Appendix 4

(this text is a summary of a review of monitoring methods conducted as part of the SCANS-II project. For a full version of the review see Hammond et al. in prep.)

Methods available for harbour porpoise monitoring

Several methods can be used to monitor the distribution and abundance of harbour porpoises.

Small cetaceans (i.e. porpoise and dolphin species) occur in relatively low densities and are highly mobile. They are difficult to spot and to follow at sea, even during good survey conditions because they typically only show part of their head, back and dorsal fin while surfacing and spend the majority of their time underwater.

Currently, there are at least seven potential approaches used in monitoring small cetaceans:

1. Satellite tracking of individual animals
2. Fixed land or sea based surveys
3. Dedicated vessel or aircraft surveys
4. Acoustic monitoring
   a. Passive acoustic ship surveys; towed hydrophones
   b. Static acoustic monitoring; e.g. T-PODs
5. Incidental sightings and platforms of opportunity
6. Strandings and bycatches
7. Photo-identification and mark-recapture analysis.

When choosing a monitoring method it is important to consider the limitations of each approach. In general, surveys from ship or aircraft have a low temporal resolution, ship surveys may have bias due to responsive movements of animals, stationary acoustic systems have low spatial resolution and logistical problems with deployment, photographic identification relies on visual differences between individuals to allow identification, and telemetry typically only allows small samples resulting in much inter-individual variation.

1) Satellite tracking of individual animals

Information on the movements and home range of individual animals can help to identify important habitats, migration routes and to define boundaries between populations. Effective conservation of animal populations is enhanced by this information, which can also be valuable when designing monitoring programmes. In recent years satellite tagging of cetaceans has been increasingly used to obtain information on seasonal movements, distribution and diving behaviour. These types of information are difficult to get with other methods for most species.
Many kinds of tags have been used in studies of cetaceans, including VHF transmitters, satellite tags and dataloggers. Satellite telemetry has the advantage that because data are transmitted to an earth based station via a satellite, it is possible to follow animals all over the world without retrieval of the tag. Several smaller cetaceans have been followed for long periods using VHF or satellite tags, e.g. belugas (*Delphinapterus leucas*), up to 126 days (Richard et al. 2001), 104 days (Suydam et al. 2001); harbour porpoises, up to 212 days (Read and Westgate 1997), 50 days (Westgate et al. 1998), 349 days (Teilmann et al. 2004); Dall’s porpoise, up to 378 days (Hanson 2001) and narwhals (*Monodon monoceros*), backpacks have worked for more than 14 months while tusk tags have been observed on the tusk after more than 5 years (Heide-Jørgensen et al. 2003, Heide-Jørgensen et al. in press.). Dataloggers that store high resolution dive data within the instrument usually for a few hours or days have also been deployed on small cetaceans, including the harbour porpoise (Westgate et al. 1995; Otani et al. 1998; Schneider et al. 1998; Akamatsu 2007; Baird et al. 2001; Laidre et al. 2002).

Transmitters are attached to smaller odontocetes usually by attaching the transmitters to the dorsal fin using pins (Teilmann et al. 2007) or to the body using suction cups (Schneider et al. 1998) and in the case of male narwhals the tags can be secured around the tusk of the animals (Dietz et al. 2001). The pins ensure that the tag stays on the animal for a longer period of time. Using suction cups for attachment allows the tag to stay on for only some hours (Akamatsu et al. 2007).

Each tagged animal can provide a wealth of information but the limitation is that typically only a few animals can be tagged in a study due to limited funding or access to live animals and general conclusions may therefore be difficult to make.

**Strengths and weaknesses of using telemetry:**

<table>
<thead>
<tr>
<th>Strengths</th>
<th>Weaknesses</th>
</tr>
</thead>
<tbody>
<tr>
<td>• Can provide information on movements, migration and range of individuals.</td>
<td>• Potential animal welfare issues from tagging process.</td>
</tr>
<tr>
<td>• Detailed information on animals without human disturbance (after release).</td>
<td>• Possible effect of tagging on behaviour.</td>
</tr>
<tr>
<td>• Can provide information on behaviour.</td>
<td>• Equipment and data recovery are relatively expensive.</td>
</tr>
<tr>
<td>• Can provide information on habitat preferences and areas of special importance to e.g. reproduction.</td>
<td>• Many individuals need to be tagged to make general conclusions.</td>
</tr>
</tbody>
</table>

**2) Fixed land or sea based surveys**

Regular land-based watching for defined periods of time has been used to identify coastal areas important for particular species and to determine variation in relative densities both seasonally and over the longer term at respective sites. For example, 50 sites around mainland Shetland were monitored by standardized watches at a similar time over four summers and indicated that porpoises mainly occurred on the east coast with concentrations at particular locations (Evans et al. 1996). A major disadvantage with fixed-point sampling is that the area of coverage is limited, generally to marine areas immediately adjacent to elevated vantage point on land, or the oil/gas platform where the observers are lo-
cated. Some of the large cetaceans (e.g. gray whales, bowhead whales, and some humpback and southern right whale populations) undertake directional seasonal migrations between calving and feeding areas passing near headlands that allow them to be counted. These counts can be used to estimate the abundance of the migrating population (see e.g. Best 1990). However, there are no such occurrences in Europe and we are not aware of any small cetacean populations that show similar, directional and predictive migrations that would allow counting the animals and the use of this information to estimate abundance.

