes for the apparent failure of the Baltic Proper porpoise to recover is thought to lie in the continuing bycatch in fisheries (Scheidat et al. in press). A recovery plan by ASCOBANS has been set up for harbour porpoises in the Baltic Sea (Jastarnia Plan; ASCOBANS 2002).

Little data existed on distribution and abundance of harbour porpoises in the German North Sea as no dedicated surveys were conducted in the overall area before 2002. Inference can be drawn from the SCANS survey in 1994 (Hammond et al. 2002). However, SCANS was a large-scale survey that aimed at a synoptic coverage of a huge survey area and did not include the area offshore the East Frisian Islands. In the 1990s, surveys in small coastal areas were conducted and resulted in an estimated abundance of 4,288 (in 1995) and 7,356 harbour porpoises (in 1996) in an 8,000 km^2 area offshore the island of Sylt (Siebert et al. 2006). The relative high proportion of mother-calf pairs west of the islands of Sylt and Amrum led to the designation of the first cetacean sanctuary in the North Sea (Sonntag et al. 1999). In 1999, the sanctuary was nominated as a Special Area of Conservation (SAC) within the existing National Park Wadden Sea of Schleswig-Holstein. However, especially density in offshore areas remained unknown. Nothing has been known about focal areas of harbour porpoises and how these could change during seasons.

General biology and life history in the North and Baltic Seas

The harbour porpoise has some unique characteristics among cetaceans. It is known to 'live in the fast lane', i.e. all reproductive and life history traits are accelerated during a short life span of about ten years (Read & Hohn 1995). Sexual maturity occurs at a young age of three to four years in both sexes, with corresponding length of about 135 cm in males and 143 cm in females (Benke et al. 1998, Bandomir et al. 1999, Lockyer & Kinze 2003). The reproductive cycle exhibits strong seasonality (Börjesson & Read 2003): after a gestation period of about 10 months, the majority of births in the North Sea occur from June to mid July (Hasselmeier et al. 2004), shortly before mating. In the Baltic Sea the birth period was found to occur about one month later than in the North Sea (Hasselmeier et al. 2004). The lactation period lasts for about eight to ten months and most adult females are pregnant and lactating at the same time as they give birth each year (Read & Hohn 1995, Lockyer 2003). This points to a very demanding energetic schedule, underlining the importance of habitats with abundant and energy-rich prey (Lockyer 2007). Harbour porpoises in the North Sea primarily feed upon sandeel (*Ammodytes* spp.) and sole (*Solea solea*), whereas porpoises in the Baltic Sea prey on goby (*Pomatoschistus* sp.), herring (*Clupea harengus*) and cod (*Gadus morhua*) (Benke et al. 1998).

POLICY-ORIENTED BACKGROUND

As described above, before the beginning of the 21st century, very little data existed on distribution and abundance of harbour porpoises in German waters. Two recent legislation amendments (Federal Nature Conservation Act in 2002 and Renewable Energy Sources Act in 2004) were in principle responsible for funding of strong efforts of field studies and put German researchers in the unique position of explicitly investigating spatial and seasonal dynamics of harbour porpoise distribution. Findings of this study were incorporated within decisions of German agencies and ministries: important habitats for harbour porpoises could be described and NATURA 2000 areas were nominated to the EU (Scheidat et al. 2006, Gilles et al. 2008).

THESIS OUTLINE

This thesis is divided into five independent chapters, each focusing on different aspects of harbour porpoise ecology.

Chapter I & II

A reasonable understanding of the ecology of harbour porpoises is impossible without having reliable estimates of abundance. Until now, this measure was not available for German waters. In the first two chapters, the abundance of harbour porpoise in the southwestern Baltic Sea and German North Sea was estimated following standard line transect methodology using aerial surveys. In the case of cetaceans abundance estimation is generally challenging as methods must consider the unseen proportion on the transect line. This has been applied, however, in this study. The estimates of the Baltic Sea abundance were set in relation to bycatch estimates of the region.

Chapter III

In this chapter I focussed on spatial distribution patterns of harbour porpoise in the German North Sea. I investigated how these patterns changed during the seasons and identified hot spot areas that could be particularly important for foraging and during the calving and mating season. In addition, I estimated the proportion of porpoises potentially affected by the imminent construction of large offshore wind farms in the area.

Chapter IV

The fourth chapter summarises the results of predictive habitat modelling of harbour porpoise density. This is the first study that assesses porpoise distribution in relation to the complex and dynamic environment of the German Bight. I investigated seasonal shifts in porpoise density in relation to several fixed (e.g. depth, slope) and dynamic (e.g. sea surface temperature, salinity, chlorophyll) habitat predictors. Further, I validated model predictions using an independent data set, originating from the SCANSII survey. In addition, a comparison of different modelling approaches was conducted: the generalised additive model (GAM), that ignores potential spatial autocorrelation (SAC), was compared with a mixed model (GAMM) that accounts for SAC.

Chapter V

In the last chapter, I elucidated the feeding ecology of harbour porpoises by using the traditional method of stomach content analysis and a fairly new method, the quantitative fatty acid signature analysis (QFASA). As the last diet analysis was conducted more than ten years ago (Benke et al. 1998), up-to-date information on porpoise diet is lacking. Besides this general update of diet preference and prey inventory, I also investigated whether inter-annual and seasonal differences in prey choice could be observed. The application of QFASA in this study is presented as a pilot study and it is investigated whether predicted diet is reasonable in comparison to those of the stomach content analysis. This is the first study that applied QFASA for a harbour porpoise diet study.

Chapter I

Harbour porpoise (*Phocoena phocoena*) abundance in the southwestern Baltic Sea

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ABSTRACT

The harbour porpoise (*Phocoena phocoena*) is the only cetacean species resident in the Baltic Sea. At least two different subpopulations occur in this area, with a presumed demarcation line in the western Baltic Sea. Aerial surveys were conducted during different seasons in the years 2002 to 2006 to obtain estimates of porpoise abundance for the southwestern Baltic. Within the survey area, three strata were defined. In total, 46 surveys were completed for these strata. Abundance estimates and corresponding confidence intervals (CI) were calculated for each stratum separately for each survey. Density between areas varied seasonally and spatially, the western study area (Kiel Bight) showing generally the highest density. Whenever all three strata were covered within 25 consecutive days, abundance for the overall survey area was calculated. Ten surveys met these criteria. Overall abundance in the western Baltic varied between surveys with the lowest value in March 2003 (457 ind.; 95% CI = 0–1,632) and the highest estimate in May 2005 (4,610 ind.; 95% CI = 2,259–9,098). The results of all other surveys were in the range from 1,352 to 2,905 animals, with largely overlapping confidence intervals. Applying the only available bycatch estimates (which include no measure of precision) currently available for the German Baltic region, the percent of porpoise bycatch in the western Baltic lies within a range of 1.78% to 17.94% of the local population. To increase the precision of bycatch rates, more detailed bycatch estimates for this region are needed. Nevertheless, the results indicate that bycatch is a major threat to harbour porpoises throughout the western Baltic Sea.

INTRODUCTION

The harbour porpoise *Phocoena phocoena* inhabits temperate to cold waters throughout the northern hemisphere and is the only cetacean species resident in the Baltic Sea (Berggren 1994, Kinze 1994, Berggren & Arrhenius 1995a, b, Benke et al. 1998). The Baltic Sea is one of the world’s largest brackish water basins (Voipio 1981). It is connected to the Kattegat Sea through the Øresund Strait, the Great and the Little Belt. The term 'Baltic Proper' is used as formulated by Fonselius (1974) and includes the waters to the east of the Darss and Limhamn ridges with the Bothnian Sea forming the northern border. A number of studies on genetics, morphology and contaminant load of porpoises indicate that several subpopulations of harbour porpoises occur in the Skagerrak-Kattegat Seas, the Belt Seas and the Baltic Proper (Kinze 1985, Andersen 1993, Börjesson & Berggren 1997, Wang & Berggren 1997, Berggren et al. 1999). Porpoises summering in the area east of the Darss and Limhamn ridges probably belong to a different population than the animals occurring in summer in the western Baltic Sea (Kiel and Mecklenburg Bights) (Tiedemann et al. 1996, Huggenberger et al. 2002).

Surveys have shown densities of 0.644 ind. km^{-2} in the Belt Seas (stratum I’ in Hammond et al. 2002). In contrast, the density and range of porpoises are believed to be much reduced in the Baltic Proper (Andersen 1982, Skóra et al. 1988, Määttänen 1990, cf. Koschinski 2002). The reasons for this are unclear. Possible causes have been discussed by a number of authors (e.g. Berggren 1994, Kinze 1994, Teilmann & Lowry 1996, Koschinski 2002) and include the commercial hunting of porpoises (e.g. in Poland and Denmark) that ended after the Second World War, high numbers of bycatch, increased mortality during severe ice winters and general habitat degradation (Skóra et al. 1988, Kinze 1994), as well as impaired health status when compared with other subpopulations (Siebert et al. 2001, 2006, Wünschmann et al. 2001). The impaired health status may be caused by high concentrations of contaminants (e.g. Bruhn et al. 1999, Siebert et al. 1999, Beineke et al. 2005, Das et al. 2006b).

One of the probable causes for the apparent failure of the Baltic Proper porpoise to recover lies in the continuing bycatch in fisheries. The incidental mortality in fishing gear is well documented for many parts of the Baltic Sea (e.g. Skóra et al. 1988, Christensen 1991, Skóra 1991, Berggren 1994, Kinze 1994, Kock & Benke 1996). However, the impact of the bycatch numbers on porpoise populations can only be determined when reliable abundance estimates are available. The aim of the present study was to determine the abundance of harbour porpoises and to evaluate the effect of bycatch in the southwestern Baltic Sea.

MATERIAL AND METHODS

Study area

The study area in the southwestern Baltic Sea reached from the German coastline north to the Danish islands. The area was divided into three strata (E: 4,696 km², F: 7,248 km², G: 10,990 km²) (Fig. 1). One survey stratum could usually be surveyed within 1 d (5 to 9 flying hours).

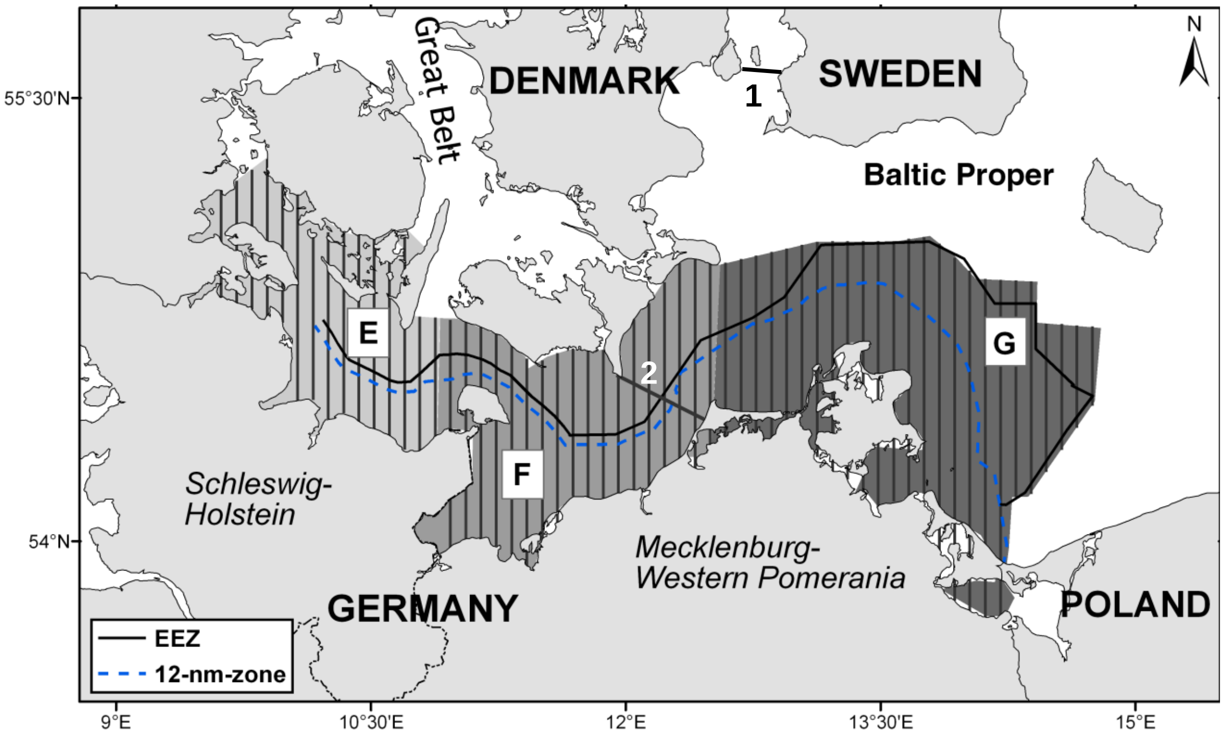

Figure 1: Study strata for aerial surveys in the southwestern Baltic Sea. North-south transect lines in strata E, F and G are indicated by solid grey lines. Transect lines are equispaced at intervals of 6 km. 1: Limhamn ridge; 2: Darss ridge. EEZ: Exclusive Economic Zone

Survey Design and Data Acquisition

Surveys were carried out following standard line-transect methodology for aerial surveys (Hiby & Hammond 1989, Buckland et al. 2001). The first survey was conducted in July 2002, the last survey in June 2006. Surveys were flown along a predetermined, systematic set of parallel transect lines with a random starting point, superimposed on the study area. The direction of transects was north-south to follow depth gradients, in order to minimise variance in encounter rate (Buckland et al. 2001). To ensure an adequate chance of harbour porpoise sightings, surveys were only conducted during good weather conditions with good visibilities (>3 km) and a sea state according to the Beaufort scale of ≤3.

The aircraft used was a high-wing two-engine Partenavia 68, equipped with bubble windows, flying at an altitude of 183 m (600 feet) with a speed of 167 to 186 km h^{-1} (90 to 100 knots). Data collection was based on the 'VOR' software designed by Lex Hiby and Phil Lovell and described in Hammond et al. (1995). Every 2 s the aircraft's position and time (to the nearest second) were recorded automatically onto a laptop computer connected to a GPS. Sighting information and details on environmental conditions were entered by a third person, the data recorder. Sea state (according to the Beaufort scale), glare, cloud cover (parts of eight), turbidity (judged visually on a scale of 0 [clear water with several meters of visibility] to 2 [very turbid water with no visibility under the surface] and subjective sighting conditions ('good', 'moderate' or 'poor') were entered at the beginning of each transect and whenever any environmental condition changed. Sighting data were acquired by two observers located at the bubble windows left and right of the aircraft. Sighting data included declination angle measured from the aircraft abeam to the porpoise group, group size, presence of calves, behaviour, swimming direction, cue and reaction to the survey plane. The perpendicular distances from the transect to the group were later calculated from aircraft altitude and declination angle.

The aircraft surveyed using the 'racetrack' method, which involves some doubling-back to re-survey previously flown transect segments for the estimation of effective strip width (ESW; Burnham et al. 1980). The synchronous recording of GPS data, abeam times and declination angles allows the positions of pods sighted on the first and second sweeps of the plane ('overflights') to be calculated. When deciding which of the pods seen on the first and second overflights were duplicates, the likelihood of these observed positions can be maximised with respect to (1) the parameters of models for the distribution of intervals between successive pods; (2) the succession of a pod's near-surface and diving phases; (3) its horizontal displacement between the times it comes abeam of the first and second overflights and (4) the probability of it being detected as a function of its perpendicular distance from the aircraft.

However, as it is impossible to determine which pod sightings on the first and second overflights are duplicates, it is necessary to sum the likelihood over all possible pairings. Some of the sighting times from the two overflights are too far apart to be duplicates. The remaining sightings form groups within which pairs of sightings from the first and second overflights may or may not be of the same pod. A recursive code was used to generate all possible pairings of sightings within each group (including the special case of no duplicates at all). These arrangements form an exhaustive set of mutually exclusive events so that the probability for the observed sighting positions equals the sum of the probabilities for each possible arrangement. In this way we calculated the likelihood for the data on each section of the survey conducted under consistent conditions; the log likelihood for the entire survey was obtained as the sum of the log likelihood for each section. Further details of the race-track method and the analyses are described in Hiby & Lovell (1998) and Hiby (1999).

Synchronous recording of GPS data and sighting conditions allows the sighting locations to be assigned to sections of effort completed under consistent conditions (good and moderate) and, hence, allows the estimates of ESW appropriate to those conditions to be applied to those sections. The large number of free parameters involved in estimating ESW meant that it was not possible to derive estimates for >2 levels of sighting conditions. Subjective assessment of 'good' and 'moderate' conditions, assessed separately to the left and right of the transect, was chosen to define the sections completed under consistent conditions.

Data analysis

Only transects flown in 'good' or 'moderate' conditions were considered in the analysis. Detection curves and estimates of ESW were found to be similar under similar conditions in different years so aerial survey data from 2002 to 2006 were pooled to provide an estimate of ESW for good and for moderate conditions.

Investigation of possible school size-bias indicated that no such bias was present. The mean school size was therefore estimated using the mean of the observed school sizes separately within each stratum.

Animal abundance in stratum *v* was estimated using a Horvitz-Thompson-like estimator as:

$$\hat{N}_v = \frac{A_v}{L_v}\left(\frac{n_{gsv}}{\hat{\mu}_g} + \frac{n_{msv}}{\hat{\mu}_m}\right)\bar{s}_v \qquad (1)$$

where A_v is the area of the stratum, L_v is the length of transect line covered on-effort in good or moderate conditions, n_{gsv} is the number of sightings that occurred in good conditions in the stratum, n_{msv} is the number of sightings that occurred in moderate conditions in the stratum, $\hat{\mu}_g$ is the estimated total effective strip width in good conditions, $\hat{\mu}_m$ is the estimated total effective strip width in moderate conditions and $\bar{s}_v$ is the mean observed school size in the stratum.

Group abundance by stratum was estimated by $\hat{N}_{v(group)} = \hat{N}_v / \bar{s}_v$. Total animal and group abundances were estimated by

$$\hat{N} = \sum_v \hat{N}_v \text{ and } \hat{N}_{(group)} = \sum_v \hat{N}_{v(group)} \qquad (2)$$

respectively. Densities were estimated by dividing the abundance estimates by the area of the associated stratum. Mean group size across strata was estimated by $\hat{E}[s] = \hat{N} / \hat{N}_{(group)}$.

Coefficients of variation (CV) and 95% confidence intervals (CI) were estimated by a non-parametric bootstrap test (999 replicates) within strata, using transects as the sampling units. The variance due to estimation of ESW was incorporated using a parametric bootstrap procedure that assumes the ESW estimates in good and moderate conditions to be normally distributed random variables. For each bootstrap pseudo-sample of transect lines, a bivariate lognormal random variable was generated from a distribution with a mean and a variance-covariance matrix equal to those estimated by Hiby (1999), i.e.

$$\hat{\mu} = (0.153, 0.054), \text{ and } \hat{\Sigma} = \begin{pmatrix} 0.0452^2 & 0.000721 \\ 0.000721 & 0.0162^2 \end{pmatrix}. \qquad (3)$$

This was used as the ESW for the pseudo-sample. The 95% CIs were calculated using the percentile method.

RESULTS

In the study period from 2002 to 2006, 43 surveys were conducted: 12 in stratum E, 18 in stratum F and 13 in stratum G. Combined survey effort for all strata was 32,448 km; the total number of sightings was 363 and the total number of animals was 516. An overview of all sightings in the study area is given in Fig. 2.

The selected detection function, using Akaike's information criterion (AIC), was a hazard rate model with sea state, turbidity, subjective sighting condition and observer as covariates providing the best fit. Using this functional form Hiby (pers. comm.) estimated a total ESW (x 2, including g(0)) to be 0.153 km (SD = 0.0452) under good conditions and 0.054 km (SD = 0.0162) under moderate conditions, with estimated covariance of 0.000721. The g(0) values were thus 0.37 for good sighting conditions and 0.14 for moderate sighting conditions. The resulting half-strip widths (excluding g(0)), thus, are 0.207 km in good and 0.193 km in moderate sighting conditions.

Density (ind. km^{-2}), CIs and CVs were calculated for each survey and are listed in Table 1. The survey in July 2002 showed densities of >1 porpoise km^{-2} in stratum G, caused by a fairly high number of aggregated sightings within a small area on the Oder Bank in the Pomeranian Bight. Such an occurrence of porpoises could not be confirmed after 2002, although coverage of the stratum was high. When excluding this unusual outlier, stratum G showed the lowest sighting rates, as well as estimated densities of <0.06 porpoises km^{-2}.

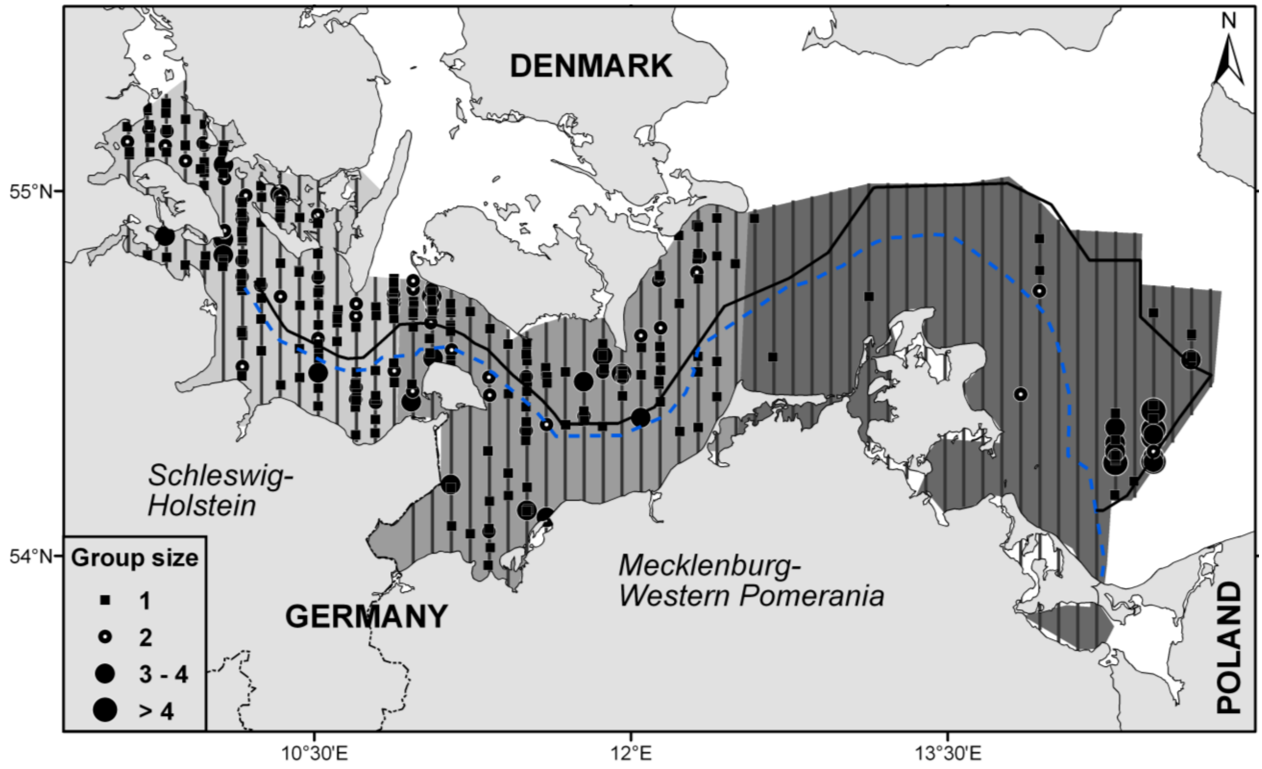

Figure 2. Overview of all tracklines covered and harbour porpoise sightings made in the study area. The area between the dashed and solid lines indicates the EEZ of Germany.

A survey of the entire Baltic Sea study area was considered to be complete, when (1) all three strata were surveyed within a period of 25 consecutive days and (2) representative coverage of the transect lines in good or moderate conditions was achieved.

Ten surveys met these criteria, and we were able to estimate abundance for March 2003, March/April 2005, April 2006, May (2005 and 2006), June (2003 and 2005), July 2004 and September (2004 and 2005). The resulting abundance estimates are listed in Table 2. In March 2003, the abundance estimate was lowest with 457 individuals. For all other studies, the abundance estimates for the overall study area varied between 1,635 and 4,610 individuals.

Table 1. Survey dates, survey effort and number of harbour porpoise sightings and animals. Mean group size and estimated density are given for each survey. CV: Coefficient of variation, CI: Confidence interval

Survey date (dd-mm-yy)	Effort (km)	No. of sightings	No. of ind.	Mean group size	Density (ind. km^{-2}) (95%CI low-high)	CV
Western Baltic (Kiel Bight): stratum E						
28-08-02	387	5	9	1.80	0.152 (0.00–0.42)	0.65
22-03-03	732	1	1	1.00	0.009 (0.00–0.40)	1.12
28-06-03	503	21	26	1.24	0.367 (0.17–0.80)	0.39
18-07-04	474	4	5	1.25	0.132 (0.02–0.35)	0.61
04-09-04	611	13	15	1.15	0.206 (0.09–0.47)	0.40
20-03-05	727	3	5	1.67	0.100 (0.00–0.37)	0.98
22-05-05	794	48	61	1.27	0.636 (0.30–1.35)	0.37
19-06-05	787	35	42	1.20	0.422 (0.18–0.96)	0.43
03-09-05	647	8	15	1.88	0.256 (0.08–0.59)	0.48
16-04-06	702	16	24	1.50	0.249 (0.06–0.60)	0.53
13-05-06	757	3	3	1.00	0.026 (0.00–0.07)	0.59
10-06/11-06-06	701	11	12	1.09	0.186 (0.07–0.43)	0.45
Total	**7822**	**168**	**218**			
Western Baltic (Mecklenburg Bight): stratum F						
15-08-02	659	7	9	1.29	0.113 (0.00–0.38)	0.81
05-09-02	559	2	3	1.50	0.035 (0.00–0.10)	0.72
30-10-02	316	3	3	1.00	0.138 (0.01–0.38)	0.64
10-12-02	553	2	3	1.50	0.100 (0.00–0.30)	0.73
20-03-03	571	2	5	2.50	0.057 (0.00–0.21)	1.05
17-06/18-06-03	735	0	0	–	0 (–)	–
01-08-03	432	7	11	1.57	0.254 (0.05–0.69)	0.59
16-07/18-07-04	675	12	16	1.33	0.178 (0.07–0.41)	0.41
02-09-04	935	16	28	1.75	0.218 (0.09–0.48)	0.42
16-01/03-02-05	643	0	0	–	0 (–)	–
13-04-05	548	1	1	1.00	0.034 (0.00–0.12)	0.99
13-05-05	1043	24	31	1.29	0.224 (0.08–0.52)	0.45
03-06-05	862	14	16	1.14	0.121 (0.02–0.38)	0.68
06-09-05	578	12	14	1.17	0.207 (0.02-0.49)	0.54
15-01/16-01-06	607	0	0	–	0 (–)	–
19-04/24-04-06	929	6	7	1.17	0.064 (0.01–0.18)	0.64
10-05/15-05-06	1123	24	33	1.38	0.236 (0.09–0.55)	0.45
11-06/12-06-06	681	26	28	1.08	0.345 (0.15–0.80)	0.45
Total	**12449**	**158**	**208**			
Baltic Proper (Pomeranian Bight): stratum G						
12-07-02	726	32	84	2.63	1.016 (0.06–3.19)	0.73
05-11-02	465	0	0	–	0 (–)	–
11-12-02	493	0	0	–	0 (–)	–
21-03/28-03-03	1143	0	0	–	0 (–)	–
07-06/17-06-03	683	0	0	–	0 (–)	–
16-07/17-07-04	831	1	1	1.00	0.008 (0.00–0.03)	1.06
03-09-04	1147	0	0	–	0 (–)	–
14-04-05	647	2	3	1.5	0.058 (0.00–0.20)	0.84
11-05/12-05-05	1562	0	0	–	0 (–)	–
09-06-05	1595	1	1	1.00	0.004 (0.00–0.02)	1.07
05-09/07-09-05	1112	1	1	1.00	0.006 (0.00–0.02)	1.13
24-04 /25-04-06	861	0	0	–	0 (–)	–
10-05/11-05-06	912	0	0	–	0 (–)	–
Total	**12177**	**37**	**90**			

Table 2. Overall abundance estimates for the surveys in the total study area (strata E, F and G) of the Baltic Sea (95% Confidence interval (CI) and coefficient of variation (CV) both based on bootstrap estimates). Survey length indicates the time period (in days) in which the survey was completed. Calculation of bycatch rates per survey were based on an estimated bycatch of 82 (Rubsch & Kock 2004). n.a.: not available

Survey	Survey length (d)	Effort (km)	Abundance	CV	CI low	CI high	Percent bycatch (% bycatch rate for CI)
March 2003	8	2446	457	0.97	0	1632	17.94 (n.a.–5.02)
June 2003	21	1921	1726	0.39	778	3750	4.75 (10.54–2.19)
July 2004	2	1980	2001	0.39	916	4318	4.10 (8.95–1.90)
Sep. 2004	2	2693	2547	0.36	1312	5461	3.22 (6.25–1.50)
March - April 2005	25	1922	1352	0.61	230	3840	6.07 (35.65–2.14)
May 2005	11	3400	4610	0.35	2259	9098	1.78 (3.63–0.90)
June 2005	16	3244	2905	0.41	1308	6384	2.82 (6.27–1.28)
September 2005	4	2337	2763	0.41	1193	5902	2.97 (6.87–1.39)
April 2006	8	2492	1635	0.45	607	3560	5.02 (13.51–2.30)
May 2006	5	2792	1833	0.44	752	4225	4.47 (10.90–1.94)

DISCUSSION

Density and abundance

Few abundance estimates for the study area are available. In July 1994, the project SCANS (Small Cetacean Abundance in the North Sea and adjacent waters) estimated the abundance of harbour porpoises *Phocoena phocoena* in the North Sea and adjacent waters (Hammond et al. 2002). The abundance estimation for stratum X (Kiel Bight, a major part of stratum E in the present study) was 588 ind. (CV = 0.48) which corresponds to a density of 0.101 ind. km^{-2} (Hammond et al. 2002) and is similar to the density in the July 2004 survey of stratum E (Kiel Bight) which was estimated at 0.13 ind. km^{-2} (95% CI = 0.02–0.38).

Densities for stratum G (east of the Darss ridge) were very low, ranging from 0 to 0.008 ind. km^{-2} during all but two surveys (July 2002 and April 2005). In fact, in eight of the 13 surveys of stratum G no sightings were recorded despite considerable survey effort (Table 1). An aerial survey in July 1995 estimated an abundance of 599 ind. (CV = 0.57) for an area around the island of Bornholm (Hiby & Lovell 1996), which corresponds to a density of approximately 0.009 ind. km^{-2}.

During our July 2002 survey an unusually high number of porpoises were seen east of the island of Rügen in stratum G. The mean group size of 2.63 was the highest ever recorded during our surveys. The estimated density of 1.04 for stratum G is associated with a very large confidence interval (95% CI = 0.07–3.42) due to the patchy occurrence of the sightings which caused a high variation in sighting rates between transects (Table 1).

Stranded porpoises are collected routinely along the German coastline (Siebert et al. 2006). It is interesting to note that from 2003 to 2006, no porpoises were reported from the area east of Rügen (H. Benke, pers. comm.). However, in 2002, a total of five porpoises was found stranded or directly reported as bycatch by fishermen (H. Benke, unpubl. data). This unusually high mortality in the German part of the Baltic Proper might be linked to the short-term local increase in the abundance of porpoises. The reasons for such relocation are unclear, but could be related to a change in food availability.

Apart from this unusual event in July 2002, the density of porpoises declined from west to east during all other study months and years, with the highest densities in strata E and F and the lowest densities in stratum G. These findings are consistent with the results of the SCANS survey in 1994 (Hammond et al. 2002). A decrease in frequency of strandings and incidental sightings (Siebert et al. 2006) and in relative occurrence (Scheidat et al. 2004) along the German coast from Schleswig-Holstein to Mecklenburg-Western Pomerania in the east has also been reported. Additionally, the frequency of porpoise click detections on stationary hydrophones (T-PODs) was shown to decrease from west to east (Verfuss et al. 2007).

During ten surveys, all three strata were covered within 25 consecutive days allowing the estimation of overall abundance. In March 2003, only a few sightings were made and the resulting low abundance estimate was associated with a large CV. For the remaining surveys in spring, abundances were low with 1352 (March/April 2005) and 1635 (April 06) individuals. All remaining estimates from May to September ranged between 1726 and 2905 ind. and had largely overlapping confidence intervals. We found no obvious seasonal patterns in our data, but we did not sample from October to February. Verfuß et al. (2007) showed seasonality in porpoise click activity in the German Baltic Sea with the highest click activity recorded in spring and summer months.

