Resident harbour porpoises *Phocoena phocoena* in the Oosterschelde (Netherlands): their behaviour compared to the behaviour of migratory harbour porpoises in the southern North Sea

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Abstract

Harbour porpoises *Phocoena phocoena* are most abundant in the southern North Sea during winter and early spring. In late spring, densities become low and porpoises are suggested to migrate northward in the direction of Scotland or the Sylt Outer Reef near Denmark, where calving takes place. However, a small resident population seems to have established in the Oosterschelde. This area, which is part of the Dutch Delta Area, is semi-seperated from the North Sea by a storm surge barrier, where tidal currents are strong. The study presented here has been conducted to gain more knowledge about harbour porpoises in the Oosterschelde, how their behaviour is related to that of the migratory porpoises in the North Sea and to determine what the role is of the storm surge barrier. To investigate this, acoustic research, visual surveys and stomach content analyses had been performed. Data of these studies were analyzed and combined with information from existing literature.

This research confirms that porpoises in the Southern North Sea are most abundant in winter and early Spring. Porpoises were hardly observed in summer, to return again in September, which suggests that they still leave the area in spring. In the Oosterschelde however, porpoise presence has been observed in all months. Evidence is provided for migration between the North Sea and the Oosterschelde, but the results suggest that this does not occur very frequently. Nocturnal activity patterns of harbour porpoises in the North Sea have been reported in earlier research. In the Oosterschelde, clicks have been recorded in relatively more time intervals at night in winter and at day in summer. The influence of tidal currents was also earlier reported, but in this study, the direction of the water currents did not have a significant effect on the swimming direction of porpoises in the North Sea. In the Oosterschelde, the tidal currents of the storm surge barrier did have a significant effect: the stronger the currents, the less presence of harbour porpoises. Furthermore, porpoises seemed to be present in more time intervals at rising tide, but produce more echolocation click trains at falling tide. So an impact of the storm surge barrier on the Oosterschelde porpoises has been found. However, since evidence was found for migration between the North Sea and the Oosterschelde, crossing the storm surge barrier is apparently not impossible for porpoises.

The diet of porpoises along the Dutch coast seems to be influenced by prey availability. In the Oosterschelde, harbour porpoises were also observed mostly at hotspots of their prey species. It is possible for the Oosterschelde harbour porpoises to cross the storm surge barrier, but apparently, the conditions are favorable enough to stay here all year, which makes it unnecessary to migrate northwards in spring.

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1. Introduction

1.1 Background

The harbour porpoise (*Phocoena phocoena*) is the most numerous cetacean species in the North Sea (Klinowska, 1991; Haelters & Camphuysen, 2009). In 1994, the total number of harbour porpoises in this area was estimated at 270 000 individuals, with the highest densities in the north-western North Sea and along the German and Danish west coasts (Hammond *et al.*, 2002). However, since the end of the twentieth century, harbour porpoises have increased in the southern part of the North Sea (Haelters & Camphuysen, 2009). From the mid-1990s to the early 21st century, an annual increase of about 41% was found. Because this increase exceeds the yearly potential population growth of about 10%, it is suggested that distribution shifts or immigration have been underlying the observed trend. The redistribution of harbour porpoises in the North Sea may have been stimulated by changes in prey availability, especially in the northern part of the North Sea (Camphuysen, 2004; Haelters & Camphuysen, 2009). Because of their small size, harbour porpoises are unable to carry large energy stores. Therefore, they must stay close to their prey species (Koopman, 1998).

Santos *et al.* (2004) showed that harbour porpoises show seasonal and geographical variation in diet. Seasonal fluctuations are also reflected in the distribution of porpoises in the southern North Sea. The highest abundance of harbour porpoises along the Dutch coast is reached in winter and early spring (Gilles *et al.,* 2009; Jak *et al.,* 2010). In late spring, a northward migration of harbour porpoises is observed (Osinga, 2005). In June and July, pregnant females give birth to calves. The Sylt Outer Reef near Denmark has already been identified as a calving ground for porpoises (Sonntag *et al.*, 1999), but some calves have also been observed near Aberdeenshire (Scotland). Although calves only comprised 3.2% of the total observed porpoises, which is too low to indicate Aberdeenshire as calving ground, it does suggest that some porpoises utilize this area to breed in summer (Weir *et al.,* 2007). By then, the number of harbour porpoises in Dutch coastal waters has become low (Haelters & Camphuysen, 2009).