Strengths and weaknesses of fixed land or sea based surveys:

<table>
<thead>
<tr>
<th>Strengths</th>
<th>Weaknesses</th>
</tr>
</thead>
<tbody>
<tr>
<td>Normally and inexpensive way of collecting data.</td>
<td>Data will only allow abundance calculation for populations with regular migration routes and when all individuals pass within range of the observation point once during each migration.</td>
</tr>
<tr>
<td>Provide information on temporal and spatial distribution in the area covered if allowance can be made for changes in sighting conditions (and a very rough measure for trend analyses if effort is available).</td>
<td>Limited area covered</td>
</tr>
<tr>
<td>Non-intrusive data collection.</td>
<td></td>
</tr>
<tr>
<td>Can provide an important resource for environmental education and ecotourism.</td>
<td></td>
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</tbody>
</table>

3) Dedicated vessel or aircraft surveys

For monitoring programmes involving dedicated visual surveys both ship-based and aerial methods are well established.

For both vessel and aircraft surveys, line transect sampling is typically used to estimate abundance or sightings per unit effort (Hiby & Hammond 1989, Buckland et al. 2001; 2004). In line transect sampling a survey area is defined and surveyed along pre-determined transects. The distance to each detected animal is measured, and these distance measurements are used to determine a detection function from which an estimate of the effective width of the strip that has been searched can be calculated. This is necessary because the probability of detecting an animal decreases with increased distance from the transect line. Changes in sighting conditions influenced by factors such as wind speed and sea state also affect the probability of sighting an animal. Estimation of effective strip width should therefore take account of sighting conditions (Teilmann 2003). Abundance is then calculated by extrapolating estimated density in the sampled strips to the entire survey area.

When estimating absolute abundance using the line transect method, it is assumed that all animals on the track line are detected. This will never be the case as animals may be diving, avoiding the ship or simply just missed by observers. It is therefore necessary to estimate how large this bias is for each survey and for each species. On shipboard surveys this is usually estimated by collecting data from two independent observation platforms on the same vessel and then using this to calculate the proportion of detected animals between the platforms. In aerial surveys this can be done by using two aircrafts surveying the same track line in tandem or using one aircraft circling back after a sighting to simulate the second aircraft (Hiby & Lovell 1998, Hiby 1999).
Relative abundance using only one platform may be sufficient for detecting population trends and distribution. This reduces the cost considerably and may be a good way of monitoring the status of the population between large-scale expensive absolute abundance surveys.

Declining trends in harbour porpoise abundance have been described in central California based on aerial surveys conducted from 1986 to 1995 (Forney 1999). Forney (1999) noted that harbour porpoise abundance was negatively correlated with positive sea surface temperature anomalies. It is therefore possible that a perceived population decline in central California is the result of small-scale changes in porpoise distribution, given that aerial survey transects have remained unchanged since 1986.

To estimate the population size of harbour porpoises in the Gulf of Maine/Bay of Fundy region, four line transect sighting surveys were conducted during the summers of 1991, 1992, 1995, and 1999 (Palka 2000). Possible reasons for inter-annual differences in abundance and distribution include experimental error, inter-annual changes in water temperature and availability of primary prey species (Palka 1995), and movements between population units.

A proper design of the survey is critical to address monitoring issues of cetacean populations, and in particular that a large enough area is covered so that shifts in distributions can be accounted for when analyzing the data.

**Strengths and weaknesses of using dedicated visual vessel or aircraft surveys:**

<table>
<thead>
<tr>
<th>Strengths</th>
<th>Weaknesses</th>
</tr>
</thead>
<tbody>
<tr>
<td>Data allow estimation of absolute or relative abundance and can be used for abundance trend analyses.</td>
<td>Data collection typically expensive, often preventing frequent surveys.</td>
</tr>
<tr>
<td>Can cover entire range of population.</td>
<td>Data collection sensitive to weather conditions.</td>
</tr>
<tr>
<td>Provide an important resource for environmental education and ecotourism.</td>
<td>No night time information</td>
</tr>
<tr>
<td>Long-term data sets can be collected.</td>
<td>High sampling variation may prevent detection of smaller population changes.</td>
</tr>
<tr>
<td>Provide information on spatial distribution.</td>
<td>Unusable in low density areas.</td>
</tr>
</tbody>
</table>

**Comparison of vessel and aircraft survey platforms:**

<table>
<thead>
<tr>
<th>Vessel</th>
<th>Aircraft</th>
</tr>
</thead>
<tbody>
<tr>
<td>+ Allows collection of additional data: acoustic, environmental, photo-identification data.</td>
<td>+ Covers large areas in short time and can make efficient use of good weather windows.</td>
</tr>
<tr>
<td>+ Large vessels can cover wide ocean areas.</td>
<td>+ Responsive movement of animals not a problem.</td>
</tr>
<tr>
<td>+ Methods to account for animals missed on the transect line and responsive movements of animals results well established.</td>
<td>+ Area coverage limited by fuel and airport location.</td>
</tr>
<tr>
<td>− Large vessels are expensive and may be labour intensive to operate</td>
<td>− Concurrent collection of supplemental environmental data usually not possible.</td>
</tr>
<tr>
<td>− Small vessels are limited to coastal areas</td>
<td></td>
</tr>
</tbody>
</table>

61
4) Acoustic monitoring

Acoustic data collection for cetaceans has some significant advantages over visual methods in that acoustic methods can be automated, data can be collected 24-hrs a day, the methods are not dependent on observer skill and are less sensitive to weather conditions. Disadvantages are that these methods rely on animals making sounds that have a useful detection range and are identifiable to species, and that methods to estimate abundance are not well-developed (except for the sperm whale).

