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Geographical and seasonal variation of harbour porpoise (*Phocoena phocoena*) presence in the German Baltic Sea revealed by passive acoustic monitoring

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The harbour porpoise is the only resident cetacean species in the German Baltic Sea. Within the last several decades this harbour porpoise stock declined drastically, causing deep concern about its status. Plans of the German government for proposing Marine Protected Areas (MPAs) to implement *Natura 2000* and for assessing the impact of offshore windmill constructions on the marine environment led to an increased research effort on the harbour porpoise in German waters. For the first time, long-term passive acoustic monitoring has been conducted in the German Baltic Sea from the Kiel Bight to the Pomeranian Bay from August 2002 to December 2005. Porpoise detectors (T-PODs) have been installed five to seven metres below the water surface at up to 42 measuring positions throughout the investigated area, registering the exact times of echolocation signals of passing harbour porpoises. The proportion of monitored days with porpoise detection in each quarter of the years has been analysed. A correlation of the results with the longitude of the measuring position revealed a significant decrease from west to east in the percentage of days with porpoise detections. Comparison of data gathered in the first quarters with the third quarters of the monitoring years displayed a seasonal variation with fewer days of porpoise detections in winter time than in summer time. Nevertheless, harbour porpoises have been detected year-round at most of the measuring positions in the German Baltic Sea. The present study clearly indicates a regular use of the German Baltic Sea by harbour porpoises with a geographical and seasonal variation in the usage of the German Baltic Sea. The larger numbers of harbour porpoise detections in spring to autumn compared with winter suggests that the German Baltic Sea is an important breeding and mating area for these animals.

INTRODUCTION

Harbour porpoises occur throughout temperate shelf waters of the northern hemisphere (Read, 1999). In the Baltic Sea they were very common up to the middle of the 20th century (Schulze, 1996). While the former range of the harbour porpoise extended into the easternmost and northernmost parts of the Baltic Sea (Koschinski, 2002), the population size decreased severely within the last several decades (Kröger, 1986; Benke et al., 1998; Kinze, 1995; Siebert et al., 1996) with a drastic reduction of the porpoises' range (Koschinski, 2002). Since 1988, the harbour porpoise has been included in Appendix II of the Convention on the Conservation of Migratory Species of Wild Animals (CMS), an intergovernmental treaty (http:/www.cms.int). The CMS initiated the Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS), focusing upon the conservation status of the Baltic Sea harbour porpoise. Other international agreements such as OSPARCOM and HELCOM also consider the conservation of this species.

In the German Baltic Sea, the harbour porpoise is the only resident cetacean species (Benke et al., 1998). Long-term investigations on harbour porpoises in Germany so far have included the collection of strandings and incidental by-catches, giving the opportunity for assessing distribution and health status of these animals in the German Baltic Sea (e.g. Siebert et al., 2001; Das et al., 2004; Siebert et al., 2006), their population structure (Tiedemann et al., 1996; Huggenberger et al., 2002) and their reproductive status (Benke et al., 1998). Furthermore, incidental sightings have been collected for several decades (H. Benke, personal communication; Siebert et al., 2006).

Until recently, all abundance estimates of harbour porpoises covered the German Baltic Sea only partly, either restricted to the western part up to the Kiel Bight (Heide-Jørgensen et al., 1992; Heide-Jørgensen et al., 1993; Hammond et al., 2002) and the Darss Sill (Gillespie et al., 2003), or to the area east of the Darss Sill (reviewed in Vesper & von Dorrien, 2001). Plans of the German Government for assessing the impact of offshore windmill constructions, as well as for proposing Marine Protected Areas (MPAs) to implement

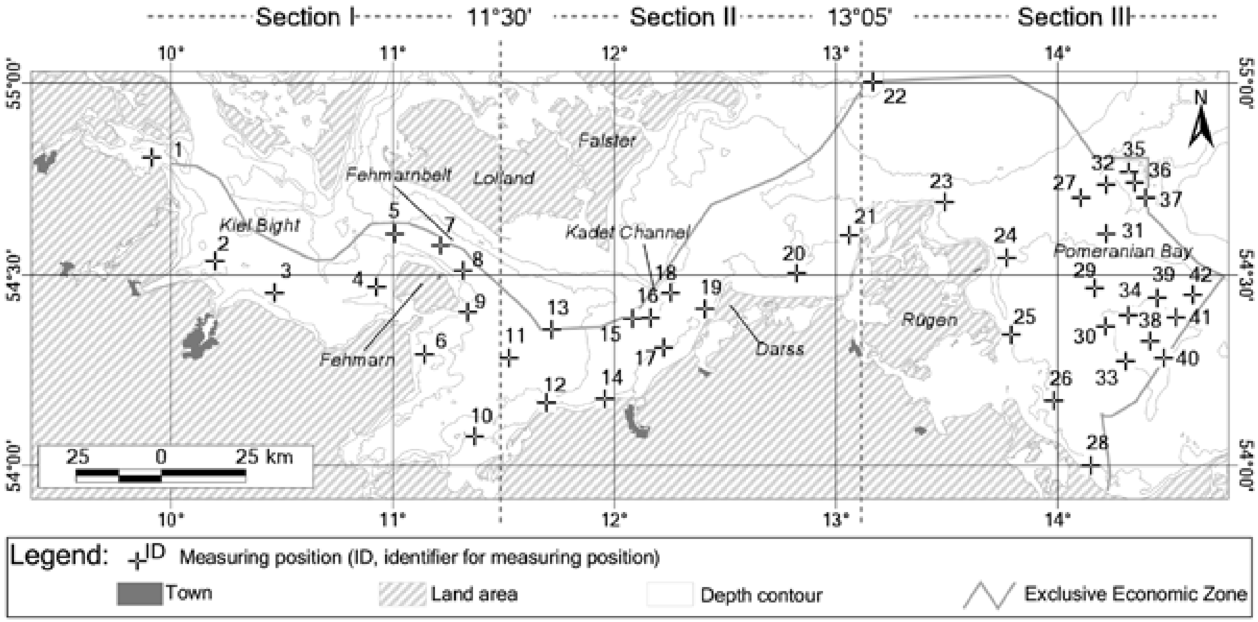


Figure 1. Timing porpoise detector (T-POD) measuring positions (crosses) in the German Baltic Sea. Longitudes 11°30'E and 13°05'E subdivide the German Baltic Sea into Sections I, II, and III for further analysis.