Besides the population in the North Sea, a small resident population seems to have established in the Oosterschelde, a semi-closed part of the Dutch Delta Area. Since the completion of the storm surge barrier in 1986, two harbour porpoises have been observed in this area for the first time in 1996 (Witte, 2001). Because little is known about this population, the Rugvin Foundation started a survey in 2009. In September of that year, 37 individuals were counted under almost windless conditions, among which five calves. Research in Swedish coastal waters showed that mother-calf pairs swim back and forth within an area of 100 kilometers, compared to 800 kilometers of independent immature porpoises (Teilmann *et al.*, 1997 in: Witte, 2001). Since calves are born in summer, it is unlikely that the observed calves crossed the distance from neither the Sylt Outer Reef nor Scotland all to the Oosterschelde. In May 2010, a second survey was conducted under less favored weather conditions by the Rugvin Foundation, resulting in fifteen counted porpoises.

Because harbour porpoises were observed in May and September by the Rugvin foundation and at different dates throughout the year from coasts and ships, it is suggested that these animals occur year-round in the Oosterschelde, which is different from the described migration route. It is unclear why these porpoises stay in the Oosterschelde instead of migrating northwards in spring. Apparently they are behaving differently from the North Sea porpoises. The storm surge barrier might play a functional role in the behaviour of the Oosterschelde porpoises, either in a positive or a negative way. It is possible that enough food is available in and around the Oosterschelde throughout the year and that tidal currents of the storm surge barrier are used for foraging. It has already been shown that harbour porpoises wait for specific states of the tide to feed. They often forage in waters where tidal currents are strong (Watts & Gaskin, 1985), because these currents are believed to concentrate prey which are funneled towards the waiting porpoises (Piermont, 2008). During flood, water from the North Sea is flowing into the Oosterschelde through the storm surge barrier, where porpoises may wait for the incoming fishes. If so, it is expected that harbour porpoises are more often present at high tide near the storm surge barrier.

The storm surge barrier may also form a barricade for harbour porpoises. The noise of the water currents passing through the storm surge barrier may hinder the harbour porpoises from swimming to the North Sea. It has already been shown that harbour porpoises are very sensitive to underwater sounds and that they show avoiding behavior towards the sound source by swimming away and increasing the respiration rate (Kastelein *et al.*, 2005; Kastelein *et al.*, 2006). They are deterred by low frequency playbacks of wind turbines (Koschinski *et al.*, 2003) as well high-frequency acoustic alarms (Culik *et al.*, 2001). In addition, females with calves may also avoid the strong tidal currents because of the risk of separation from calves that might experience difficulty swimming against the tidal stream (Piermont, 2008). Four times a day, during slack tide, the tidal currents cease. At these moments, the noise and tidal currents are minimal, which may provide chances for the porpoises to migrate between the Oosterschelde and the North Sea. If porpoises are hindered by the storm surge barrier, it is expected that they will be observed near the Oosterschelde barrier mostly during slack tide.

Earlier research by Todd and colleagues (2009) revealed that day light can also have an influence on the behaviour of harbour porpoises: porpoises around North Sea off-shore gas installations showed a diurnal pattern: the number of visits was greater at night than by day, and also a pronounced diel pattern in echolocation was found. An interpretation of this pattern was that porpoises were feeding below or around the platform at night. No information is available about the effect of day light on porpoises in the Oosterschelde yet.

To investigate to what extent the behaviour of the Oosterschelde porpoises differs from that of the migratory North Sea porpoises, a comparison has been made between their migratory behaviour, the effect of day light and tide on their daily movement patterns, spatial usage of their habitat and diet. Devices for static acoustic monitoring, called C-pods, have been deployed on both sides of the storm surge barrier to record the echolocation sounds of harbour porpoises. In this way, it is possible to determine whether harbour porpoises occur year-round in the Oosterschelde, whether migration between the North Sea and the Oosterschelde occurs, whether harbour porpoises can be observed near the storm surge barrier more frequently in particular periods of the day or year and what the influence is of tide on the presence and echolocation activity of porpoises near the storm surge barrier. Next to the two Oosterschelde surveys performed in September 2009 and May 2010, a third survey has been done in June 2011. Results of these three Oosterschelde surveys conducted by the Rugvin Foundation provide information about the spatial usage of this area by the harbour porpoises. Stomach content analysis of porpoises stranded in the Oosterschelde, performed by M. Leopold and O. Jansen, will give an indication of the diet.