Estimating bycatch rates

Rubsch & Kock (2004) provided the only available estimate of porpoise bycatch along the German Baltic coast. They included data from stranded bycaught animals and bycatch reported directly by fishermen, as well as data from interviews with the local fishing community from the years 1996 to 2002. Their conclusion was that on average 57 animals are caught in the German western Baltic Sea (corresponding to strata E and F) and 25 animals are caught in the German Baltic Proper (corresponding to stratum G) per year. Thus, when applying the total annual bycatch of 82 animals to our abundance estimates for porpoises in the German Baltic Sea, bycatch rates can be calculated for each of the overall surveys (Table 2).

The results indicate that the lowest annual bycatch rate is 1.78%. All bycatch rates calculated in this way exceed the recommendations for maximum sustainable bycatch of 1% in harbour porpoises given by the Bergen Declaration (ASCOBANS 2002) and by the International Whaling Commission (IWC 2000). It also exceeds the recommendation given in the Agreement on the Conservation of Small Cetaceans of the North and Baltic Seas (ASCOBANS) that total anthropogenic removal of than 1.7% must be considered unacceptable

(ASCOBANS 2000). When using the lower confidence limit of the abundance estimates, as a precautionary principle would require, all bycatch rates are >3.6%. A further point to note is that our abundance estimates included Danish waters, whereas the bycatch estimate by Rubsch & Kock (2004) did not include porpoises recorded on the Danish coast as bycatch. Therefore, these bycatch rates are likely minimum estimates. It is apparent that the aim to reduce bycatch rates to levels that would not risk a further decline or to allow the recovery of porpoise is not reached along the German coast.

Bycatch rates depend on many different factors, such as the fishing effort and method, the local abundance of porpoises, as well as their local distribution in relation to fishing activities. Thus, it is certain that bycatch will vary between seasons, as well as between years. The present estimates of bycatch for the western Baltic have no measure of precision. In the future, detailed studies on seasonal and regional differences in bycatch are needed, which could then be put into a relationship with abundance estimates on the same spatial and temporal scales. Independent observer schemes are considered the only way to obtain reliable quantitative bycatch estimates (Northridge 1996, CEC 2002); recommendations for the design of monitoring schemes and for the best practises are given by Northridge (1996). However, the application of these recommendation will be difficult, due to the large number of small fishing boats in the Baltic Sea area, that have little or no place for observers.

As described in the introduction, there is sufficient evidence to suggest that at least two different populations of porpoises occur in Baltic waters. The tentative demarcation line between these two populations lies in German waters. Our data show that, in most cases, the density of porpoises east of the Darss ridge was extremely low. A short-term migration of porpoises into this area (as probably seen in July 2002) can be considered an unusual event. In areas of very low densities, any visual survey will struggle to get reliable results: therefore, alternative monitoring methods, such as passive acoustics, need to be further developed and standardised. Berggren et al. (2002) have shown that porpoises from the subpopulation east of the Darss and Linham ridges (Baltic Proper) are bycaught at an unsustainable rate. Our results indicate that the fairly abundant animals of the western Baltic in the Kiel and Mecklenburg Bights face similar threats. Even though porpoise density is still fairly high compared to the Baltic Proper population, the estimated percentage of bycatch is cause for concern. It is also conceivable that the porpoise population in the western Baltic may depend on immigrants from other areas to maintain itself. If such a 'sink population' exists, the estimated bycatch rates might not be accurate until total abundance and bycatch for each particular population area have been estimated.

The effort of the aerial surveys between 2002 and 2006 was very high, resulting in reliable abundance estimates for the local populations of porpoises in the southwestern Baltic Sea. However, to estimate bycatch rates, it is very important to have access to equally reliable and precise bycatch numbers. None of the smaller fishing boats are covered by observer programs that are now implemented throughout the European Union (ICES 2007a), and thus it is doubtful that the data will be sufficient to estimate bycatch of porpoises in Baltic waters. The ASCOBANS recovery plan for harbour porpoises in the Baltic Sea (Jastarnia Plan) provides guidelines for the reduction of bycatch and proposes more research on porpoise population structure in the Baltic (ASCOBANS 2002). Potentially, these results could allow us to interpret the occurring bycatch on different temporal and spatial scales. This, in turn, would enable us to suggest the best measurements polocies for mitigation and to increase the chances for survival of the harbour porpoise in all Baltic Sea waters.

ACKNOWLEDGEMENTS

The data presented were collected within the scope of projects funded by the following agencies: the German Federal Ministry of Food, Agriculture and Consumer Protection, the German Federal Ministry for the Environment, Nature Conservation and Nuclear Safety within the Investment-In-Future Program (ZIP) and the Federal Agency for Nature Conservation. We thank L. Hiby, P. Lovell and K. Kaschner for their help with data analyses. Our thanks go to P. Siemiatkowski from Sylt Air, L. Petersen from the Danish Air Survey and S. Hecke from FLM Kiel. The completion of the surveys was only possible through the enthusiastic dedication of the observers and navigators J. Adams, P. Börjesson, D. Risch, A. Gomez, H. Herr, I. Kuklik, K. Lehnert, L. Lehnert, M. Marahrens, C. Rocholl, T. Walter, U. Westerberg and S. Zankl. We thank H. Giewat for maintaining and managing the database and R. Mundry for programming several programs to facilitate statistical analyses. We also greatly appreciate the help of D. Borchers, L. Burt and F. Samarra, who provided the code for data and bootstrapping analyses. We thank L. Hiby and D. Borchers for reviewing the methods section of this paper. We also thank S. Koschinski for his comments on an earlier version of the manuscript.

Chapter II

Harbour porpoise abundance in the German North Sea – setting the scene

ABSTRACT

For the German North Sea, a baseline of robust abundance estimates for harbour porpoises (*Phocoena phocoena*) is needed in order to account for possible effects during the planned construction of offshore wind farms and other human activities. This study provides the first abundance estimates for the entire German EEZ and 12 nm zone. Aerial surveys, that covered waters in the German Exclusive Economic Zone (EEZ) and the 12 nautical mile zone of the North Sea were conducted from May 2002 to May 2006, following standard line transect methodology. In total, 43 surveys in four strata were completed; in all seasons except in winter. The aircraft, a Partenavia 68 equipped with bubble windows, covered 26,551 km of track lines within an area of 41,045 km^2. A total of 1,984 harbour porpoise sightings with 2,449 individuals was recorded on effort. The racetrack method was applied to account for missed animals on the transect line. Abundance estimates and corresponding confidence intervals (CI) were calculated for each stratum separately for each survey. The estimated abundance in the North Sea was highest in April/May 2005 with an estimate of 38,089 individuals (95%CI = 19,628-81,126) and in May/June 2006 with an estimate of 51,551 ind. (95%CI = 27,879-98,910). Porpoise density was found to be highest in late spring to early summer. Lower numbers were estimated in autumn, e.g. 10,849 ind. (95%CI = 5,544-22,202) in Oct./Nov. 2005. The highest density was found in stratum C throughout the year, followed by the offshore strata B and A, whereas lowest densities were estimated for stratum D. The seasonality in stratum D differed in comparison to the other studies as highest density was estimated for spring, lowest in summer and intermediate for autumn. The contribution of the estimated German stock to the putative sub-population 'Southern and Central North Sea' was determined to be 34% in summer and 7% in autumn.

INTRODUCTION

The harbour porpoise (*Phocoena phocoena*) is a small odontocete inhabiting temperate to cold waters throughout the northern hemisphere (Gaskin 1984) and is the only cetacean species found regularly in the German North Sea (Reijnders 1992, Benke et al. 1998, Scheidat et al. 2004, Siebert et al. 2006). Due to its occurrence, mainly but not exclusively, in coastal waters the porpoise is threatened by a variety of anthropogenic impacts (e.g. Kaschner 2001, Scheidat & Siebert 2003), including by-catch in fishery (Kock & Benke 1996, Vinther 1999, Lockyer & Kinze 2003, Vinther & Larsen 2004, Scheidat et al. in press) and habitat degradation due to chemical pollution (e.g. Aguilar & Borrell 1995, Jepson et al. 1999, Siebert et al. 1999, Beineke et al. 2007) as well as noise pollution (Richardson et al. 1995, Lucke et al. 2008).

To address concerns on human impacts, the protection of harbour porpoises was made the subject of several international agreements and conventions in EU waters (e.g. Convention on the Conservation of Migratory Species (CMS), EU Habitats and Species Directive). The Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS), that entered into force in 1994, aims to maintain a favourable conservation status for small cetaceans.

Until recently, very little data existed on distribution and abundance of harbour porpoises in the German North Sea. Most information was based on results of the SCANS[1] survey from July 1994 (Hammond et al. 2002). In 1994, harbour porpoise abundance was estimated at 341,366 animals (95% CI = 260,000-449000) within an area of 1 mio. km^2. Eleven years later, in July 2005, SCANS II estimated abundance at 385,617 animals (95% CI = 261,266-569,153) which is higher than in 1994 but for a larger survey area (1.4 mio. km^2) (SCANSII 2008).

However, as large-scale surveys SCANS and SCANS II aimed at a synoptic coverage of a huge survey area. Concerning local porpoise abundance in the German Bight they are of limited value. At the same time no other surveys have ever been conducted that were designed to explicitly cover the complete Exclusive Economic zone (EEZ) and the 12 nm zone of Germany. In the beginning of the 90ies, several surveys were conducted in coastal areas off the island of Sylt only (Heide-Jørgensen et al. 1993, Sonntag et al. 1999, Siebert et al. 2006). The status

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[1] **S**mall **C**etacean **A**bundance in the **N**orth **S**ea and Adjacent Waters

of the offshore areas, however, remained unknown. Especially in these areas constructions are planned, as particular attention is being paid to the production of wind energy in offshore locations (BMU 2007). To be able to evaluate the effects of human impacts, such as the construction of wind farms, information on the status of harbour porpoises in German waters with respect to recent distribution and density is needed.

The objectives of this study were to obtain a complete picture of harbour porpoise abundance in the German Bight by performing dedicated line transect surveys (Buckland et al. 2001) over the entire area of the German North Sea. Surveys were repeated all year round during five consecutive study years in order to assess seasonal as well as annual variation. The results can be seen as a baseline for management decisions with respect to the proposed construction of wind farms or other human activities.

MATERIAL AND METHODS

Study area and survey design

The study area was divided into four strata (A: 3,903 km^2, B: 11,650 km^2, C: 13,668 km^2, D: 11,824 km^2) on the basis of prior knowledge and on logistical constraints (e.g. plane refuelling). The size of the total study area was 41,045 km^2 and included the German EEZ and 12 nm zone of the North Sea (Fig. 3). The survey design consisted of a grid of systemically spaced transect lines randomly superimposed on the study area. Transects were placed either in east-west or north-south direction (Fig. 3) to run perpendicular to water depth gradients, as recommended by Buckland et al. (2001). It was planned to cover all four strata four times a year in order to account for seasonal variability. A survey of the total study area was considered to be complete when a representative coverage of the transect lines in good or moderate conditions was achieved in a short period of time, i.e. in a maximum of 40 days.

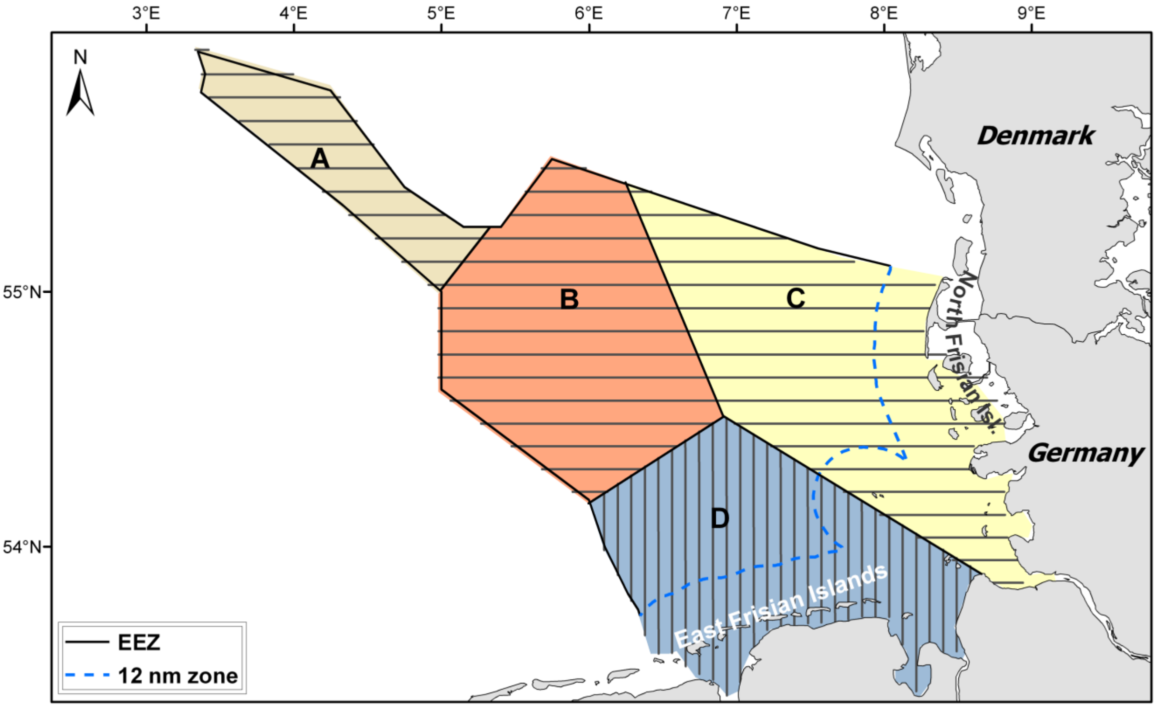


Figure 3. Study strata for aerial surveys in the south-eastern North Sea. East-west transect lines in strata A, B, C and north-south transects in stratum D are indicated by solid grey lines. Transect lines are equispaced at intervals of 10 km and 6 km (only in D). EEZ: Exclusive Economic Zone.

Aerial survey methodology

The methodology followed standard line transect distance sampling techniques, where the observer travels along a line, recording detected objects and the distance from the line to each object (Hiby & Hammond 1989, Buckland et al. 2001). Line transect sampling is one of the most widely used techniques for estimating the size of wildlife populations (Buckland et al. 2001). The idea behind line transect sampling is to estimate the density of the target species in strips sampled by surveying along a series of transects, and to extrapolate this density to the entire survey area. The calculated number is therefore an estimate of abundance in an defined area at a particular time (Evans & Hammond 2004).

Aerial surveys were flown at 100 knots (185 km/h) at an altitude of 600 feet (183 m) above the water surface in a Partenavia P68, a two-engine high-wing aircraft, equipped with two bubble windows to allow scanning directly underneath the plane. Details of the field protocol are provided by Scheidat et al. (in press).

During surveys for cetaceans it is never possible to detect all objects present on the transect line, which, however, is a central assumption in conventional line transect theory (Buckland et al. 2001). Two factors influence detection: i) availability bias and ii) perception bias (Marsh & Sinclair 1989, Laake et al. 1997). The availability bias describes the probability of an animal being available for detection (i.e., at or near the surface) whereas the perception bias incorporates the probability that an animal, when it is physical available for detection, is missed by the observer (e.g. due to fatigue, observer experience or environmental condition). To account for these bias, the 'racetrack' method, which involves some doubling-back to re-survey previously flown transect segments for the estimation of effective strip width (ESW; (Burnham et al. 1980) was applied during surveys (Hiby & Lovell 1998, Hiby 1999). From the time and position of the original as well as the re-sightings, the Hiby algorithm determines the probability that the sightings are the same group. Details of the racetrack method are found in chapter 1.

Data analysis

Only transects flown in good or moderate conditions were considered in the analysis. Detection curves and estimates of ESW were found to be similar under similar conditions in different years and aerial survey data from 2002 to 2006 were pooled to provide an estimate of ESW for good and for moderate conditions. Abundance estimates and associated confidence intervals were determined as described in Scheidat et al. (in press).

In order to evaluate the contribution of the German stock to the North Sea population, estimates of this study were related to the recent abundance estimate for the total North Sea (SCANSII 2008). The SCANSII blocks H, L, U, V and Y have been grouped to correspond as closely as possible to the borders of the putative sub-population 'Southern and Central North Sea'. Porpoises in the area south of a line between Bergen/Norway and St. Peterhead/Scotland and down to the Dutch coast are regarded as a single sub-population (IWC 2000).

RESULTS

In the study period from May 2002 to May 2006, 37 aerial surveys were conducted: 5 in stratum A, 9 in stratum B, 13 in stratum C and 10 in stratum D. Combined survey effort for all strata resulted in 26551 km; the total number of sightings was 1,984 and the total number of individuals was 2,449 (Table 3). Highest effort could be achieved in the coastal strata, C and D. Harbour porpoise densities exhibited significant seasonal variations in all strata and showed spatial differences across strata. Highest densities were estimated for stratum C in June/July 2003 (3.61 ind. km^{-2}) and lowest density for stratum D in October 2002 and November 2005 (both, 0.08 ind. km^{-2}). Mean school size varied from 1 to 2.57.

A coverage of all survey strata, i.e. in a synoptic attempt to cover all strata, could be achieved in six times. Due to unfavourable weather conditions it was not always possible to achieve a good coverage of stratum A. Thus, for better comparison between surveys, the six abundance estimates in Table 4 refer to data collected in strata B, C and D only. The abundance estimates ranged between 10,849 animals in Oct./Nov. 2005 (95% CI = 5,544–22,202) and 51,551 animals in May/June 2006 (95% CI = 27,879–98,910). This difference is significant (α=0.05) as estimate for Oct./Nov. 2005 is outside the 95% CI of May/June 2006.

Table 3. Survey dates, survey effort and number of harbour porpoise sightings and animals. Mean group size and estimated density are given for each survey. CV: Coefficient of variation, CI: Confidence interval

Survey date (dd-mm-yy)	Effort (km)	No. of sightings	No. of ind.	Mean group size	Density (ind. km^{-2}) (95%CI low-high)	CV
Doggerbank: stratum A						
28-05-02	93	2	4	2.0	0.80 (0.00–1.83)	0.56
30-05-03	135	30	41	1.37	1.99 (0.58–4.95)	0.51
04-08-03	384	30	38	1.27	0.81 (0.34–1.64)	0.40
22-04-05	390	5	9	1.80	0.15 (0.00–0.45)	0.69
23-11-05	241	9	10	1.11	0.60 (0.00–1.92)	0.79
Total	**1243**	**76**	**102**			
Offshore: stratum B						
20-07/03-08-02	414	27	32	1.19	1.06 (0.41–2.22)	0.44
01-10/15-10-02	631	7	18	2.57	0.24 (0.01–0.68)	0.75
25-03/23-04-03	575	45	55	1.22	0.62 (0.24–1.36)	0.43
13-07/04-08-03	327	30	43	1.43	1.02 (0.39–2.31)	0.46
28-07-04	895	56	65	1.16	0.58 (0.28–1.21)	0.39
03-05-05	646	33	40	1.21	0.72 (0.29–1.84)	0.48
16-08/22-08-05	835	29	40	1.38	0.39 (0.18–0.85)	0.39
03-10-05	590	15	16	1.07	0.18 (0.07–0.43)	0.48
11-05-06	826	59	63	1.07	0.55 (0.27–1.16)	0.38
Total	**5739**	**301**	**372**			
North Frisia: stratum C						
04-06/10-06-02	412	15	16	1.07	0.53 (0.14–1.33)	0.56
15-07/29-07-02	881	58	70	1.21	1.09 (0.37–2.56)	0.48
02-09-02	655	82	97	1.18	1.38 (0.48–3.13)	0.47
26-03-03	541	38	57	1.50	0.69 (0.33–1.45)	0.39
27-06/31-07-03	875	278	358	1.29	3.61 (1.66–7.33)	0.37
22-07-04	912	149	231	1.55	2.31 (0.90–4.75)	0.44
09-09-04	678	31	43	1.39	0.68 (0.30–1.46)	0.40
07-11/11-11-04	659	19	20	1.05	0.47 (0.19–1.01)	0.42
28-04-2005	1056	130	151	1.16	1.25 (0.68–2.46)	0.34
25-07-05	588	68	86	1.26	1.06 (0.40–2.24)	0.42
21-09-05	808	51	80	1.57	0.83 (0.33–1.87)	0.44
17-11/18-11-05	1045	27	37	1.37	0.58 (0.28–1.17)	0.36
10-05/12-05-06	1045	308	315	1.07	2.84 (1.54–5.39)	0.32
Total	**10155**	**1254**	**1561**			
East Frisia: stratum D						
17-06/18-06-02	980	25	42	1.68	0.32 (0.14–0.67)	0.42
01-10/02-10-02	708	5	9	1.80	0.08 (0.00–0.25)	0.71
02-09/30-09-04	1012	30	37	1.23	0.27 (0.10–0.59)	0.44
01-11/07-11-04	733	20	25	1.25	0.43 (0.12–1.03)	0.53
03-05-2005	775	53	62	1.17	1.07 (0.19–3.18)	0.66
15-06/16-06-05	1577	11	12	1.09	0.09 (0.03–0.22)	0.48
13-09-05	709	11	13	1.18	0.14 (0.04–0.30)	0.46
22-11-05	977	4	4	1.00	0.08 (0.00–0.22)	0.71
15-04/21-04-06	1117	141	156	1.11	1.46 (0.70–3.12)	0.38
02-05-06	826	53	54	1.02	0.55 (0.24–1.11)	0.37
Total	**9414**	**353**	**414**			

Table 4. Overall abundance estimates for the surveys in the total study area (strata B, C and D) of the North Sea (95% Confidence interval (CI) and coefficient of variation (CV) both based on bootstrap estimates). Survey length indicates the time period (in days) in which the survey was completed. Proportion of German stock on North Sea population has been estimated. Estimates of North Sea population are based on SCANSII blocks H, L, U, V and Y (SCANSII 2008).

Survey	Survey length (d)	Effort (km)	Abundance	CV	CI low	CI high	% North Sea population
Sep. - Oct. 2002	43	1995	22562	0.44	9112	49850	14.8
March - April 2003	30	1296	17556	0.37	8791	36231	11.5
April - May 2005	5	2476	38089	0.38	19628	81126	25.0
Aug. - Sep. 2005	36	2352	17618	0.38	8786	36574	11.6
Oct. - Nov. 2005	50	2612	10849	0.36	5544	22202	7.1
May 2006	10	2696	51551	0.32	27879	98910	33.9

DISCUSSION

This study achieved the first abundance estimates for harbour porpoises in the entire German EEZ and 12 nm zone. There now exist robust baseline estimates of abundance that can be used to evaluate anthropogenic impacts in the German North Sea.

It was possible to conduct a high number of successful surveys in the course of five study years. The estimates for the total study area are all robust as CVs are low. Although it was thought to estimate abundance for the total study area only when strata have been covered within 40 consecutive days, an exception was made for the survey in Oct./Nov. 2005 as the coverage has been very good and as data for the autumn months were scarce. No survey between December and February resulted in a good coverage of strata due to unfortunate weather conditions and, thus, no estimate could be provided for winter.

It was found that the abundance in the German North Sea was highest in May/June 2006 with an estimate of 51,551 animals (%CV = 32) and in April/May 2005 with an estimate of 38,089 animals (%CV = 38). Thus, highest numbers were found from end of April to June. Significant lower numbers were estimated in autumn, e.g. 10,849 animals (%CV = 34) in Oct./Nov. 2005. When comparing individual strata it was found that highest porpoise density occurred in stratum C throughout the year, followed by the offshore strata B and A whereas lowest densities were estimated for stratum D. The seasonality in stratum D differed in comparison to the other studies: here, highest density was estimated for spring, lowest in summer and intermediate for autumn.

Between 2002 and 2004, Thomsen et al. (2007) surveyed a 2,600 km^2 area in the central German Bight, which corresponds to the south-eastern part of stratum B in this study. Estimated densities ranged between 0.14 and 1.54 ind. km^{-2} and were in the same range as estimated in this study. No apparent seasonal trend was found (Thomsen et al. 2007). In the present study, however, stratum B showed a clear seasonality with increasing densities in spring, highest in summer and lowest in autumn.

When estimating the importance of the German stock in relation to the North Sea population, based on estimates of the SCANSII survey in summer 2005, a high proportion of up to 34% could occur in German waters during summer. In autumn, when abundance is lowest, 7% of the North Sea (summer) population are found in German waters. There are no abundance estimates available for the neighbouring countries, the Netherlands and Denmark; besides areas covered by the SCANS and SCANSII surveys. It is thus difficult to evaluate the significance of this proportion. However, highest density of all 16 blocks were estimated for the SCANSII block U, that covered German waters in large parts. The comparison between SCANS and SCANSII revealed no difference in the abundance of harbour porpoises in 1994 and 2005. However, in 2005 the average density in survey blocks north of 56°N was approximately half the density estimated in 1994, and the average density in survey blocks south of 56°N in 2005 was approximately twice the density estimated in 1994. Both these differences are significant at the 5% probability level (SCANSII 2008). In the present study, an increase in density in the southernmost stratum D in May 2005, April 2006 and May 2006 has been observed and further underlines the findings from SCANSII. In addition, the southern neighbouring countries, The Netherlands, Belgium and northern France, were reporting an increase in harbour porpoise strandings and sightings (Camphuysen 2004, Kiszka et al. 2004). The reasons for this large distribution shift from the north to the south are unknown but it is suspected that, in turn, major distributional shift of prey species could be responsible (SCANSII 2008).

This study is a valuable start to improving our knowledge of harbour porpoise occurrence and density in the German North Sea. Continued effort, however, is of the essence. Abundance must be monitored in the future to detect changes in numbers early. As the building of the first offshore windmill farm in German waters is approaching, it will be necessary to monitor animal distribution closely in order to follow possible shifts in distribution and abundance. Areas of highest harbour porpoise densities found in Europe have been identified in our waters and Germany shares the responsibility for the conservation of this species.

ACKNOWLEDGEMENTS

The data presented were collected within the scope of projects funded by the following agencies: the German Federal Ministry of Food, Agriculture and Consumer Protection, the German Federal Ministry for the Environment, Nature Conservation and Nuclear Safety within the Investment-In-Future Program (ZIP) and the Federal Agency for Nature Conservation. We thank L. Hiby, P. Lovell and K. Kaschner for their help with data analysis. Our thanks go to P. Siemiatkowski from Syltair, L. Petersen from the Danish Air Survey and S. Hecke from FLM Kiel. Completion of the surveys would have been impossible without the enthusiastic effort of the observers and navigators J. Adams, P. Börjesson, D. Risch, A. Gomez, H. Herr, I. Kuklik, K. Lehnert, L. Lehnert, M. Marahrens, C. Rocholl, T. Walter, U. Westerberg and S. Zankl. We would like to thank H. Giewat for managing the database.

Chapter III

Seasonal distribution shifts of harbour porpoises and wind farm developments in the German North Sea

ABSTRACT

The seasonal distribution of harbour porpoises in the German North Sea was investigated, hot spot areas were identified and the proportion of porpoises potentially affected by the imminent construction of offshore wind farms was estimated. Data were collected during dedicated aerial surveys conducted year-round between 2002 and 2006 following line transect methodology. Survey effort amounted to 44,739 km during which a total of 5,121 harbour porpoises was detected, including 258 calves. The data suggest that porpoises move to distinct areas on a seasonal basis as their biological requirements change. They move into German waters in early spring, reach maximum numbers in early summer and move out of the area in autumn. Important aggregation zones were detected in offshore waters: in spring, two hot spots, Borkum Reef Ground and Sylt Outer Reef (SOR) were identified as key foraging areas. In summer, only the large hot spot SOR persisted, causing a strong north-south density gradient. In autumn, porpoises were more evenly distributed. Most mother-calf pairs were observed during spring and summer in the area of SOR, underlining its importance as foraging area when reproductive costs are high. Spatial overlap exists between important areas for porpoises and areas where offshore wind farms are licensed or planned. The proportion of the national stock possibly exposed to the construction noise of 18 licensed wind farms was estimated applying different scenarios. Within a 20 km zone of responsiveness - as worst case scenario - nearly 40% of the harbour porpoise national stock could be affected during construction.

INTRODUCTION

The approaching construction of offshore wind farms will possibly impact on marine mammals (Madsen et al. 2006). Major disturbances arise from construction activities like pile-driving and drilling, increased vessel traffic, pollutant emissions and stirred-up bottom sediments (Carstensen et al. 2006). Thorough knowledge of the distribution, density and seasonal movements of species present in the area is one key to assess and mitigate potential effects of such human activities.

Beyond doubt, the global response to climate change must involve a move to carbon-free sources of electricity (Schiermeier et al. 2008). However, if plans are realised the construction of wind farms could be the greatest human impact in the North Sea next to the fisheries (Hüppop et al. 2006). The offshore wind industry in Germany has the most ambitious plans in the world: by June 2008, 18 wind farms were approved and 47 more farms are in the approval process in the North Sea (Fig. 4; BSH 2008). The construction sites show spatial overlap with the designated Sites of Community Importance (SCI), according to the Habitats Directive of the European Union (Fig. 4), and it is therefore imperative to obtain baseline data on marine mammals in order to assess the risk of, and mitigate for, the impact of construction and compare with a post construction situation.

The south-eastern North Sea is an area with a wide range of human activities (OSPAR Commission 2000, Ducrotoy et al. 2000, Halpern et al. 2008). The harbour porpoise *Phocoena phocoena* (Linnaeus, 1758) is the most common cetacean in the North Sea (Hammond et al. 2002) and the only cetacean species found regularly in German waters (Scheidat et al. 2004, Siebert et al. 2006). There is evidence that harbour porpoise abundance in the south-eastern North Sea has declined since the 1940s (Smeenk 1987, Reijnders 1992, Camphuysen & Leopold 1993). Various pressures were identified, such as by-catch (Kock & Benke 1996, Vinther & Larsen 2004), prey depletion (Smeenk 1987) or habitat degradation due to chemical pollution (Siebert et al. 1999, Wünschmann et al. 2001, Beineke et al. 2005, Das et al. 2006a, b). Recently, an increase in sightings as well as strandings has been observed in the southern North Sea (Camphuysen 2004, Kiszka et al. 2004, SCANSII 2008).

The harbour porpoise depends on sound for orientation and foraging (Teilmann et al. 2002, Verfuss et al. 2005) and is very sensitive to different types of acoustic signals. Underwater noise is produced both during construction, operation and dismantling of offshore wind farms. Especially during piling hydraulic hammers create noise with considerable sound power levels (Nedwell & Howell 2004). The same holds for dismantling if foundations are blasted of the sea floor after 20 years of operation (Nedwell & Howell 2004). The potential effects on harbour porpoises are hearing loss (either temporary or permanent), masking of natural noise, increased stress levels or abandonment of important habitat (Tougaard et al. 2003, Carstensen et al. 2006, Nowacek et al. 2007, Weilgart 2007, Lucke et al. 2008). Disturbance is the most commonly observed effect of noise on cetaceans (Richardson et al. 1995). It could be significant if animals were to be displaced from areas that are particularly important for feeding, reproducing or care of young (National Research Council (NRC) 2005). Still the population-level impacts of such disturbance are largely unknown and would probably depend on the scale of the disturbance

A lack of basic data on harbour porpoise distribution, both in space and in time, has been acknowledged in the study area. To this point, two kinds of dedicated surveys have assessed the abundance and distribution of harbour porpoises: (1) two large-scale surveys conducted in summer, covering the complete North Sea and adjacent waters in a synoptic way (July 1994 and July 2005 during the SCANS surveys; Hammond et al. 2002, SCANSII 2008) and (2) surveys of selected smaller areas for case studies, conducted during recent years on a monthly basis (Thomsen et al. 2006, 2007) or in the 1990s only in summer (Heide-Jørgensen et al. 1993, Siebert et al. 2006). Thus, surveys either provided a snapshot of a precise time interval or a detailed picture for a fraction of the area of interest.

The aim of this study was to obtain a spatially and temporally explicit picture of harbour porpoise distribution in the German North Sea in order to assess the overlap with the planned construction of offshore wind farms and the potential impact to this species. Therefore, dedicated aerial line transect surveys were conducted throughout the year during five consecutive years. The seasonal distribution patterns of harbour porpoises were assessed and focal areas identified. Spatial overlap of preferred areas with offshore wind farms was investigated and the proportion of the national stock possibly affected by the imminent construction of offshore wind farms in the German North Sea was estimated. This study provides the baseline for future comparisons.