Natura 2000, led to an increased research effort on the harbour porpoise in Germany. In this context, Scheidat et al. (2004a, b) included the entire German Baltic Sea area in their abundance study. Results of aerial surveys conducted in 1995 and 1996, which include the entire German Baltic Sea, have also been published recently (Siebert et al., 2006).

CMS (http:/www.cms.int) considers the harbour porpoise as a migratory species. The porpoise populations of the western North Atlantic move into coastal waters during summer. In some areas, they move offshore in winter to avoid advancing ice cover (Read, 1999). Seasonality in harbour porpoise abundance is also found around the coast of Iceland (Saemundsson, 1939) and the Faroe Islands (IWC, 1996). Historical catches in the Little Belt area of Denmark in spring and winter point towards a seasonal migration of harbour porpoises inhabiting the Baltic Sea (Kinze, 1995). Anecdotes and the historical tradition of Danish fishermen hunting those porpoises imply that the animals followed herring schools into the Baltic Sea in spring and left the inner Baltic waters, escaping from sea ice formation in autumn and winter (reviewed in Koschinski, 2002). Incidental sightings and strandings data collected in the German Baltic Sea from 1988 to 2002 and 1990 to 2001, respectively, also show seasonality when summed over the study period, with maximum numbers in July to September (Siebert et al., 2006). Nevertheless, these methods contain some bias, for example due to unequal sightings effort or due to differences in the submersion time of carcasses depending on the seasons (Siebert et al., 2006). Therefore, it has not yet been conclusively shown if, and how, harbour porpoise abundance in the German Baltic Sea changes over seasons, i.e. if seasonal migration takes place in the harbour porpoise population inhabiting the German Baltic Sea.

Like other odontocete species, harbour porpoises emit short pulsed high frequency click sounds for echolocation (Au, 1993). As an active sensory system, echolocation in porpoises is used for orientation (Verfuß et al., 2005) as well as for foraging (Verfuß & Schnitzler, 2002). Harbour porpoise echolocation clicks are very distinct and differ from most dolphin echolocation clicks (Au, 1993). Their main energy is focused upon a small frequency bandwidth around 130 kHz (Goodson et al., 1995; Kamminga et al., 1999). The distinct and easily distinguishable click structure provides a good opportunity to set up an automatic system that specifically monitors this species, such as a porpoise detector (T-POD). The advantage of static passive acoustic monitoring with T-PODs is that the devices are suitable for long-term deployment. They register the presence of harbour porpoises over months.

The study presented here has been conducted to gain knowledge about the spatial usage of the German Baltic Sea by harbour porpoises. This knowledge provides data for proposing protection areas and gives a baseline for future monitoring programmes in areas of interest such as windmill construction or protection areas. The results of 3.5 years of year-round harbour porpoise monitoring in the German Baltic Sea are presented. The spatial and seasonal variation of the relative abundance of harbour porpoises was investigated with a network of static passive acoustic monitoring instruments, the T-PODs.

MATERIALS AND METHODS

The T-POD

Timing porpoise detectors, (T-PODs, Chelonia Ltd., Long Rock, United Kingdom) are self-contained data loggers for cetacean echolocation clicks, consisting of a hydrophone, filter and digital memory. They register, at a 10 μsec resolution, the presence and length of high frequency click sounds matching specific criteria, logging for 24 hours a day over a period of eight to ten weeks. After this period, the data are downloaded and batteries have to be replaced.