To gain more insight in the recent distribution and movement patterns of harbour porpoises in the southern North Sea, a cetacean monitoring program was set up by the Rugvin Foundation in January 2005. This monitoring program is associated with the Atlantic Research Coalition: a partnership between several European cetacean monitoring programs operating on ferry services with the same research methods. Observations were done between January 2005 and December 2010 from the bridges of the Stena Line ferries between Hook of Holland (NL) and Harwich (UK) on regular transects and on a monthly basis. In this way it is possible to detect coastal movements and to detect trends whether porpoises still migrate in spring or whether more porpoises are also observed in the southern North Sea in summer. Together with already existing literature, a reconstruction of annual, seasonal and daily movement patterns of the North Sea harbour porpoises could be made.

The study presented here has been conducted to gain more knowledge about harbour porpoises in the Oosterschelde and how their behaviour is related to that of the migratory porpoises in the North Sea. This information is important for gaining insight in the status and possible chances but also threats for the harbour porpoise in the Oosterschelde: since plans have been made to build tidal turbines within the gaps of the storm surge barrier, this research intends to provide insight into porpoise behaviour for taking more effective measures to conserve the harbour porpoise population in the Oosterschelde and to minimize their threats.

1.2 Research Questions

To what extent does the behaviour of harbour porpoises in the Oosterschelde differ from harbour porpoises in the southern North Sea and what is the role of the storm surge barrier?

1. Is there any difference in migratory behavior throughout the year and can trends be detected?
2. Does exchange take place between harbour porpoises in the Oosterschelde and the North Sea?
3. Is there any difference in daily movement patterns?
   - Does day light play a role?
   - Do tidal currents play a role?
4. Is there any difference in diet and how is that related to prey availability and spatial usage of the habitat?

2. Methods

2.1 Study area

To investigate how the movement patterns of the harbour porpoises in the Oosterschelde are related to those of the migratory harbour porpoises in the North Sea, observations were done in both areas. Data from monthly visual surveys in the southern North Sea between January 2005 and December 2010 have been used (Fig. 1a). Together with already existing literature, this study gives information about daily, seasonal and yearly movement patterns of harbour porpoises. In the Oosterschelde, acoustic research has been performed on both sides of the storm surge barrier to investigate the movement patterns of porpoises in the Oosterschelde and to see whether migration between the Oosterschelde and the North Sea occurs. Data from January 2010 to March 2011 have been used in the analysis. Furthermore, visual surveys have been performed in the Oosterschelde in September 2009, May 2010 and June 2011 to investigate the abundance, distribution and spatial usage of harbour porpoises in this area. Stomach content analyses from harbour porpoises stranded in the Oosterschelde were performed by M. Leopold and O. Jansen. This data was compared with literature to study the differences and diet preferences of porpoises in the southern North Sea and the Oosterschelde.