Monitoring these sounds offers possibilities to obtain information on spatial and temporal habitat use, as well as estimation of relative density. However, little is known about the detailed use (when, how often, etc) of these sounds by cetaceans in the wild and, hence, if no sounds are recorded it does not necessarily mean that there are no animals in the area. Information on diurnal and seasonal sound production by individuals is therefore necessary to ensure that acoustic data are comparable. This is especially relevant for static recordings of clicks where the natural echolocation behaviour is recorded rather than the response to the passing vessel which may occur when using towed hydrophones. Recently, high frequency tags have been developed for small cetaceans such as porpoises (Akamatsu et al. 2005; 2007). These tags provide information on the natural echolocation behaviour of particular individuals.

There are currently two types of systems available for passive acoustic detection of small cetaceans; towed hydrophones and static autonomous click detectors (e.g. T-PODs).

4a) Passive acoustic ship surveys; towed hydrophones

Since 1994, the International Fund for Animal Welfare (IFAW) has been developing systems for the automatic detection of high frequency harbour porpoise clicks. The first system, used between 1994 and 1999 (Chappell et. al. 1996) relied primarily on analogue electronics to shape the high frequency signals and to detect clicks which were then logged by a PC. This system was used with some success by vessels during the first SCANS survey in 1994. Further advances in computing speed, have now enabled the elimination of the analogue electronics section altogether with all processing being done real time. This has lead to improved positioning accuracy, lower costs and the possibility of making the complete detection system easier to reproduce or implement on different processing platforms. This new acoustic detection and recording system was further developed as part of the SCANS-II project in 2005 and was used by all vessels in the pilot and main surveys.

4b) Static acoustic monitoring; e.g. T-PODs

So far only the T-POD or PORpoise Detector has been documented in static acoustic monitoring of harbour porpoises (Verfuss et al. 2007, Kyhn et al. in press.). The T-POD is a relatively small and cheap self-contained data-logger (developed by Nick Tregenza, http://www.chelonia.demon.co.uk) that records echolocation clicks from porpoises and dolphins. It is programmable and can be set to specifically detect and record the echolocation signals from e.g. harbour porpoises. The T-POD consists of a hydrophone, an amplifier, a number of band-pass filters and a data-logger that logs echolocation click activ-
ity. It may be anchored or deployed on marine structures and can operate down to depths of 500m (N. Tregenza pers. com.).

The T-POD processes signals in real-time and logs time and duration of sounds fulfilling a number of acoustic criteria set by the user. These criteria relate to click-length (duration), frequency spectrum and intensity, and are set to match the specific characteristics of echolocation-clicks. Like the IFAW towed array (see above) the T-POD relies on the highly stereotypical nature of porpoise sonar signals. These are unique in being short (50-150 microseconds) and containing virtually no energy below 100 kHz. The main part of the energy is in a narrow band 120-150 kHz, which makes the signals ideal for automatic detection. Most other sounds in the sea are characterised by being either more broadband (energy distributed over a wider frequency range), longer in duration, with peak energy at lower frequencies or combinations of the three.

The T-POD operates with six separate and individually programmable channels. This allows e.g. for one channel to log low frequency boat activity while remaining channels log porpoise echolocation activity. Each of the six channels operates sequentially for 9 seconds, with 6 seconds per minute assigned for change between channels. This is done with a resolution of 10 µs. T-PODs are battery powered and have memory and power to log data for several months. Data from the T-POD can be downloaded in the field for storage on a PC.

Since 2001 T-PODs have been used for monitoring area use by harbour porpoises in e.g. Denmark, Germany, Holland, and U.K. A statistical model has been developed to treat T-POD data collected in Danish waters. Further, an acoustic calibration method has also been developed to measure the exact sensitivity of each T-POD. From experiments with captive animals it has been shown that T-POD software can differentiate between porpoises clicks and other sounds, although some porpoise sounds may be lost in the filtering process (Thomsen et al. 2005, Carstensen et al. 2006). In a study of wild porpoises 98% of the animals sighted within 150m of its location were detected by the T-POD (Koshinski et al. 2003). The T-POD can obtain information on seasonal variation and relative density in specific areas. It is cheap and may be used to detect trends in density over many years. T-PODs can also be used in specific areas such as narrow straits or areas of low density where long term monitoring of presence, migration or time trends is needed (Carstensen et al. in 2006). Currently the prospects of using T-PODs or other static acoustic dataloggers to determine an absolute density of porpoises is being developed.
5) Incidental sightings and platforms of opportunity

In areas where little or no previous information is available, the collection of incidental sightings can provide the first indications of temporal and spatial distribution in an area.

Incidental sightings by non-specialists (e.g. bird watchers, ferry and other marine operators, coast guard, fishermen and recreational yachts) provide a low cost data source. In several European countries organized regional or national networks for recording of cetacean sightings have been in operation during the last decades (Evans 1976, Berggren & Ar-rhenius, 1995a,b, [http://www.hvaler.dk/](http://www.hvaler.dk/), [http://www2.nrm.se/tumlare/](http://www2.nrm.se/tumlare/)). The data can provide a rough measure for assessing trends in distribution and occurrence. Without any information on effort and sightability quantitative analysis of data from incidental sightings for monitoring trends of cetacean populations is not possible. However, the collected information can be very useful for planning dedicated surveys.