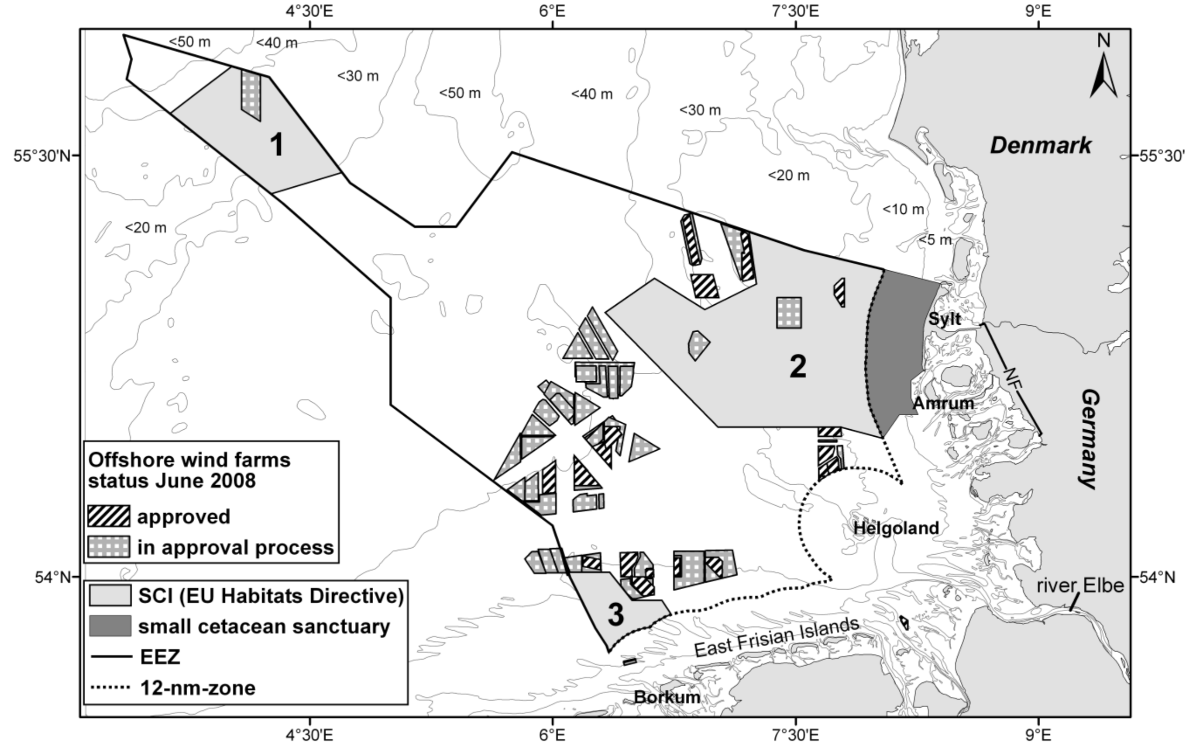


Figure 4. Offshore wind farm sites (BSH 2008) and sites of marine protected areas in the German North Sea. SCI (Sites of Community Interest): 1-Doggerbank, 2-Sylt Outer Reef and 3-Borkum Reef Ground. Bathymetry is indicated by isobaths. NF = North Frisian Islands

MATERIALS AND METHODS

Study area

The study area (41,045 km^2) ranged from 3° to 9°E and from 53°30’ to 56°N and included the exclusive economic zone (EEZ) and the 12 nautical mile zone of the German North Sea (Fig. 5). The bottom topography of this shelf sea region is characterised by the shallow Wadden Sea (<10 m) and the post glacial valley of the river Elbe (>30 m), which extends from the Elbe estuary to the northwest and passes the Dogger Bank on the eastern side of Dogger Tail End (Becker et al. 1992). The hydrography is characterised by tidal currents and substantial gradients in salinity that are formed by the encounter of different water bodies. Two distinct water masses occur: the Continental Coast water mass is characterised by low salinity and low clarity and the Central North Sea water mass by high salinity, high clarity and a thermal stratification in summer (Becker et al. 1983).

Data collection

Aerial surveys were conducted year round between 20 May 2002 and 10 October 2006. The area was divided into four geographic strata (Fig. 5, Table 5). One survey stratum could usually be surveyed within one day (5 to 9 flying hours).

The methodology followed standard line transect distance sampling techniques (Buckland et al. 2001). Surveys were flown along a systematic set of parallel transects (Fig. 5) placed either in east-west or north-south direction to run perpendicular to water depth gradients as transect direction should not parallel physical or biological features (Buckland et al. 2001).

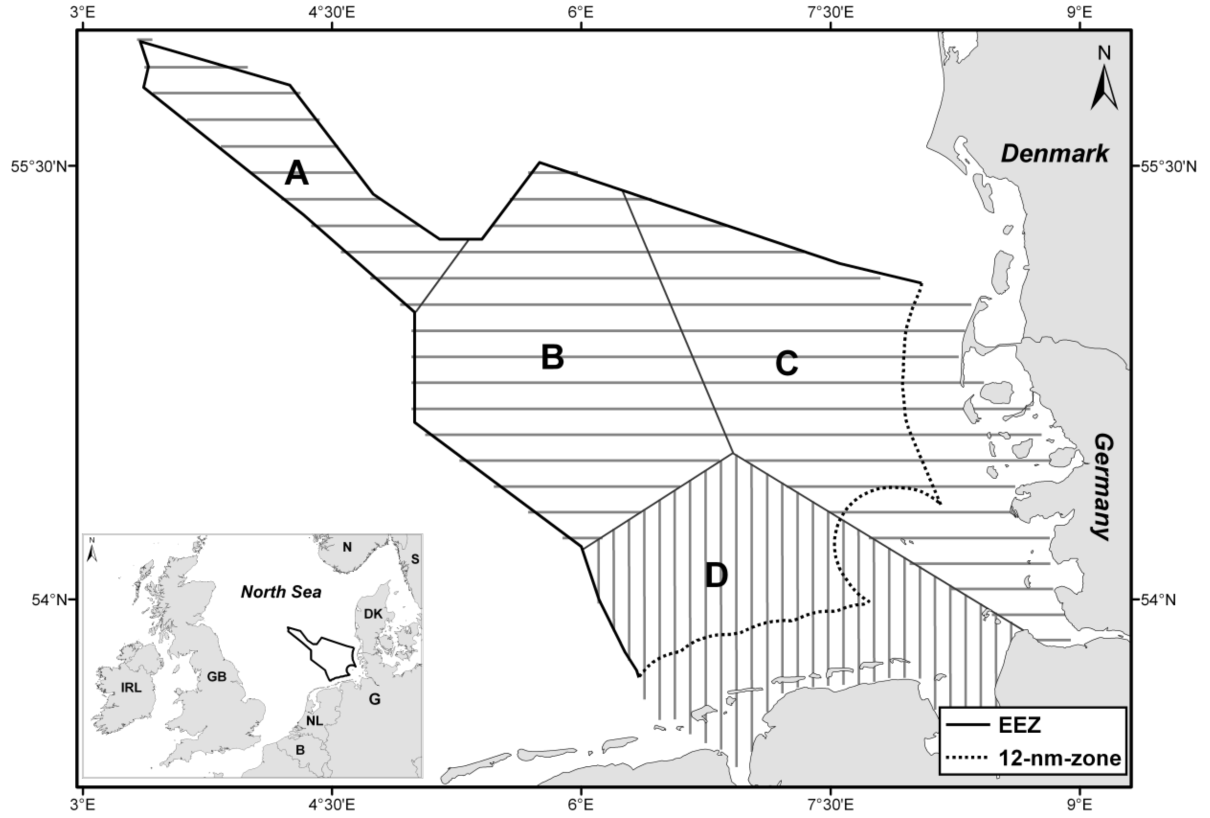


Figure 5. Study area in the SE North Sea. Transects were equispaced: 10 km in strata A to C and 6 km in stratum D.

Surveys were flown at 100 kn (185 km/h) at an altitude of 600 ft (183 m) in a Partenavia P68, a two-engine, high-wing aircraft equipped with two bubble windows to allow scanning directly underneath the plane. The survey team consisted of two observers, one data recorder (navigator) and the pilot. Communication between all team members was ensured via the intercom system. Sighting data were acquired simultaneously by the observers, each positioned on one side of the aircraft at a bubble window, scanning for animals with the naked eye. Observers rotated during breaks, i.e. every 2-3 hours. The navigator entered all reported data directly into a laptop computer interfaced with a Global Positioning System (GPS). The aircraft's position was stored every two seconds. Additionally, the start and end positions of the transect lines and the exact sighting positions were recorded.

Table 5. Survey design by geographic stratum.

Stratum	Area (km^2)	n transects	Total transect length (km)	Mean duration of transect (min)
A	3903	11	396	12
B	11650	15	1165	26
C	13668	18	1369	25
D	11824	28	1912	22
Total	**41045**	**72**	**4842**	**21**

A calm sea surface and good visibility are crucial during fieldwork as the harbour porpoise is one of the smallest cetacean species and shows an elusive behaviour at the water surface (Teilmann 2003). Surveys were only conducted during Beaufort sea states 0 to less than 3, and with visibilities greater than 5 km. Environmental conditions were recorded at the beginning of each transect and updated with any change. Conditions included (1) Beaufort sea state, (2) water turbidity (judged visually: 0 - clear water with several meters of visibility to 2 - very turbid, no visibility under the surface), (3) percentage of cloud cover, and for each observer side, (4) glare (angle obscured by glare and intensity of glare) and (5) the observer's subjective view of the likelihood that, given all of the conditions, they would see a harbour porpoise should one be present. These subjective conditions could be either good, moderate or poor.

Data recorded for each harbour porpoise sighting included: (1) angle of declination to the group, (2) estimated group size and (3) number of calves (individuals were classified as calves if their size was less than half the size of the adult). The declination angle was measured by hand-held inclinometers when the group passed abeam of the plane.

Other marine mammal species recorded during the study included seals (370 sightings, no species identification possible), white-beaked dolphin and minke whale (2 sightings each).

Data analysis

All data recorded in poor conditions were excluded from subsequent analysis. To estimate the proportion of animals missed on the transect line, the racetrack data collection method was used (Hiby & Lovell 1998, Hiby 1999). This method allows estimation of effective strip width (ESW; Buckland et al. 2001), taking into account both the availability and the perception bias (Marsh & Sinclair 1989, Laake et al. 1997). Synchronous recording of GPS and sighting conditions allowed the assignment of sighting locations to sections of effort completed under consistent conditions. Hence, the estimates of esw appropriate to those conditions could be applied to those sections. The above mentioned subjective assessment of good and moderate conditions, assessed separately to left and right of the transect, was chosen to define the sections completed under consistent conditions. Further details of the application of the racetrack method are described in Scheidat et al. (in press).

Encounter rates in each stratum were calculated by the ratio s_k/L_k, where s_k is the total number of sightings and L_k is the total number of km spent on effort in each survey month k, respectively. In order to test for significant differences in encounter rate between the four strata, generalised linear models (GLM, McCullagh & Nelder 1989) were fitted. The Bonferroni correction was applied to lower the alpha value (to 0.0125) in order to account for multiple pair-wise comparisons (Zar 1998).

For the spatial analysis in ArcGIS 8.3 a grid with a resolution of 10x10 km was created, corresponding to the inter-transect spacing. Grid cells with a survey effort lower than 10 km were excluded from analysis, resulting in a single set of representative cells per season. The overall number of harbour porpoises (n_i) and the effectively searched area (EA_i) per grid cell i were determined and mean density estimates were calculated by the ratio n_i/EA_i.

EA_i was computed by:

$$EA_i[km^2] = esw_L * L_i + esw_R * L_i$$

with:

esw_L = esw, left side of the plane [km]

esw_R = esw, right side of the plane [km]

L_i = effort in good or moderate conditions [km]

Similarly, the seasonal density per stratum *j*, that is used in the wind farm scenarios (see below), was estimated by the ratio n_j/EA_j.

Latitude and longitude were assigned to the centre of each grid cell when testing for inter-annual and seasonal differences in spatial distribution.

Statistical analysis

Data of the five study years (2002-2006) were pooled when collected in the same season. Seasons were defined as spring (March-May), summer (June-Aug.) and autumn (Sep.-Nov.). The winter months (Dec.-Feb.) were excluded due to low search effort. Prior to pooling generalised additive models (GAM) were fitted (Hastie & Tibshirani 1990, Wood 2006) to detect any significant spatial variation between data collected in the same season but during different years. Harbour porpoise density values were normalised applying the Z-transformation (Zar 1998), before running the GAMs. A quasi error distribution was found to be appropriate. Two different approaches were chosen (following Wood 2006): First, assuming a symmetric distribution in two study years but same season, all data were pooled and harbour porpoise density was modelled using the locational covariates latitude and longitude. Secondly, an asymmetric model was applied assuming differences in spatial distribution patterns. Both models were compared by an analysis of variance (ANOVA). If there was no significant difference between both models, no difference between the two tested years was assumed. In all seasons, all but two pairings showed no significant spatial variation. The number of pairs without significant variation totals four in spring and autumn respectively and eight in summer. The lower number of pairs to be tested in spring and autumn are due to no coverage in strata A, B and D in spring 2004 and autumn 2006. Pooling was appropriate as the main aim of this study was to identify focal areas that are used by harbour porpoises on a regular basis.

In addition, generalised additive mixed models GAMM (Lin & Zhang 1999, Wood 2006) were applied to examine latitudinal density gradients during the three seasons. Longitude was added as random effect factor.

For GAM and GAMM the package 'mgcv' (Wood 2006) was used in R v.2.6.2 (R Development Core Team 2008).

Wind farm scenarios

In order to estimate the proportion of porpoises potentially affected during the construction of the 18 licensed wind farms, a few different scenarios were considered. According to Richardson's zones of impact around an anthropogenic sound source (Richardson et al. 1995) buffers were created around each of the 18 wind farm sites. If buffers overlapped, only combined buffers were used. If buffers extended to Danish or Dutch waters, this area was subtracted as no data on porpoise density were collected outside German borders. The radii of buffers were chosen based on existing knowledge. In scenario 1 no buffer was applied. In scenario 2 a small buffer of 2 km was applied in order to account for effects close to the constructions. In scenarios 3 and 4 (10 and 15 km buffer) empirical values from Horns Rev (Denmark), the first offshore wind farm in the North Sea, were applied. At Horns Rev behavioural reactions (e.g. displacement) of animals were recorded in 10-15 km away from the construction site. As no visual surveys or acoustic data logging were conducted at greater distances than 15 km (Tougaard et al. 2003), it can be assumed that 15 km represents a minimum radius in which behavioural effects can be attributed to the construction. This, and results of a recent TTS (temporary threshold shift) study conducted in Denmark (Lucke et al. 2008), is the reason why it is hypothesised in scenario 5 that behavioural reactions of harbour porpoises could be triggered in even larger distances, up to 20 km away from the sound source (K. Lucke, pers. comment).

The underlying temporal assumption is that all 18 wind farms will be constructed at the same time. These projects represent pilot phases where about 80 turbines (5-6 MW each), erected on steel multipile foundations, will be built in each field. In following planned expansions, that goes along with an enlargement of the area affected not taken into account here, the number of turbines will increase. In Horns Rev, it took between 0.5-2.5 hours to drive one pile into the bottom and it finally took 6 months until all 80 monopiles were founded (Tougaard et al. 2003).

To obtain an estimate of the number of harbour porpoises potentially affected by the construction a simplified approach was used: (1) the 18 pilot projects were assigned to the survey strata (B, C or D; see Fig. 5), for which seasonal densities were estimated, (2) densities were multiplied with the size of the area affected including various buffer zones, (3) the number of potentially affected individuals was related to the estimated abundance for the total study area ('German stock') and affected proportion calculated.

RESULTS

Survey effort and harbour porpoise sightings

During 91 survey days, 44,739 km of transect lines were surveyed within the 41,045 km^2 study area. A total of 4,169 sightings of harbour porpoise groups were made on-effort. The number of sighted individuals totalled up to 5,121, including 258 calves (Table 6). In most survey strata, encounter rates (ER) were highest during the period May to August (Fig. 6). In stratum D values were highest in April, May and September. ERs in stratum C were significantly higher ($p < 0.0125$) than ERs in stratum B in May, June and August. ERs in stratum C were significantly higher ($p < 0.0125$) than ERs in stratum D in all months but in April and November.

Due to stable weather conditions highest survey effort could be achieved during the summer months. However, it was also possible to obtain a good coverage in spring and autumn (Table 6). In spring and summer more than 60% of the transects were surveyed in Beaufort sea states 0 and 1. In autumn, surveys were conducted in sea states 0 and 1 for 43% and in sea state 2 for 36% of the survey time (Table 7).

Group sizes ranged from one to six. However, single individuals were sighted in 87% of all recordings in spring and in 77% in summer and autumn respectively, resulting in an overall median group size of 1 in all seasons.

Table 6. *Phocoena phocoena*. Effort summary per season and main aerial survey results in good and moderate conditions. Data from the study years 2002 to 2006 were pooled. EA: effective search area

Season	Flight days	Track line length (km)	EA (km^2)	No. of groups	No. of indiv.	No. of claves
Spring	28	14838	1637	1932	2225	28
Summer	38	17128	1711	1826	2355	199
Autumn	25	12773	1185	411	541	31
Total	**91**	**44739**	**4533**	**4169**	**5121**	**258**

Table 7. Length (km) and percentage of track lines surveyed in Beaufort sea state conditions 0-3. Data from the study years 2002 to 2006 were pooled.

	Spring		Summer		Autumn	
Beaufort	Track line	%	Track line	%	Track line	%
0	1616	10.9	1288	7.5	353	2.8
1	9694	65.3	9723	56.8	5219	40.5
2	2996	20.2	4662	27.2	4638	36.3
3	532	3.6	1455	8.5	2564	20.1

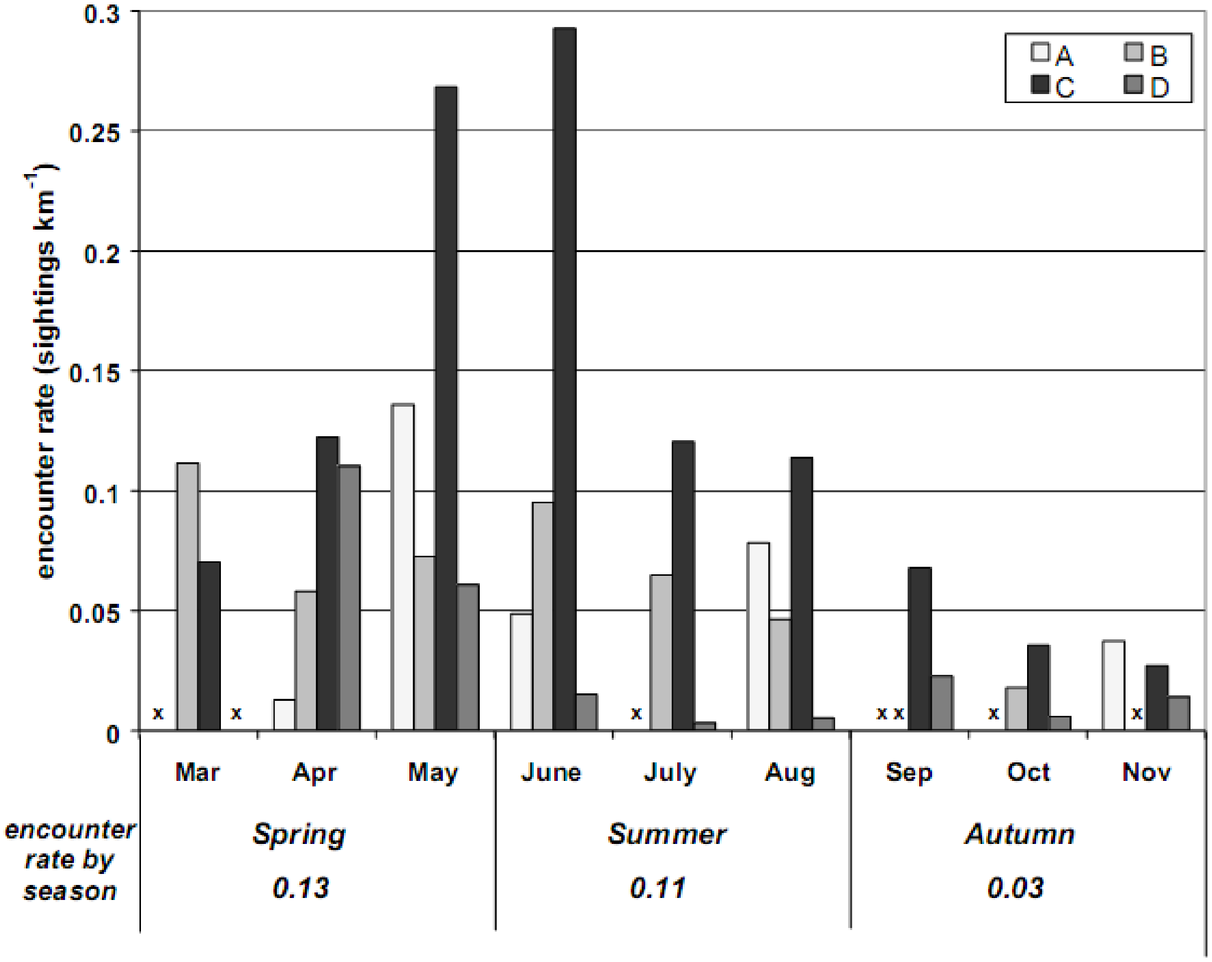


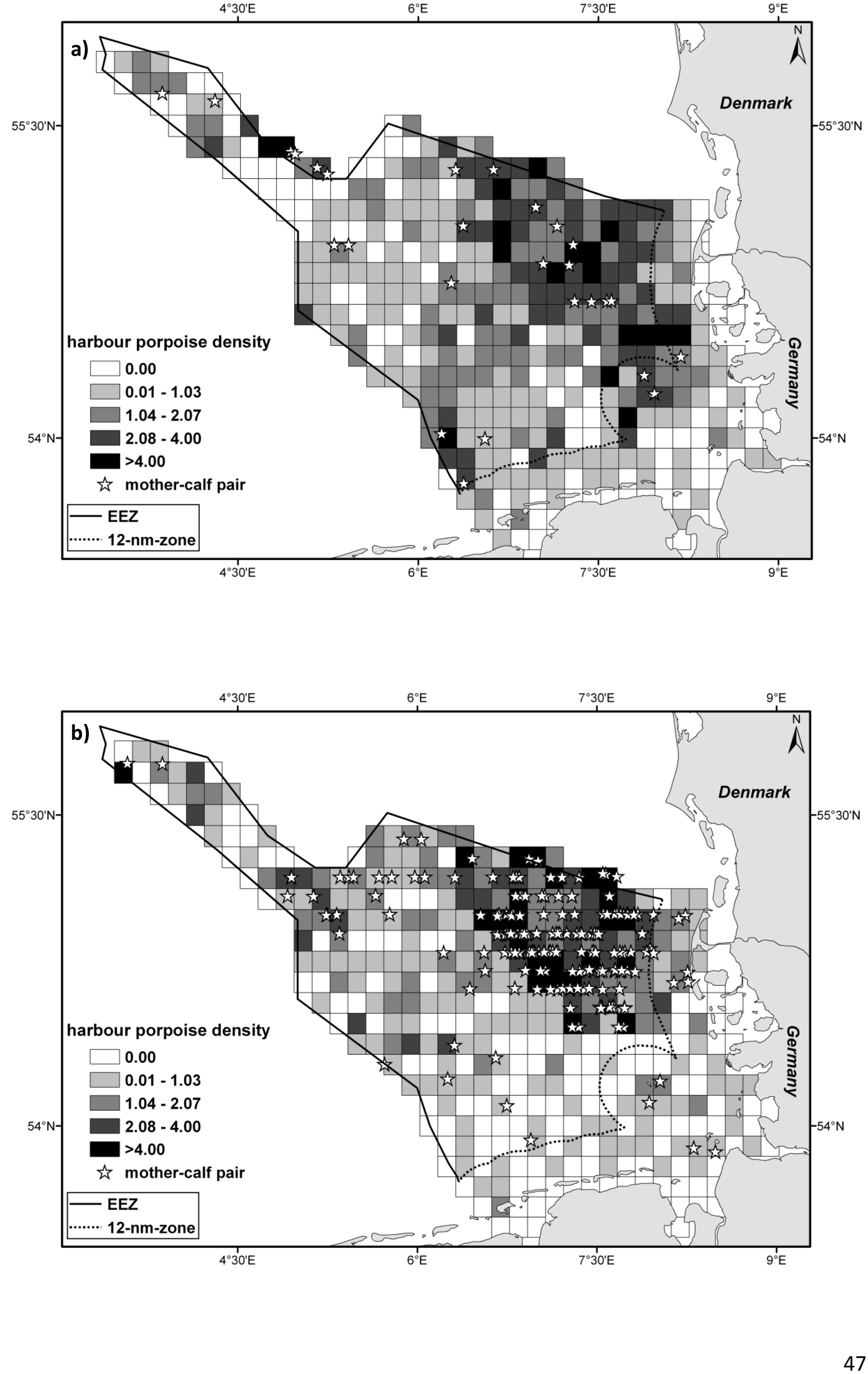
Figure 6. ***Phocoena phocoena.*** **Encounter rate from March to November, separated by survey stratum (A-D, see Fig. 5). Encounter rates by season are indicated as well. Data from the study years 2002 to 2006 were pooled. x: no effort.**

Seasonal changes in distribution

In spring, harbour porpoise distribution was highly clumped. Two hot spot areas of particularly high densities could be detected (Fig. 7a). Porpoise densities reached highest values in the north-eastern part of the German EEZ in an area from 40 to 130 km west of the North Frisian islands of Amrum and Sylt, in the Sylt Outer Reef (SOR, see Fig. 4). This large aggregation zone was consistently found during all study years. The second, but smaller aggregation, was located in the south-western part of the German EEZ, approx. 60 km offshore the East Frisian Islands, in an area called Borkum Reef Ground (BRG, see Fig. 4). This hot spot could be observed from 2004 onwards and only in spring. In addition, high densities were observed in the vicinity of the island of Helgoland and on the submerged sandbank Dogger Bank (stratum A) in the most westerly part of the EEZ. Most mother-calf pairs were found in the areas of higher densities, SOR having 46% of the total observed, 25% on the Dogger Bank and 11% around BRG and around Helgoland.

In summer, a distinct north-south density gradient was observed (Figs. 7b & 8). This was mainly due to large aggregations of harbour porpoises that were detected in the north-eastern part of the German EEZ in contrast to much lower densities south of 54°30’N. This gradient was also detected in the distribution of the mother-calf pairs: more than 84% were sighted in the area of SOR.

In autumn, porpoises were more evenly dispersed throughout the study area (Fig. 7c). There was no specific aggregation area. Low-density cold spots were detected instead. Overall highest densities occurred in the area of SOR and near the island of Helgoland. The sighting rate was lowest in comparison to spring and summer (Fig. 6), indicating a migration of animals out of the German Bight during autumn. The harbour porpoises remaining in the area were sighted mainly (90% of all sightings) in waters east of 6°30’E but the coverage in the offshore strata (namely in area A) was poor. In comparison to the summer months a higher number of porpoises was detected in the waters around the East Frisian Islands, although the densities were lower than during spring. The majority (76%) of the 31 mother-calf pairs were found in the area of SOR.


a)
4°30'E
6°E
7°30'E
9°E
55°30'N
54°N
N
Denmark
Germany
harbour porpoise density
0.00
0.01 - 1.03
1.04 - 2.07
2.08 - 4.00
>4.00
☆ mother-calf pair
EEZ
12-nm-zone
b)
4°30'E
6°E
7°30'E
9°E
55°30'N
54°N
N
Denmark
Germany
harbour porpoise density
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EEZ
12-nm-zone

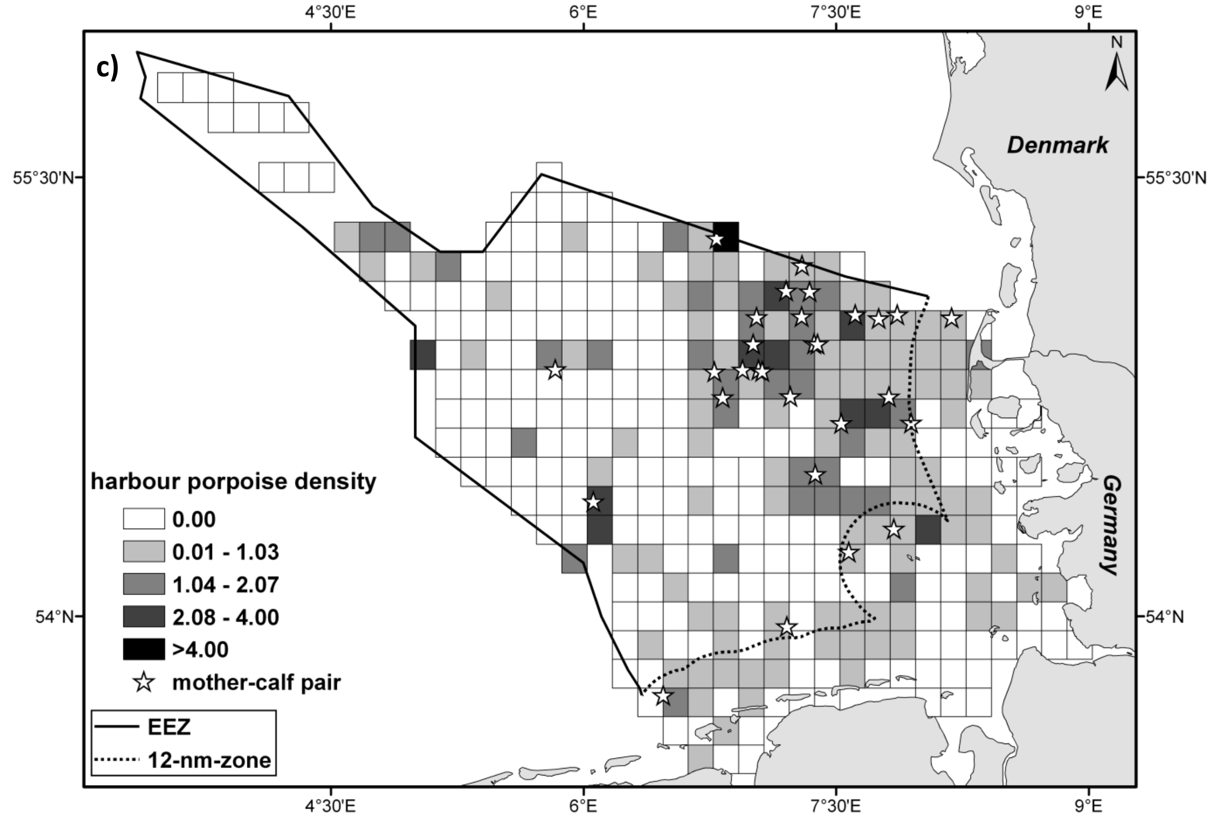

Figure 7 (a-c). ***Phocoena phocoena.*** **Spatial distribution of harbour porpoise density (ind. km^{-2}). Data from the study years 2002 to 2006 were pooled. Grid cell size: 10 x 10 km. a) spring (March-May), b) summer (June-Aug.), c) autumn (Sep.-Nov.)**

The results of the GAMMs confirmed significant ($p < 0.001$) spatial differences in latitudinal distribution (Fig. 8). In all three seasons a north-south density gradient was observed, that was most pronounced in summer.