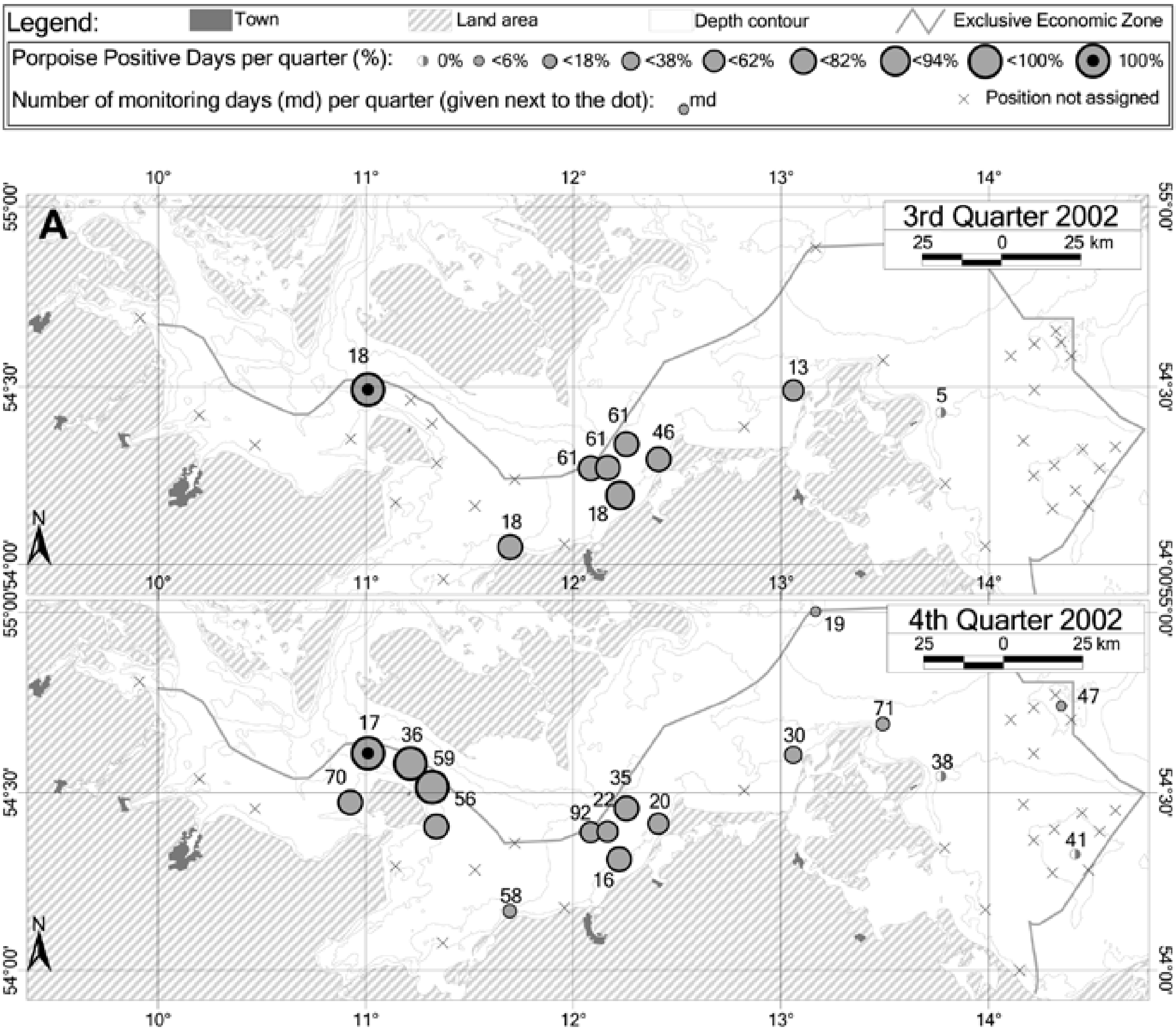


Figure 2. Percentage of porpoise-positive days per monitoring period at the measuring positions for each quarter of the years (A) 2002; (B) 2003; (C) 2004; and (D) 2005. The size of the dots is proportional to the percentage. The number of monitoring days is given next to the dots. Measuring positions at which no data were gathered for the specific quarter are marked with grey crosses.

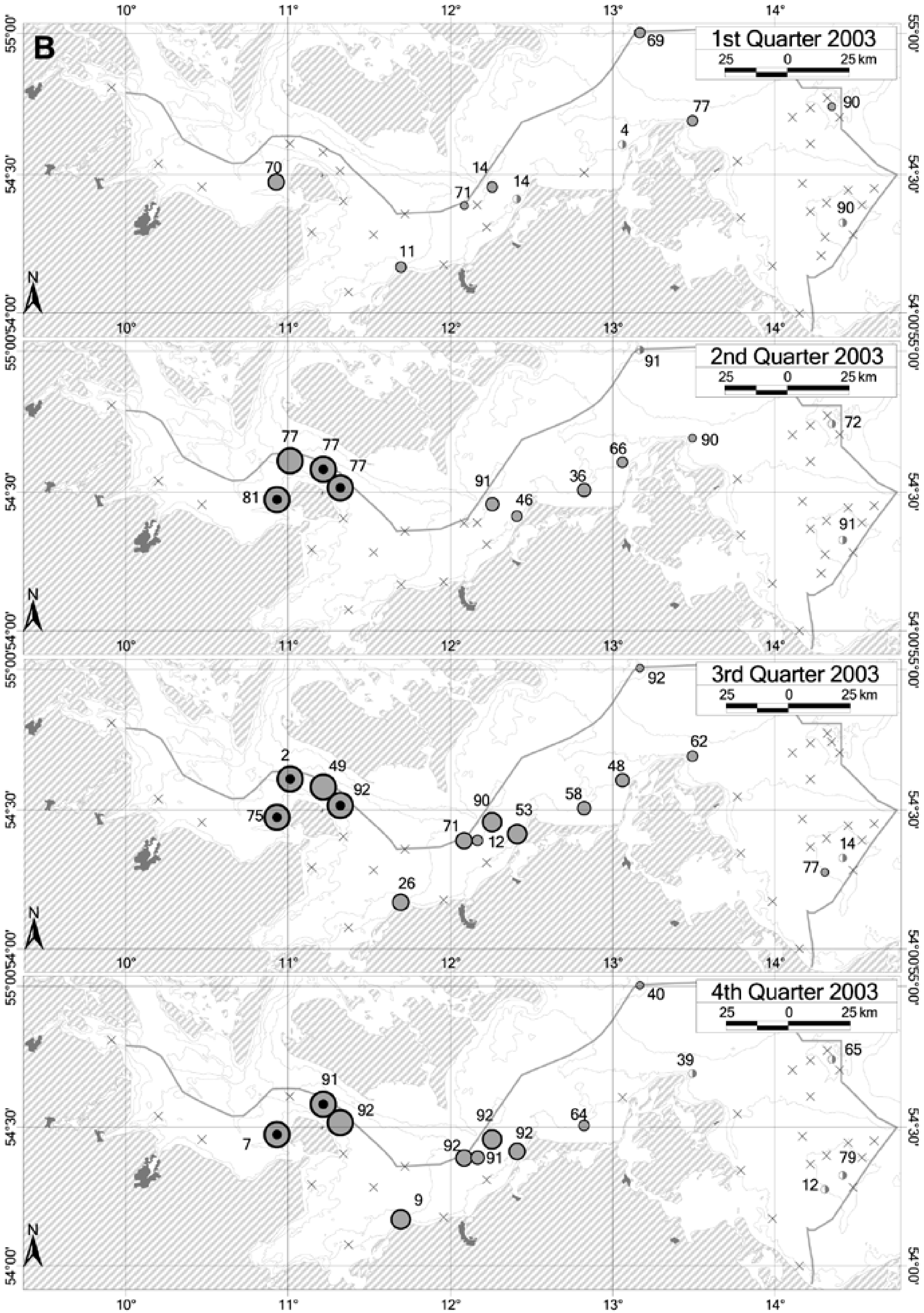
The T-POD software comprises a train detection algorithm, that detects and then classifies trains of registered clicks according to how likely they are to be a cetacean train.

T-POD application

Up to 42 measuring positions were selected to monitor the German Baltic Sea from the Kiel Bight to the Pomeranian Bay (Figure 1) between summer 2002 and the end of 2005. This network of measuring positions contained 17 positions in 2002, and grew, especially at the beginning of 2005, to its final size. Water depth at the measuring positions ranged from 7 m up to 28 m. Measuring positions have been allocated throughout the German Baltic Sea in order to cover the area as appropriately as possible. Emphasis was laid upon proposed MPAs as well as — since 2005 — on the Pomeranian Bay. The positions met the demands of the German Water and Shipping authorities.

At each measuring position, one T-POD at a time was deployed on a mooring, fixed five to seven metres under the water surface. T-PODs of versions 2, 3 and 4 were used. The mooring consisted of a 30-kg weight and anchor connected to several surface buoys via a rope. From the beginning of the recordings in 2002 until spring 2005, the listening criteria of the T-PODs were set to *porpoise-only high sensitivity* as given in the T-POD programme (T-POD version 2: *filter A*=130 kHz, *filter B*=90 kHz, *ratio A/B*=4, *'A' filter sharpness*=10, *'B' filter sharpness*=18, *minimum intensity*=6, *scan limit on number (N) of clicks logged*=240; T-POD version 3: *filter A*=130 kHz, *filter B*=90 kHz, *ratio A/B*=4, *'A' integration period*=short, *'B' integration period*=long, *minimum intensity*=6, *scan limit on N clicks logged*=240; T-POD version 4 was not used during that time). Eventually the *ratio A/B* was set to 6, which reduced the registration of high frequency background noise.