Data for monitoring cetacean population can also be collected in conjunction with other research projects. Several organisations in the UK and elsewhere have collected low-cost sightings data making use of so-called “platforms of opportunity” (PoO). These are vessels or other platforms engaged in other activities (e.g. fish or bird surveys, ferries or cruise liners) that can be used to collect sightings or acoustic data by placing equipment or observers on board. The main advantage of this methodology is the possibility of collecting a large amount of data for a fraction of the cost of a dedicated survey. The disadvantages are that it is not usually possible to influence where, when and at what speed the vessels travels, which may result in uncomparable effort. Research cruises, however, such as fisheries surveys, may utilise designed surveys repeated every year. In some cases PoOs also lack good observations locations on the vessel.

There are two major sources of platform of opportunity data. Recently, the Joint Nature Conservation Committee in UK (JNCC) has funded an initiative to merge these major datasets to provide a single cetacean distribution database for the north-west European waters (Reid et al. 2003).

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**Strengths and weaknesses of using acoustic data from towed hydrophones and static click detectors:**

<table>
<thead>
<tr>
<th>Strengths</th>
<th>Weaknesses</th>
</tr>
</thead>
<tbody>
<tr>
<td>• Data collection can be relatively inexpensive.</td>
<td>• Methods to estimate abundance are not well developed.</td>
</tr>
<tr>
<td>• Data can be used to monitor relative abundance if click rates are assumed to be constant over time.</td>
<td>• High frequency vocalisations have a limited detection range of approximately 200m.</td>
</tr>
<tr>
<td>• Data are independent of daylight and most weather conditions.</td>
<td>• Species identification is currently difficult for other species than harbour porpoises.</td>
</tr>
<tr>
<td>• Towed hydrophones provide high spatial resolution.</td>
<td>• Performance is dependent on the noise level of the vessel</td>
</tr>
<tr>
<td>• Smaller vessels can be used than for sighting survey.</td>
<td>•</td>
</tr>
<tr>
<td>• Stationary click detectors provide high temporal resolution.</td>
<td>•</td>
</tr>
<tr>
<td>• Long-term data sets can be collected.</td>
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</tr>
</tbody>
</table>

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64
The database, called the Joint Cetacean Database (JCD), contains more than 20,000 cetacean sightings records of more than 60,000 individuals from 1977 to 1997. Over 600,000 km have been covered during these 21 years, collected over almost 38,000 person-hours. This database is potentially a valuable source of information on trends in the relative abundance of cetaceans in space and time. Bravington et al. (1999) used the PoO data in the JCD to investigate trends in relative abundance of harbour porpoises over space and time in the North Sea. If it can be assumed that protocols or sightability have not changed substantially over the period they were collected, PoO data offer the possibility of detecting trends or even sudden changes in abundance within restricted areas.

<table>
<thead>
<tr>
<th>Strengths and weaknesses of using platforms of opportunity:</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Strengths</td>
<td>Weaknesses</td>
</tr>
<tr>
<td>• Cheap way of collecting data.</td>
<td>• Normally not possible to dictate time or area covered.</td>
</tr>
<tr>
<td>• Long-term data sets can be collected.</td>
<td>• Data will not allow estimation of absolute abundance.</td>
</tr>
<tr>
<td>• Provide useful information for planning dedicated surveys.</td>
<td>• Variation in data can confound information on trends in abundance.</td>
</tr>
<tr>
<td>• Potentially provide information on temporal and spatial distribution if effort data are available.</td>
<td></td>
</tr>
<tr>
<td>• Provide an important resource for environmental education and ecotourism.</td>
<td></td>
</tr>
</tbody>
</table>

6) Strandings and bycatches

Data collected from animals found stranded or incidentally taken (by-caught) in fishing gear can provide some information on distribution. The actual geographical origin of a stranding is, however, not known. In tidal regions or other areas with strong currents a dead animal could be taken a long way from its place of dead and hence provide misleading information. These data cannot provide reliable information on trends in abundance. Changes in the number of stranded and/or bycaught animals does not reflect only changes in the number of animals in a population or area, but reflect confounded factors such as changes in distribution, effort (searching along coasts for stranded animals or fisheries effort for bycatch), weather conditions (e.g unusual storms) and natural mortality rates.

7) Photo-identification and mark-recapture analysis

Mark-recapture methods were initially developed for studies in which individual animals are physically captured and marked (e.g. by painting, branding or tagging), released and then physically recaptured. These methods were implemented on cetaceans using so-called Discovery tags that were fired into the blubber of large cetaceans and then recovered when the animal was flensed after being harpooned in harvesting operations. More recently, individual-based studies of cetaceans have relied upon the photographic recognition of individuals from natural marks on their bodies or genetic identification of biopsied individuals. Photo-identification is a widely used technique in cetacean research that can provide estimates of abundance and population parameters e.g. survival and calving rate. The technique relies on being able to obtain good qual-
ity photos and on most animals having unique recognisable markings. If species like harbour porpoises do not have these marks the method is not possible. Using the genetic fingerprint from biopsies is possible but require an efficient biopsy method to be developed.