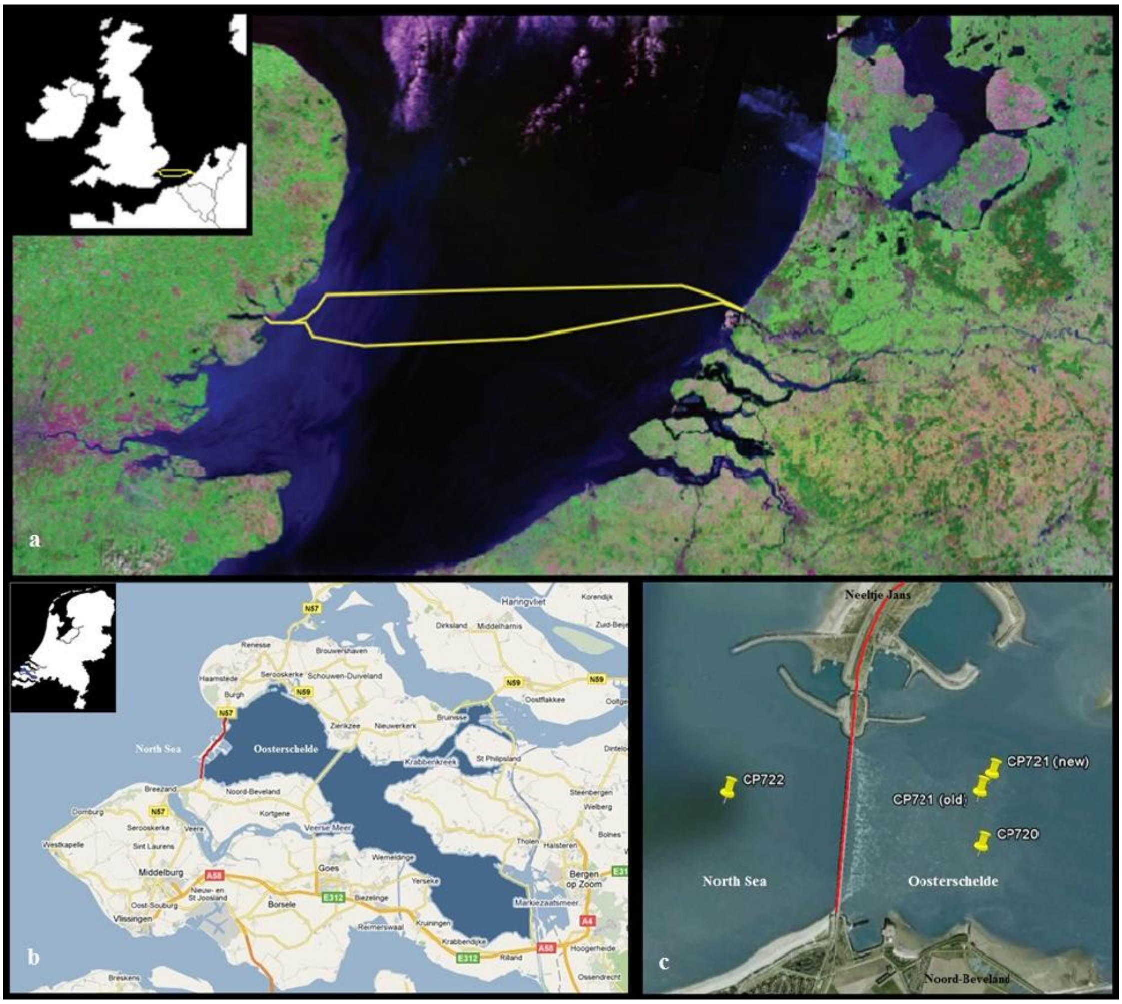

Figure 1: maps of the study areas. Figure 1a shows the routes of the Stena Hollandica and the Stena Britannica. The northern line indicates the route from Hook of Holland to Harwich; the southern line represents the route from Harwich to Hook of Holland (Osinga, 2005). Figure 1b shows the location of the Oosterschelde (dark blue). The red line indicates the storm surge barrier. Figure 1c shows the position of the C-pods. The red line indicates the storm surge barrier. CP721 (old) indicates the location of C-pod 721 before 12 January 2011; CP721 (new) indicates the location of C-pod 721 since 12 January 2011.

2.2 Migratory behaviour

To compare the migratory behaviour of harbour porpoises in the southern North sea and the Oosterschelde, data was used from monthly visual surveys from Stena Line ferries in the southern North Sea and from acoustic research in the Oosterschelde.

2.2.1 Stena Line monitoring program

In January 2005, a monitoring program was set up by the Rugvin Foundation to gain more insight into the movement patterns of harbour porpoises in the southern North Sea. This monitoring program is associated with the Atlantic Research Coalition (ARC): a partnership between several European cetacean monitoring programs operating on ferry services with similar research methods.
Between January 2005 and December 2010, observations were done from the bridges of the Stena Line ferries between Hook of Holland (NL) and Harwich (UK) on a monthly basis. In the period January until June 2005, surveys were conducted twice a month within the framework of the graduation research of N. Osinga. In 2007, surveys were carried out only in September, October, November and December due to ship reconstruction works.

Every survey consists of two survey days with an observation period of approximately six hours per day during day light: the first day of observation is on the Stena Hollandica travelling from Hook of Holland to Harwich (departure in the afternoon); the second day is on the Stena Britannica travelling back from Harwich to Hook of Holland (departure in the morning). Both transects measure approximately 200 kilometers and the routes remained the same throughout the years (Fig. 1a). The border between the Netherlands and England is in the middle of the transect line.