The T-PODs were calibrated before deployment as described in Verfuß et al. (2004a,b) in order to determine



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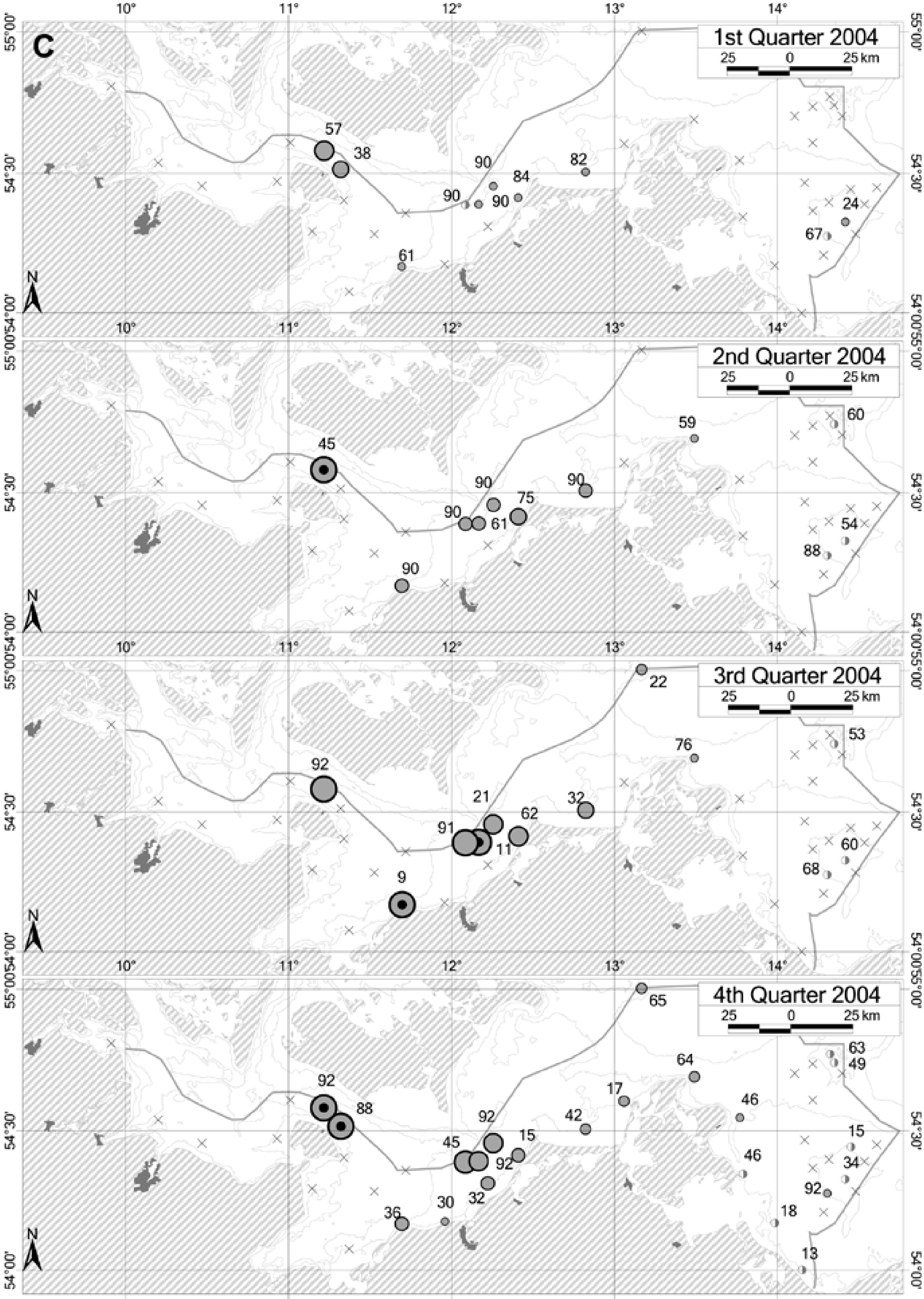

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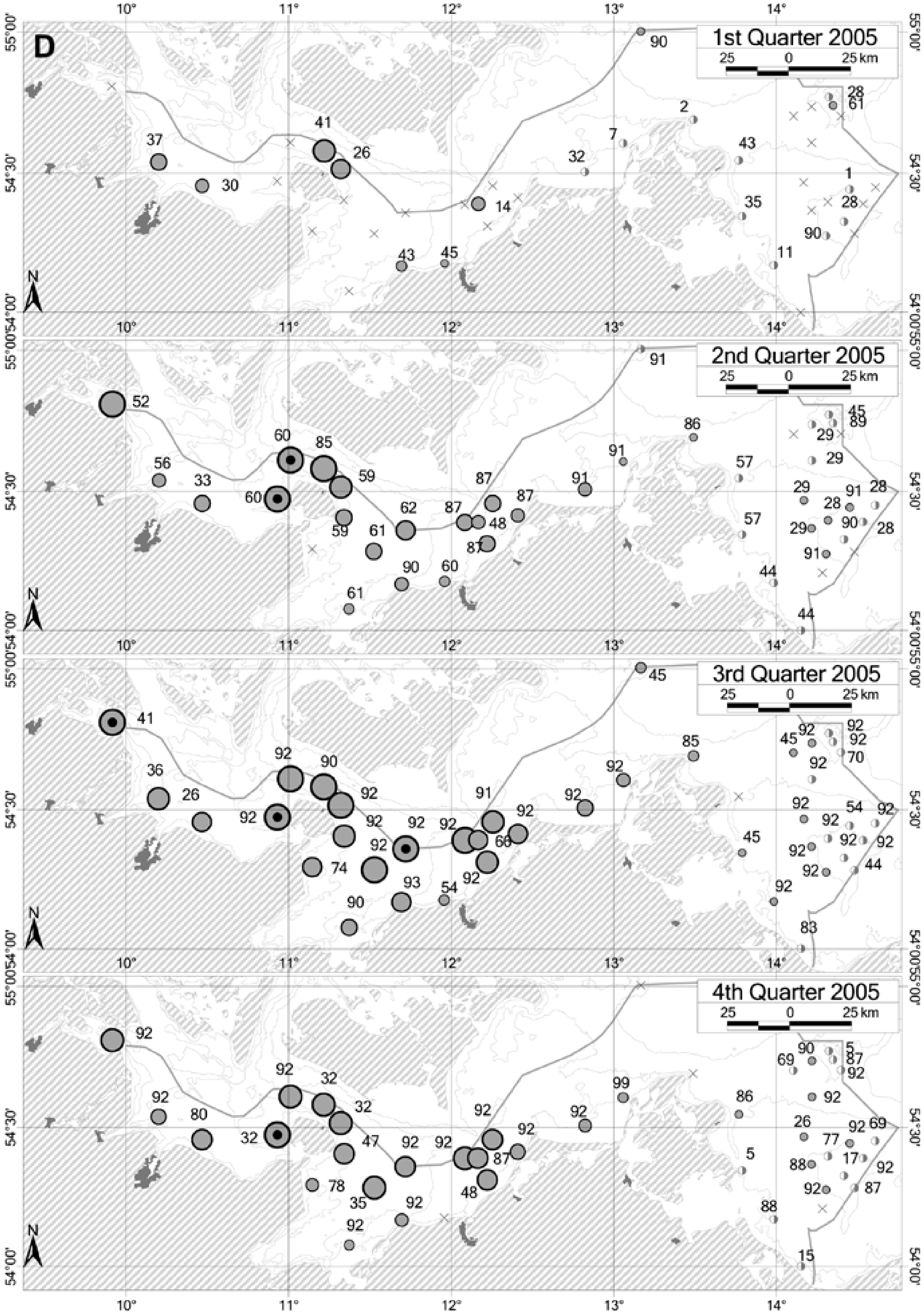