Strengths and weaknesses of using mark-recapture sampling for monitoring (modified from Thompson et al. 2004):

<table>
<thead>
<tr>
<th>Strengths</th>
<th>Weaknesses</th>
</tr>
</thead>
<tbody>
<tr>
<td>• Valuable method for estimating total population size and survival rates.</td>
<td>• Require that individuals are recognizable or that biopsies can be obtained.</td>
</tr>
<tr>
<td>• Data sets can provide good basis for long-term monitoring.</td>
<td>• Labour-intensive data collection</td>
</tr>
<tr>
<td>• Estimates of population size can be based upon surveys made in discrete sampling areas within the population’s range.</td>
<td>• Low sightings frequency may prevent estimation of annual abundance, or reduce precision.</td>
</tr>
<tr>
<td>• Data from these studies can provide an important resource for environmental education and ecotourism.</td>
<td>• Surveys can only be carried out during good weather conditions.</td>
</tr>
<tr>
<td>• Raw data can be archived to permit re-analyses and reliable comparison between years.</td>
<td>• Potential disturbance of animals by boats during data collection.</td>
</tr>
<tr>
<td></td>
<td>• Relatively labour intensive data management, image matching and analyses.</td>
</tr>
</tbody>
</table>
High density areas for harbour porpoises (*Phocoena phocoena*) in Danish waters identified by satellite tracking

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Word count: 5015

Abstract

1. The population status of harbour porpoises has been of concern for several years, and the establishment of Marine Protected Areas (MPA) has been suggested as a method to protect the harbour porpoise and other small cetaceans. In order to designate MPAs, high density areas for the species must be identified.
2. Spatial distribution of small cetaceans is usually assessed by surveys from ships or planes. As an alternative, this study examined the movements of 63 harbour porpoises satellite tagged between 1997 to 2007, in order to determine the distribution in Danish waters.
3. Results show that harbour porpoises are not evenly distributed but congregate in certain high density areas. These areas are subject to some seasonal variation. In the Danish study area, the high density areas are Store Middelgrund, northern Øresund, northern Samsø Belt, Little Belt, Great Belt, Flensborg Fjord, Fehmarn Belt and the tip of Jylland.
4. This novel method of identifying high density areas for harbour porpoises and possibly other small cetaceans will be of key importance when designating MPAs. For harbour porpoises it is currently of particular interest regarding the identification of Special Areas of Conservation in the EU.
5. Synthesis and applications. The establishment of Marine Protected Areas has been suggested as a method of protecting harbour porpoises in high density areas. This study examined 63 satellite tracked porpoises in Danish waters in order to identify these areas. The harbour porpoises did not distribute evenly and eight high density areas were identified in the study area. This novel method of examining distribution of harbour porpoises will be of key importance when designating MPA for the species.
Introduction

The proper conservation of cetaceans depends on knowledge of several aspects of their population ecology. Ideally, information of population size, genetic structure, and seasonal distribution as well as data on mortality and breeding activity should be available. However, this is rarely the case. The knowledge of the harbour porpoise distribution (*Phocoena phocoena*, Linnaeus 1758) is limited due to its shy behaviour; harbour porpoises are submerged most of the time and surface only briefly (Koopman and Gaskin 1994). In the last few decades the need to protect these small cetaceans and thus maintain sustainable populations has become increasingly apparent. Like other small cetaceans, harbour porpoises face threats of incidental by-catch in fishing gear (e.g. Vinther & Larsen 2004), pollution, food depletion (e.g. Reijnders 1992) and other human disturbances such as underwater noise, shipping, oil and gas exploration and exploitation as well as constructions at sea including bridges and off shore windfarms (Carstensen *et al.* 2006).

The establishment of Marine Protected Areas (MPA) has been suggested as a method to protect small cetaceans. In the EU, all member states are thus legally obliged to protect the harbour porpoise as well as the bottlenose dolphin (*Tursiops truncates*, Montagu 1821) by designating MPAs, here named Special Areas of Conservation (SAC), according to the Habitats Directive (92/43/EEC). The selection of SAC in the EU is scheduled to be completed in 2012 (European Commission 2007).

A first step towards designation of MPAs is to identify the key habitats of a species. Key habitats (as defined in Article 3.1 of the Habitats Directive) refer to those parts of a species’ range that are essential for day-to-day survival, as well as for maintaining a healthy population growth rate. Areas that are regularly used for feeding, breeding, raising calves, and migration are all part of the key habitats (sensu Hoyt 2005). For the harbour porpoises, knowledge of the physical and biological factors defining key habitats is currently insufficient. It may, however, be assumed that the areas with the highest porpoise densities are also the areas where essential factors to life and reproduction are best fulfilled (European Commission 2007). Hence, the designation of MPAs may be based on the distribution of harbour porpoise density.

Up until recently, distribution of small cetaceans has always been estimated by visual surveys from vessel or aircraft (e.g. Heide-Jørgensen *et al.* 1992; 1993; Hammond *et al.* 1995; Scheidat *et al.* 2004). In the last decade, acoustical surveys, in which an array of hydrophones is towed behind a vessel, have been applied (Gillespie *et al.* 2005). In Germany, the surveys intended to identify SACs for harbour porpoises were supplemented in areas of expected low density by an extensive use of stationary acoustic dataloggers (T-PODs) (Verfuss *et al.* 2007). These methods have, however, limitations in identifying distribution and thus high density areas. Visual surveys can only be conducted in daylight under calm weather conditions and the range from an airplane is limited in time and space (Teilmann 2003). Consequently, visual surveys have mainly been
conducted in the summer. Acoustic studies, both stationary and surveys, may be conducted throughout the year, as they are rarely affected by weather. However, large numbers of acoustic dataloggers are needed to obtain adequate spatial coverage, due to their limited detection range. Acoustic surveys have a wide spatial range but – unless repeated - only provides an instant view of the distribution.