Observations were done by two observers from the bridges of the ship, one on starboard and one on port board, always including one of the project coordinators, either F. Zanderink or N. Osinga. The bridge of the Stena Hollandica is 32m high and the bridge of the Stena Britannica is 35m high. The observers scanned each 45° of the course line. The average speed of the ship is 20 knots (=37km/h). The total travel time per day was approximately seven hours. In winter, day length limited the hours of observation on the first survey day.
During the surveys two record forms were filled in. One form includes parameters such as date, time, location, course and speed of the ship, sea state, visibility, clouds, swell height, wind speed, wind direction and the type and intensity of precipitation. This form was filled in every 30 minutes. The second form was filled in once cetaceans were spotted: time, position, sea state, visibility, species, swimming direction, distance and angle to the individual and sometimes behavior was registered.

The distribution of the harbour porpoises has been mapped with ArcGis Explorer. The data points were plotted for each month and each year to visualize seasonal and annual trends. To detect east-west shifts, a zero point was set on the most eastern point of the Stena Line route, namely Hook of Holland (51°59'11"N and 4°05'02"E). The perpendicular horizontal distances in kilometres to this longitude were measured using ArcGis Explorer. Although the route remained the same over the years, it is possible that porpoises have been observed more on the northern or southern part of the route in particular months or years. Therefore, also north-south movements were detected: latitude 52°08'31"N was used as northern zero point and ArcGis Explorer was used to measure the perpendicular vertical distances to this latitude. Together with already existing literature, a reconstruction of the migratory patterns of the North Sea harbour porpoises was made.

2.2.2 Acoustic research in the Oosterschelde

To investigate the migratory behaviour of harbour porpoises in the Oosterschelde (Fig. 1b) , three C-pods, which are devices for acoustic monitoring, were deployed on the safety lines on both sides of the Oosterschelde barrier in 2009: one in the North Sea and two in the Oosterschelde (Fig. 1c, Table 1). The data of the C-pods give information about the presence of harbour porpoises on both sides of the storm surge barrier throughout the year. The C-pods use digital waveform characterization to select the clicks of cetaceans (Tregenza, 2011). Time, centre frequency, sound pressure level, duration and bandwidth of each clicks were registered by these C-pods. Every two months, batteries were changed and data was collected. Within the first two months, the C-pods did not work properly. Data was used from February 2010 until March 2011. The C-pod in the North Sea did not work in May and December of 2010. At least one C-pod was working in the Oosterschelde in every month of data collection. On 12 January 2011, C-pod 721 was moved because it was enfolded in the safety line.

Table 1: table showing the locations of the three C-pods. CP721 was moved on 12 January 2011 because it was enfolded in the safety line. Since the safety lines are floating with the currents, these locations are somewhat variable.

Location	C-pod	GPS points
North Sea	**CP722**	51°36'34.56"N and 3°40'1.44"E
Oosterschelde	**CP720**	51°36'19.02"N and 3°42'2.04"E
Before 12-01-2011	**CP721 old**	51°36'34.86"N and 3°42'1.50"E
Since 12-01-2011	**CP721 new**	51°36'39.84"N and 3°42'7.20"E

To open the raw data, software called CPOD.exe v2.001 was used (Tregenza, 2011). This software uses the KERNO classifier to detect cetacean click trains in the data. Only high and moderate quality click trains were used. Harbour porpoise click trains were searched by putting on the setting ‘NBHF cetacean’, coding for species that produce Narrow Band High Frequency clicks. Trains with features of WUTS (Weak Unknown Train Sources) were excluded. The data was sorted with this software in time-intervals of ten minutes. Data was available as:

- the number of clicks per ten-minute time-interval. This dataset gives information about the production of echolocation clicks near the storm surge barrier.
- DPM = Detection Positive Minutes = the number of minutes (from zero to ten) in which harbour porpoise clicks were recorded per time-interval of ten minutes;

An additional dataset was created from the above-mentioned datasets, in which a 1 codes for presence of harbour porpoises during the ten-minute interval and in which a 0 stands for no recording of porpoise sounds. This dataset was used to show if porpoises were more often observed in particular parts of the day or year. In the other two datasets, intervals without observations have been eliminated to investigate patterns in click production and time that porpoises spend near the storm surge barrier when they are present. Data from C-pod 720 and C-pod 721, both located in the Oosterschelde, were put together.

2.3 Migration between the North Sea and the Oosterschelde

To demonstrate whether harbour porpoises cross the storm surge barrier, the dataset was used in which the 0 codes for absence in a particular time-interval of ten minutes, and a 1 codes for presence. Migration was assumed to occur when porpoise clicks were recorded in the Oosterschelde and in the next time interval the North Sea or vice versa (Table 2).