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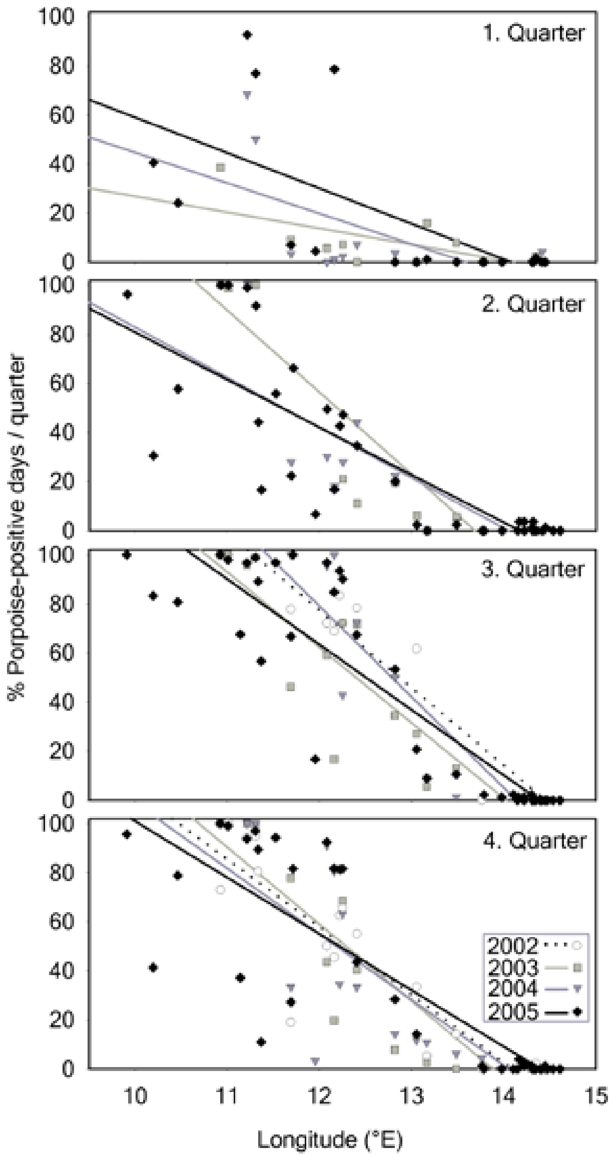

Figure 3. Percentage of porpoise-positive days per quarter of the monitoring years 2002 (circle), 2003 (square), 2004 (triangle) and 2005 (diamond), plotted against the longitude of the corresponding measuring position. The corresponding regression lines for each quarter of the years 2002 (dotted), 2003 (light grey), 2004 (dark grey) and 2005 (black) are also given.

the specific minimum receiving level up to an accuracy of ±1 dB. This is the minimum sound pressure level that a porpoise click needs to have at the device's hydrophone to be registered. The minimum receiving level of the deployed T-PODs was in the range of 117 dB re 1 V_{pp}/μPa up to 144 dB re 1 V_{pp}/μPa. From spring 2005 onwards, the T-PODs were set as close to a standard sensitivity of 127 dB re 1 V_{pp}/μPa as possible by adjusting the parameter *minimum intensity*. From this time onwards, also version 4 T-PODs were used, set to: *filter A*=130 kHz, *filter B*=92 kHz, *click bandwidth*=5, *noise adaptation*=++, *sensitivity*=adapted to our standard sensitivity of 127 dB re 1 V_{pp}/μPa.

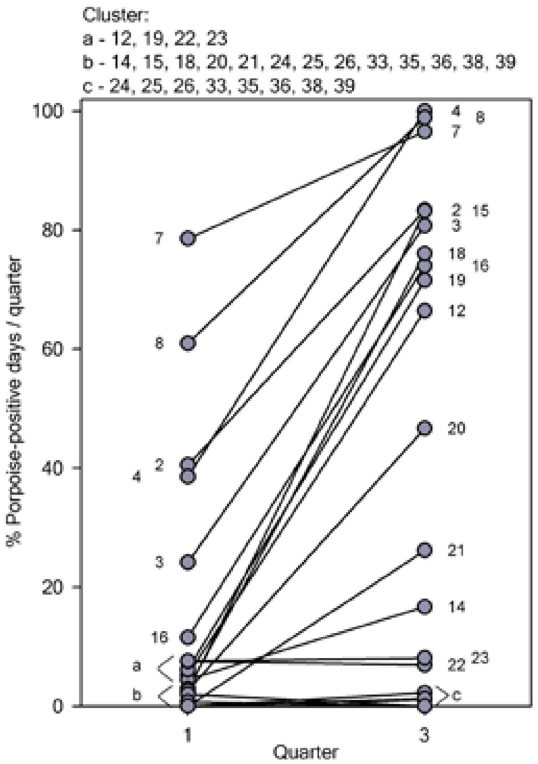

Figure 4. Percentage of porpoise-positive days of 23 measuring positions, each averaged over the years for the first quarters (mainly winter) and third quarters (mainly summer). The numbers next to the symbols give the identifier for the measuring position. The identifiers for the clustered values (a, b, c) are given above the graph.