In the last decade, satellite tagging has been used to investigate harbour porpoise movement and behaviour (e.g. Read & Westgate 1997; Teilmann et al. 2004; Johnston et al. 2005). Satellite tracking of animals can provide detailed information on an individual’s movement for up to a year. Satellite telemetry has never been used for identifying high density areas of small cetaceans, although it potentially represents a method that has the advantage of combining temporal and spatial information on a broader scale. Based on previously conducted surveys (Heide-Jørgensen et al. 1993; Hammond et al. 2002; Scheidat et al. 2004), we hypothesise that harbour porpoises are not evenly distributed within the Danish waters and that we, by means of satellite telemetry data can identify key habitats, i.e. high density areas of the species.

Materials & Methods

Study area
Due to the locations of tagging (see below), the study area were divided into two areas, namely the Inner Danish Waters (IDW) including the southern Kattegat, and Skagerak including the northern North Sea. The IDW is defined as the waters (both Danish, Swedish and German) between Læsø (57°20’N) and the Baltic German coast (13°00’E) and covering 46,700 km² (Fig. 1). The main part of this area is between 10 and 40m deep and due to the many islands the only passage from the Baltic Proper to Kattegat is through the narrow straits of Little Belt (<2 km wide in the narrowest place), Great Belt (18 km wide) and Øresund (<7 km). The North Sea and Skagerrak, here defined as the waters north and west of Læsø (57°20’N), include deeper waters, in particular, the Norwegian Trench that runs along the northern Danish border and represents a sudden drop from 100 m up to 700 m.

Satellite tagging of harbour porpoises
This study examines 63 harbour porpoises tagged with satellite transmitters in Danish waters from 1997 to 2007. Twenty-four harbour porpoises were tagged on the northern tip of Jylland (Skagen) at the border between Skagerrak and Kattegat and 39 harbour porpoises were tagged in the Inner Danish Waters. In the analysis, the porpoises were divided in two groups; the IDW group and the Skagerak group. Each porpoise were assigned to the group residing in area in which it spent the majority of its time. This division was made in order to examine high density areas within groups of harbour porpoises residing in different areas.

Porpoises were caught incidentally in pound nets and tagged within a maximum of 48 hours of entrapment. Satellite-linked transmitters were attached to the dorsal fin of each porpoise.
Six different types of transmitters were used: Telonics ST-10 and ST-18; Wildlife Computers SDR-T10, SDR-T16 and SPOT2; and Sirtrack Kiwi 101. The transmitters weighed 105-240g in air. Prior to attachment, the dorsal fin was cleaned with antiseptic and anaesthetized with lidocaine. Each transmitter was attached by perforating the fin and subsequently the transmitter was fastened using three 5mm polyoxymethylen pins covered with Dacron Cuffs (by Sulzer Ascutek, Scotland). The pins were attached to the transmitter on one side of the dorsal fin and were secured with a clasp nut on the opposite side. The tagging procedure took 0.5-1 hour from the animal was obtained from the pound net to its release.

The tagging of porpoises was not evenly distributed throughout the year, e.g. thirty-two of the 63 harbour porpoises were tagged in spring (March-May) which is the main season for pound net fishery. Details on monthly distribution of porpoises with active transmitters in accordance to sex and age group are listed in Table 1.

Fig. 1. Map of the study area with names mentioned in the text indicated. The locations of the pound nets where the harbour porpoises were caught and tagged are indicated with red dots. Blue line indicates the Danish Exclusive Economic Zone (EEZ).
Data analysis

The locations of the tagged animals were determined by the ARGOS system maintained by Service Argos. In short, the satellite transmitters are programmed to send signals (uplinks) at periodic intervals whenever the animal is at the surface. Uplinks are received by satellites in polar orbit and if two or more signals are received from the same transmitter during one satellite pass the position of the transmitter can be determined. The accuracy of positioning varies and is determined by factors such as number of uplinks received during a satellite overpass, time interval between individual uplinks and angle from the transmitter to satellite. All positions are classified by Service Argos into one of six location classes (LC) according to level of accuracy (LC 3, 2, 1, 0, A, B), with LC3 being the most accurate and LCB the least. See Keating (1994) and Vincent et al. (2002) for details on accuracy of individual location classes. To remove positions most likely to be inaccurate the positions were filtered by a SAS-routine, Argos_Filter v7.03 (by Dave Douglas, USGS, Alaska Science Center, Alaska, USA). The filter applies user-defined settings such as maximum swim speed to filter out the most unlikely positions, i.e. positions resulting in unrealistic swimming speed or movements, using the methods described by Keating (1994) and McConnell et al. (1992). The settings used in this study were as follows; maxredun=5 (Distance between locations in km - if two positions are within close distance, here <5km, of each other, they are both retained, since the likelihood of them both being wrong is small), minrate=10 (max. swim speed km/h), ratecoef=10 (Angle between lines to previous and following location - if this angle is too small and distance too long, the position is excluded). All other settings were set as default. Positions from all six location classes were filtered and thus all six location classes were included in the dataset used for further analysis. For further details and explanation see Douglas (2006).