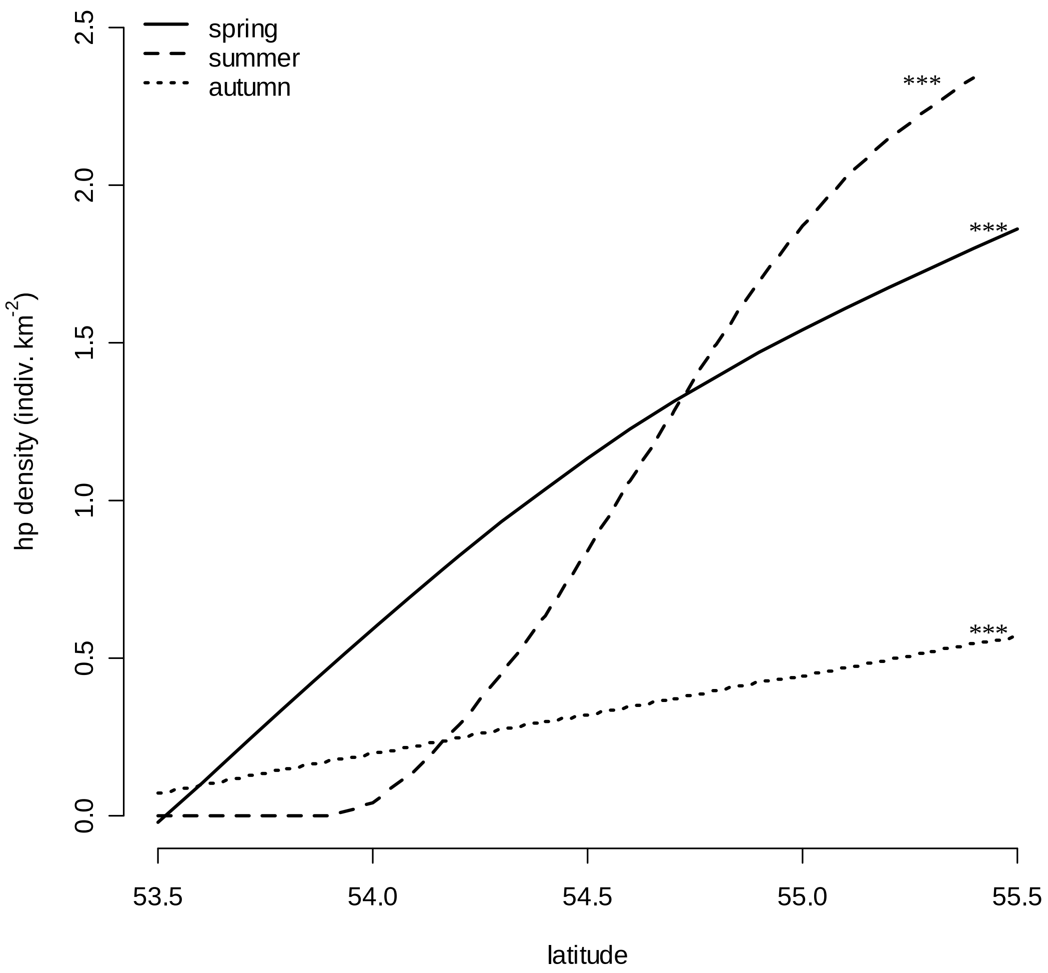

Figure 8. *Phocoena phocoena.* Fitted models (GAMM) show north-south density gradient. Data from the study years 2002 to 2006 were pooled. ***P < 0.001.

Effects of offshore wind farm construction

Table 8 summarises the different scenarios. The total area occupied by the 18 licensed wind farms in their pilot phases will encompass 730 km^2. In the first scenario, without any buffer, approx. 2% of the harbour porpoise national stock could be affected during construction. Within this close proximity to the sound source, individuals could suffer from hearing impairment (e.g. TTS, Lucke et al. 2008). The area affected by construction is largest in stratum C and as porpoise density is very high in this area, the estimated proportion of porpoises that could be exposed to the noise from the offshore constructions is highest in C for all scenarios in all seasons. The density in stratum D is highest in spring and autumn, therefore the proportion of porpoises affected in summer is likely to be low in D.

Table 8. ***Phocoena phocoena.*** **Estimated proportion of harbour porpoises that could be exposed to the noise from the construction of offshore wind farms (OWF) in the German North Sea. As buffers overlapped between survey strata when buffer radii are larger than 15 km, it was not possible to present results per stratum for scenario no. 5.**

Szenario (no.)	Stratum	Spring	Summer	Autumn	Area (affected by OWF) [km^2]	Zone of impact[1]	Reference
		% of national stock affected					
no buffer (1)	B	0.27	0.31	0.31	190	1,2,3,4	Lucke et al. 2008
	C	1.53	1.72	1.43	344		
	D	0.30	0.06	0.24	196		
	Total	**2.10**	**2.10**	**1.98**	**730**		
2 km buffer (2)	B	0.71	0.83	0.83	505	1,2,3	K. Lucke, pers. comm.
	C	4.27	4.80	3.99	959		
	D	0.84	0.17	0.68	550		
	Total	**5.82**	**5.81**	**5.49**	**2013**		
10 km buffer (3)	B	2.30	2.72	2.71	1645	1,2	Carstensen et al. 2006, Tougaard et al. 2003
	C	14.99	16.84	13.99	3364		
	D	3.09	0.64	2.50	2032		
	Total	**20.39**	**20.19**	**19.20**	**7041**		
15 km buffer (4)	B	3.05	3.59	3.59	2176	1,2	Lucke et al. 2008, Tougaard et al. 2003
	C	24.99	28.07	23.31	5608		
	D	5.31	1.10	4.29	3489		
	Total	**33.35**	**32.76**	**31.19**	**11273**		
20 km buffer (5)	**Total**	**36.27**	**39.98**	**37.61**	**13575**	1,2	K. Lucke, pers. comm.

[1] Zones of impact around an anthropogenic sound source (Richardson et al. 1995): (1) zone of audibility, (2) zone of responsiveness, (3) zone of masking, (4) zone of hearing loss, discomfort or injury

DISCUSSION

The data collected during this 5-year study provide year-round information on seasonal changes in harbour porpoise density and distribution. A consistency was shown for one of the identified hot spots: the Sylt Outer Reef (SOR) was a focal area in all study years and across all seasons. A lack of consistency was shown for the second (spring) hot spot in Borkum Reef Ground (BRG), that could not be detected before 2004. This study is important for all countries bordering the North Sea as information on seasonal movements and focal areas are provided and as possible impacts on porpoises during the construction of offshore wind farms were quantified. In the worst case scenario nearly 40% of the harbour porpoise national stock could possibly be affected during construction.

Hot spot areas

This study documented a patchy distribution with harbour porpoises showing clear preferences for several discrete areas. Although aerial surveys cannot provide information on behavioural patterns, the observed hot spots suggest that these are areas where prey availability is high. Other top predators, like seals, were recorded as well in the hot spots. Marine populations aggregate mainly during feeding, reproduction, protection from predators and migration (Palacios et al. 2006). Porpoises in the North Atlantic feed mainly on small shoaling fish species from both demersal and pelagic habitats (Santos & Pierce 2003). Recent analysis of harbour porpoise stomach content from the study area revealed that goby (Gobiidae), cod (*Gadus morhua*), sole (*Solea solea*), sandeel (*Ammodytes* sp.) and herring (*Clupea harengus*) are important constituents of the overall diet (chapter IV). Standardised fisheries data show that within the area of SOR the pelagic clupeids herring and sprat (*Sprattus sprattus*) are most abundant followed by the demersal fish species dab (*Limanda limanda*), whiting (*Merlangius merlangus*) and plaice (*Pleuronectes platessa*) (Ehrich et al. 2006). In BRG the same species are abundant, with the exception of whiting where highest densities occur in the northern areas of the German EEZ (Ehrich et al. 2006). Additionally, SOR seems to be an important habitat for sandeels as the area is targeted by the industrial fishery that generally starts at the beginning of April, yielding highest catches from May to July (ICES 2007b).

In spring, the two hot spots BRG and SOR seem to play an important role as key foraging areas from where porpoises spread out. In summer, the pronounced north-south density gradient could have been caused by animals moving from the south to the north. It might also be that harbour porpoises entered the area of SOR from the north. Indeed, Danish aerial surveys along the border to Germany in the North Sea, revealed a high density area about 50-100 km off the coast which complements the high density area found during our surveys in SOR (Teilmann et al. 2008). A similar area was detected during the SCANS II survey in July 2005, where the hot spot extended northwest across the Danish North Sea sector (SCANSII 2008). In autumn, porpoises seemed to start moving out of the study area. The described seasonal pattern is also reflected in data on strandings and incidental sightings (Siebert et al. 2006). Although a coverage of the total study area could not be achieved during winter, the few surveys in winter resulted in consistent lowest sighting rates, completing the annual cycle of distribution patterns.

The density of porpoises in the south-west increased in the course of the study period from 2004 onwards, mainly in spring. A second hot spot was registered in the area BRG. That could also explain the absence of spatial symmetry for two of the study years that were checked for pooling. At the same time the southern neighbouring countries, The Netherlands, Belgium and France, were reporting an increase in harbour porpoise strandings and incidental sightings (Camphuysen 2004, Kiszka et al. 2004). In fact, a return of harbour porpoises to Dutch coastal waters is reported after their virtual disappearance from the area in the early 1960s (Camphuysen 2004). A study in the area off Eastern Frisia and in parts of Dutch waters support the results, as an increase in sightings from February 2004 until the beginning of May 2004 was reported (Thomsen et al. 2006). Besides that, the SCANSII survey showed that in comparison to the SCANS survey from 1994, porpoise density estimated in the survey blocks north of 56°N was approximately half the density estimated in 1994, and density in survey blocks south of 56°N in 2005 was approximately twice the density estimated in 1994 (SCANSII 2008). As there was no difference in the overall abundance of porpoises in the North Sea in 1994 and 2005, it is thought that the geographical shift could be due to changes in distribution of harbour porpoises as response to distributional change of their prey (SCANSII 2008).

Occurrence of mother-calf pairs

The identification of areas where mating and calving occur might be important as this period is of special significance in the annual life cycle. However, in the case of smaller odontocetes, there is often no clear separation between feeding and breeding areas, as opposed to most of the mysticetes (Hindell 2002). The harbour porpoise is known to 'live in the fast lane', i.e. all reproductive and life history traits are accelerated during a short life span of about 10 years (Read & Hohn 1995). As female harbour porpoises are thought to be 'income breeders' (Sibly & Calow 1986, Read 2001) and reproductive costs are significant (Lockyer 2007), it is concluded that they must be able to continually locate areas, where prey species with high energy content are abundant. The harbour porpoise exhibits strong seasonality in the reproductive cycle (Börjesson & Read 2003) and the majority of births occurs from June 6 to July 16 in the study area (Hasselmeier et al. 2004), shortly before mating. Occurring in high densities could have advantages for locating mates. The return to particular grounds, maybe to those ones where foraging was successful in the previous year, might therefore be essential in order to meet mating partners but also to find enough food for the high energy demand of birth, mating and the first months of lactation (Lockyer et al. 2003).

Potential impact of offshore wind farms

The presented distribution patterns of harbour porpoises show considerable spatial overlap between preferred areas of porpoises and areas where offshore wind farms are licensed, most notably in the north-east and south-west of the study area. This is the first study that addressed the potential effects during construction and showed that - in the worst case - nearly 40% of the German national porpoise stock could be affected within the 20 km zone of responsiveness. However, for this scenario we assumed that all pile-driving in the 18 approved wind farm sites would occur in one year. This is not totally unrealistic, as according to statements of the various operators, first projects are scheduled to start construction in 2009, others follow in 2010/2011. If pile-driving is spread in a few years, a smaller percentage of porpoises could possibly be affected in each year. Although our approach of estimating the proportion exposed is simplified, it should be seen as pilot study that incorporates best knowledge available at the moment from the few existing offshore wind farms. It would have been biologically more meaningful to assess the significance of numbers exposed in relation to an abundance estimate for the North Sea population as a whole, by incorporating estimates of the recent SCANS II survey. However, for this approach one would also have to include all offshore activities and construction plans of all countries bordering the North Sea. This has been beyond the scope of this contribution.

Both, behavioural and physiological effects on porpoises could be expected during construction (Tougaard et al. 2003, Carstensen et al. 2006, Weilgart 2007). Porpoises displaced by construction activities would not be lost to the population but they might be displaced to less suitable areas. The absence of an obvious behavioural reaction would not yet prove the absence of a response but rather reflect the inability of measuring it. It was formerly assumed that animals that move away from disturbance do so because they are more affected than those that remain. However, recent studies suggest that departing animals may be the ones with sufficient condition to do so (Bejder et al. 2006, Beale 2007). Moreover, where disturbance is concentrated in or nearby critical habitat, animals may have no other option but to stay. An example of bottlenose dolphins (*Tursiops* sp.) in Australian waters showed that long-term population impacts of disturbance may occur without dramatic or even observable short-term reactions (Bejder et al. 2006).

It was not possible to include temporal scenarios at this stage as it is unknown for how long harbour porpoises will be affected. From the operating large wind farms Horns Rev (North) and Nysted (Baltic Sea) it is known that construction lasted 6-12 months. In Nysted, porpoises avoided the area to a large extent and this avoidance still persisted after two years of operation, however with indications of a slow, gradual recovery (Carstensen et al. 2006). Thus, it cannot be assumed that construction impacts are only short-term. Especially when considering the cumulative effects of a large number of wind power projects over time, there will be installations under construction at any given time (Madsen et al. 2006) as the actual plans in Germany clearly show.

Wind farms in the German EEZ require the approval of the Federal Maritime and Hydrographic Agency (BSH 2008). Authorisation has to be refused if the safety and easy flow of shipping is hindered or if the marine environment is endangered (Wustlich & Heugel 2006). Following legislation, a step-by-step expansion (pilot phase: maximum 80 turbines) is intended where the next step (enlargement of area) presupposes a positive result with regard to environmental impacts. During and after construction of the pilot phase the owner is obliged to carry out an effect monitoring according to guidelines of the BSH.

In any way, mitigation measures are widely used in order to minimise effects. These measures are mandatory in Germany, according to state of the art. Methods could include a soft-start/ramp-up procedure to allow animals to move away before the sound gets too loud (Richardson et al. 1995), air-bubble curtains to reduce the source level of the pile-driving noise (Würsig et al. 2000) or acoustic harassment devices AHD (like pingers, seal scarer) to 'scare' marine mammals from the vicinity of construction activity (Tougaard et al. 2003, Carstensen et al. 2006). However, some of these are controversial as they may lead to habituation (e.g. soft-start, AHD) or attract animals by initially weak sounds (Compton et al. 2008).

We would like to highlight the possibility of temporal and spatial restrictions following the precautionary principle. For the identified focal areas SOR and BRG the following suggestions arise: we recommend not to license the wind farm sites in approval process on the Sylt Outer Reef and advise that construction in the area of Borkum Reef Ground should not be carried out during spring, unless surveys showed that the spring hot spot has disappeared.

Finally, the potential cumulative effects of the construction of several wind farms in the range of the harbour porpoise has to be assessed strategically, and in certain areas through the collaboration of neighbouring countries. Other pressures to this species should also be taken into account, such as bycatch (main threat in the area), pollutants and food depletion. Future work should incorporate the assessment of significance to the population. This study is a first step towards the estimation of numbers potentially affected by the construction of wind farms. Although the data represent a good time series of data for any cetacean species in European waters covering a large area, a mobile species like the harbour porpoise might change its distribution quite dramatically within a decade (as SCANSII has shown) and consequently hot spots can move. Nevertheless, detailed baseline data on porpoise distribution were collected over a 5-year study period and provide a reasonable temporal window and may serve for any before-after comparison.

ACKNOWLEDGEMENTS

Data were collected under financial support of the German Federal Ministry for the Environment, Nature Conservation and Nuclear Safety (BMU; MINOS and MINOSplus projects), Federal Ministry of Food, Agriculture and Consumer Protection (BMELV) and the Federal Agency for Nature Conservation (BfN; project EMSON). We thank L. Hiby, P. Lovell and K. Kaschner for their help with data analysis, H. Giewat for managing the database and S. Adler for help with statistical analysis. Our thanks go to the pilots P. Siemi and K.-U. Breuel from Sylt Air, L. Petersen from the Danish Air Survey and S. Hecke from FLM Kiel. Completion of the surveys would have been impossible without the enthusiastic effort of the observers and navigators J. Adams, P. Börjesson, D. Risch, A. Gomez, H. Herr, I. Kuklik, K. Lehnert, L. Lehnert, M. Marahrens, C. Rocholl, T. Walter, U. Westerberg and S. Zankl. P. Schwemmer, K. Lehnert, H. Herr, F. Colijn, K. Lucke and three anonymous reviewers provided valuable comments on the manuscript.

Chapter IV

Modelling harbour porpoise seasonal density in relation to the German Bight environment

ABSTRACT

The harbour porpoise is an important top predator in the North Sea and as such an indicator species for its environment. There is growing demand for predictive models of porpoise distribution to support conservation and management plans. In this study, we used physical and biological parameters to predict porpoise density during different seasons in the German Bight. Sightings data were collected during dedicated aerial surveys conducted year-round between 2002 and 2005 following standard line transect methodology. Survey effort amounted to 38,720 km during which a total of 3,887 harbour porpoises were seen. Observed aggregations of porpoises shifted between seasons. We investigated differences in these seasonal hot spots in relation to several fixed (e.g. depth, slope) and dynamic (e.g. sea surface temperature, chlorophyll) predictors. We applied generalised additive models (GAM) and mixed models (GAMM) that, unlike GAM, explicitly account for potential spatial autocorrelation. Internal cross validation indicated that all models were robust. Besides, the successful model validation with an external data set, derived from the SCANSII survey, further underlines the robustness of the summer (GAM) model and enabled us to extrapolate our predictions to a more regional scale. The key habitat descriptors as selected by our models varied between seasons. Predictors explaining most of the variance were the hydrographical parameter 'residual currents' and proxies for primary production and fronts (chlorophyll and nutrients) as well as the interaction 'distance to coast/water depth'. Our comparison of GAM and GAMM outputs indicated that model predictions were very similar, however the GAM performed better. Our models provide important new information in understanding the determinants of harbour porpoise habitat in the North Sea and are a valuable tool to help managers address concerns about potential impacts from human activities.

INTRODUCTION

Ecological theory of species distribution modelling assumes that species distributions are determined at least in part by environmental variables, and that reasonable approximations for these variables can be estimated (Austin 2007). Predictive cetacean-habitat modelling is by now a powerful tool in marine science as it integrates heterogeneity in marine ecosystems and provides essential information for ecological studies, management purposes and the mitigation of anthropogenic impacts (Cañadas et al. 2005, Guisan & Thuiller 2005, Kaschner et al. 2006, Redfern et al. 2006). It is an effective method for understanding the processes that affect the interannual and seasonal variability in species distribution (Ferguson et al. 2006, Lea et al. 2006, Giannoulaki et al. 2008). Further, the incorporation of oceanographic variability can precise conventional abundance estimates by reducing the variance (Forney 2000, Hedley & Buckland 2004, Gómez de Segura et al. 2007).

The harbour porpoise (*Phocoena phocoena)* is one of the most common cetaceans in coastal waters of the northern hemisphere (Gaskin 1984, Hammond et al. 2002) and as such an important top predator and indicator species for its environment. It still remains unclear what environmental factors drive harbour porpoise distribution at both large and small scales in the south-eastern North Sea. However, there is a growing demand for predictive models of porpoise distribution to support conservation and management action to protect harbour porpoises in the North Sea, where the species might be affected by a wide range of human activities, including the recent progress of wind farm industries in offshore waters (OSPAR Commission 2000, Ducrotoy et al. 2000, Garthe & Hüppop 2004).

Although behavioural factors such as migration, predator avoidance and social interactions influence cetacean distributions (Redfern et al. 2006), many of the distribution patterns are determined by the response of cetaceans as predators foraging in a patchy prey resource environment (Karczmarski et al. 2000). This holds especially true for porpoises which, due to their small size and their distribution in temperate waters, have a high energy demand but only limited energy storage capacities (Koopman 1998). Thus, we can hypothesise that their pattern of movement will be strongly related to prey distribution. Unfortunately, the 'optimal' proximal gradient, such as prey density, is not available for the analysis at the required spatial resolution or at the necessary biological accuracy to be used for habitat prediction models. As prey availability is ultimately determined by physical and biological properties of the ocean (e.g. Maravelias et al. 2000a, b, Arnott & Ruxton 2002, Dulvy et al. 2008), we can use these indirect gradients or proxies to model the link between observation and environment. This approach is supported by a recent study demonstrating that models of dolphin habitat selection were more powerful if environmental variables were used as predictor variables rather than relying on prey data as explanatory variables (Torres et al. 2008).

While the ecological processes determining harbour porpoise distribution are still not well understood, our knowledge of factors found to influence porpoises has increased during the last years. Examples are (1) water depth and slope (Carretta et al. 2001, Hamazaki 2002, MacLeod et al. 2007, Kiszka et al. 2007), (2) sea surface temperature SST (Forney 1999), (3) thermocline gradient (Tynan et al. 2005), 4) salinity (Tynan et al. 2005), 5) island wake (Johnston et al. 2005), 6) frontal system (Skov et al. 2003) or 7) tidal flow (Goodwin 2008, Pierpoint 2008). However, species may have different habitat preferences in different geographic regions and investigations of environment correlates cannot be ready extrapolated beyond the original study area. Until now, no habitat prediction model has been developed for harbour porpoises in the German Bight.

It is known that porpoises exhibit seasonal variations in diet (Santos & Pierce 2003), and we can therefore expect the functional relationship between porpoise occurrence and the environment to change on a seasonal basis. With this study, we have the unique opportunity to analyse a large amount of porpoise sighting data, collected at a very high spatial and temporal resolution during three seasons of four consecutive study years using standard line transect aerial surveys (Buckland et al. 2001). Hence, we will be able to develop seasonal habitat models.

Generalised additive models GAMs (Hastie & Tibshirani 1990) are in widespread use to quantitatively explore species-habitat relationships when little is known about the underlying mechanisms responsible for generating the observations (Guisan et al. 2002). GAMs effectively address many of the statistical challenges associated with field survey data, like e.g. non-normally distribution of the response variable as well as non-linear and non-monotonic relationships between the response and the set of habitat variables (Jensen et al. 2005). However, survey data often display spatial autocorrelation (SAC), which means that values of variables sampled at nearby locations are not independent from each other

(Dormann 2007). Methods that ignore SAC (like the traditional GAM approach) could possibly overestimate the correlation between response and environmental variables (Ferguson & Bester 2002, Keitt et al. 2002, Hedley & Buckland 2004) or omit important variables during model selection (Keitt et al. 2002). Recent advances in the development of spatial generalised additive mixed models GAMM (Lin & Zhang 1999, Wood 2008) makes it possible to extend the GAM approach to account for autocorrelated data. In this study we applied non-spatial (GAM) and spatial (GAMM) models on the same data set, compared the model fit and associated errors.

We aim to identify possible physiographic, hydrographical and biological factors that influence harbour porpoise distribution during different seasons on a mesoscale resolution. Using identified predictors we want to develop robust seasonal habitat prediction models and test them with available data. Subsequently, we will further validate model predictions using an independent data set, originating from the SCANSII survey (SCANSII 2008).

MATERIALS AND METHODS

Study Area

Our study area is situated in the shallow south-eastern North Sea. We collected data on harbour porpoises mainly in the German EEZ and 12-nm-zone, whereas data on environmental properties were also compiled for an adjacent area (Fig. 9) as we aimed to predict harbour porpoise summer density on a regional scale. The bathymetry of the German Bight is characterised by the (1) shallow Wadden Sea (<10 m) with the estuaries of the large rivers Ems, Weser, Elbe and Eider, (2) the deep wedge-shaped post-glacial Elbe river valley (>30 m), that extends from the Elbe estuary to the northwest and passes the Dogger Bank on the eastern side of Tail End, and (3) the central part of the German Bight area, with depths between 40 and 60 m (Becker et al. 1992) (Fig. 9). The residual currents run generally in an anti-clockwise direction and transport the water masses of the inner German Bight in northern direction with a long term residual current of 5 cm/s (Becker et al. 1992). The hydrographical situation is complex and characterised by tidal currents and substantial gradients in salinity that are formed by the encounter of different water bodies. (Krause et al. 1986) classified three different types of fronts in the German Bight: a thermal, an up-welling and a salinity front due to the river runoff of the river Elbe. The thermal front (i.e. the boundary between the stratified and well-mixed water) is a seasonal, the up-welling front a transient and the river plume front a permanent phenomenon.

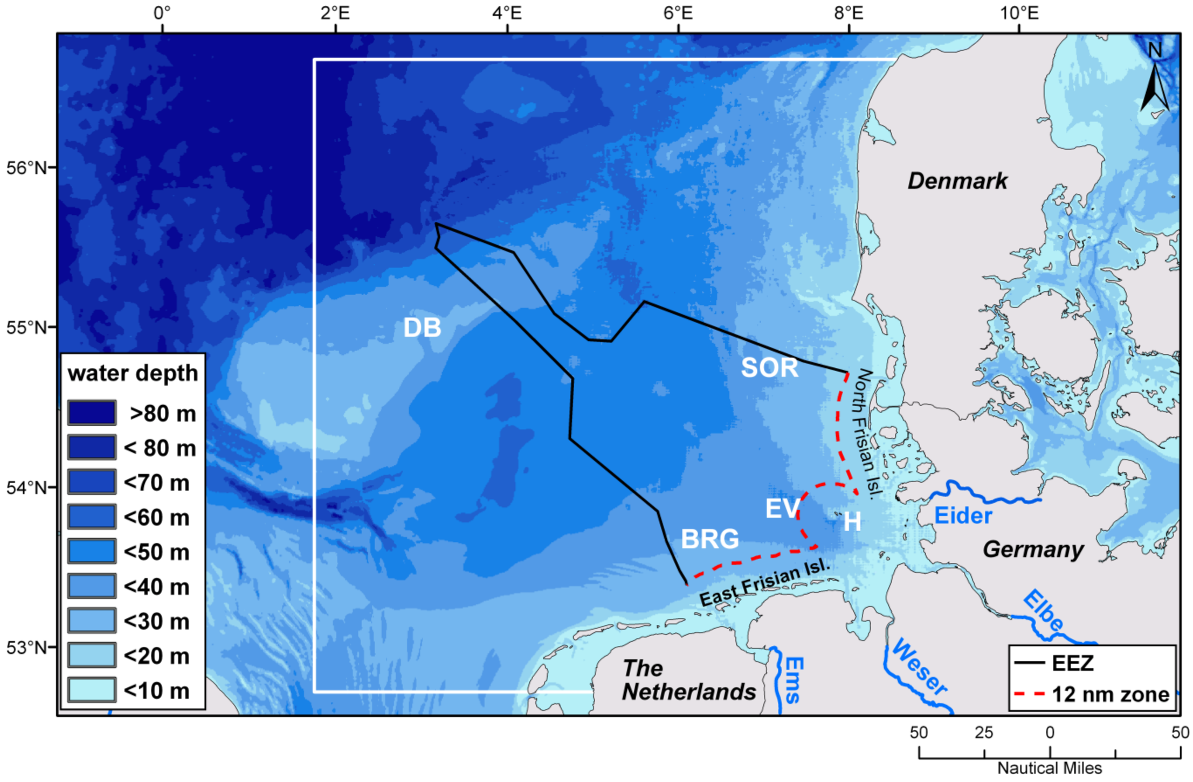

Figure 9. Study area in the SE North Sea; with bathymetry. Data on harbour porpoise seasonal distribution were collected in the German EEZ and 12 nm zone. Environmental data were compiled for a wider area, indicated by the white border. DB: Doggerbank, BRG: Borkum Reef Ground, SOR: Sylt Outer Reef, EV: Elbe valley, H: Island of Helgoland

Harbour porpoise distribution data

High-quality data on harbour porpoise distribution are available from dedicated surveys that we conducted year-round in the German EEZ and the 12 nm zone between May 2002 and November 2005 using standard line transect methodology (Buckland et al. 2001). The study area (41,045 km^2) was divided into four geographic strata where we designed a systematic set of 72 parallel transects with a total transect length of 4,842 km (chapter III). Aerial surveys were flown at 100 kn (185 km h^{-1}) at an altitude of 600 ft (183 m) in a Partenavia P68, a two-engine, high-wing aircraft equipped with two bubble windows to allow scanning directly underneath the plane. Surveys were only conducted during Beaufort sea states 0 to typically less than 3. Detailed field protocols are found in chapter III. Estimation of effective strip widths and g(0), following the racetrack data collection method (Hiby & Lovell 1998, Hiby 1999), allowed for precise effort correction and accounted for missed animals and sighting conditions Scheidat et al. (in press).

We completed 76 survey days in the study area, resulting in a total effort of 38,720 km and 3,088 sightings of harbour porpoise groups (Table 9). Data of the four study years were pooled when collected in the same season. We defined seasons as spring (MAM), summer (JJA) and autumn (SON) The effort was comparable between the three seasons (Table 9). The winter months (DJF) were excluded due to low search effort.

Table 9. Harbour porpoise sighting data. Results of the line transect aerial survey in the German EEZ and 12 nm zone. Effort summary per season and main survey results in good and moderate sighting conditions are shown. Each season was pooled over the years 2002 to 2005.

	Flight days	Track line length (km)	No. of groups	No. of individuals
Spring	19	10,081	1,234	1,470
Summer	32	15,511	1,462	1,900
Autumn	25	13,128	392	517
Total	**76**	**38,720**	**3,088**	**3,887**

As we aimed to study porpoise-habitat relationship on a meso-scale resolution (Redfern et al. 2006), we decided to use a resolution of 10x10 km for all spatial analyses in ArcGIS 9.2 (ESRI). Subsequently, porpoise sighting data were extracted for each 10 km segment of on-effort transect as described in chapter III. We derived an estimate of porpoise density corrected for the detection probability (see chapter III) and used these estimates as the response variable. Additionally, the survey effort in each grid cell was weighted and included in the model equation as weight factor in order to prevent potential bias resulting from over- or under sampling subregions within each stratum. We decided to standardise weights for effort on the interval 0.5-1 (Zuur et al. 2007). The total number of surveyed grid cells was 427 in spring, 444 in summer and 416 in autumn.

Testing for seasonal differences

We carried out an initial test to establish whether or not there are significant shifts in harbour porpoise distribution between different seasons in our study area. Earlier tests indicated that spatial patterns in harbour porpoise distribution did not vary inter-annually over the study period when collected in the same season (chapter III), thus allowing us to pool all data across season.

We modelled porpoise density based on the locational covariates latitude and longitude and followed an approach developed by Wood (2006; p 239) to test for the effect of season. At first, assuming no difference in spatial distribution throughout the year, all data were pooled. A second model was applied assuming differences in spatial distribution patterns caused by season (using *by* variables in mgcv). Both models were then compared by their residual deviance (using the anova.gam function). If there was a significant difference between both models, we conclude that there is evidence against symmetry and that this effect is due to the factor 'season'. This approach was carried out for all seasons.

Modelling approaches

We used GAMs to investigate the relationship between observed harbour porpoise seasonal density (response variable) and our selected environmental predictors (independent variables). We modelled the estimated probability of porpoise density at any site as an additive function of the selected environmental predictors using a logarithmic link and a quasi-likelihood error distribution to account for overdispersion in the data. We performed modelling in R v.2.7.2 (R Development Core Team 2008) with GAM setup based on the 'mgcv 1.4-1' package (Wood 2008). GAMs fit flexible functional forms to the response variable as they allow non-parametric smoothers, in addition to parametric forms, combined with a range of link functions. The degree of smoothness is estimated as part of model fitting (Crawley 2007); in 'mgcv' the smoothing parameter is estimated by the generalised cross validation (GCV) criterion (Wood & Augustin 2002, Wood 2006). Smoothing parameters are chosen to minimise the GCV.

In addition, the GAM was further extended to a mixed effect model including random effects (Lin & Zhang 1999, Wood 2008). Generalised additive mixed models (GAMM) allow modelling of non-linear relationships while explicitly taking into account the spatial autocorrelation (Dormann et al. 2007). The spatial autocorrelation structure that we implemented in the GAMMs has an exponential structure. It is implemented by the 'corExp' functions of the 'nlme' package in R (Pinheiro & Bates 2000) and described as follows: letting *d* denote the range and *n* denote the nugget effect, the correlation between two observations a distance *r* apart is (1-*n*)**exp(-r/d*), when a nugget effect is assumed. The GAMM procedure is computationally very time consuming as for every candidate set of predictors a numerical approximation of the likelihood over all possible realisations of the models random effects needs to be performed (Aarts et al. 2008).

We developed both GAMs and GAMMs using the same data sets in order to compare model fit and predictive power statistically and to gain ecological insight into variables and functional forms included in each type of model. As GAMMs are estimated by penalised quasi likelihood (PQL) iterations in 'mgcv', only approximate likelihoods of working linear mixed models are determined (Wood 2008). It is thus not possible to compute the explained deviance and we can only present adjusted R^2 values for the GAMMs, as proposed by Pierce et al. (2007).

Explanatory variables

The explanatory variables were selected based on *a priori* knowledge of factors known to indirectly determine harbour porpoise distribution by influencing patterns in prey occurrence. As it was not possible to collect *in-situ* oceanographic data during aerial surveys, we compiled spatially referenced oceanographic and remote sensed data from a number of different oceanographic databases. All data sets were processed in ArcGIS 9.2 to generate corresponding gridded environmental data at the selected resolution of 10x10 km.

We used a combination of static and dynamic predictors to fit the models, as listed in Table 10 and discussed in detail in the following:

a) Static predictors

Distance to shore (DIST) was calculated in ArcGIS 9.2 as the shortest distance between the midpoint of each grid cell and the closest point on the coastline (mainland). Water depth (DEPTH) data were obtained from a digital bathymetric map set with a spatial resolution of 617 m. As DIST and DEPTH are correlated (R^2=0.8, p<0.05), these two variables were included as interaction term (DIST,DEPTH) in all models. We hypothesise that this interaction term could be very important to capture the complex topography of the German Bight, as there a number of offshore shallows (e.g. Amrum & Dogger Bank). Bottom slope (SL) was derived from the depth data by using the Spatial Analyst extension (Surface Analyst - slope) in ArcGIS. Although derived from the bathymetry, the slope at a particular location is independent of its depth (here: $R^2=-0.5$, $p<0.05$).

b) Dynamic predictors

We compiled dynamic predictor data for the spring, summer and autumn season across all four consecutive study years in order to capture the range of seasonal and inter-annual environmental variability. We strove for matching each survey day with corresponding data for each dynamic predictors highest available resolution to capture the environmental situation at every single flight day as accurately as possible. Temporal variables were then subsequently pooled for each season and averaged across all years.