Influence of T-POD version / settings / sensitivity

Knowledge of the effect on the data of differences in the versions of T-POD, their settings and/or their sensitivity is of particular importance when comparing data gathered with different T-PODs. Therefore, several tests have been conducted to test the comparability of the data gathered for this project.

The change of the settings from ratio 4 to ratio 6 affected neither the sensitivity nor the comparability of the gathered data (Verfuß et al., 2004a). Also, data recorded with version 2 T-PODs were comparable with the data of version 3 T-PODs (Verfuß et al., 2004b), so long as all train classes mentioned in section 'data analysis' (see below) were included in the data analysis.

The sensitivity of the T-PODs was included in the statistical analysis of the first year's data presented and described in Verfuß et al. (2006), so as to reveal any influence of differences in T-POD sensitivity. It could be shown that there was no influence of sensitivity on the results.

Recordings of one T-POD of version 3 and two T-PODs of version 4, set to the same sensitivity, obtained at the same spot within a porpoise-rich area for 4 days showed comparable results when comparing the amount of hours with porpoise detections. During this test, one v4 was set to *noise adaptation*=++ while the other was set to *noise adaptation*=+.

Data analysis

The train detection algorithm (V2.2) has been used to identify click trains within the gathered data. Click trains classified by the algorithm as *high probability cetacean click*

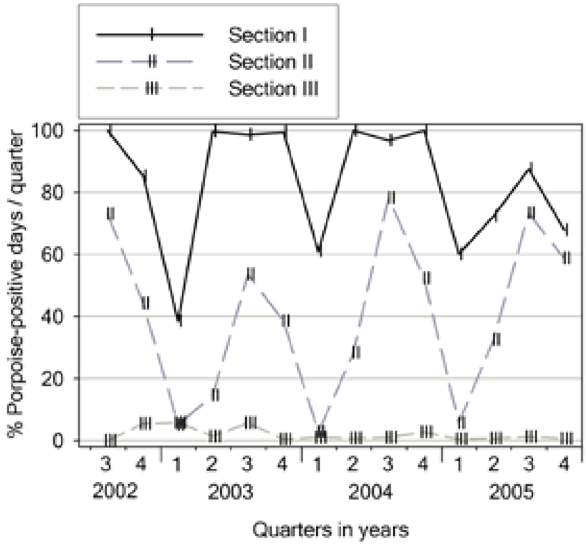

Figure 5. Percentage of porpoise-positive days per quarter for section I, lying west of longitude 11°30'E (solid black line), section II, lying between longitudes 11°30'E and 13°05'E (long dashed dark grey line) and section III, being east of longitude 13°05'E (short dashed light grey line). Please note that from 2005 onwards, the observation area was expanded to the Kiel Bight, probably influencing the results of section I.

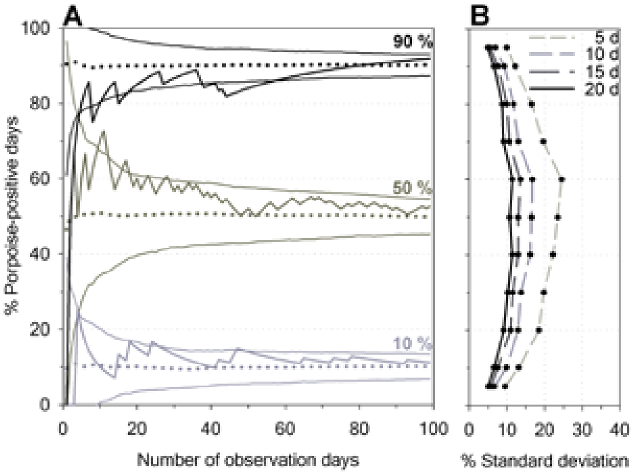

Figure 6. Mean percentage of porpoise-positive days (A, dotted lines) and +/- standard deviation (A, thin lines) from 250 simulations each of a range of numbers of observation days (B, 5 d: light grey short dashed line; 10 d: middle grey middle dashed line; 15 d: dark grey long dashed line, 20 d: black line) and a range of underlying %PPD values (A, 10%: light grey; 50%: grey; 90%: black; B, black dots). Thick (serrated) lines in (A) show one simulation for each sample size.

trains down to *very doubtful trains* were manually reviewed for harbour porpoise echolocation click trains, as described in Verfuß et al. (2004a,b). Click trains which were manually attributed to porpoise origin, were included in the data set, while those manually attributed to boat noise or background noise were excluded from the data set. For further analysis, porpoise-positive days, defined as a day with at least one classified porpoise click train, were determined from all data recordings. The percentage of porpoise-positive days per monitoring days within a quarter of a year (*%PPD/Q*) was calculated for each position. A monitoring day is defined as a day in which a T-POD gathered usable data.

Statistics

The resulting *%PPD/Qs* have been tested for geographical and seasonal differences.

Geographical differences

We tested the null hypothesis that there is no relationship between *%PPD/Q* and the longitude of the measuring positions: Spearman's rank correlation coefficient was calculated separately for each combination of year and quarter (a total of 14 correlations between the *%PPD/Qs* and the longitudes of the corresponding measuring positions). The correlation-coefficient was then tested with a sign test to examine the null hypothesis that positive and negative correlation coefficients are equally likely.

P-values were calculated with the permutation method (1000 permutations each). The alpha-level adjustment to correct for multiple testing was conducted using a binomial approach after Cross & Chaffin (1982) as well as Fisher's omnibus test (Haccou & Meelis, 1994).

We also tested the null hypothesis that there is no relationship between the geographical distance of the measuring positions to each other and the comparability of their results: for the quarter with the highest sample size, the third quarter of 2005, a correlation of the geographical distances and differences between the results of the measuring positions was investigated. Therefore, for each pair (1; 2) of measuring positions, the dissimilarity (C_U) of their data was calculated:

$C_U=(\%PPD/Q1-\%PPD/Q2)/(\%PPD/Q1+\%PPD/Q2)$,
if $\%PPD/Q1+\%PPD/Q2>0$, otherwise 0.

The relationship between the dissimilarity and the geographical distance of the measuring positions was determined with a matrix correlation. The significance of this correlation was calculated using a Mantel test (Sokal & Rohlf, 1995).

Seasonal variation

We tested the null hypothesis that the results of each measuring position gathered in the first and third quarter respectively, are not different from each other: the means over the years of the *%PPD/Qs* for the first and the third quarters respectively, were calculated for each measuring position and tested with a Wilcoxon matched-pairs signed-ranks test.