Table 2: table showing the patterns that were assumed to represent migration between the Oosterschelde and the North Sea. A 1 is coding for porpoise presence and 0 for porpoise absence.

	North Sea	Oosterschelde
Migration from North Sea to Oosterschelde		
Ten-minute time-interval 1:	1	0
Ten-minute time-interval 2:	0	1
Migration from Oosterschelde to North Sea		
Ten-minute time-interval 1:	0	1
Ten-minute time-interval 2:	1	0

By randomizing the dataset, it was possible to investigate whether these patterns were found more often than random. After the first trial of one month, these patterns were found significantly more often by the randomizer than in the original dataset, since multiple 1 in subsequent time-intervals were separated after randomizing. Therefore, a data correction was applied to count multiple 1 in subsequent time-intervals as one observation. Data was randomized 1000 times for each month using the algorithm Mersenne Twister. When the chance on finding the pattern minimally as often as in the original dataset is lower than 0.05, the results are considered not to be based on coincidence.

Note: although more possibilities in the dataset exist that might code for migration (i.e. in time interval 2 both the North Sea and the Oosterschelde score a 1), these were not used in the analysis. When clicks were recorded at both sides of the storm surge barrier in the same time interval, it cannot be excluded that the clicks were produced by two individuals instead of one individual that crosses the barrier, which means that this possibility is no evidence.

2.4 Daily movement patterns

To answer the question whether day light and/or tide have an effect on the daily movement patterns of North Sea porpoises and Oosterschelde porpoises, the following methods have been used:

2.4.1 The effect of day light and tide on harbour porpoises in the Oosterschelde

The effect of day light and tide on porpoises was tested for all three datasets. For the influence of tide, the water levels of the locations *Roompot binnen* (within the Oosterschelde) and *Roompot buiten* (outside the Oosterschelde) were compared (Rijkswaterstaat, 2011). These waterlevels were given in centimeters compared to NAP per 10 minutes. For all data, Greenwich Mean Time + 1 was used. The water height from *Roompot binnen* was subtracted from the water level of *Roompot buiten*. A positive value indicates a water flow from the North Sea into the Oosterschelde, whereas a negative value means that the direction of the water currents is into the North Sea. The difference in water level was classified into eleven classes (Table 3). There has been tested whether a significant difference between the classes could be found in the number of clicks per ten minute time interval, in the detection positive minutes per ten minute time interval and in the presence of porpoises.

Table 3: table showing the eleven classes in which the differences in water levels of *Roompot buiten* and *Roompot binnen* were classified.

Class
From -100 to -81 cm
From -80 to -61 cm
From -60 to -41 cm
From -40 to -21 cm
From -20 to -1 cm
From 0 to 19 cm
From 20 to 39 cm
From 40 to 59 cm
From 60 to 79 cm
From 80 to 99 cm
From 100 to 119 cm

For the influence of day light on porpoises, the exact points of time (GMT+1) of sunrise, sunset and astronomic darkness were used (Meteo Delfzijl, 2009). Astronomic darkness starts when the sun is minimal eighteen degrees below the horizon. 'Day' was defined as the time from sunrise to sunset, 'night' was defined as the time from the start of astronomic darkness until the end of astronomic darkness. The end of astronomic darkness to sunrise and the time from sunset to the start of astronomic darkness were both classified as 'twilight'. The ten-minute time-intervals with transitions between 'twilight' and 'day' plus 'twilight' and 'night' were always classified as twilight, to be sure that the intervals classified as 'day' were fully day light and the intervals classified as 'night' were fully dark. All three datasets have been tested on significant differences between night, day and twilight.

2.4.2 The effect of day light and tide on harbour porpoises in the North Sea

To study the effect of tide on the daily movement patterns of harbour porpoises in the North Sea, the swimming direction of the harbour porpoises (noted during the Stena Line surveys) has been compared to the direction of tidal currents. The tidal stream atlas was used, published by Rijkswaterstaat (2001). By entering the times of high tide in Hook of Holland, the tidal current directions in the southern North Sea could be reconstructed. The tide-tables for Hook of Holland for 2005 until 2010 were found in the Dutch journal *Getijtafels voor Nederland voor het jaar...* also published by Rijkswaterstaat. In this way it was possible to see whether porpoises are usually swimming upstream or downstream.