Sea surface temperature (SST) data were available at a weekly resolution. In order to derive mean seasonal values, we processed a total of 16, 21 and 21 weekly composites for spring, summer and autumn respectively. Data were provided by the German Federal Maritime and Hydrographic Agency (BSH) and derived from satellite data (NOAA satellites) combined with ground-truth data in order to diminish the absolute error of the satellite measurements (Becker et al. 1986, Becker & Pauly 1996).

Data on residual currents (CURR) were provided by the BSH with a spatial resolution of 1 nm on a daily basis. They were computed in the BSH by the operational circulation model 'BSHcmod' (Dick et al. 2001). Residual currents are characterised by only those currents generated by wind and density differences when tidal currents are eliminated by averaging over two tidal periods (Dick et al. 2001). As we gathered data on residual currents for seven days before up to seven days after the porpoise survey day, we processed a total of 850 daily observations to derive mean seasonal values.

Surface chlorophyll concentration (CHL) was obtained from the multispectral sensor MERIS[1] on-board ESA’s ENVISAT satellite and were provided by the GKSS[2]. MERIS is used to derive in-water optical properties and concentrations from the reflectance spectra. The sensor has a spatial resolution of 300 m for full resolution images, a revisit period of 1-2 days at mid-latitudes and a set of 15 spectral bands (Rast et al. 1999, Doerffer et al. 1999). We displayed and analysed the satellite images using the BEAM software (Brockmann Consult, ESA 2006).

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[1] Medium Resolution Imaging Spectrometer

[2] GKSS Research Centre. Institute for coastal research, http://www.gkss.de/institute/coastal_research/index.html.en

We selected the suitable spatial and band subset (algal_2, chlorophyll absorption) and produced a GeoTIFF, a TIFF[3] file with embedded georeferenced data. We imported a total of 12 GeoTIFFs in ArcGIS 9.2 where mean values of surface chlorophyll concentration could be extracted for each grid cell.

We derived the predictor 'chlorophyll range' (CHL_r) from the chlorophyll data. It describes the range of surface chlorophyll and is the difference between the maximum and minimum pixel value within our 10x10 km grid cells. This predictor was included to approximate fronts or upwelling zones, which could be characterised by chlorophyll anomalies.

We processed data on sea surface salinity (SAL) and selected nutrients (silicic acid (SI) and total nitrogen (N)) from in-situ measurements taken at oceanographic stations. Salinity data were provided by the International Council for the Exploration of the Seas (ICES Oceanographic database[4]) and data on nutrients were provided by the German Oceanographic Data Centre (NODC[5]). We used these point coverages of salinity and nutrient concentrations to create interpolated raster surfaces across the study area. For interpolation we used the ordinary kriging function in ArcGIS (Geostatistical Analyst) that forms weights from surrounding measured values to predict values at unmeasured locations and accurately interpolates spatial trends between data points (Mueller et al. 2004). However, we were only able to calculate seasonal values of nutrient concentration for spring and autumn 2004 resp. and for summer 2002 as the number of sampled stations was too low in the other years to compute a robust interpolation by season.

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[3] Tagged Image File Format

[4] http://www.ices.dk/ocean/INDEX.asp

[5] http://www.bsh.de/en/Marine_data/Observations/DOD_Data_Centre/index.jsp

Table 10. Overview of explanatory variables used for harbour porpoise-habitat modelling. Abbreviations as used throughout the text.

Explanatory variable	Abbreviation	Unit	Predictor category
distance to shore	DIST*	km	static
water depth	DEPTH*	m	static
slope	SL	°	static
sea surface salinity	SAL	PSU	dynamic
sea surface temperature	SST	°C	dynamic
residual current	CURR	cm/s	dynamic
sea surface chlorophyll	CHL	mg/m^3	dynamic
chlorophyll range	CHL_r	mg/m^3	dynamic
silicate	SI	µmol/l	dynamic
nitrogen	N	µmol/l	dynamic

* DIST/DEPTH included as interaction term

Model selection

We fitted GAMs and GAMMs independently for each of the three seasons, thus obtaining six models. For each model, model selection was based on identifying which explanatory variables had significant effects. We performed the backward (stepwise) selection, where an initial model contained all environmental variables and was subsequently simplified by removing insignificant variables with lowest F-values until all predictors were significant (α=0.05) and the most parsimonious model has been selected (Redfern et al. 2006). We then determined the model error for the best-fit models as mean value of the response residuals, which denote the difference between observed and fitted value for each grid cell in the study area.

However, model selection may be biased due to (1) residual spatial autocorrelation violating the assumption of independence of observations (Legendre 1993) as well as (2) multicollinearity, i.e. inherent correlations between predictors (Schröder 2008).

To assess the effect of these biases on the most parsimonious models, as determined by the backward selection process, we conducted a visual inspection of response residuals to determine whether patterns of spatial autocorrelation could be detected. We also used the Kolmogorov-Smirnov test (K-S test) to test for normality of residual distribution.

In addition, we checked all predictors included in the final models for collinearity using R^2x, the variance in each independent variable x explained by the other independent variables (Gregr & Trites 2001). Non-independence of predictors is best addressed by dropping one of the two correlated predictors from the model, if the bivariate correlation coefficients exceed a certain threshold. In other cetacean-habitat studies, this threshold has been set to R^2x = 0.8 or 0.9 (Gregr & Trites 2001, Laran & Gannier 2008). We decided to use a pre-defined threshold of 0.7. In case of detected strong collinearity exceeding this threshold, variables were nonetheless retained, when a comparison of models with and without variable x showed significant differences between models and the residual deviance increased in the model without variable x. If, however, the root mean square error of prediction (see below) increased substantially at the same time, the variable was dropped.

Assessment of model performance and validation

To assess model performance, we compared observed harbour porpoise densities with predicted density surfaces as produced by our best models for each season. Predicted densities were shown as smooth surfaces where isolines denote areas of same density. Additionally, the spatial distribution of the response residuals were mapped in order to identify areas where the model over- (i.e. residuals are negative) or underestimated (i.e. residuals are positive) density. Response residuals were calculated on the basis of the 10x10 km grid cells. Finally, residuals of the resulting best-fit GAM and GAMM were plotted against each other to evaluate which model had lower error distribution. If both models are equal the points should lie close to the first angle bisector.

We used a k-fold cross validation procedure to validate the predictive accuracies of the resulting best-fit models using withheld data. During cross validation, subsets of the original data set are iteratively used as training data sets while other subsets are withheld during model fitting and are then used to test model performance (Fielding & Bell 1997, Schröder 2008). Alternatively, independent data can be used to assess model performance and robustness (Guisan & Zimmermann 2000, Schröder 2008). Here, we carried out both internal and external validations based on an enlarged study area (i.e. white box, Fig. 9) which encompassed a sufficiently large proportion of survey providing our independent data (see below).

We performed internal validation of each seasons best model by using subsets of the original data. Additionally, we performed an external validation by using independent data to validate the summer model. The independent data set was collected during the SCANSII survey (SCANSII 2008) which estimated small cetacean abundance in the North Sea and European Atlantic continental shelf waters in July 2005 using sightings data from large-scale line transect surveys. We only used harbour porpoise sightings collected in survey blocks that overlapped with our study area (i.e. blocks H, L, U, V and Y).

The procedure of the cross validation worked as follows: (1) The data set was divided in 9 spatial subsets of equal size. (2) Models were fitted with 8 subsets (= training set) only and the fitted model was then used to predict porpoise density for the remaining subset (= test set). (3) Test and training datasets were switched until each subset was the test set exactly once. (4) The error distribution for each test set was assessed in order to determine the root mean square error of prediction (RMSEP). RMSEP, commonly used to compare the predictive power of multiple models (Redfern et al. 2008), was calculated as follows:

$$\text{RMSEP} = \sqrt{\frac{\sum(observed - predicted)^2}{n}}$$

where *n* is the number of observations.

RESULTS

Testing for seasonal differences

The investigation of potential seasonal longitudinal and or latitudinal shifts in harbour porpoise density indicated significant differences (all $p<0.001$) between all of the three seasons. Consequently, we developed three distinct seasonal habitat prediction models for the harbour porpoises in the German North Sea.

Model selection

The model statistics for best-fit seasonal GAM and GAMM are presented in Table 11. In general, the mixed model approach selected fewer significant predictors during the backward model selection than the GAM and showed lower values for adjusted R^2. Except for autumn, the GAMM did not select different predictors than the GAM. The GAM models used a higher number of estimated degrees of freedom (edf), especially for the interaction DIST/DEPTH, whereas the GAMMs spent a maximum of 2.9 edfs (Table 11). This suggested that most of the effects of explanatory variables in our GAMMs were linear (edf=1) or very close to linear as fewer degrees of freedom indicated a greater degree of smoothing.

Both methods agreed that the summer model explained the highest deviance, followed by spring and autumn (Table 11). The residual current (CURR) and the interaction (DIST,DEPTH) were the predictors most often selected in all six models, followed by chlorophyll concentration (CHL) and bottom slope (SL). The higher the F-value the more deviance is explained by selected factors. Highest F-values were found for nitrogen (N), CHL and CURR.

In general, the mean error for all best-fit models was near zero, indicating a robust fit (Table 11). The GAMM summer model displayed the highest error with 0.07. As a measure of goodness of fit we analysed diagnostic plots and spatial structure of GAM and GAMM residuals that indicated no autocorrelation structure in the residuals. None of the tests reached the significance level (K-S test, all $P>0.05$), indicating that the distribution of residuals did not deviate from a normal distribution.

Assessment of model performance and validation

In spring observed harbour porpoise distribution was highly heterogeneous (Fig. 10a). Two hot spot areas of particularly high densities were observed. Porpoise density was highest in the north-eastern part of the German EEZ in the Sylt Outer Reef (SOR, see Fig. 9). The second aggregation was located in the south-western part of the German EEZ, about 60 km offshore of the East Frisian Islands, in an area called Borkum Reef Ground (BRG, see Fig. 9). Other high density areas were found at the Dogger Tail End (Fig. 10a).

The modelled response surfaces of both GAM (Fig. 10b) and GAMM (Fig. 10c) showed a good fit of the observed density distribution and captured the two hot spots in SOR and BRG very well. The small-sized hot spot at the edge of the submerged Dogger Bank was predicted successfully as well. Both approaches predicted increasing porpoise density, when moving from the island of Helgoland north towards SOR and further north-west. Whereas predicted density in SOR was similar in the GAM and GAMM approach (around 3 Ind. km^{-2}), the GAMM predicted porpoise density to be lower at BOR and Dogger Bank (Fig. 10c). Associated GAMM residuals were higher in those areas (Fig. 10f), suggesting a better fit of the GAM for this season (Fig. 10e). Moreover, the high number of positive residuals indicate that the GAMM tended to underestimate density (Fig. 10f).

In summer, porpoise densities within our study area reached their maximum and a substantial northwards shift in distribution was observed, as densities decreased in the southern German Bight and further increased in the North. Again, large aggregations of harbour porpoises were observed in the north-eastern part of our study area. Areas of high density also remained at the Dogger Tail End, while the aggregation around BOR disappeared in summer (Fig. 11a). The response surfaces of the GAM and GAMM showed a very good fit with the observed spatial pattern (Figs. 11b & 11c). Whereas the GAM predicted densities up to 4.5 Ind. km^{-2} in the north-east at the national border to Denmark, the maximum densities predicted by the GAMM amounted to 3 Ind. km^{-2} (Fig. 11c). However, as the spatial distribution of residuals show, the GAMM clearly underestimates the density around SOR (Fig. 11f).

The aerial surveys in autumn revealed that harbour porpoises were more evenly dispersed throughout the study area and that they occurred in lower densities in comparison to the other seasons (Fig. 12a). This pattern was captured equally well by GAM and GAMM (Figs. 12b & 12c). The density surface, as predicted by the GAM, showed two focal areas, one again around the reef structure of the SOR and another one at the Dogger Tail End (Fig. 12b). The GAMM predicted this pattern as well but also another hot spot on the BRG (Fig. 12c), similar as in spring. Residuals show low values (Figs. 12e & 12f) for both models but again indicate a possible underestimation of density for the GAMM (Fig. 12f).

In general, GAM and GAMM tended to perform equally well in terms of reliable predicting harbour porpoise densities across all three seasons, as indicated by the scatter plots of GAM and GAMM residuals which showed a similar distribution of values lying closely along the 1st angle bisector for all three seasons (Figs. 10d, 11d & 12d).

Table 11. Best-fit model based on backward model selection for a) GAM and b) GAMM. F-values, significance test p-values and estimated degrees of freedom (edf) are given for the explanatory variables (abbreviations in Table 10). The adjusted R^2, deviance explained (%) and mean error of residuals are also shown. Terms that were not significant (ns, p>0.05) were dropped from the model. ni: not included due to multicollinearity.

Explanatory variable		a) GAM			b) GAMM		
		Spring	Summer	Autumn	Spring	Summer	Autumn
Intercept	t	-4.76	-8.45	-13.24	-0.47	-1.96	-6.86
	Pr(>|t|)	<0.001	<0.001	<0.001	0.641	<0.001	<0.001
	estimate	-0.37	-0.74	-1.63	-0.08	-0.74	-1.24
DIST,DEPTH	F	4.46	3.90	3.55	4.01	6.74	
	p	<0.001	<0.001	<0.001	0.012	<0.001	ns
	edf	23.5	10.25	18.8	2.0	2.0	
SL	F	4.53			4.03		6.58
	p	0.004	ns	ns	0.005	ns	0.004
	edf	2.4			2.9		1
SST	F	5.17			6.34		
	p	<0.001	ni	ns	0.005	ns	ns
	edf	6.3			1.0		
SAL	F	4.82		3.48			
	p	0.004	ns	<0.001	ns	ns	ns
	edf	2.2		8.5			
CURR	F	9.64	3.35		5.36	5.85	6.74
	p	<0.001	0.002	ns	0.010	0.007	0.004
	edf	1.0	6.22		1.0	1.0	1
CHL	F	2.21		2.31			13.62
	p	0.03	ns	0.031	ns	ns	<0.001
	edf	6.9		5.8			1.0
CHL_r	F	5.81		5.95			
	p	0.007	ns	0.007	ns	ns	ns
	edf	1.0		1			
SI	F	2.44					
	p	0.057	ns	ns	ns	ns	ns
	edf	2.9					
N	F		15.25			7.42	
	p	ns	<0.001	ns	ns	0.002	ns
	edf		2.11			1.0	
n		389	419	388	389	419	388
R^2 adj.		0.51	0.56	0.40	0.28	0.41	0.212
deviance expl. (%)		56.2	56.9	42.6	-	-	-
mean error		-0.01	-0.01	0.00	0.00	0.07	0.02

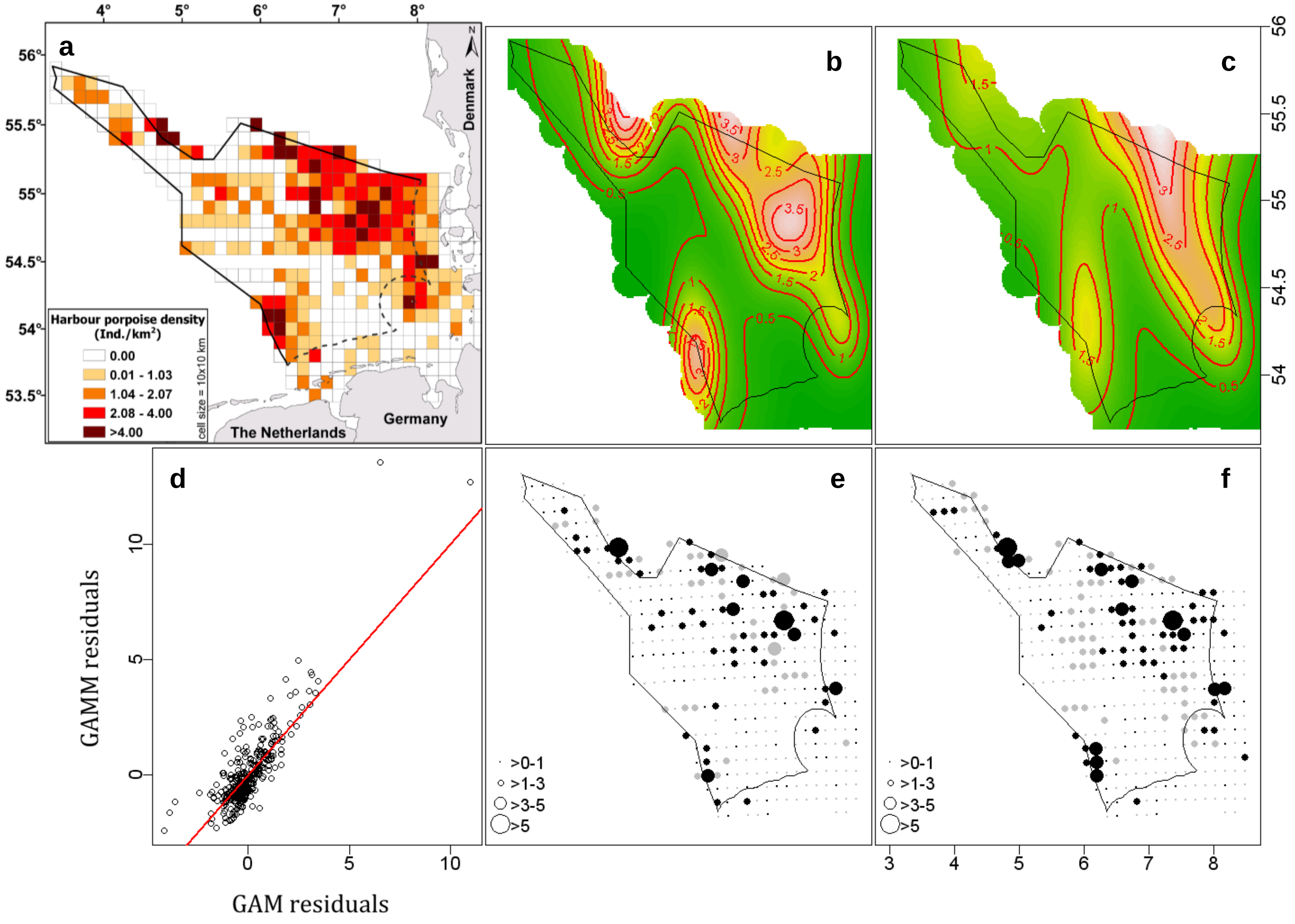

Figure 10. Harbour porpoise distribution in spring; a) observed during aerial surveys, b) predicted porpoise density surface by selected predictors using GAM (see Table 11a for selected predictors) c) predicted porpoise density surface by selected predictors using GAMM (see Table 11b for selected predictors), d) residual plot GAM vs GAMM, e) spatial distribution of residuals (GAM), f) spatial distribution of residuals (GAMM). Contour lines in b) and c) are isolines of porpoise density (Ind. km^{-2}); d)-f) response residuals are shown (observed-fitted values); positive values of residuals in black, negative in grey.

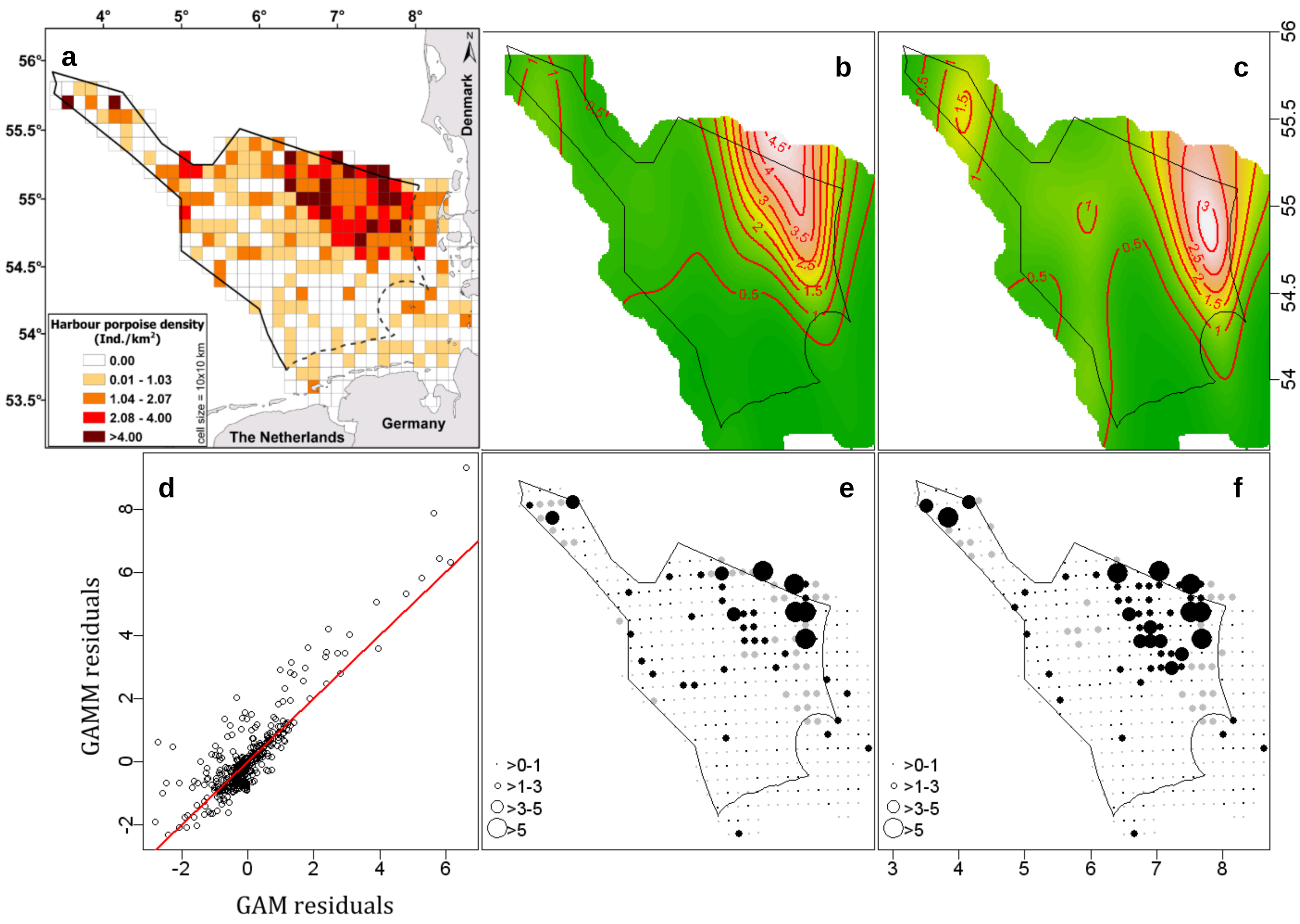

Figure 11. Harbour porpoise distribution in summer; a) observed during aerial surveys, b) predicted porpoise density surface by selected predictors using GAM (see Table 11a for selected predictors) c) predicted porpoise density surface by selected predictors using GAMM (see Table 11b for selected predictors), d) residual plot GAM vs GAMM, e) spatial distribution of residuals (GAM), f) spatial distribution of residuals (GAMM). Contour lines in b) and c) are isolines of porpoise density (Ind. km^{-2}); d)-f) response residuals are shown (observed-fitted values); positive values of residuals in black, negative in grey.

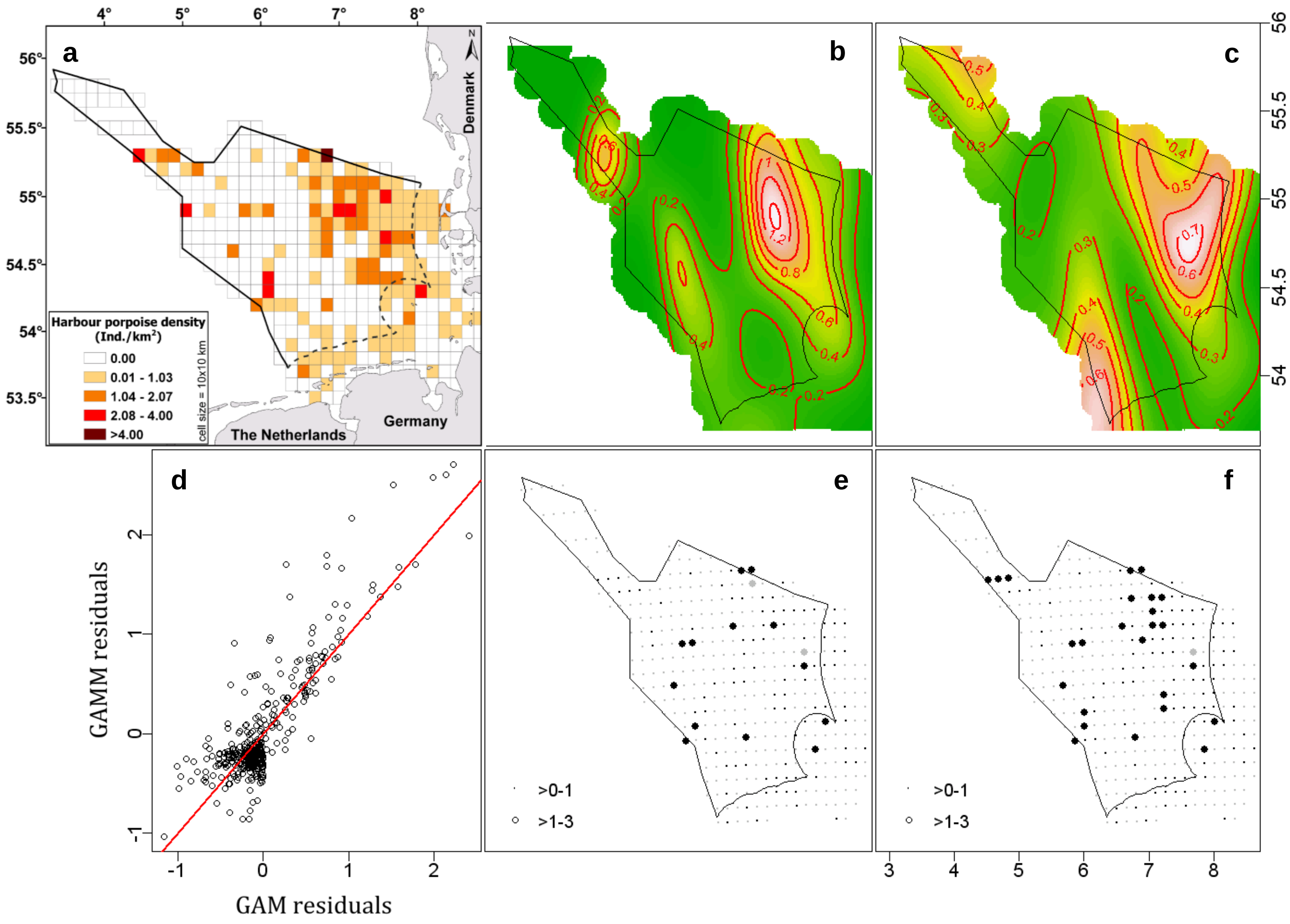

Figure 12. Harbour porpoise distribution in autumn; a) observed during aerial surveys, b) predicted porpoise density surface by selected predictors using GAM (see Table 11a for selected predictors) c) predicted porpoise density surface by selected predictors using GAMM (see Table 11b for selected predictors), d) residual plot GAM vs GAMM, e) spatial distribution of residuals (GAM), f) spatial distribution of residuals (GAMM). Contour lines in b) and c) are isolines of porpoise density (Ind. km^{-2}); d)-f) response residuals are shown (observed-fitted values); positive values of residuals in black, negative in grey.

Internal and external cross validation also indicated a good fit for all three seasons and both modelling approaches, as indicated by the low RMSEPs (Table 12). RMSEPs based on internal validation were very similar for GAM and GAMM in all seasons, except for spring. Predictive power was highest in autumn for both modelling approaches (Table 12). The external validation with the independent data set SCANSII focused on the transferability and generalisability of the model. The validation of the summer model resulted in a positive validation of the GAM (RMSEP=1.21) but did not provide support for the GAMM (RMSEP=9.44) (Table 12). As a consequence, we used the GAM best-fit model based on the local summer data to predict porpoise density for a more regional scale as supported by the SCANS validation (Fig. 13). The results show that the summer hot spot in the north-eastern German Bight was predicted to extend far into Danish waters. Additional high density areas of harbour porpoises were predicted in the southern North Sea offshore the West Frisian Island in the Netherlands and on the Dogger Bank.

Table 12. Root mean squared error of prediction (RMSEP) of best-fit GAM and GAMM (see Table 11) as determined by internal and cross validation (cross val.).

	GAM			GAMM		
	spring	summer	autumn	spring	summer	autumn
RMSEP - internal cross val.	2.79	1.51	0.57	1.62	1.93	0.49
RMSEP - external cross val.	-	1.21	-	-	9.44	-

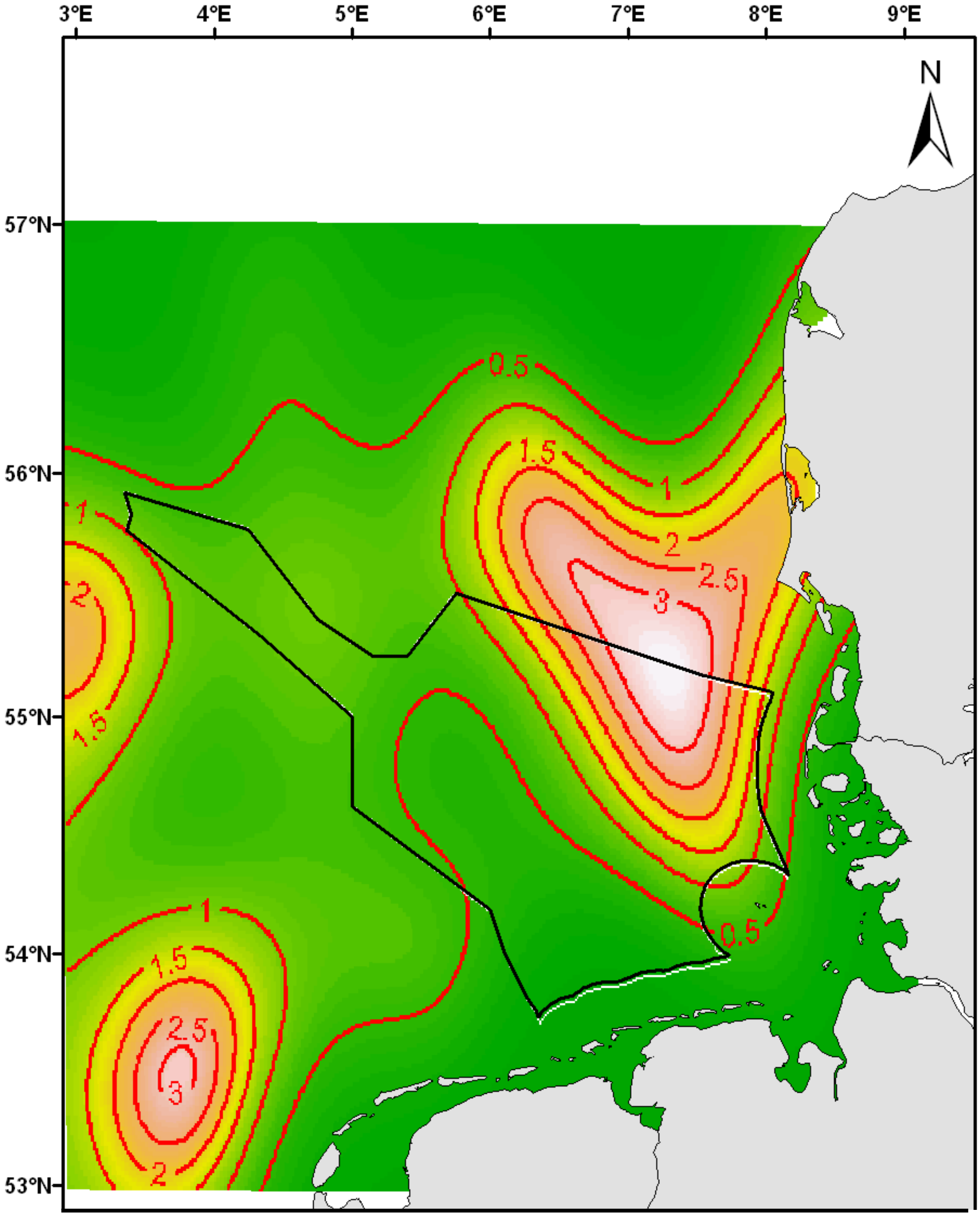

Figure 13. Predicted harbour porpoise density (Ind. km^{-2}) surface in summer by selected predictors using GAM (see Table 11a for selected predictors). Model validation with SCANS II data.