To summarize the outcome of the statistical analysis (see results) in one graph, the study area has been divided into three sections, with *section I* lying west of longitude 11°30'E, *section II* being between longitudes 11°30'E and 13°05'E, and *section III* lying east of 13°05'E (Figure 2). *%PPD/Qs* have been calculated for each section by summing the porpoise-positive days, as well as the observation days, of all measuring positions lying within the corresponding section, and calculating their quotient.

Table 1. *Number of monitoring days and number of measuring positions per quarter (given in brackets) of the monitoring years 2002 to 2005 for section I to III.*

		No. of monitoring days (No. of measuring positions)			
Year	Quarter	Section I	Section II	Section III	Total
2002	3.Q	18 (1)	278 (7)	5 (1)	301 (9)
	4.Q	238 (5)	273 (7)	216 (5)	727 (17)
2003	1.Q	70 (1)	114 (5)	326 (4)	510 (10)
	2.Q	312 (4)	239 (4)	344 (4)	895 (12)
	3.Q	218 (4)	218 (7)	218 (4)	821 (15)
	4.Q	190 (3)	440 (6)	235 (5)	865 (14)
2004	1.Q	95 (2)	497 (6)	91 (2)	683 (10)
	2.Q	45 (1)	496 (6)	261 (4)	802 (11)
	3.Q	92 (1)	226 (6)	279 (5)	597 (12)
	4.Q	180 (2)	401 (9)	505 (11)	1,086 (22)
2005	1.Q	133 (4)	141 (5)	389 (10)	663 (19)
	2.Q	525 (9)	851 (11)	985 (18)	2,361 (38)
	3.Q	725 (10)	948 (11)	1,575 (20)	3,248 (41)
	4.Q	669 (10)	821 (10)	1,269 (19)	2,759 (39)
Total		3,510 (10)	6,083 (11)	6,725 (21)	16,318 (42)

No., number.

Influence of the number of monitoring days on the reliability of the results

To evaluate the degree of reliability of the percentage of porpoise-positive days gained in a specific monitoring period, the following simulation has been conducted.

Eleven fixed percentages of porpoise-positive days per hundred monitoring days (5%, 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, 90% and 95%) have been attributed to a supposed area. Random series of porpoise-positive days and porpoise-negative days (i.e. no detection on that day) that could be obtained in that area were simulated 250 times for each specific outcome. For each of the 250 simulations for the eleven data sets, the percentage of porpoise-positive days was calculated for each number of monitored days from 1 to 100. For each of these numbers of monitored days, the mean and the standard deviation of the 250 calculated percentages of porpoise-positive days was determined for each fixed percentage of porpoise-positive days.

RESULTS

Harbour porpoises have been registered at nearly all measuring positions throughout the German Baltic Sea, except for a very few positions in the Pomeranian Bay (Figure 2). The data show a regular and year-round use of the German Baltic Sea by these animals, but with geographical differences and seasonal variation in the percentage of porpoise-porpoise positive days.

Geographical differences

A significant decrease of the *%PPD/Q* from west to east was seen in nearly all quarters of the different years (Figures 2&3), except for those with a sample size lower than 12 (nearly all $P \leq 0.001$; with rho from −0.756 (N=19, 1st quarter 2005) to −0.966 (N=14, 4th quarter 2003), except: 2nd quarter 2004: P=0.002; rho= −0.842; N=11; 3rd quarter 2002: P=0.071; rho= −0.627; N=9; 1st quarter 2003: P = 0.146; rho= −0,497; N=10; and 1st quarter 2004: P=0.338; rho= −0.328; N=10); sign test: P=0.00012; alpha-correction after Cross & Chaffin (1982): $P < 0.0001$; Fisher's omnibus test: χ^2=161.9; df=28; $P < 0.0001$).

The matrix correlation of the geographical distances between the measuring positions and the differences between their data obtained in the third quarter of 2005 revealed a significant correlation (rho= 0.573, P=0.001). This means that neighbouring measuring positions show similar results and data become more dissimilar with increasing distance between positions.

Seasonal differences

Seasonal differences have been revealed for the *%PPD/Q* (Figure 4). At 23 measuring positions, data were gathered for the first and third quarter. Those data showed a significantly higher percentage of porpoise-positive days in the third quarter (July to September) — which mainly mirrors summer — compared with the first quarter (January to March), largely corresponding to winter time (Wilcoxon test: z=3.509; N=23 (2 ties); $P < 0.001$).

The *%PPD/Qs* calculated for the sections I to III clearly mirror the statistically significant seasonal variation and geographical difference in *%PPD/Q* (Figure 5; Table 1). Figure 5 shows the aggregated data, in which quarters are not strictly comparable e.g. the reduction in the *%PPD/Q* in 2005 in section I compared to the years 2002 to 2004 might be due to the inclusion of measuring positions in the Kiel Bight from 2005 onwards rather than due to changes in the porpoise population.

Influence of the number of monitoring days on the reliability of the results

The simulation we conducted shows that the reliability of the results depends on the number of monitoring days as well as on the prevailing situation causing a specific percentage of porpoise-positive days: The variability of data gets smaller with increasing number of monitoring days (Figure 6A&B). For a fixed number of monitoring days, the standard deviation rises with rising predetermined values for the percentage of porpoise-positive days up to around 50%, and then decreases again with rising predetermined values (Figure 6B). This fact has been taken into account when deciding on the bin width of the percentage of porpoise-positive days for Figure 2 (largest bin width for middle range percentages, decreasing bin width towards 0% and 100%, respectively).

For monitoring periods with a minimum of 14 monitoring days, the percentage standard deviation resulted in values below ±15%.

DISCUSSION

Our data show the importance of the German Baltic Sea as a habitat for harbour porpoises. We found that the species was present in the German Baltic Sea all year round (Figure 2), with decreasing acoustic detections of harbour porpoises from west to east, as well as increasing porpoise detections during the breeding and mating seasons (spring and summer), and a subsequent decrease in winter time (Figures 3—5).

We interpret the changes in the proportion of porpoise-positive days throughout the year and differences across areas as temporal changes and geographical differences in harbour porpoise density. Abundance estimates with visual surveys, showing that the density of harbour porpoises in the German Baltic Sea decreases from west to east (Scheidat et al., 2004a,b; Siebert et al., 2006), confirm our statement, that the percentage of porpoise-positive days reflects the density of harbour porpoises in our study area.