The influence of light on the movement patterns of harbour porpoises could not be tested with the use of the Stena Line data, because visual observations were always done during day light. Therefore, literature was used to make a comparison between the influence of light on the daily patterns on porpoises in the Oosterschelde and in the North Sea.

2.5 Diet and spatial usage of the habitat

Information about the diet of harbour porpoises at different locations in the North Sea was found in literature, but no information was available yet about prey consumption of porpoises in the Oosterschelde. Therefore, a stomach content analysis was performed by M. Leopold and O. Jansen. For this analysis, stomachs were used from twelve individuals (both adults and juveniles), stranded in the Oosterschelde. Furthermore, three surveys were performed in the Oosterschelde to study the distribution, abundance and spatial usage of harbour porpoises in this area: one in September 2009, one in May 2010 and one in June 2011. Eight or nine ships sailed parallel to each other from the Oosterschelde storm surge barrier (west) to the outer limits in the east where the water became too shallow (Fig. 2), with an average cruising speed of six knots. The water surface to be scanned by the observers of a ship was always overlapped by ships on both sides to ascertain complete coverage. The distance between each pair of ships and between the outer ships was maximum 200m. One trained coordinator was on board of each ship together with at least two observers. The coordinator and captains kept contact with the other ships to control the track, speed and distance. Every half an hour the coordinates, speed, direction of the ship and state of the weather were recorded on observation forms. Once a harbour porpoise was observed, time, location, distance, swimming direction and angle to the individual was noted. The locations of the observations were mapped using Google Earth and a depth chart of the Oosterschelde to visualize the spatial usage of the harbour porpoise.