DISCUSSION

This is the first study that assessed harbour porpoise distribution and density as a function of the complex and dynamic German Bight environment. We were able to develop models generating high-quality predictions without using standard locational covariates latitude and longitude, that are often used but are difficult to interpret ecologically. By including a range of static as well as dynamic habitat predictors we were able to increase the resolution of the density prediction. This fine resolution would not be available by using stratified line-transect analysis only and we are now able to calculate density for any subarea within the large study area. Moreover, we were in the unique position to develop seasonal models that allowed the visualisation of shifts in harbour porpoise distribution throughout the year. Extensive validation of our models provided support for the robustness and precision of the predicted patterns of harbour porpoise density in the south-eastern North Sea.

Seasonal focal areas

Our models suggest that there are remarkable differences in the seasonal distribution patterns of harbour porpoises. Porpoises were not uniformly distributed but aggregated in distinct hot spots within their seasonal range. The Sylt Outer Reef (SOR) is the most important focal region throughout the year (chapter III). Besides, Borkum Reef Ground (BRG) and the Dogger Bank were highly frequented in spring and autumn. The area in-between SOR and BRG seems to be no focal area in the wider sense, although we have to consider its function as migration corridor. By transferring our predictions for summer to a more regional scale, we showed that the hot spot in SOR extends into Danish waters and that this large focal area could be of great importance throughout the north-eastern North Sea.

Factors affecting harbour porpoise distribution

Given the complexity of marine trophic interactions, it is difficult to identify specific individual predictors that directly affect prey aggregations or otherwise determine predator fidelity. Our findings suggest that a range of different dynamic and static parameters play important roles in determining porpoise distribution in the German Bight, since all best-fit models included at least one type of physiographic as well as hydrographical and biological predictors.

Residual currents appeared to play an important role in determining porpoise distribution during most seasons. The functional form of the response curve of this variable showed a positive relationship with porpoise density indicating that porpoises preferred areas with stronger currents. Since prey often aggregates or is aggregated in such regions, porpoises are known to actively seek out areas of permanent or predictable enhanced relative velocity, such as islands and headland wakes (Johnston et al. 2005) or tide race areas (Pierpoint 2008) as a proxy for foraging sites.

The same positive dependence holds for chlorophyll anomalies: the larger the range between minimum and maximum surface chlorophyll concentration the higher the density of porpoises. A large range in chlorophyll concentration could be indicative of localised patches of primary production and fronts as these coincide with areas of high primary and secondary productivity (Mann & Lazier 2006). Frontal structures are known to increase food availability for top predators, like marine mammals and seabirds (Guinet et al. 2001, Ballance et al. 2006). This has been shown for seabirds in the German Bight (Garthe 1997, Skov & Prins 2001, Markones 2007) and for harbour porpoises around the Faroese Islands (Skov et al. 2003) and in the Bay of Fundy in Canada (Johnston et al. 2005).

Fronts are very dynamic oceanographic features and of great ecological relevance in the German Bight (Becker et al. 1999). A tidal mixing front (i.e. thermal as well as haline), between warm stratified and tidally mixed water, develops in the south-western part of the German Bight at the East Frisian coast in summer (Schrum 1997). At the convergence zone at the edge of the front, downwelling occurs. This feature near the East Frisian coast, also known as 'cold belt' (Krause et al. 1986), can cover the whole southern German Bight in its east-west extension (Otto et al. 1990). It could be the explanation for the hotspot at BOR, given a high solar radiation has preceded which is not unlikely in May.

A permanent front, however, is the estuarine front of the German Bight which exists through-out the year in the eastern part of the German Bight (Krause et al. 1986). The discharges of the large Weser and Elbe rivers lead to large fluctuations in salinity and nutrients over a yearly cycle (Otto et al. 1990). The fact that salinity is an important predictor in spring and summer might be indicative of the role of this front. Studies in the California Current System showed that surface salinity was an important predictive variable to explain the variance in harbour porpoise occurrence, where the species occurred in upwelled waters of higher salinity near the coast (Tynan et al. 2005).

Besides, a topographically induced up-welling of cold nutrient-rich water may locally increase primary production and aggregation of zooplankton, that in turn might lead to the aggregation of suitable prey species for harbour porpoises. This would explain the successful incorporation of physiographic factors in the models and the preference of harbour porpoises to forage along areas with higher bottom slope as well as on the edge of offshore shallows. The post-glacial Elbe River valley, which is basically a submarine canyon, could be particularly important at a local scale since it creates a dynamic topography which could direct many fish assemblages and delineate fish habitat. In the German Bight it is in fact mainly depth and distance from the coast that have a major impact on the composition of typical fish assemblage (Ehrich et al. 2006). Ephemeral upwelling was described to occur in the area of the Elbe River valley close to the island of Helgoland when easterly winds prevail (Krause et al. 1986). In fact, our predicted surfaces show that the focal region in the area SOR extends to the vicinity of Helgoland, and thus runs along the northern edge of the Elbe River valley. In Wales, preferred areas of porpoises were also found adjacent to a narrow, steep-sided trench (Pierpoint 2008).

Nutrient data are, besides salinity and temperature, a valuable tool to differentiate water masses and provide, in addition, information on recent state of biogeochemical turnover processes (Ehrich et al. 2007). Nutrient depletion e.g. is possibly a sign of a preceding phytoplankton bloom and could indicate the on-set of secondary production. In our summer model, total nitrogen concentration was the most influential predictor on porpoise. The functional relationship was a negative one, thus porpoise densities were higher in areas where nitrogen concentration was low. This makes sense as we have to account for sufficient time for zooplankton abundance to rise, fish to locate the area and top predators to arrive.

Comparison of different model approaches

We used two methodological approaches on the same data set - the GAM that ignored potential spatial autocorrelation (SAC) and the GAMM that accounts for SAC. Dormann (2007) stated that there is a need to evaluate whether a more sophisticated 'true' spatial model is actually less biased than more simplified non-spatial models that do not account for SAC. Although the need to incorporate SAC is recognised for cetacean-habitat models (Redfern et al. 2006), it is seldom taken into consideration (Laidre et al. 2004, Yen et al. 2004, Parra et al. 2006, Panigada et al. 2008). We are only aware of two other studies implementing the GAMM approach within cetacean data (Pierce et al. 2007, De Stephanis et al. 2008). We therefore state that it has been important to run this comparison on the basis of the presented data.

Our comparison of GAM and GAMM outputs indicated that model performance and predictions were very similar. For all three seasons, GAM vs. GAMM residuals scatter plots showed unskewed distributions of residuals indicating similar predictive ability of both models. Similarly, the mean error and the spatial distribution of the residuals were comparable during all seasons for both approaches, although the GAMM in fact performed worse than the less complex GAM in spring and summer. We therefore conclude that there is no substantial difference between GAM and GAMM performance in our study. Consequently we propose that - in accordance to the principle of parsimony - the results of the less complex model (i.e. GAM) should be used for further analysis. This does by far not mean that we advice to ignore SAC. We agree with Redfern et al. (2006) who strongly recommend that SAC should be systematically controlled for in studies of cetacean habitats.

Limitations

The application of GAMs requires a survey design with good coverage in space and time (Augustin et al. 1998). High survey effort in three seasons of four consecutive years in an area spanning 41,000 km^2 is clearly an advantage of our study. We showed that the distribution of harbour porpoises in our study area exhibited significant differences between seasons but similar patterns throughout the 4-year-study period (chapter III). Pooling the data enabled us to derive robust seasonal habitat models. As a consequence the dynamic habitat predictors needed to be seasonally averaged as well. Thus, we will not be able to predict harbour porpoise distribution at shorter time scales. However, by integrating data across multiple spatial and temporal scales we addressed the general ecological relationship in an adequate way. Besides, by evaluating associated errors all uncertainties within our predictions were sufficiently addressed.

The selection of spatial scale is crucial in the development of cetacean-habitat models as relationships are scale dependent. It is of importance that the unit of observation, where porpoise and habitat data are summarised, match the spatial scale determined by the purpose of the model (Redfern et al. 2006). We conclude that our spatial resolution of 10x10 km was probably fine enough to capture local porpoise-habitat relationships on a meso-scale and, additionally, coarse enough to eliminate spatial autocorrelation.

In conclusion, our models provide important new information in understanding the determinants of harbour porpoise habitat in the North Sea. The models provide a valuable tool to help managers address concerns about potential impacts from human activities. They could be applied for calculating abundance and associated confidence intervals for any subarea of the German Bight, irrespective of pre-designed survey strata. Further modelling exercises could include food competitors (like harbour seals) and disturbance factors (e.g. anthropogenic noise).

ACKNOWLEDGEMENTS

Survey data were collected under financial support of the German Federal Ministry for the Environment, Nature Conservation and Nuclear Safety (BMU; MINOS and MINOSplus projects; FKZ 0327520, 0329946B), Federal Ministry of Food, Agriculture and Consumer Protection (BMELV; 514-33.29/03HS059) and the Federal Agency for Nature Conservation (BfN; project EMSON, FKZ 80285260). We thank L. Hiby and P. Lovell for their help with data analysis and H. Giewat for managing the survey database. Our thanks go to all pilots, observers and navigators during the aerial surveys. We thank the following institutions for provisioning the various data sets: German Federal Maritime and Hydrographic Agency (BSH), International Council for the Exploration of the Seas (ICES) and the GKKS Research Centre, Department of Operational Systems. Thanks to P. Hammond and all people and institutions involved in SCANSII for providing the SCANSII data.

Chapter V

Feeding ecology of harbour porpoises in German waters

ABSTRACT

This study used hard-part analyses from stomachs to investigate the diet of harbour porpoises in the German North and Baltic Sea and adjacent Danish waters in the period 1994-2006. A total of 36 fish taxa could be identified in 120 stomachs. Otolith size was corrected for partial digestion and used to estimate the proportion by mass (M) of each species in the diet. Overall, the diet was dominated by goby (Gobiidae spp., 41%M), cod (*Gadus morhua*, 23%M), sole (*Solea solea*, 15%M), sandeel (*Ammodyte*s spp., 5%M) and herring (*Clupea harengus,* 4%M). A multivariate analysis revealed significant seasonal and between-year fluctuations in the relative importance of prey fishes: in spring, mainly sandeel, goby and herring contributed with high masses whereas cod was most important in summer. Goby and flatfish species appeared to be more important before 2001, whereas in the period 2002-2006 sandeel, herring and sprat contributed more to the diet. Cod appeared to be an important prey species throughout the study period.

Additionally, the fairly new quantitative fatty acid signature analysis (QFASA) was used on blubber samples of 95 porpoises from the same area and period. Findings of QFASA were compared with the more traditional diet assessment method. QFASA predicted that mean diets consisted mainly of dab (*Limanda limanda,* 26.6%M), sprat (*Sprattus sprattus*, 22.2%M) and herring (15.9%M) in the North Sea. For the Baltic Sea, it was predicted that herring (18.3%M) and sprat (17%M) dominated the diet. As it is envisaged to expand the prey database, the QFASA results are preliminary, but they seem reasonable. This is the first study that used QFASA for a harbour porpoise diet study.

INTRODUCTION

Knowledge of the feeding ecology of top predators within an ecosystem is essential in order to elucidate predator-prey dynamics (e.g. Read 2001, Baumgartner et al. 2003, Read & Brownstein 2003, Wanless et al. 2005) as well as interactions with fisheries (e.g. Trites et al. 1997, Kaschner et al. 2001, Herr et al. 2008). Whenever changes in distribution and abundance of cetacean species are observed, the interpretation depends to some extent upon reliable information on diet as movements could be linked to those of their prey (Read & Westgate 1997). Therefore, accurate information on the type of prey, quantity, relative importance and temporal aspects of prey choice are needed.

The harbour porpoise (*Phocoena phocoena*) is an important top predator in the North Sea (Santos & Pierce 2003). It is the only cetacean species common in German waters (Benke et al. 1998, Siebert et al. 2006). However, due to its small size and elusive behaviour it is one of the most difficult species to study at sea. As a small endothermic with limited energy storage capacity (Koopman et al. 2002), it can only survive a few days without feeding, depending on age and initial physical condition as well as water temperature (Kastelein et al. 1997). Most accounts of porpoise diet are based on stomach content analysis of dead animals found stranded or by-caught in fishing nets (reviewed in Santos & Pierce 2003). Throughout the geographic range, porpoises feed on both pelagic schooling and demersal or benthic fish species (Santos & Pierce 2003). The diet in the north-eastern Atlantic is held to be more diverse than in the western Atlantic (Donovan & Bjørge 1995). However, there are large variations with respect to individual, geographical and temporal aspects (e.g. Börjesson et al. 2003, Santos et al. 2004, Spitz et al. 2006).

The most recent study of harbour porpoise diet in German waters dates back to the beginning of the 1990s. Benke et al. (1998) analysed 40 stomachs, collected in the period 1991 to 1993. They found that, according to relative weight, porpoises in the North Sea fed primarily on sandeel (*Ammodytes* spp.) and sole (*Solea solea*), whereas porpoises in the Baltic Sea preyed upon goby (*Pomatoschistus* sp.), herring (*Clupea harengus*) and cod (*Gadus morhua*).

A decade later, updated information is needed as shifts in porpoise diet are probable. On the one hand, stocks of commercially exploited fish species have declined (e.g. Corten 2001, Christensen et al. 2003, Daan et al. 2005, Ehrich et al. 2007). On the other hand, the distributions of fish species in the North Sea has responded to an increase in sea temperature by an average of 1.05°C from 1977 to 2001 (Perry et al. 2005). Corresponding to this temperature increase a northward shift of several warm-water species, including anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*), was reported (Beare et al. 2004). Studies have suggested two important shifts in porpoise diet, both related to decrease and increase of the herring stocks in the north-eastern Atlantic: (1) Reijnders (1992) associated the decline of porpoise abundance in the southern North Sea with the massive decline of Atlantic herring during the 1980s (Corten 1990). Porpoises shifted their diet from clupeid fish (mainly herring) to sandeels and gadoid fish (Santos & Pierce 2003). (2) In recent times, it has been proposed that a shift back to a clupeid dominated diet could have occurred, in relation to the increase of herring stocks in the southern North Sea in the late 1990s. This is also thought to be the reason for the come-back of the harbour porpoise in the southern North Sea (Camphuysen 2004, Kiszka et al. 2004). However, the recovery of the North Sea herring stock has not yet been shown in porpoise diet (Santos et al. 2004).

Recently, aerial surveys revealed that the distribution of harbour porpoises in German waters is not homogeneous. In contrast, porpoises re-visit focal areas and show seasonal shifts (chapter III). Individuals could be following movements of their prey. Thus, it is of importance to know whether their diet preference change with season. This has been shown in Scotland, where to some extent, the seasonal variation in diet could be attributed to variation in prey abundance (Santos et al. 2004). In the study of Benke et al. (1998) the low number of available samples did not allow for investigation of seasonality in prey choice.

This study is primarily based on the analysis of stomach contents of harbour porpoises stranded or bycaught at the North and Baltic Sea coasts. Although the analysis of stomach contents provide important information on diet, the problems associated with hard prey remains for diet analysis are well known (Pierce & Boyle 1991, Santos & Pierce 2003). These include that the remains only reflect the last meal and that otoliths, that are used for identification and size estimation, are subject to erosion during digestion and otoliths from different species are degraded at different rates (Wijnsma et al. 1999, Grellier & Hammond 2006). Recently developed techniques for obtaining information on marine mammal diets such as fatty acid (FA) signature analysis have not yet been applied to porpoises on a large scale (Santos & Pierce 2003). It is well-established as a technique for studies on seals though (e.g. Iverson et al. 1997, Beck et al. 2005). One advantage of FA signature analysis is that it integrates dietary intake over periods of weeks or even months and can thus provide information on more than just the last meal (Hooker et al. 2001, Iverson et al. 2004, Budge et al. 2006). Another advantage is that in FA studies all major components of the diet can in principle be identified even prey species that do not contain hard parts. By examining changes in FA signatures of the predator qualitative questions about spatial or temporal variations in diets, both among and within individuals or populations can be answered (e.g. Iverson et al. 1997, Walton & Pomeroy 2003, Beck et al. 2005, Walton et al. 2008). This study approached the second use of FAs – that is to quantitatively estimate diet from FA signatures of predator and prey (Budge et al. 2006). The quantified fatty acid signature analysis (QFASA) (Iverson et al. 2004) uses a multivariate least-squares model to compute the most likely combination of prey FA signatures that comes closest to matching those observed in the predator. In this study, we applied QFASA for harbour porpoises and sampled their blubber as well as potential prey species from the North and Baltic Seas.

The objective of this study was to update knowledge on harbour porpoise diet in German and adjacent waters, taking both inter-annual as well as seasonal variation into account. The application of QFASA in this study is presented as pilot study. Its effectiveness is examined by testing whether predicted diet is reasonable in comparison to those of the stomach content analysis.

MATERIAL AND METHODS

Stomach content analysis

Stomachs (with content) were recovered from 131 harbour porpoises, stranded or by-caught in the German North and Baltic Sea as well as in adjacent Danish areas (Fig. 14) between 1994 and 2006. Whole stomachs were collected during necropsies, performed regularly in the frame of a dedicated stranding monitoring scheme of the county of Schleswig-Holstein (Benke et al. 1998, Siebert et al. 2001, Siebert et al. 2006). Post-mortem examinations were performed as described in Siebert et al. (2001). Digestive tracts were opened, contents were collected by rinsing with water in a sieve. Stomach contents were stored at -20°C for later examination. Porpoises were classified in three age classes, based preferably on growth layer counts in teeth (Lockyer 1995) or, in cases where this was not possible, on body length and sexual maturity (Siebert et al. 2001, Siebert et al. 2006).

The methodology of stomach contents analysis followed the standard for marine top predators (Pierce & Boyle 1991). Main issues relevant for this study are described in the following. During examination of stomach contents intact or partially digested food items were identified and measured. Remaining stomach contents were separated using a series of sieves with mesh sizes of 0.5-2 mm. Hard parts collected for identification of ingested food items included sagittal otoliths and bones from fish, cephalopod beaks as well as crustacean remains (e.g. claws, carapace). Whole fish and larger fish fragments were identified according to (Muus & Nielsen 1998) and prey remains were identified using published guidebooks (Härkönen 1986, Leopold et al. 2001) as well as an own reference collection. Not all prey remains could be identified to species, and some composite categories were therefore used.

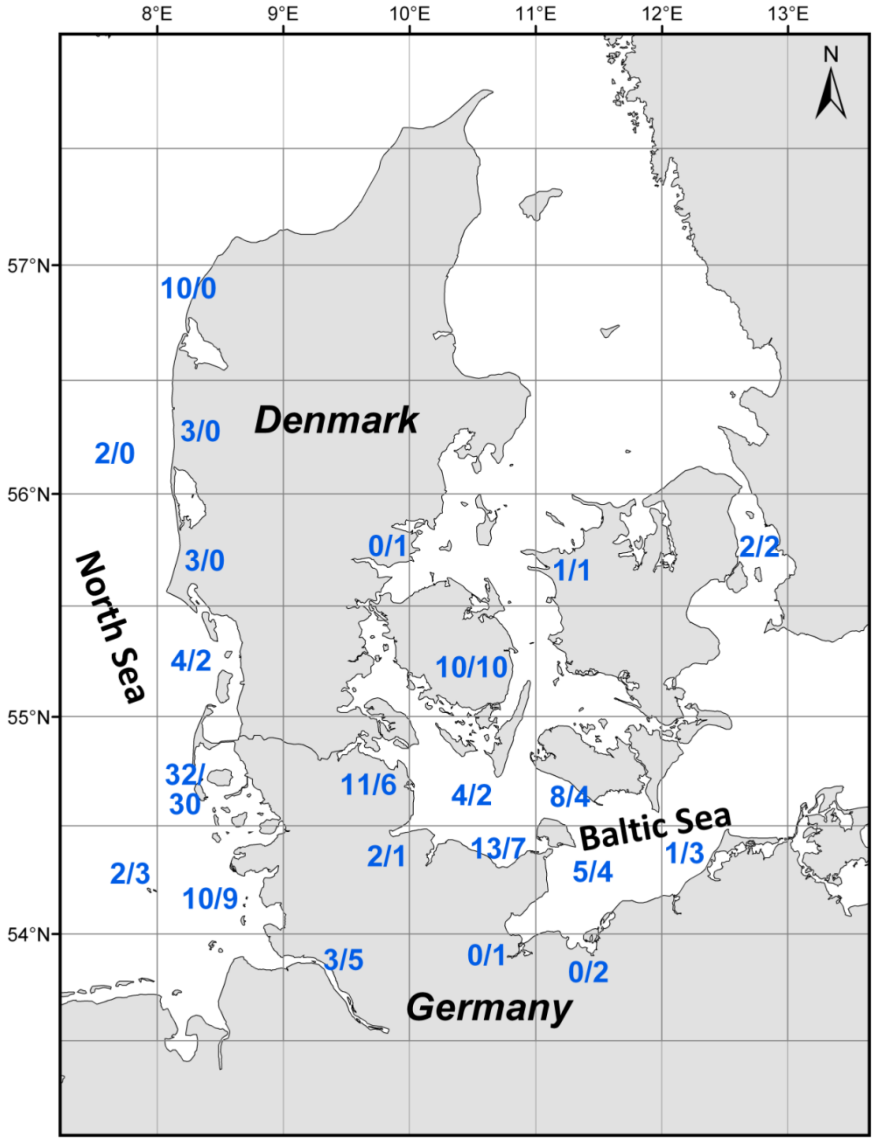

Figure 14. Locations from where harbour porpoise samples were collected, summed across ICES rectangles (0.5° latitude x 1° longitude). The first number denotes the number of stomachs, whereas the second indicates the number of blubber samples.

Prey number and prey size estimation

The minimum number of fish and cephalopods consumed by each porpoise was estimated by adding the number of intact food items to the number estimated from identified remains. For fish it was assumed that each sagittal otolith represents 0.5 fishes (Pierce & Boyle 1991). The number of cephalopods was estimated as number of upper and lower mandible whichever was greatest (Börjesson et al. 2003). Individual prey length and wet weight were calculated from the length or width of the otoliths based on established otolith size regressions (Leopold et al. 2001). In cases where otoliths could only be identified to family or genera level, like *Ammodytes* spp., Callionymidae and Gobiidae, the otolith size regression for *Callionymus lyra*, *Ammodytes marinus* and *Pomatoschistus minutus* were used respectively (all from Leopold et al. 2001).

If more than 100 otoliths were present for one prey taxon in a stomach, a randomly selected sub-sample of 120 otoliths was measured. Otherwise all otoliths were measured resulting in a total of 5,839 measured otoliths. Correction factors for otoliths were applied to take account of size reduction and degradation of the peripheral structure due to digestion (Wijnsma et al. 1999). The approach by Recchia & Read (1989) and Börjesson et al. (2003) was adopted. At first, each otolith was scored on a scale depending on otolith wear: (1) A-otoliths (according to the scale of 0-1 in Recchia & Read (1989)) have well-defined surface structures such as convex lobes on the edge/margin (pristine), (2) B-otoliths (Recchia & Read 1989: 2) have smooth edges/margins, shine less and surface structure are less visible (moderately digested) and (3) C-otoliths (Recchia & Read 1989: 3-5) have concave lobes on the edges/margins, shine less and surface structure are least visible (considerably digested). Otolith length (or width) was assumed to follow a normal distribution. Size differences between A, B and C otoliths were assessed for each prey species and when size B or C differed significantly from A, the correction factor was simply the difference between the two means and otoliths were corrected accordingly. The difference between A and B otoliths was not significant. For 8 prey taxa a correction factor for C-otoliths was determined, that corrected for a maximum difference of 15% between A and C-otoliths.

For cephalopods, mantle length and wet weight were estimated from intact upper mandibles using the regressions given by (Clarke 1986). As cephalopod beaks are relatively robust to mammalian digestive processes (Tollit et al. 1997), no correction factor was determined.

The overall contribution of each prey type in the diet of porpoises was assessed by (1) the occurrence of a given prey taxon, which is the number of stomachs in which the taxon was observed and is given by the frequency of occurrence (%O). (2) The relative abundance is given by the number of individuals of the same taxon found throughout the sample set. (3) The estimated biomass is given by the product of the average reconstituted body mass and the number of individuals of the same taxon in each stomach, summed throughout the sample set. The last two measures of contribution, for which prey items were pooled over all examined stomachs, are presented for better comparison with previous studies. However, in order to account for variation among individuals, the reconstructed size for every prey taxon within each individual stomach was taken into account in the following multi- and univariate analyses. A bootstrapping routine was written using R v.2.7.2 (R Development Core Team 2008) in order to calculate mean values of prey length and mass and to determine sampling errors (Efron & Tibshirani 1993).

Multivariate analysis

Dietary variations were analysed in relation to season and year. To examine multivariate patterns in diet and to identify which environmental descriptors best explained these patterns a constrained correspondence analysis (CCA) (ter Braak 1986, Legendre & Legendre 1998) was applied. In constrained ordination only the variation that can be explained by the used environmental variables is displayed. Each variable to be included in the model was tested for significance using a permutation test (Legendre & Legendre 1998). The CCA and the permutation tests were run in R v.2.7.2 (R Development Core Team 2008) with setup based on the 'vegan 1.15-0' package.

For this analysis only the results of 107 porpoise stomachs could be used, as for these information on year as well as on season were available. Sample sizes for winter, spring, summer and autumn were 16, 32, 43 and 16 respectively. Only prey species were incorporated that occurred at least in three stomachs and, thus, the total number of prey species totalled to 18. The dietary data was a matrix consisting of the biomass (g) consumed by each porpoise (i.e. number of prey species in each stomach multiplied by the reconstructed wet weight determined explicitly for each individual stomach).

Quantitative fatty acid signature analysis – QFASA

Blubber samples were retrieved during necropsies (described above). Carcasses were stored frozen at -20°C before necropsies. Blubber was sampled from 95 harbour porpoises, stranded or bycaught in in the German North and Baltic Sea as well as in adjacent Danish areas (Fig. 14) in the period 1998-2006. As the blubber of porpoises exhibits considerable stratification in lipid composition (Koopman et al. 2003), entire blubber cores (consisting of skin, blubber and some muscle) were obtained. The fatty acid (FA) composition of the inner blubber layer can vary with location on the body (Koopman et al. 1996). Therefore, all tissue samples were removed from the same part of the body, i.e. in front of the dorsal fin (Learmonth 2006). As samples were taken from dead animals and oxidation of lipids could be a problem, a large piece of blubber was placed in a sealed plastic bag and frozen at -20°C. Prior to extraction, the exterior margins of the tissue were trimmed, in order to remove oxidised tissue.

FA analysis was conducted as described in Budge et al. (2006). In the following, the most important steps are described. Lipid was only extracted from the inner layer, i.e. the layer nearer to the muscle, of the blubber sample by the method of Folch et al. (1957). The lipids were hydrolysed and fatty acid butyl esters (FABES) prepared. FABES were separated on a DB-23 column by gas chromatography and 82 fatty acids were quantified. Quantitative information were obtained using the software FASCALC which has been developed to perform the QFASA procedures described by Iverson et al. (2004). The model requires two important inputs: (1) a database of prey species and (2) a set of FA calibration coefficients (FA-CCs) or weighting factors (Iverson et al. 2004) that account for the differential deposition and synthesis of FA during lipid metabolism. To address the first point a total of 281 specimens out of 15 prey taxa was collected. Fish were sampled in the North and Baltic Seas in 2005 and 2006 during various research cruises of the Johann Heinrich von Thünen Institute[1] and along the Dutch North Sea between 2002 and 2005 during various cruises of IMARES[2] in late summer and autumn (S. Brasseur, pers. comm.). Immediately upon sampling, fish were frozen whole in plastic bags on board and later, upon return from sea, kept in the lab at -20°C. As harbour porpoises consume their prey whole (Lowry & Teilmann 1994), the whole fish specimen was homogenised and then analysed using the same methods as described above for the blubber samples. Lipids are extracted from a subsample (ca. 1.5 g) of the homogenised fish material.

FA-CCs were only available for phocid species (Iverson et al. 2004) and are usually obtained by feeding several animals of a given species for a long time (preferably >6 months) on a known diet and then determining the fatty acid profiles of both the diet and the blubber. For

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[1] formerly known as Federal Research Centre for Fisheries BfAFi

[2] Wageningen IMARES, Institute for Marine Resources & Ecosystem Studies, Texel

this study, FA-CC could be obtained from a single porpoise, which had been fed on a known diet and later died in captivity.

A sub-set of 34 fatty acids, including all FAs that could be derived from dietary origin, was used in the application of the QFASA model. The amounts of these FAs in the blubber were divided by the calibration coefficient and then compared against a set of FA profiles of possible prey species. The model calculates the 'best-fit' of the prey profiles to match the blubber profile. In each case the values of the individual FABES were normalised so that the sum came to 100%. Corrections were also applied for the different fat contents of different prey species.

RESULTS

Composition of porpoise samples

The number of stomachs examined each year, tabulated by area, season, sex, age class, and bycatch are summarised in Table 13a. Analogous figures for blubber samples, collected for QFASA, are listed in Table 13b.

Stomach content analysis

Remains of 36 fish and five invertebrate taxa could be recovered and identified in 120 harbour porpoise stomachs. In nine out of the 129 examined stomachs, only polychaetes and non-cephalopod mollusk remains were found, which were accounted for as secondary food. These nine stomachs were not used for subsequent analysis. The majority of the recovered prey remains could be identified to species level (Table 14), while some otoliths could only be identified to family or genus level; sandeel (*Ammodytes* spp.), dragonet (*Callionymus* spp.), herrings, shads, sardines and menhadens (Clupeidae), cods and haddocks (Gadidae), gobies (Gobiidae) and righteye flounders (Pleuronectidae). A number of otoliths that were too damaged to be identified with certainty, were classified as unspecified fish (fish-unsp.).

The number of prey taxa recorded in each stomach varied between 1 and 10 (median=2). However, 25% of the stomachs contained one, 24% two and 27% contained three prey taxa.

In stomachs from the North Sea, goby was the most frequently occurring species (33%), followed by sandeel (28%), cod (27%) and herring (25%). In the Baltic Sea, cod (51%) was the most frequently occurring species, followed by goby (38%) and herring (30%) (Table 14).

Table 13: Summary of samples in each year, by area (NS: North Sea, BS: Baltic Sea), by season (1: winter (DJF), 2: spring (MAM), 3: summer (JJA), 4: autumn (SON), by sex (F: female, M: male), by age class (calf, juv.: juvenile, ad.: adult) and by bycatch. a) Stomach analysis. Seven sample were of unknown origin, in three cases no age class could be assessed, in five cases it was not possible to determine sex and in 12 cases the by-catch status was unknown b) QFASA. One sample of unknown origin; by-catch status unknown in four samples.

a)		by area		by season				by sex		by age class			by bycatch	
Year	***n***	NS	BS	1	2	3	4	F	M	calf	juv.	ad.	yes	no
1994	**1**	1	0	0	0	1	0	1	0	0	0	1	0	1
1996	**1**	1	0	0	0	1	0	0	1	1	0	0	0	1
1997	**4**	3	1	0	0	3	1	2	2	1	2	1	1	1
1998	**14**	8	6	4	4	5	1	8	6	0	7	7	6	7
1999	**1**	1	0	0	1	0	0	0	1	0	1	0	0	1
2000	**4**	1	3	0	1	1	2	2	2	0	4	0	3	1
2001	**8**	2	5	4	1	3	0	5	3	0	5	3	3	4
2002	**6**	1	5	0	1	2	3	3	3	1	3	2	5	0
2003	**8**	3	5	1	4	2	1	5	2	1	4	3	5	2
2004	**8**	3	3	2	2	3	1	2	6	0	4	4	1	7
2005	**45**	25	20	4	17	15	9	14	29	1	24	19	6	36
2006	**25**	17	8	3	10	11	1	10	15	0	12	13	7	17
Date unkn.	**4**	0	0	0	0	0	0	0	2	1	1	1	0	2
Total	**129**	**66**	**56**	**18**	**41**	**47**	**19**	**52**	**72**	**6**	**66**	**54**	**37**	**80**

b)		by area		by season				by sex		by age class			by bycatch	
Year	***n***	NS	BS	1	2	3	4	F	M	calf	juv.	ad.	yes	no
1998	**1**	0	1	1	0	0	0	1	0	0	1	0	1	0
2000	**9**	3	6	1	2	1	5	2	7	2	7	0	6	3
2001	**16**	7	8	6	3	5	2	8	8	1	11	4	5	9
2002	**10**	2	8	1	2	4	3	5	5	3	5	2	7	3
2003	**9**	2	7	1	4	2	2	5	4	2	7	0	7	2
2004	**12**	9	3	2	4	3	3	6	6	3	6	3	0	12
2005	**25**	18	7	6	8	3	8	8	17	1	14	10	4	19
2006	**13**	8	5	1	6	5	1	6	7	2	6	5	1	12
Total	**95**	**49**	**45**	**19**	**29**	**23**	**24**	**41**	**54**	**14**	**57**	**24**	**31**	**60**

Table 14: Frequency of occurrence (%O) and overview of identified prey remains, by area (NS: North Sea, *n*=60; BS: Baltic Sea, *n*=53) and combined for all areas (NS+BS, *n*=120; including 7 samples with unknown origin).