The decrease in the proportion of porpoise-positive days per quarter from west to east has been shown in all observation years. Whereas the decrease is prominent with a large slope in the second to third quarters of the years, the slope of regression for the first quarter is not as steep and is only significant for the first quarter of one year, 2005 (Figure 3), mirroring the seasonal changes then.

In the first year of our study, seasonal changes in the detection rate of harbour porpoises in the German Baltic Sea were already obvious (Figures 2&5) and were confirmed in the subsequent years of static acoustic monitoring. Seasonality is only prominent for measuring positions in sections I and II (Figures 1, 4&5).

One could argue that harbour porpoises, like other cetaceans, might show seasonality in their vocalization, and that a decrease in acoustic detection is more a matter of non-vocalization than of a decrease in the number of porpoises present. The mating song of some baleen whales, e.g. humpback whales (*Megaptera novaeanglia*), is heard during the winter breeding season, but seldom at other times (Gordon & Tyack, 2001). However, in contrast to the echolocation behaviour of harbour porpoises, those vocalizations do have a communication function. Echolocation is an active sensory system delivering information about the porpoise's environment. Verfuß et al. (2005) demonstrated the importance of echolocation for harbour porpoises. Porpoises, which were living in a well-known, semi-natural outdoor pool, continuously used echolocation, even in easy orientation tasks during daylight, regardless of the season. Differences in the environmental complexity (uncluttered versus cluttered) or in behavioural status (orientation and foraging) only affected the rate of click production, but did not result in an interruption of echolocation. A wild harbour porpoise carrying an acoustic datalogger also used its sonar system almost continuously (Teilmann et al., 2005). Pauses between click trains were logged with a maximum of 222 seconds, but 90% of the silent periods were less than 15 seconds. Therefore, almost continuous use of echolocation by harbour porpoises is very likely.

Until the mid-20th century, a migration of harbour porpoises between the North and Baltic Seas was believed to occur (reviewed in Koschinski, 2002). In spring, the porpoises were thought to have followed movements of herring, passing through Danish waters into the Baltic Sea. In late autumn and winter, when the Baltic tended to freeze over in some years, the porpoises may have migrated back out of the Baltic Sea. Nowadays, the porpoise populations are too small to easily prove such migrations. Teilmann et al. (2004) were able to prove seasonality in the use of areas in Danish waters with the help of satellite tags on porpoises. Siebert et al. (2006) also showed seasonality, in more than ten years' data collection of incidental sightings and strandings in the German Baltic Sea, with a maximum of sightings and strandings in the summer months July to September. The authors discuss the possibility that the data from incidental sightings might be biased by a lower effort in winter (e.g. fewer sailing boats), whereas the strandings data, obtained by a year-round observer scheme and standard procedure ensuring stable monitoring efforts, may be biased by a longer submersion time of carcasses when water temperature is low (Moreno et al., 1993) and because of the unknown drift route that they may take.

Geographical and seasonal changes in environmental conditions might be an argument for explaining geographical and seasonal changes in the T-POD data. Temperature and salinity can affect the speed of sound in water (Richardson et al., 1995), but does not affect the absorption of sound that could influence the detectable range of a porpoise click train. Therefore, the decreasing concentration of salinity prevailing in the Baltic Sea (Janssen et al., 1999) is unlikely to cause the decrease of porpoise registrations from west to east. Variation in temperature and salinity along with water depth, on the other hand, does affect sound propagation (Richardson et al., 1995), as sound bends when travelling through water strata of different temperature and salinity. This effect of refraction can affect the sound intensity over kilometres. However, very high frequencies, as found in porpoise echolocation clicks, do have a high loss of sound density due to absorption, resulting in a short detection range of the clicks. Therefore, refraction cannot affect the clicks' sound intensity over a range of kilometres as it would for low frequency sound.

Furthermore, harbour porpoises are very mobile animals, passing through different water depths (Lucke et al., 2000; Read & Westgate, 1997) during the course of swimming, feeding and breathing. This reduces the risk of an animal being undetectable by a T-POD. For analysing porpoise-positive days, only a short part of a click train must be detected by the T-POD to make a day porpoise-positive. Furthermore, analysis of porpoise-positive days per quarter showed that neighbouring measuring positions obtained similar results and became more dissimilar with growing distance in between the positions. Thermo- and haloclines in the Baltic Sea are very heterogeneous with respect to space and time, especially when passing through different water depths. If this phenomenon did have an influence on the data, neighbouring positions at different water depths would not gather such comparable data.

The number of monitoring days per quarter of each year, as given in Figure 2 and Table 1, has also been sufficient at most of the measuring positions to give representative data, following the results of the model shown in Figure 6. Also the varying and increasing number of measuring positions does not change the replication of seasonal and geographical variation in each of the monitored years.

The measuring positions in section III (east of 13°05'E) did not show any obvious seasonality (Figures 1, 4 & 5). Huggenberger et al. (2002) hypothesized that porpoises inhabiting the waters east of the Darss Sill do not migrate over longer distances to the west in ice free winters. Their morphological studies revealed the existence for a separate sub-population of harbour porpoises in the Baltic proper, i.e., east of Darss Sill. Those data have been confirmed by genetic investigations (Tiedemann, 2001). The low density of this sub-population raises serious concern for the survival of the population, which is especially emphasized in the Recovery Plan for Baltic harbour porpoises (the Jastarnia Plan of ASCOBANS). The T-POD data confirm a very low density of harbour porpoises in the German part of the Baltic proper. Further east and north, in the Swedish and Polish Baltic proper, harbour porpoise encounters become rare (reviewed in Koschinski, 2002). This area is now considered as the north-easterly distribution range of harbour porpoises in the Baltic Sea (Koschinski, 2002). The very low density of the Baltic-proper harbour porpoise makes this sub-population very vulnerable. Any negative anthropogenic influence (e.g., fishery by-catch, chemical or noise pollution) on this very small and therefore highly endangered sub-population might sooner or later lead to its extinction if no action is taken.

The method of T-POD deployment proved to be a very valuable tool for investigating changes in harbour porpoise density within the German Baltic Sea on a temporal and geographical scale. The present study proves a regular use of the German Baltic Sea by harbour porpoises with geographical differences in porpoise density and a seasonal migration pattern of the harbour porpoises inhabiting the German Baltic Sea. The higher numbers of harbour porpoise detections in spring to autumn compared with winter indicate that the German Baltic Sea is an important breeding and mating area for these animals. The infrequent detections of harbour porpoises north and east of the island of Rügen confirm a very low density of the Baltic-proper harbour porpoise sub-population, and raise an immediate need for protection measures.

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