To standardize data and reduce autocorrelation for the home range calculations only the location judged most accurate for each day was selected. This selection was based on LC level and number of uplinks per transmission and was done automatically by the SAS-routine. Furthermore, to avoid overrepresentation of the area of the tagging site, all locations from day 0-2 were removed from the analysis.

To localize key habitats for harbour porpoises, kernel density estimation grids were produced in ArcMap using the fixed kernel density estimator.
(Worton 1989) by means of Hawth’s Analysis Tool (by Beyer 2004). Smoothing factor (bandwidth) was set to 20,000 and output cell size to 1 km². The kernel density estimate is a nonparametric estimation that calculates the density distribution from a random sample of Argos locations e.g. from one or more satellite tagged porpoises. By determining the smallest possible area that contains a user specified percentage of the positions the kernel grid was divided in percentage volume contours from 10% to 90% with 10% intervals. For instance, the 90% volume contour consists of the smallest possible area containing 90% of the locations that were used to generate the original kernel density grid. This means that the 10% contour area represents the areas with the highest density and the 90% contour almost the entire range of the porpoises.

We defined high density areas as kernel percent volume contours of 30% density or higher (10% and 20%). This is a subjectively chosen threshold and consequently, the exact boundaries of the 30% volume contour should be considered advisory and not fixed. The volume contours of lower levels (≥40%) should not be disregarded. However, the volume contours of 40% or higher often connects the 30% areas, which gives the areas irregular forms and relatively large sizes, thus making them more difficult to manage and therefore to be designated for MPAs.

As the transmitters on the different animals had very variable lifetime a bias towards animals with long transmitter lifetime is introduced into the analysis. To counteract this bias an analysis in which all porpoises were weighted evenly was also performed. This method introduces a bias in the opposite direction, i.e. areas visited by animals with short transmitter lifetime are overrepresented. Results of both methods are presented for comparison.

To challenge the validity of the high density areas determined with the kernel density estimator, results were compared to results obtained with another grid-based analysis, which takes into account the inaccuracies in the Argos positioning system (Tougaard et al. 2008). The grid analysis divides the study area into 10x10 km grid cells and calculates the most likely number of true positions inside each grid cell by weighting each position according to the accuracy of the associated location class. The method has the advantage over kernel density analysis that each estimate is a local estimate, whose value depends only on positions within the grid cell and immediately neighbouring cells. Thus, in contrast to kernel methods, where the whole dataset is included in the analysis and data geographically far apart therefore may influence each other, the grid method produces the same results locally, regardless of whether the entire dataset is analysed or only a small geographical region of the dataset is used.

This method was applied with and without weighting by individual porpoises as for the kernel density analysis.

Seasonal variation in the distribution of porpoises was assessed by dividing the dataset into subsets, which were analysed separately. Seasons were defined as winter (December to February), spring (March to May), summer (June to August) and autumn (September to November).
Results

Satellite telemetry
The lifetime of the individual transmitters varied with the shortest transmitting locations for 9 days and the longest for 349 days (median=102 days). The 63 porpoises were grouped according to the area in which they spend the majority of their time. The 24 porpoises tagged at Skagen were all grouped with the Skagerrak group. These animals never moved south of Anholt. Of the 39 porpoises tagged in the IDW, 3 of them briefly swam north of Skagen, but two other porpoises, tagged in the northern part of the IDW, swam immediately after tagging north into Skagerrak and the North Sea and stayed there for the entire contact period. Consequently, they were moved to the Skagerak group. Once grouped, there was little overlap between tracks from the IDW group and the Skagerrak group. One animal tagged in the IDW moved into the Baltic Proper but came back again after 12 days. Locations of the 63 porpoises (one location per day) are shown in Fig. 2.

Fig. 2. Locations (1 per day) of the 63 porpoises tracked between 1997 and 2007. Locations from porpoises tagged in the IDW are red and locations from porpoises tagged in Skagen are blue (N=63 porpoises, n=4287 locations). Map projection universal transverse Mercator, Zone 32N, WGS84.
Distribution
Kernel densities

The kernel density percent volume contours of all 39 IDW porpoises are shown in Fig. 3a (unweighted) and 3b (weighted). Results of the grid-analysis are showed in 3c (unweighted) and 3d (weighted). The corresponding analyses for the Skagerrak porpoises are displayed in Fig. 4a-d. The figures show good correspondence between weighted and unweighted analyses.

Fig. 3. Distribution of porpoises tagged in the IDW between 1979 and 2007. Comparison of methods of analysis: a) unweighted Kernel, b) weighted Kernel c) unweighted grid analysis, d) weighted grid analysis. Projections as in Figure 2.
These results confirm that the abundance of harbour porpoises in the Inner Danish Waters is not evenly distributed. The distribution of porpoises for the entire year in the IDW and in Skagerrak is displayed in Fig. 5. The high density areas were found to be Store Middelgrund, northern Øresund, northern Samsø Belt, Little Belt, Great Belt, Flensborg Fjord and Fehmarn Belt in the IDW and the tip of Skagen for the Skagerrak.