Family	Species	Common name	No. of stomachs (%O NS)	No. of stomachs (%O BS)	No. of stomachs (%O NS+BS)
Agonidae	*Agonus cataphractus*	Hooknose	0 (0.0)	1 (1.9)	2 (1.7)
Ammodytidae					
	Ammodytes spp.*	Sandeel	17 (28.3)	4 (7.5)	21 (17.5)
	Hyperoplus lanceolatus	Great sandeel	4 (6.7)	3 (5.7)	7 (5.8)
Anguillidae	*Anguilla anguilla*	European eel	2 (3.3)	2 (3.8)	4 (3.3)
Atherinidae	*Atherina presbyter*	Sand smelt	1 (1.7)	0 (0.0)	1 (0.8)
Bothidae	*Arnoglossus laterna*	Scaldfish	1 (1.7)	0 (0.0)	1 (0.8)
Callionymidae					
	Callionymus lyra	Dragonet	4 (6.7)	1 (1.9)	5 (4.2)
	Callionymus maculatus	Spotted dragonet	2 (3.3)	0 (0.0)	3 (2.5)
	Callionymus reticulatus	Reticulated dragonet	0 (0.0)	1 (1.9)	1 (0.8)
	Callionymus spp.		4 (6.7)	1 (1.9)	5 (4.2)
Carangidae	*Trachurus trachurus*	Atlantic horse mackerel	2 (3.3)	1 (1.9)	3 (2.5)
Clupeidae					
	Clupea harengus	Atlantic herring	15 (25.0)	16 (30.2)	33 (27.5)
	Sprattus sprattus	European sprat	10 (16.7)	6 (11.3)	17 (14.2)
	unspecified Clupeidae		2 (3.3)	3 (5.7)	6 (5.0)
Cottidae	*Myoxocephalus scorpius*	Shorthorn sculpin	0 (0.0)	2 (3.8)	3 (2.5)
Gadidae					
	Gadus morhua	Atlantic cod	16 (26.7)	27 (50.9)	47 (39.2)
	Melanogrammus aeglefinus	Haddock	0 (0.0)	1 (1.9)	1 (0.8)
	Merlangius merlangus	Whiting	8 (13.3)	6 (11.3)	17 (14.2)
	Raniceps raninus	Tadpole fish	1 (1.7)	0 (0.0)	1 (0.8)
	Trisopterus esmarkii	Norway pout	0 (0.0)	1 (1.9)	1 (0.8)
	Trisopterus luscus	Pouting	2 (3.3)	0 (0.0)	2 (1.7)
	unspecified Gadidae		4 (6.7)	14 (26.4)	18 (15.0)
Gasterosteidae	*Spinachia spinachia*	Sea stickleback	0 (0.0)	1 (1.9)	1 (0.8)
Gobiidae					
	Gobius niger	Black goby	3 (5.0)	4 (7.5)	8 (6.7)
	Pomatoschistus minutus	Sand goby	5 (8.3)	1 (1.9)	6 (5.0)
	unspecified Gobiidae		20 (33.3)	20 (37.7)	42 (35.0)
Lotidae					
	Ciliata mustela	Fivebeard rockling	1 (1.7)	0 (0.0)	1 (0.8)
	Enchelyopus cimbrius	Fourbeard rockling	0 (0.0)	1 (1.9)	1 (0.8)
Osmeridae	*Osmerus eperlanus*	European smelt	7 (11.7)	0 (0.0)	7 (5.8)
Pleuronectidae					
	Limanda Limanda	Dab	8 (13.3)	1 (1.9)	9 (7.5)
	Platichthys flesus	Flounder	0 (0.0)	1 (1.9)	2 (1.7)
	Pleuronectes platessa	European plaice	1 (1.7)	0 (0.0)	1 (0.8)
	unspecified Pleuronectidae		5 (8.3)	1 (1.9)	7 (5.8)
Soleidae	*Solea Solea*	Common sole	8 (13.3)	2 (3.8)	11 (9.2)
Syngnatidae	*Syngnathus* spp.	Pipefish	2 (3.3)	3 (5.7)	5 (4.2)
Zoarcidae	*Zoarces viviparus*	Eelpout	2 (3.3)	4 (7.5)	6 (5.0)
fish-unsp.			11 (18.3)	8 (15.1)	19 (15.8)

Family	Species	Common name	No. of stomachs (%O NS)	No. of stomachs (%O BS)	No. of stomachs (%O NS+BS)
Invertebrata					
Loliginidae	*Loligo* (*Alloteuthis*) spp.	Squid	5 (8.3)	1 (1.9)	6 (5.0)
Sepiolidae	unspecified	Bobtail squid	1 (1.7)	0 (0.0)	1 (0.8)
Omma-strephidae	unspecified	Arrow squid	1 (1.7)	0 (0.0)	1 (0.8)
Crangonidae	unspecified	Shrimp	7 (11.7)	8 (15.1)	15 (12.5)
unspecified	unspecified	Crab	5 (8.3)	7 (13.2)	14 (11.7)

* either *A. marinus (lesser or Raitt's sandeel)* or *A.tobianus (small sandeel)*

Prey size could be reconstructed for 27 prey taxa (Table 15). Prey size could be estimated for 22,676 fish, representing an estimated total weight of 281.4 kg, and for 209 cephalopods, with an estimated total weight of 0.72 kg.

Numerically seen, goby (Gobiidae spp.), sandeel and sole were the most important prey. The ingested biomass was essentially made up of four species: goby (41.3%), cod (23.4%), sole (14.9%) and sandeel (4.5%). However, this picture is probably slightly biased and overestimates goby because of one case where 21,200 goby otoliths, i.e. a minimum of 10,600 individuals, were counted in the stomach. This juvenile female stranded on the Island of Sylt (North Sea) in spring of 1998. However, of the 56 porpoise stomachs where gobies (all species of Gobiidae) have been identified in total, 14 more stomachs revealed a high number of 300 to 2,200 goby otoliths. When treating this single case as outlier, the percentage by mass would be distributed as follows: cod (32%), goby (21%), sole (20%) and sandeel (6%).

Flounder, goby, cephalopods and plaice were the smallest prey items, with lengths less than 8 cm and weights less than 7 g (Table 15. Besides eel, only occurring in four stomachs, cod was found to be on average the longest (24.2 cm) and heaviest fish (180 g).

Table 15. Harbour porpoise stomachs (n=120). Mean length (cm) and mean mass (g) of prey taxon (SD: standard deviation; 95% CI: 95% confidence interval, determined by bootstrap ($_{boot}$)). ***No. of prey*** shows the no. of individuals counted per taxon. ***Estimated biomass*** is the product of mean mass and the no. of prey.

Prey taxon	Abbrev.	Length (cm) ($\bar{x}_{boot} \pm SD$)	95% CI_{boot}	Mass (g) ($\bar{x}_{boot} \pm SD$)	95% CI_{boot}	No. of prey (% total)	Estim. biomass (g) (% total)
Agonus cataphractus		10.2 ± 0.1	10.13 – 10.33	8.4 ± 0.2	8.12 – 8.61	2 (0.01)	17 (0.01)
Ammodytes spp.[a)]	Am	12.8 ± 0.6	11.75 - 13.89	6.4 ± 0.7	4.92 - 7.70	2005 (8.8)	12778 (4.5)
Hyperoplus lanceolatus	Hl	14.4 ± 2	10.06 - 17.08	9.5 ± 2.3	4.15 - 13.31	138 (0.6)	1305 (0.5)
Anguilla anguilla		38.0		98.6		4 (0.02)	394 (0.1)
Callionymus lyra	Cl	10.4 ± 2.4	5.35 - 14.87	14.3 ± 6.8	2.5 - 30.26	46 (0.2)	657 (0.2)
Callionymus maculatus		15.7 ± 0.6	15.0 – 17.0	19.7 ± 1.8	17.44 – 24.08	52 (0.2)	1023 (0.4)
Callionymus reticulatus		11.4 ± 0.2	11.02 - 11.70	13.5 ± 0.6	11.97 - 14.39	2 (0.01)	27 (0.01)
Callionymus spp.[b)]		17.1 ± 2.9	10.96 - 22.94	53.6 ± 21.3	9.96 - 97.17	103 (0.5)	5516 (2.0)
Trachurus trachurus	Tt	13.3 ± 5.1	3.5 - 24.7	51.1 ± 35.5	0.81 - 137.2	103 (0.5)	5258 (1.9)
Clupea harengus	Ch	17.1 ± 1.3	14.6 - 19.62	48.5 ± 8.9	32.77 - 67.17	226 (1.0)	10950 (3.9)
Sprattus sprattus	Ssp	10.8 ± 0.7	9.49 - 12.12	12.0 ± 2.5	7.43 - 17.25	147 (0.6)	1768 (0.6)
Myoxocephalus scorpius		10.3 ± 0.01	10.33 - 10.26	17.7 ± 0.1	17.62 - 17.8	15 (0.1)	266 (0.1)
Gadus morhua	Gm	24.2 ± 1.8	20.88 - 27.65	180.3 ± 26	131.3 - 232.58	366 (1.6)	65990 (23.4)
Merlangius merlangus	Mm	14.8 ± 1.8	11.52 - 18.57	52.6 ± 21.3	21.4 - 100.8	160 (0.7)	8414 (3.0)
Trisopterus esmarkii		9.40		7.37		1 (0.004)	7 (0.003)
Spinachia spinachia		13.5		5.2		1 (0.004)	5 (0.002)
Gobiidae spp.[c)]	Gob	5.1 ± 0.3	4.58 - 5.63	6.9 ± 0.6	5.84 - 8.0	16970 (74.2)	116414 (41.3)
Gobius niger	Gn	5.8 ± 0.1	5.52 - 5.98	2.5 ± 0.2	2.21 - 2.84	194 (0.8)	489 (0.2)
Pomatoschistus minutus	Pm	4.7 ± 0.6	3.55 - 5.87	1.9 ± 0.7	0.86 - 3.26	586 (2.6)	1119 (0.4)
Ciliata mustela		12.9 ± 0.4	12.12 - 13.65	18.2 ± 1.8	14.74 - 21.75	5 (0.02)	91 (0.03)
Osmerus eperlanus	Oe	9.0 ± 2.0	5.24 - 12.72	10.9 ± 4.5	3.43 - 19.97	238 (1.0)	2601 (0.9)
Limanda limanda	Ll	15.5 ± 1.5	12.69 - 18.32	51.3 ± 15.1	25.53 - 84.41	59 (0.3)	3027 (1.1)
Platichthys flesus		3.2 ± 0.2	2.89 - 3.53	0.9 ± 0.1	0.77 - 1.09	25 (0.1)	23 (0.01)
Pleuronectes platessa		8.7 ± 0.2	8.29 – 9.06	7.1 ± 0.4	6.36 – 7.87	3 (0.01)	21 (0.01)
Solea solea	Sso	15.3 ± 1.1	13.19 – 17.59	35.55 ± 7.4	21.75 - 49.31	1181 (5.2)	41985 (14.9)
Zoarces viviparus	Zv	14.6 ± 2.6	9.66 - 19.75	28.4 ± 10.6	5.62 - 49.69	44 (0.2)	1248 (0.4)
Cephalopoda	Cep	5.4 ± 0.2	5.14 – 5.67	3.4 ± 0.3	3.04 – 3.83	209 (0.9)	717 (0.3)
Total						**22885**	**281088**

[a)] regression *A. marinus*

[b)] regression *C. lyra*

[c)] regression *P. minutus*

(all Leopold et al. 2001)

Multivariate analysis

Results of the CCA indicated that both factors, year and season, had a significant effect on harbour porpoise diet ($p < 0.001$; p values based on 1000 permutations).

In order to examine the effects on diet composition for each factor in more detail, univariate analyses were used. Marked seasonal differences are apparent, both within species and between species (Fig. 15). Differences are significant when the median is outside the lower and upper quartile of another boxplot. A significantly higher mass of sandeels were consumed in spring and autumn in contrast to summer. The same pattern holds for herring. Porpoises consumed more cod in summer than in other seasons (Fig. 15).

When estimating the overall consumed biomass by season, porpoises consumed more mass in spring (36.8%) and summer (27.6%) than in autumn (15.6%) and winter (19.9%).

The inter-annual differences are elucidated in Fig. 16. When comparing the time period 1994-2001 with the period 2002-2006, a shift in the relative contribution of prey species to porpoise diet is visible. In the former period, goby, sole and dab were more important; especially the relative importance of goby decreased from 49% to 23%. In the more recent period sandeel, herring, sprat and whiting appeared to contribute more to the diet. However, cod appeared to be an important prey species throughout the study period: in the period 1994-2001 with 31% and in 2002-2006 with 38%. By examining the last five study years in detail, it is obvious that distinct species varied in contribution to diet on a yearly basis (Fig. 16). Sandeel peaked in 2004 (40%) and 2006 (28%), herring in 2002 (43%). The contribution of cod to porpoise diet was highly important in every year, ranging from 68% in 2003 to only 31% in 2004, the year when sandeel peaked.

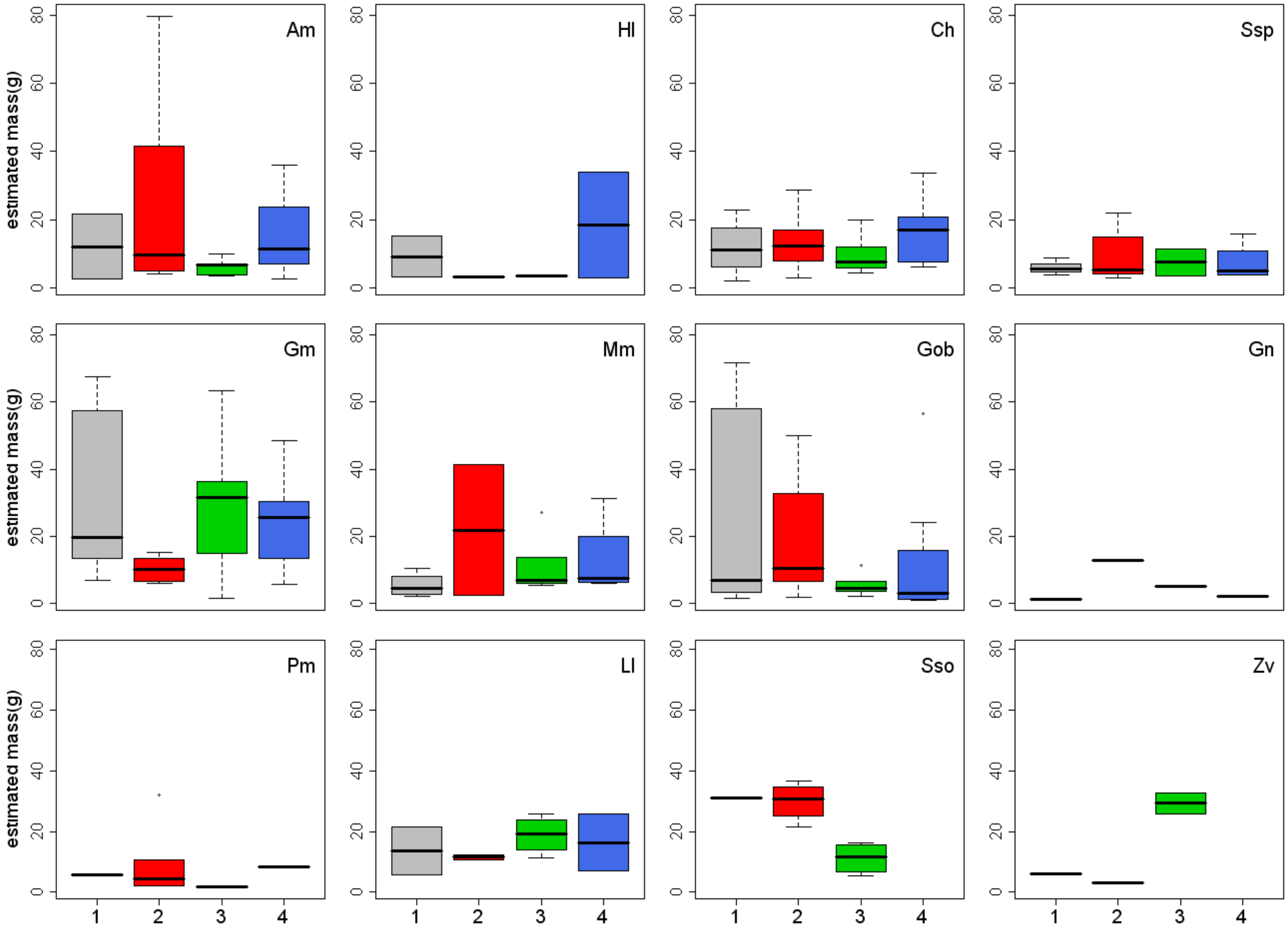
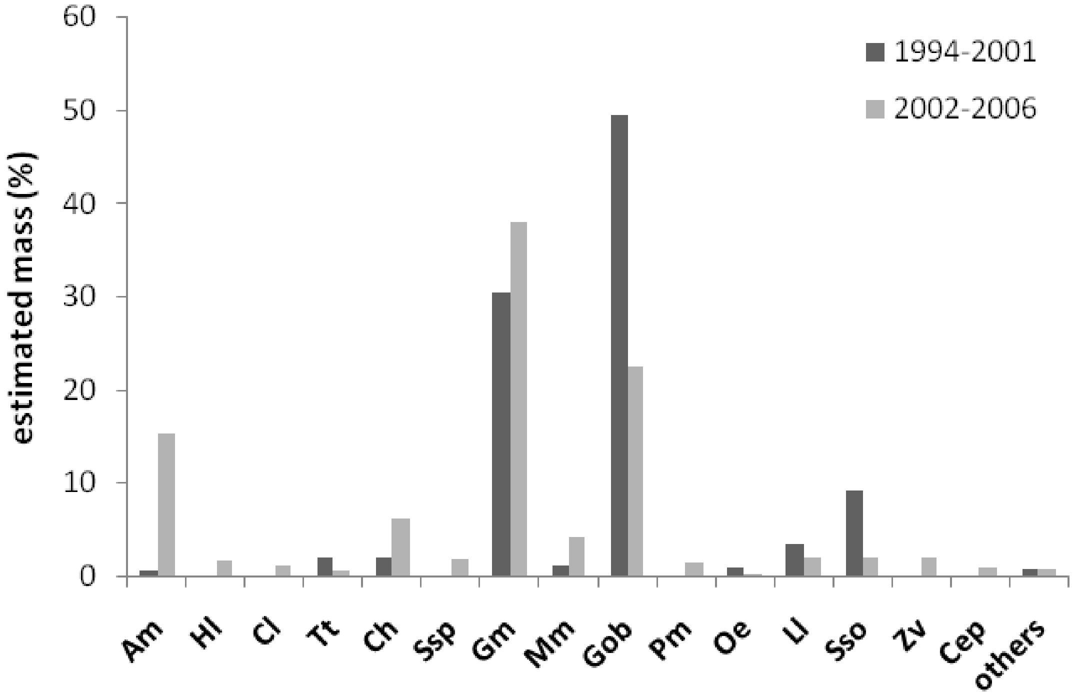


Figure 15. Stomach content analysis. Box plots of square root transformed estimated mass ingested by 107 harbour porpoises per season (1: winter (grey), 2: spring (red), 3: summer (green) and autumn: 4 (blue). Median is indicated as thick black line, 25% and 75% quartiles define the hinges of the box. See Table 15 for abbreviation of fish species.



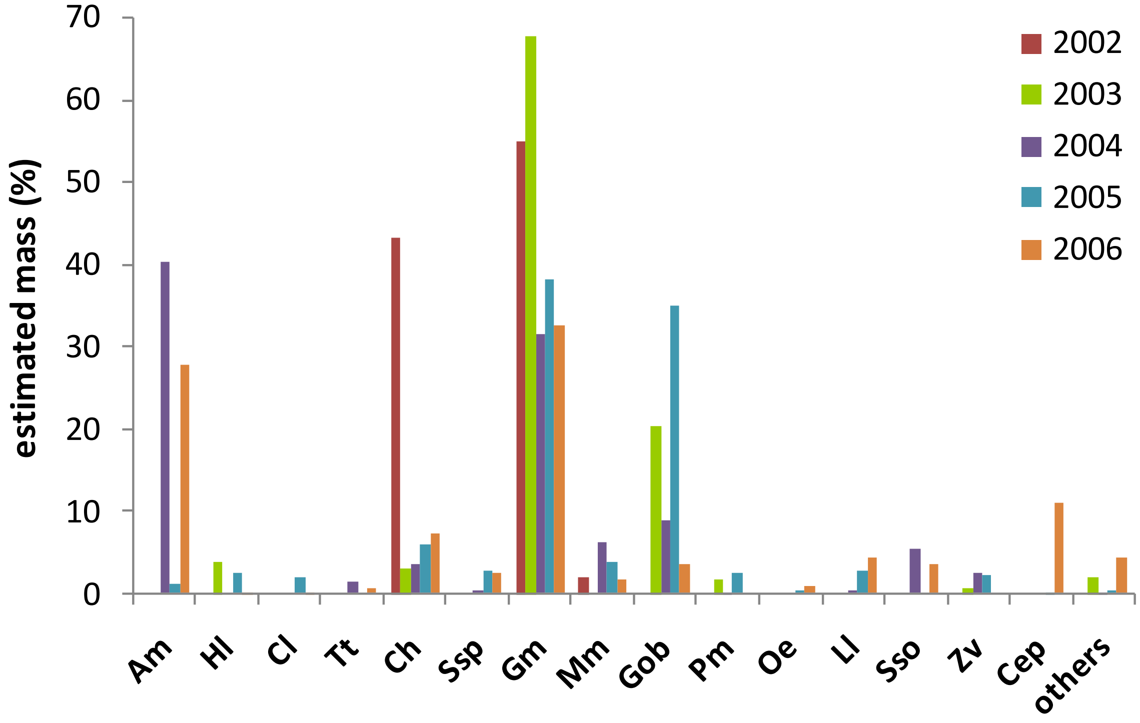


Figure 16. Stomach content analysis. Inter-annual differences in contribution (by mass in %) of prey species to harbour porpoise diet, between two distinct time periods (upper graph; n=107) and by year between 2002 to 2006 (lower graph; n=79). Only prey species with a contribution of >1% are shown; remaining species were grouped in 'others'. Abbreviation of prey species are found in Table 15. See Table 13a for composition of porpoise samples.

QFASA

The results of the calibration coefficient and the subsample of 34 FAs used for QFASA modelling are found in the appendix (Table 1A).

Table 16 shows the composition of the prey database and indicates how many individuals by species (by area) were analysed concerning their FAs and then included in the QFASA modelling.

Table 16: Composition of the prey database for QFASA and mean lipid content of prey. If not indicated, see scientific names in Table 14. NS: North Sea, BS: Baltic Sea, SD: standard deviation

Prey taxon	No. of specimens		Mean lipid content (%)	SD
	NS	BS		
sandeel (*Ammodytes* spp.)	41	10	3.67	2.31
horse mackerel	10	0	5.26	1.81
mackerel (*Scomber scombrus*)	29	0	8.86	3.84
anchovy (*Engraulis encrasicolus*)	5	0	2.19	0.51
herring	20	20	4.93	2.71
sprat	0	20	6.05	1.65
cod	7	10	1.61	0.29
whiting	18	6	1.69	0.69
goby (Gobiidae spp.)	10	0	2.06	0.52
smelt	9	0	2.76	0.59
dab	10	0	2.88	0.98
flounder	16	0	2.01	0.83
plaice	21	0	1.44	0.48
sole	9	0	1.22	0.33
shrimp (*Crangon crangon*)	10	0	1.67	0.51
Total	**215**	**66**		

Figure 17 shows the mean diets as predicted by QFASA, using a prey database consisting of 14 fish and 1 crustacean species (Table 16). It was predicted that porpoise diet in the North Sea consisted mainly of dab (26.6%), sprat (22.2%) and herring (15.9% by weight). For the Baltic Sea it was predicted that mainly herring (18.3%), shrimp (17.7%) and sprat (17%) dominated the diet.

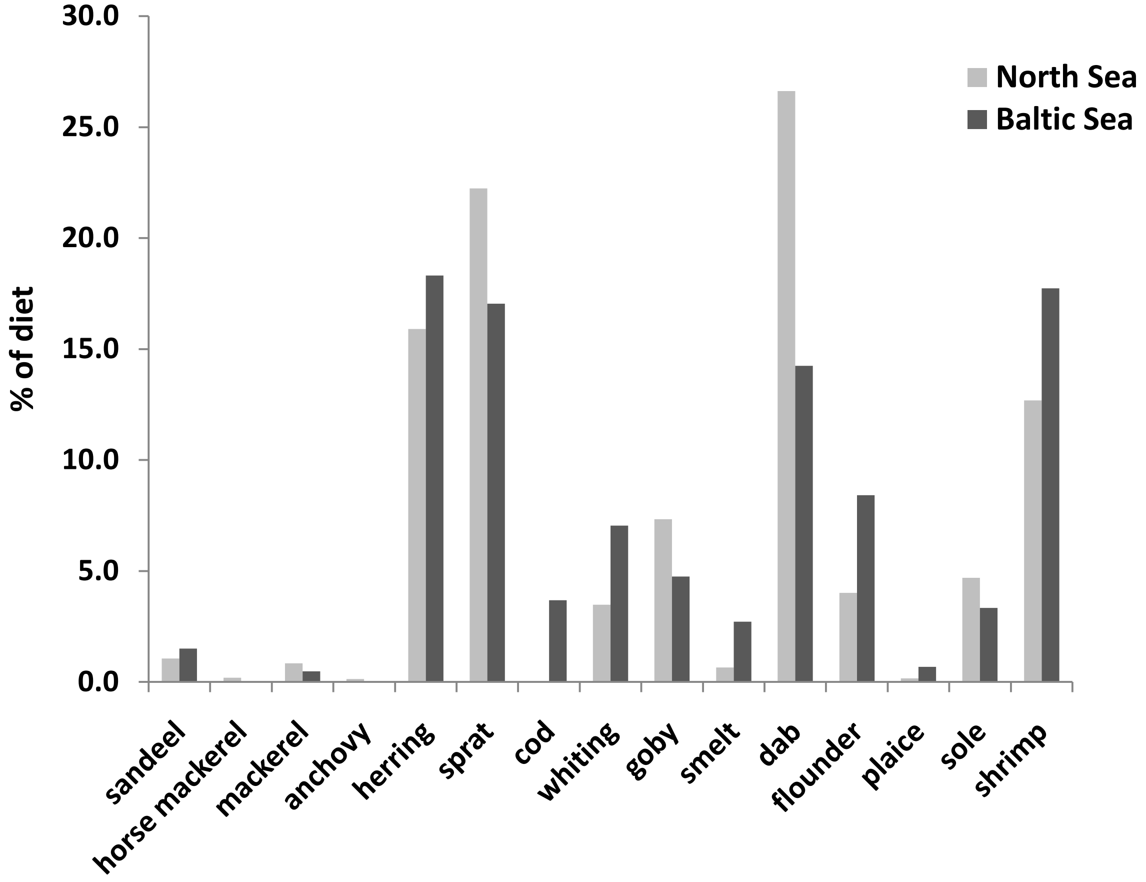


Figure 17. QFASA. Diet of harbour porpoises in the North and Baltic Sea estimated using quantitative fatty acid signature analysis. Values are mean percentages of diet by wet weight for all prey species existing in the prey database. Data from all years were combined. See Table 13b and Table 16 for composition of samples.

In 34 cases, both QFASA modelling and stomach content analysis (SCA) could be performed on the same porpoise individuals (Fig. 18). In direct comparison, SCA identified goby, cod and sandeel to be far more important parts of the diet than QFASA predicted. In turn, QFASA predicted herring, sprat, dab and flounder to be more important constituents than found out during SCA. Both methods were comparable concerning the contribution of whiting, smelt and sole.

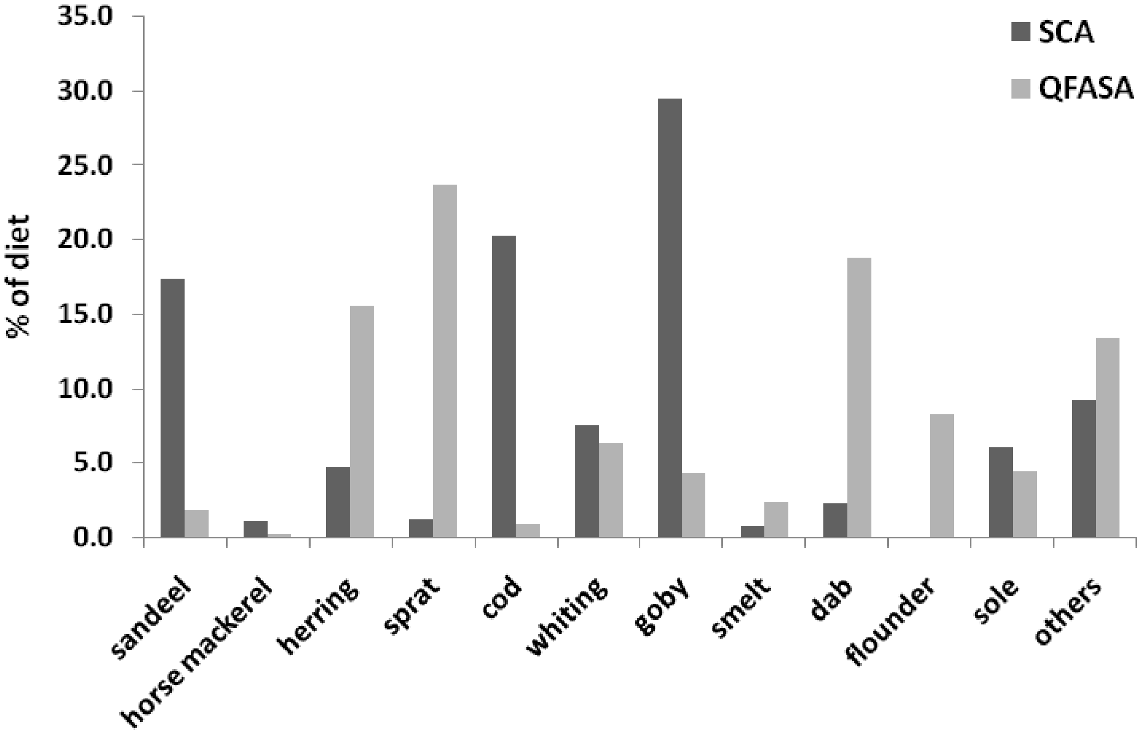


Figure 18. Comparison between stomach content analysis (SCA) and QFASA. Sample size (n=34) is restricted by the application of both methods on the same porpoise individual and by the occurrence of prey species in SCA and QFASA prey database (remaining species were grouped in 'others', resp.). For SCA: in category 'goby', Gobiidae spp., *G. niger* and *P. minutus* were pooled.

DISCUSSION

Stomach content analysis

Limitations and sampling issues

The sample size of 120 stomachs in the present study is a fairly large data set to investigate general patterns as it was found that a minimum of 35-71 stomachs is required to be confident that all common prey species will be found (Börjesson et al. 2003). However, it has to be noted that sampling in this study encompassed several years (see below) and different areas. Sampling from stranded animals is inevitably opportunistic (Pierce & Boyle 1991). Biases can be introduced by the predominance of stranded animals as such animals may not be representative for the rest of the population. In this study, more than 50% of the analysed stomachs were derived from stranded porpoises and 29% could be determined as bycatch (besides 21% of unknown status). However, the estimated number of undetected bycatch among the catalogued strandings is suspected to be high (Siebert et al. 2006).

Stomach contents can only provide a representative estimate of the diet for a limited time before the death of the animal and thus only for a spatially limited foraging area. From data on passage rate of otoliths, (Prime & Hammond 1987)Prime & Hammond (1987) estimated that grey seal faeces indicate diet of a radius of up to 100 km. It is unknown which radius would correspond to when using stomach contents.

The erosion of otoliths during digestion has been addressed in the present study by deriving species specific correction factors. The values are within the range of other studies (Tollit et al. 1997); as far as this is possible to compare as most studies on digestion rate of otoliths are based on the analysis of faeces of pinnipeds. However, it was found that digestion of the recovered otoliths in faeces could result in underestimation of the original fish size by an average of 48% (Tollit et al. 1997). Another limitation and a factor that can never be ruled out is that small, fragile otoliths break early in the digestion process and, thus, cannot be recovered or are completely digested. Otoliths from some species (e.g. Atlantic salmon) are quickly digested and are rarely found in stomach or faeces contents (Pierce & Boyle 1991). Analysis may, thus, be biased in favour of species with large and robust hard parts (e.g. cod) (Tollit et al. 1997, Bowen 2000). However, in the present study a high number of small otoliths like those from herring and goby could be successfully retrieved and could be seen as an index for abundant occurrence of this species. In addition to possibly underestimating otolith size, also the number of recovered otoliths underestimates the number of ingested otoliths and therefore the number of ingested prey. Bowen (2000) determined the mean prey number correction factor to be as high as 4.8 for sprat, 3.6 for sandeel and 3.0 for herring. However, as these factors were derived from hard parts recovered in faeces of pinnipeds, it is not clear whether these are readily transferable to hard parts recovered from stomach contents. Kastelein et al. (1997) recorded the passage time of carmine red dye in porpoises and found that mean initial passage times of porpoises fed on herring and sprat varied between 143 and 196 minutes. Examination of the stomach content of a porpoise, which died 30 minutes after eating several thawed herring, showed that only bones remained in the forestomach (Kastelein et al. 1997). They concluded that the porpoise has one of the shortest mean passage time in comparison to other mammals (marine & terrestrial) which could be due to a high metabolic rate and because fish is easy to digest (Kastelein et al. 1997).

Overall diet composition

Harbour porpoises investigated in this study exhibited a broad diet that is similar to that found in other regions of the North and Baltic Sea (Börjesson et al. 2003, Santos & Pierce 2003, Santos et al. 2004). However, a lot of the inventoried fish taxa in the present study occurred in a few porpoise stomachs only and a small number of benthopelagic and demersal fish species contributed substantially to the overall diet: goby, cod, sole and herring together formed >80% of the calorific contribution.

In comparison to earlier studies in German waters, the most striking finding is that cod form a more important part of the porpoise diet in the present study. This is, however, not supported by QFASA (see below). Benke et al. (1998) reported that cod contributed with a maximum of 15% (by weight). The prey spectrum with 13 fish species was also lower than in this study. The importance of goby as prey for porpoises could be confirmed in this study. However, Benke et al. (1998) reported that goby occurred mainly in porpoise stomachs from the Baltic Sea (%O; Baltic Sea=53% *Pomatoschistus* spp. and *G. niger*) whereas this study showed that goby occurred in the same frequencies (%O: Baltic Sea=47%, North Sea=47%; all Gobiidae). It is often suspected that small prey, like gobies, would appear in the stomach as a result of secondary predation; when fish that do feed upon gobies (like cod) are also found in the same stomach. However, direct ingestion of gobies has been observed in harbour porpoises in the Normandy and it was found that gobies made up more than 95% of prey (De Pierrepont et al. 2005). Therefore, it is assumed that gobies are important primary prey.

The estimated size for cod and herring in this study was compared with others: Börjesson et al. (2003) estimated cod to have a mean length of 28.1 cm ± 5.8 SD and a mean mass of 208 g ± 11.9 SD, which is a bigger size than estimated in this study (Table 15). The same holds for herring (Börjesson et al. (2003): 26.1 cm ± 4.9 SD, 163 g ± 88 SD). In comparison to Benke et al. (1998), however, the lengths of the fish were similar. They reported that length of herring ranged between 15-21 cm.

Inter-annual differences

The data suggest a change of relative importance of some prey species in the course of the study years. Besides cod, an important species throughout the study period, the flatfish species, sole and dab, as well as goby proved to be more important in porpoise diet before 2001. Goby even provided more mass than cod in the period 1994-2001. Herring appeared to be more frequently consumed in the period 2002-2006 than before. However, it has to be noted that the number of sampled stomachs was not equally distributed between the study years. The bulk of stomachs was sampled in the most recent years, i.e. 2005 and 2006. Yet, a higher number of stomachs has also been sampled in 1998 and by pooling the years 1994-2001 and 2002-2006 a reasonable comparison could be made. It also has to be noted that samples from North and Baltic Sea were pooled for the analysis of inter-annual and seasonal differences. A further stratification of the sample size, e.g. by location, would have resulted in low subsamples. We explored, however, the contribution of prey species when stratifying by location and could not detect a major change in pattern.

Especially the results for Atlantic cod could be very interesting as many stocks, especially in the North Sea, have declined significantly in abundance and biomass over the last 20 years and are said to be close to collapse (Christensen et al. 2003). Although cod showed a frequency of occurrence of 51% in the Baltic Sea in contrast to 27% in the North Sea, consumed masses were also high in the North Sea. Harbour porpoises obviously still find cod to prey on. Estimated size suggests that cod eaten by harbour porpoises is much smaller than what is commercially fished. The minimum landing size for cod in ICES subarea IV and divisions IIIa and VIId is 35 cm; in Denmark it is 40 cm (ICES 2007b). Recent studies showed concentrations of mature cod in the study area of the present study, namely in the German Bight (Fox et al. 2008).

Seasonal differences

Diets of harbour porpoises in the study area showed marked seasonal changes in prey composition and importance. In general, the total ingested prey mass was highest in spring and summer, lowest in autumn and increased slightly in winter. This corresponds well with the demanding life history of harbour porpoises that imposes very high energetic demands, especially during the reproduction season from May to August (Read & Hohn 1995, Lockyer et al. 2003, Lockyer 2007). The mass of ingested sandeel was high in spring and autumn, but lower in summer, possibly reflecting the energy content and availability of sandeels (Hislop et al. 1991). Around March to April, one year and older sandeel emerge from the bottom to feed on pelagic zooplankton during daytime, but bury in sand during the night. In June to July, the majorities of older sandeel stop feeding and go into hibernation, whereas young-of-the-year sandeel continue to feed until October before hibernating (van der Kooij et al. 2008).

Significantly lower mass of cod were consumed in spring. It could be possible that porpoises switched from sandeel and herring in spring to a more cod dominated diet in summer. These prey species, especially herring, show large seasonal variation in fat, and thus energy content (Hislop et al. 1991, Pedersen & Hislop 2001). Porpoises could still prey upon high numbers of sandeels but probably retrieve more energy from cod. Santos et al. (2004) reported a change from sandeel in quarters 2 and 3 to gadoids in quarters 1 and 4. However, the size of ingested sandeels was smallest in quarter 3 (here: summer) when high numbers of 0-group sandeels become available (Santos et al. 2004). In this study sandeel were recovered from a similar number of stomachs in spring and summer (8 and 7 resp.), but numbers and individual mass of sandeel were lower in summer. It is thought that sandeels are ideal prey for porpoises in spring and summer as this is the time when they form large shoals in the water column. These swarms are of high importance in the food web of the North Atlantic (Wright et al. 2000). In autumn and winter most sandeels are buried, except of a short spawning period in December and January (Wright & Begg 1997, Bergstad et al. 2001). In this study all sandeels from the winter season were recovered from porpoises stranded in January, which could be a hint that porpoises exploit that short period of matured sandeels.

Quantitative fatty acid signature analysis - QFASA

QFASA has been shown to provide accurate estimates of diets of seals, polar bears, mink and seabirds (Iverson et al. 2004, Iverson et al. 2007, Thiemann et al. 2008). The present study demonstrated the successful application of QFASA for porpoise diet studies. However, QFASA predicted a different picture than the stomach content analysis. This could be due to various limitations. To begin with, this QFASA exercise should be seen as a pilot study: this is one of the first studies that applies this technique to porpoises and it is the first study that determines a calibration coefficient for the harbour porpoise. The latter is the first limitation that needs to be discussed as the weighting factor originates just from a single porpoise (female, juvenile). Ideally, it would be preferred to use several animals during long-term diet studies but it is not allowed to collect full depth blubber (biopsy) samples from porpoises in captivity in Europe. Another limitation is the prey database. We started with quite a number of different species but as shown by the results of the stomach content analysis a wide range of different species are consumed by the porpoise. If an important prey species is not present in the database, it obviously cannot be detected in the diet. For a lot of fish species, e.g. herring, the lipid content cycles seasonally (Hislop et al. 1991, Pedersen & Hislop 2001) and is also dependent of the size and maturity status. Ideally, a prey database would consist of an adequate sample size for each prey species to allow statistical evaluation of within- and between-species variability; e.g. Iverson et al. (2004) used a database of 28 prey species (n= 5,954 individuals). In future, it is envisaged to establish a public prey database in a joint venture of various institutions that work on marine mammal diet in the North and Baltic Sea area and thus enlarge FA signatures of (whole) prey.

Another important limitation to discuss is the storage of blubber samples and the oxidation of FA that could occur during prolonged storage. Most FA studies use blubber biopsy samples (e.g. Hooker et al. 2001, Walton et al. 2007, 2008). The blubber samples analysed in this study were stored frozen up to 5 yr, one sample even up to 7 yr. In these cases it is important to extract lipids from a core taken from the centre of the original sample (Budge et al. 2006) as has been done in this study. Learmonth (2006) reported no evidence of FA oxidation in the core of blubber of harbour porpoises stored at -20°C for 566 d and Meynier et al. (2008) analysed blubber samples of sea lions that were stored for 5 yr and did not report any problems associated with storage. The same holds for the samples used in this study, where no irregularities could be reported during lipid extraction (S. Budge, pers. comm.).

Due to a limited sampling size the direct comparison of QFASA and SCA could only be performed in 34 cases. Both methods agreed on the importance of pelagic schooling fish like herring and sprat. However, the contribution by weight of these species varied substantially. One reason for this could be a massive underestimation of herring and sprat in SCA, as otoliths of these species are difficult to recover. In contrast, SCA suggested cod (having robust otoliths) to be a very important part, whereas the contribution of cod in QFASA was outcompeted by the high proportion of herring and sprat as well as probably dab. A recent study, using stable isotope analysis of predators and their prey, showed a similar picture: porpoises in the southern North Sea occupy a trophic position of 3.4 reflecting a higher amount of zooplanktivorous fish in its diet and a lesser amount of cod and other gadoids as previously thought (Das et al. 2003). Another, or additional explanation, could be the different 'time-frame' that both methods cover. In a way, it is suspected that both methods differ. SAC, describing the last meal of the dead animal, can only provide inference on the more local fish community, whereas QFASA integrates dietary information over a longer time period. This is clearly an advantage of this new method. From studies on distribution and abundance it is known that harbour porpoises conduct seasonal movements within the study area and beyond. It has been suggested that porpoises move from the southern North Sea to the north-eastern area of the German EEZ during late spring (see chapter III). Herring abundance is suspected to be higher in the southern North Sea than in the northern part of our study area. If porpoises fed upon herring in the southern North Sea, e.g. in Dutch waters where the increase in herring has been reported, and later strand at the northern German coast, the distinct FA signature of herring should still be present in the blubber.

In any case, the reasons for the observed differences between both methods are speculative at the moment. To be more precise, the prey database needs to be enlarged and more direct comparisons are needed between QFASA and SCA.

It has been shown that the diet of harbour porpoises in German waters is dominated by a few fish species. The importance of herring in the diet, as hypothesised in the introduction should has been increased, shows a trend for such an increase in the recent years and is even more pronounced when only considering the results of the QFASA study.

ACKNOWLEDGEMENTS

This study has been funded by the German Federal Agency for Nature Conservation (BfN). We thank S. Budge and her team from Dalhousie University (Halifax) for FA analysis. Thanks to all people involved during necropsies at the FTZ for collecting stomachs and blubber samples. We are grateful to Fjord & Belt Centre and the Fisheries and Maritime Museum

Esbjerg for assistance during collection of bycatches in Denmark. We thank S. Brasseur and IMARES (Texel) for enlarging the prey database for QFASA. We would like to thank the Johann Heinrich von Thünen Institute for the possibility of collecting fish samples during their research cruises. Thanks to Denise Risch, Linn Lehnert and Helena Herr for collecting fish samples and to Sven Adler for assistance with R.

APPENDIX

Table A1: Overview of quantified fatty acids and their calibration coefficients (CC) estimated for the harbour porpoise. * dietary FA used in QFASA modelling

Fatty acid	CC
12	7.03
13	2.09
14	1.59*
14:1n-9	0.44
14:1n-7	3.25
14:1n-5	10.68
iso15	1.78*
anti15	5.50*
15	1.11*
15:1n-x	3.49
iso16	3.04
16	0.56*
16:1n-11	0.61
16:1n-9	2.64
16:1n-7	2.30
16:1n-5	1.20
16:2n-6	1.05*
anti17	1.17*
16:3n-6	0.93*
16:2n-4	0.71*
17	0.75*
16:3n-4	1.15*
17:1n-x	1.64*
iso18	1.32
16:4n-1	0.74
18	0.55*
18:1n-13	0.95
18:1n-11	42.12
18:1n-9	1.15*
18:1n-7	0.73*
18:2d5,7	0.05
18:1n-5	4.53
18:2n-6	0.54*
18:2n-4	0.32
18:3n-6	0.69*
18:3n-4	0.53
18:3n-3	0.46*
18:3n-1	0.64
18:4n-3	0.31*
18:4n-1	1.13
20	0.75*
20:1n-11	11.01*
20:1n-9	3.63*
20:1n-7	0.46*
20:2n-6	0.32*
20:3n-6	0.57*
20:4n-6	0.42*

Fatty acid	CC
20:3n-3	0.26*
20:4n-3	0.80*
20:5n-3	0.28*
22:1n-11	4.54*
22:1n-9	0.62*
22:1n-7	0.49
21:5n-3	0.47*
22:4n-6	0.70
22:5n-6	0.49
22:4n-3	1.18
24	0.16
22:5n-3	1.65*
22:6n-3	0.38*
24:1n-9	0.30

General conclusion

This thesis aimed to characterise harbour porpoise habitat in German waters by combining field studies and model exercises in an interdisciplinary approach. Investigations on abundance (chapter I & II), seasonal distribution and focal areas (chapter III), effects of human activities (chapter I & III), porpoise-habitat modelling (chapter IV) and feeding ecology (chapter V) were presented. Addressed gaps in knowledge could be filled and understanding of harbour porpoise ecology in German waters could be improved.

Each of the five chapters provides an important keystone to understand the complete picture of harbour porpoise habitat. In the following, a synthesis is given that addresses the following questions:

1) Is it possible to infer on seasonal movements of harbour porpoises in the North Sea?
2) Could these movements be linked to movements of their preferred prey?
3) Could the porpoise-habitat model be improved by including aspects of the ecology of preferred prey species?

(1) Seasonal movements in the North Sea

Within a species range, there may be regular changes in areas of occurrence as biological and ecological requirements change (Forcada 2002). As migration is defined as a seasonal change between two geographic locations, that is persistent and more or less rectilinear (Stern 2002) like in mysticetes, I use the term 'movement' in the following to describe the seasonal change in harbour porpoise distribution. The seasonal movement of harbour porpoises in the North Sea are not well known. It is generally assumed that inshore/offshore movements and movements parallel to the shore occur (Reijnders 1992, Bjørge & Tolley 2002). Tag data from the Bay of Fundy (Canada) suggested that seasonal movement patterns of individual harbour porpoises are not temporally coordinated migrations, but that the observed seasonal decline is the result of a gradual net movement of porpoises into a wider geographic region (Read & Westgate 1997). The results of this thesis suggest that harbour porpoises move to distinctly different areas on a seasonal basis. However, based on results of this study it is not possible to say much about distribution patterns outside the study area.

At the moment, we know that harbour porpoises move into German waters in early spring, reach maximum numbers in early summer and start moving out of the study area in autumn (chapter III). It is not yet possible to infer on the distribution and density in winter as only a few surveys could be conducted during the winter months. Porpoises were still present in the area of Sylt Outer Reef, but sighting rate was lowest in comparison to other seasons (A. Gilles, unpubl. data). Some individuals are possibly resident and remain in the German Bight but the significant decline in density in autumn (chapter II) suggests a temporally coordinated movement.

In the following, I attempt to derive a general picture of seasonal movements in the North Sea (i.e. beyond national borders), based on results of this study and published results of other countries. Based on systematic observations from coastal sites, it is known that harbour porpoises are winter/early spring visitors in Dutch coastal waters, with a peak from December to March and then disappearing around April (Camphuysen 2004). It is very likely that our observed hot spot around Borkum Reef Ground in spring (chapters III & IV) is actually an extension of a larger aggregation area that extends into Dutch waters. In June, porpoises are seldom reported in Dutch waters, indicating a movement away from the Dutch coast in early summer (Camphuysen 2004). This picture is also supported by our habitat model predictions in summer that, when transferred to a more regional scale, predicted a hot spot offshore the West Frisian Islands in the southern North Sea (chapter IV). Another important aspect of the habitat model predictions in summer is that, on a regional scale, the large aggregation in the north-east, i.e. on the Sylt Outer Reef, is probably extending into Danish waters (chapter IV). This is supported by results from Denmark that revealed a high density area just north of Sylt Outer Reef (Teilmann et al. 2008).

For spring and summer, I could present suggestions for movements and aggregations of harbour porpoises beyond national borders, by integrating information from Denmark and the Netherlands. The question remains where individuals move to in autumn. They have obviously partly left German waters at that time and Denmark reported lower densities in the southern Danish North Sea as well (Teilmann et al. 2008). In the Netherlands porpoises arrive around October (Camphuysen 2004). Some animals could have moved south, but the increase in Dutch waters does not mirror the high summer densities estimated in our study area. It is known that harbour porpoises are able to cover hundreds of kilometres in a relative short time (Read & Westgate 1997). They could also have moved north-west to deeper waters and/or west towards the east coast of the UK. Peak numbers of sightings and individuals occur in August and September off eastern England, with a secondary peak from February to March. In East Scotland, peak numbers occur in February and March and from August to December (Evans et al. 2003). Thus, numbers peak in the UK at times when densities are low in our waters and could point to a gradual east-west movement in autumn.

(2) Seasonal movements in relation to prey availability

Seasonal movements of top predators are believed to be related to prey availability (Read & Westgate 1997), although behavioural factors such as social interactions influence cetacean distributions as well (Redfern et al. 2006). However, predictable resources are important for the harbour porpoise being one of the smallest cetaceans with a relatively high metabolism and limited energy storage (Kastelein et al. 1997, Koopman 1998). Thus, it is assumed that the porpoise must be able to optimise food energy resources. Large-scale migration events of pelagic fish in the North Sea are usually linked to spawning and feeding but may also be triggered by seasonal changes in water temperature due to inflows, summer warming or winter cooling (Daan et al. 1990). Dab, for instance, are known to move from the relatively shallow Wadden Sea regions towards the deeper areas of the central German Bight at the onset of winter (Hinz et al. 2005). Herring is best studied concerning its seasonal migration in the North Sea. Herring stops feeding in July and gradually moves, aggregated in large pre-spawning schools, towards the east coast of Scotland and England (Maravelias 1999). Thus, it may be that porpoises from our study area follow the seasonal migration of herring or, in turn, follow other piscivorous fish that feed upon herring. In the Bay of Fundy (Canada) it has been shown that the northward migration of harbour porpoises in summer followed by southward movements in autumn may be related to the migration of Atlantic herring (Gaskin & Watson 1985, Trippel et al. 1999). During years of low herring abundance, low harbour porpoise entanglement rates were observed (Trippel et al. 1999). This suggests that porpoise movements matched the migratory behaviour of one of their preferred prey species. However, as long as no satellite transmitters have been attached to a large number of individuals dwelling in the North Sea, it will not be possible to get a complete insight into seasonal movements and the causes behind these movements.

(3) Link between porpoise-habitat model and ecology of prey

In chapter IV, results of the habitat modelling exercise were presented. Most of the variance could be explained by the hydrographical parameter 'residual currents' and proxies for primary production and fronts (chlorophyll and nutrients) as well as the interaction 'distance to coast/water depth'. Fish are attracted to areas with high concentration of food associated with productive waters (Bellido et al. 2008). Cod juveniles, which is the age class that is consumed by harbour porpoises (chapter V), are often observed in zones where coastal water masses meet water of oceanic origin and where hydrographic fronts might be established (Munk et al. 1995). The same holds for herring that prefer areas adjacent to frontal zones where zooplankton production is probably greatest (Maravelias et al. 2000a). However, static ecogeographic variables such as bathymetry are also important for fish distribution (Maravelias et al. 2000b, Giannoulaki et al. 2005). It is, thus, not unsurprising that these predictors were selected by our models. All selected habitat descriptors have to be seen as proxies for the harbour porpoise to locate areas with abundant food at the same time as fish distribution patterns are not controlled by single but are influenced by a variety of biotic and abiotic factors, especially temperature, salinity and food availability (Rose 2005). At this point one has to make clear which spatial scale is in focus and that the strategies of top predators for locating foraging grounds and prey concentrations undoubtedly varies with the spatio-temporal scale involved - from long-distance seasonal migrations over weeks down to minute-by-minute selection of the optimal prey patches within a restricted area. An excellent contribution by Kenney et al. (2001) describes a multi-scaled, hierarchical, conceptual model of North Atlantic right whale (*Eubalaena glacialis*) migratory and foraging strategies; starting at the basin scale (1000's of km), over regional scale (10's to 100's of km) and meso-scale (1-10 km) down to micro-scale (cm to 10's of metres). It is obvious that the strategy of a small odontocete, like the harbour porpoise, cannot be compared with that of a large mysticete, like the right whale, that migrate annually between high-latitude feeding grounds and low-latitude calving and breeding grounds (Kenney 2002). However, the general idea that different mechanisms work at various spatio-temporal scale connects the ecology of both species. In this thesis, I attempted to explain harbour porpoise distribution and aggregation on a meso-scale. Prey distribution and density could not be incorporated in the models due to a lack of data on appropriate temporal and spatial scales. Although it is often suggested that habitat models could be greatly improved by including such data (Redfern et al. 2006), I assume that this would not be the case for harbour porpoises, at least on a meso-scale. Even though it has been shown that the harbour porpoise prefers to prey upon a few fish species (chapter V), it cannot be designated a true specialist. It is rather a generalist predator (Santos & Pierce 2003), but a specialist in that way that prey species have to be rich in energy, which is attributable to the high metabolism and the limited energy storage. In order to incorporate prey data in habitat modelling, fish data should be available for size classes of species preyed on by harbour porpoises, together with a precise account of seasonal energy densities and seasonal distribution patterns of prey, matched to the time of porpoise surveys. However, one also has to account for limitations within studies on diet of harbour porpoises, as shown in chapter IV.

OUTLOOK

It is important to keep on monitoring harbour porpoise distribution in the North and Baltic Seas. Not only because human activities target offshore areas, but also as marine NATURA 2000 areas were designated that demand a regular monitoring. This thesis provided valuable insights of core areas of harbour porpoises in German waters and an understanding of factors that influence porpoise distribution. In future, porpoise-habitat models could be extended by including disturbance factors (e.g. anthropogenic noise) and food competitors (e.g. harbour seals). Further insights in harbour porpoise ecology could be obtained by analysing movement patterns at a finer spatio-temporal scale using telemetry techniques (e.g. tracking with satellite tags).

Although this thesis proved to be a good start in interdisciplinary work, by drawing information from the field of marine mammal science, oceanography, fishery biology and mathematics, this interdisciplinary approach should be enhanced in future in order to account for the complex dynamics and interactions of the marine environment with marine life.

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ABBREVIATIONS

ASCOBANS	Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas
BRG	Borkum Reef Ground
BSH	Federal Maritime and Hydrographic Agency
EEZ	Exclusive Economic Zone
ESW	effective strip-width
g(0)	probability of detecting an object on the transect line
GAM	Generalised Additive Model
GAMM	Generalised Additive Mixed Model
FA	Fatty acid
ICES	International Council for the Exploration of the Sea
IWC	International Whaling Commission
MPA	Marine protected area
QFASA	Quantitative fatty acid signature analysis
SCANS	Small Cetacean Abundance in the North Sea and adjacent waters (1994)
SCANS II	Small Cetaceans in the European Atlantic and North Sea (2005)
SCI	Site of Community Interest
SAC	Special Area of Conservation
SOR	Sylt Outer Reef
RMSEP	Root mean squared error of prediction
TTS	Temporary threshold shift

DESCRIPTION OF THE INDIVIDUAL SCIENTIFIC CONTRIBUTION TO THE MULTIPLE-AUTHOR PAPERS

The chapters of this thesis are in press (Chapter I), in review (Chapter III) or prepared for submission to peer reviewed journals (Chapter IV and V). Parts of Chapter II are published in a book chapter. The following list provides an overview about my personal contributions on each of the publications:

Chapter I: Harbour porpoise (*Phocoena phocoena*) abundance in the southwestern Baltic Sea

Authors: Meike Scheidat[1,2], Anita Gilles[1], Karl-Hermann Kock[3], Ursula Siebert[1,]

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in press: Endangered Species Research, special issue 'Fisheries Bycatch: Problems and solutions'

Contributions: US and KHK developed the idea of this study. AG conducted most of the field work, MS and AG conducted the data analysis, all graphical presentations were done by AG. AG, MS and US discussed the results, MS and AG wrote the manuscript. All authors read and approved the final manuscript.

Chapter II: Harbour porpoise abundance in the German North Sea - setting the scene

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Parts of manuscript published in:

Gilles A, Herr H, Lehnert K, Scheidat M, Siebert U (2008) Harbour porpoises - abundance estimates and seasonal distribution patterns. In: Wollny-Goerke K, Eskildsen K (eds) Marine mammals and seabirds in front of offshore wind energy. MINOS-Marine warm-blooded animals in North and Baltic Seas. B.G. Teubner, Wiesbaden, p 19-36

Contributions: US and MS developed the idea of this study. AG conducted most of the field work, AG conducted all data analysis. AG, MS and US discussed the results, AG wrote the manuscript. All authors read and approved the final manuscript.

Chapter III: Seasonal distribution shifts of harbour porpoises and wind farm developments in the German North Sea

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in review: Marine Ecology Progress Series

Contributions: MS and US developed the idea of this study. AG conducted most of the field work, AG conducted all data analysis and graphical presentations. AG and MS discussed the results, AG wrote the manuscript. All authors read and approved the final manuscript.

Chapter IV: Modelling harbour porpoise seasonal density in relation to the German Bight environment

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Chapter V: Feeding ecology of harbour porpoises in German waters

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Danksagung

Vielen Dank an Franciscus Colijn für die Betreuung dieser Arbeit, das immer "offene Ohr" für alle Probleme und das Korrekturlesen zum guten Schluss.

Besonderer Dank gebührt an dieser Stelle Ursula Siebert, da sie mir immer mit fachlichem und tatkräftigem Rat zur Seite stand, viele aufmunternde Worte fand (gerade in der Endphase!) und mir einen großen Freiraum verschaffte, indem ich meine Ideen ausprobieren konnte. Ursula, vielen Dank für alles!

Ein weiteres großes Dankeschön gebührt Meike Scheidat für die vielen Denkanstöße, unermüdlichen Tatendrang, große Unterstützung und vor allem für die gute Laune, die sie gerne verbreitet. Texel ist viel zu weit weg…

Meinen liebsten Mitbewohnern "hinterm Deich" Kristina und Helena möchte ich danken für den support in allen Lebenslagen, das absolute Vertrauen und die schöne Freundschaft, die ich nicht missen möchte. Schade, dass ich jetzt nicht mit euch auf Polarstern sein kann. Aber ich hatte ja eine andere Mission…

Besonderer Dank geht an unsere Statistiker Roger Mundry und Sven Adler für die äußerst spannende und immer nachzuvollziehende (!) Ein- und Weiterführung in die Statistik. Sven gebührt vor allem großer Dank bei der Einführung in die Habitatmodelle und der generellen Einführung in R (it's great)!

Vielen Dank an Stefan Garthe für spannende Flurgespräche und "updates".

Bedanken möchte ich mich auch bei Philipp Schwemmer, für das Korrekturlesen einiger Teile dieser Arbeit und die beruhigenden Worte eines jemanden "der das schon hinter sich hatte"!

Krishna, merci beaucoup pour les merveilleux moments à Warwerort. Un grand merci également d'avoir relu mon mémoire de thèse.

Vielen Dank an alle Kollegen in der Arbeitsgruppe "Ökologie mariner Säuger und Vögel" in Büsum für die gute Atmosphäre, viele hilfreiche Hände und Unterstützung bei der

Feldarbeit. Danke an Heidi Andreasen, Susanne Carstens-Michaelis, Heiko Charwat, Volker Dierschke, Henriette Dries, Hauke Giewat, Nils Guse, Ilka Hasselmeier, Bettina Mendel, Katharina Kramer, Jana Kotzerka, Kristin Kaschner, Ulrike Kubetzki, Eva Kuhn, Linn Lehnert, Klaus Lucke, Stefan Ludwig, Martje Ludwig, Katta Ludynia, Sabine Müller, Susanne Prahl, Marion Rademaker, Petra Rettmann, Denise Risch, Jacob Rye Hansen, Conny Schmidt, Henrike Seibel, Dirk Sonnenschmidt, Nicole Sonntag, Antje Steinfurth, Janne Sundermeyer, Ulrika Westerberg und alle anderen FTZlern.

Die Flugzählungen haben natürlich eine großen Teil meiner Zeit eingenommen und vielen Personen gilt es zu danken. Zum einen den Piloten Siemi, Kai-Uwe, Danny, Bernie, Clemens und Michi von Sylt Air; Hecki, Benni und Felix von Kiel FLM; und Leif vom Danish Air Survey. Hinzu kommt eine Schar an Observern und Navigatoren, die maßgeblich zum Gelingen dieser Arbeit beigetragen haben: Jörg Adams, Patrick Börjesson, Denise Risch, Amaia Gomez, Helena Herr, Iwona Kuklik, Kristina Lehnert, Linn Lehnert, Maik Marahrens, Carsten Rocholl, Thorsten Walter, Ulrika Westerberg and Solvin Zankl. Dank auch an Klaus Struve, vom Flugplatz Büsum, für die Kontrolle von EDXB!

Den Mitarbeitern der folgenden Institute bzw. öffentlichen Einrichtungen möchte ich für die Bereitstellung der externen Daten und die sehr gute Kooperation und Hilfe danken: Stefan Dick, Heiko Mauritz, Friedrich Nast und Reinhard Schwabe (Bundesamt für Seeschiffahrt und Hydrographie, Hamburg); Wolfgang Cordes, Roland Doerffer, Ulrike Kleeberg und Hajo Krasemann (GKSS, Geesthacht); vielen Dank an die Entwickler und Mitarbeiter der ICES Oceanographic Database.

Matthias Keßler sei gedankt für die tolle Hilfe bei der Erstellung von AML-Skripten in ArcInfo und Gerd Bruss sei gedankt für die Unterstützung beim import der Strömungsdaten (es lebe Fortran!).

Teile dieser Arbeit wurden finanziert im Rahmen der Projekte EMSON, MINOS, MINOSplus und Nahrung finanziert durch das Bundesministerium für Umwelt und Reaktorsicherheit sowie das Bundesamt für Naturschutz.

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Publikationen

Scheidat M, **Gilles A**, Kock K-H, Siebert U (in press) Harbour porpoise (*Phocoena phocoena*) abundance in the south-western Baltic Sea. Endangered Species Research 5, special issue (2-3): Fisheries Bycatch: Problems and solutions

Gilles A, Scheidat M, Siebert U (2008) Harbour porpoises in German waters – evaluating proposed NATURA 2000 sites. In: Evans PGH (Ed.). Selection criteria for marine protected areas for cetaceans. ECS special publication series No. 48, p 76-82

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ERKLÄRUNG

Hiermit erkläre ich, dass die vorliegende Dissertation selbständig von mir angefertigt wurde und in Inhalt und Form meine eigene Arbeit ist. Es wurden - abgesehen von der wissenschaftlichen Beratung durch meinen Betreuer - keine anderen als die angegebenen Hilfsmittel und Quellen verwendet. Die Arbeit wurde unter Einhaltung guter wissenschaftlicher Praxis entwickelt.

Diese Arbeit wurde weder ganz noch zum Teil schon einer anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegt. Dies ist mein erster Promotionsversuch. Die Promotion soll im Fach Biologische Meereskunde erfolgen. Für die Prüfung wird die Form der Disputation gewählt. Der Zulassung von Zuhörern bei der mündlichen Prüfung wird nicht widersprochen.

Kiel, den

Anita Gilles