Fig. 4. Distribution of porpoises tagged in Skagen between 1979 and 2007. Comparison of methods of analysis: a) unweighted Kernel, b) weighted Kernel c) unweighted grid analysis, d) weighted grid analysis. Projections as in Figure 2.
Seasonal distributions for both the IDW population and the Skagerrak population are shown in Fig. 6. In spring and summer, the reproductive period, the Skagerrak porpoises stay close to the tip of Jylland while the IDW animals spread out in the entire range of the IDW. In spring and summer, the high density areas in Danish waters are the tip of Jylland, Store Middelgrund, northern Øresund, Little Belt, Flensborg Fjord, Great Belt and Fehmarn Belt. In autumn and winter, the distribution is somewhat different, with the Skagerrak porpoises moving further out into the northern North Sea (although high porpoise density in this area still remains) and the IDW porpoises moving south. The main high density areas in the autumn and winter are the tip of Jylland, an area along the Norwegian Trench, the southern Little Belt, Flensborg Fjord, Great Belt, Fehmarn Belt and the Kadet Trench.

Fig. 5. Kernel distribution all year showing the 10% to 90% volume contours (IDW group: N=37 porpoises, n=2765 locations; Skagerrak group: N=26, n=1522). Projections as in figure 2.
We accept the hypothesis that harbour porpoises do not distribute evenly but aggregate in certain areas. Kernel density estimations, here confirmed by grid analysis, is a valid method of identifying high density areas. In the Danish study area these are Store Middelgrund, northern Øresund, northern Samso Belt, Little Belt, Great Belt (including Kalundborg Fjord), Flensborg Fjord, Fehmarn Belt and the tip of Jylland. Of these Little Belt and Great Belt are historically known for high abundance of harbour porpoises whereas the other areas are previously unrecognised in Danish waters.

Fig. 6. Seasonal distribution for porpoises tagged in the IDW population (green) and in Skagerrak (blue) displayed as kernel density estimations. a) spring (IDW: N=29, n=829; Skagerrak: N=12, n=213), b) summer (IDW: N=27, n=1056; Skagerrak: N=18, n=382), c) autumn (IDW: N=16, n=575; Skagerrak: N=16, n=596) and d) winter (IDW: N=8, n=305; Skagerrak: N=12, n=331). Projections as in figure 2.
Some of the high density areas found by satellite tagging are supported by previously studies. For instance, Heide-Jørgensen et al. (1993) conducted aerial surveys in the waters north of Fyn, Great Belt and the Bay of Kiel, and found that the density in Great Belt was more that twice of the other areas. Furthermore, during a ship-based line transect survey, Teilmann (2003) recorded the highest density of porpoises (4.9 porpoises km\(^{-2}\)) reported in Europe. Gillespie et al. (2005) conducted boat-based visual and acoustic surveys in 2001 and 2002 in the Bay of Kiel and the western Baltic. Both survey methods indicated an increase in porpoises from east to west with considerably more porpoises in Flensborg Fjord and in Little Belt than in any other area and almost no porpoises in the Baltic Proper. Within the same study area, Gilles et al. (2006; 2007) conducted regular aerial surveys throughout the year from 2002 to 2006. Like Gillespie et al (2005), they too found a general increase in density from east to west, but found defined high density areas around Als (Flensborg Fjord) and in the western part of Fehmarn Belt. Fehmarn Belt is divided by the Danish-German border and the German side of the Belt was recently identified by Verfuss et al. (2007) as a key habitat for harbour porpoises. They deployed acoustic data loggers, T-PODs, along the German Baltic coastline and found Fehmarn Belt to be one of the areas with the highest level of porpoise encounters. Thus, entirely different methods have confirmed several of the high density found by satellite tracking in our study.

Our study found seasonal changes in the distribution of high density areas. Porpoises tagged in the IDW moved south in the winter and porpoises tagged at Skagen moved west in the winter. This movement may be linked to changes in distribution of prey (Gaskin 1982). The winter distribution is, however based on relatively few animals (Table 1), which may influence the results. In fact, very little information is available on harbour porpoise distribution in the winter season in general, since visual surveys are difficult to conduct mainly due to poor weather conditions. Satellite tagging additional porpoises with long lasting transmission tags or conducting regular acoustic surveys could improve our knowledge in the winter time significantly.

All results are based on the assumption that the 63 harbour porpoises tagged in this study are representative for the natural populations in the area. Preferably, animals should be tagged randomly throughout the study area and contain the natural distribution of ages and sex. Tagging sites were, however, restricted to the areas where pound net fishery was carried out and porpoises were caught (Fig. 1). The harbour porpoise is a wide ranging species and may potentially spend more time in any area within its reach. Consequently, the fact that they do prefer some areas i.e. key habitats to other and that some of these e.g. Northern Øresund are relatively far away from the tagging sites, rejects that the movements are seriously dependant on sites of tagging. Eighteen of the 64 tagged porpoises were adults. There is no way of knowing whether this represents the natural age distribution or even whether age and sex influences the movements of harbour porpoises. However, several of the high density areas identified in this study are supported by studies using other methods.

If MPAs are to be selected for porpoises or any cetacean species, it is of essential importance that the key habitats do not vary greatly from year
to year. This study was conducted over a ten year period, which was
needed to catch and tag such a high number of porpoises. Compiling
data over several years may hide minor changes in distribution, but in-
spection of the individual tracks does not indicate that this is the case. A
time trend study e.g. involving regular acoustic surveys with a high cov-
erage throughout the year and/or the deployment of T-PODs in and ad-
joint to the identified key habitats could further examine changes over
time and season.

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