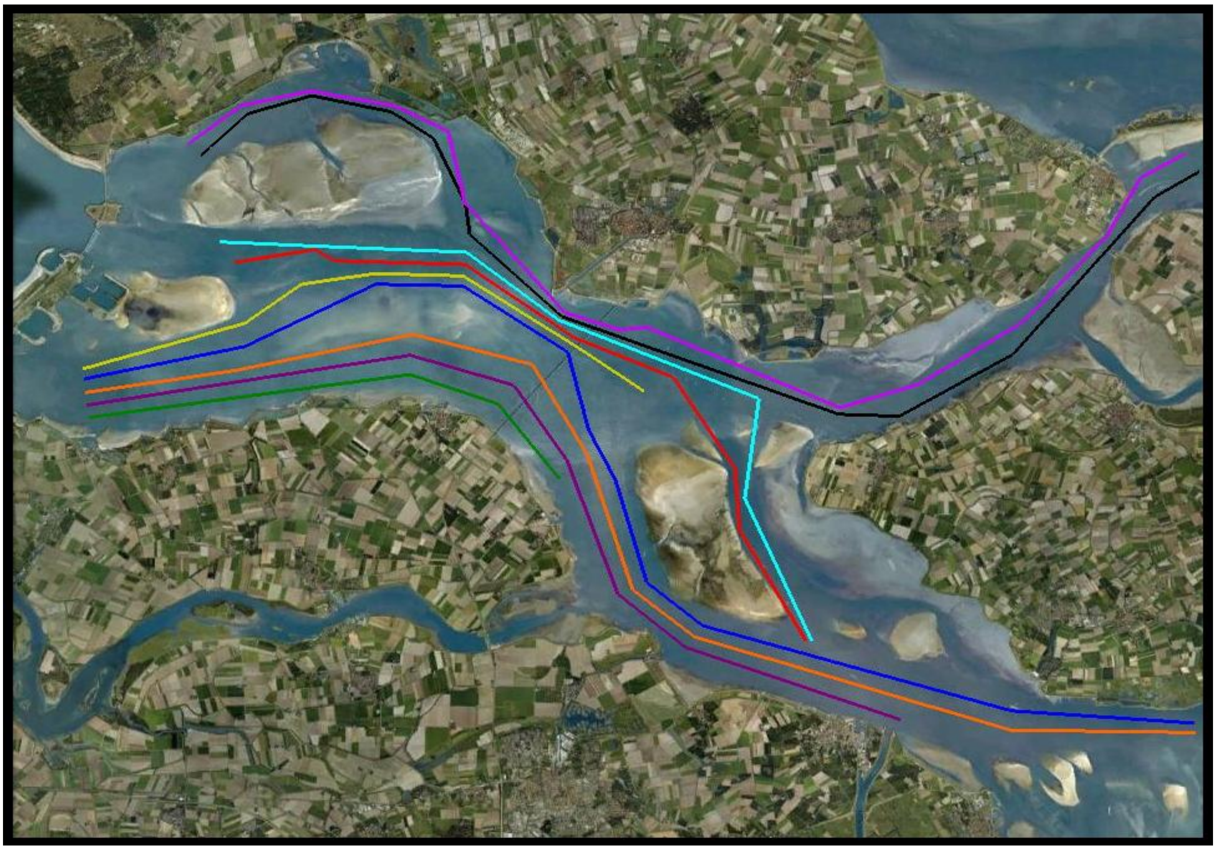

Figure 2: map showing the routes of the different ships during the Oosterschelde surveys (B. van Engeldorp Gastelaars, the Rugvin Foundation).

2.6 Data analysis

First, all data were tested for normal distribution with R by using the Shapiro-Wilk test. The differences per month and per year between locations where harbour porpoises have been observed on the Stena Line route were tested with the non-parametric Kruskal-Wallis test. This test has also been used to determine the difference in the number of porpoises observed per month on the whole Stena Line route. When only two months or years had to be compared, the Wilcoxon rank sum test was applied. To test whether porpoises were observed more frequently in certain years, a chi-square test was applied. For the C-pod data: presence near the storm surge barrier (proportion intervals in which porpoises have been recorded to the total number of ten-minute time intervals) was compared with the Chi-square test. For the number of clicks per interval and the average number of minutes present per ten-minute time interval, only positively scored time intervals have been used. Intervals without observations have been excluded. The difference in click production per month and DPM per month was tested by using the Kruskal-Wallis test. This test has also been used to investigate the effect of tide on the production of clicks and on the time that porpoises spend near the storm surge barrier. The effect of tide on the presence of porpoises near the Oosterschelde barrier has been tested by using the Chi-square test. This test has also been used to test the effect of the direction of the water currents on the swimming direction of harbour porpoises in the North Sea. To investigate the effect of day light on the click production and DPM, the Wilcoxon rank sum test was used. By using the Chi-square proportion test, it was possible to determine the effect of day light on the presence of harbour porpoises near the storm surge barrier. Correlations between the dataset ‘clicks’ and the dataset ‘DPM’ and correlations between Oosterschelde data and North Sea data have been tested with Spearman’s rank correlation test. All tests have been performed with R.

3. Results

3.1 Migratory behaviour

3.1.1 Stena Line monitoring program

Between January 2005 and December 2010, 70 surveys of each two observation days were performed to gain more insight in the recent distribution and movement patterns of harbour porpoises in the southern North Sea. In total, 688 harbour porpoises were observed in 312 sightings. A detailed overview of the number of sightings and harbour porpoises per month and per year can be found in Table 4. Maps with the locations of the sightings grouped per month of each year can be found in Appendix I.

Table 4: overview of the number of sightings (S) and the number of harbour porpoises (H) observed per survey, which consists of two observation days. Each month, one survey has been performed. From January 2005 to June 2005, surveys were carried out twice a month within the framework of the graduation research of N. Osinga. Therefore, the number of porpoises was divided by two for those months, indicated by H*. No surveys were conducted from January 2007 to August 2007 due to reconstruction works.

	2005			2006		2007		2008		2009		2010	
	S	**H**	**H***	**S**	**H**	**S**	**H**	**S**	**H**	**S**	**H**	**S**	**H**
January	0	0	0	3	6			3	5	9	13	6	9
February	8	10	5	10	14			5	12	4	6	2	4
March	35	54	27	6	6			8	10	17	20	3	3
April	10	13	6.5	1	1			6	12	3	5	62	316
May	5	9	4.5	1	1			5	6	8	13	5	7
June	0	0	0	0	0			0	0	4	6	0	0
July	0	0		0	0			0	0	1	1	0	0
August	1	2		1	3			0	0	2	3	1	1
September	0	0		1	2	0	0	4	5	4	4	19	37
October	0	0		0	0	2	3	5	6	3	4	3	3
November	3	7		0	0	1	1	2	2	3	5	9	11
December	0	0		6	9	1	1	0	0	3	5	8	12
Total	**62**	**95**		**29**	**42**	**4**	**5**	**38**	**58**	**61**	**85**	**118**	**403**

In 2009 and 2010, significantly more harbour porpoises were observed on the Stena Line route compared to the other years ($p<2.2\cdot10^{-16}$, df=4, $\chi^2=746$). Because of incomplete data, 2007 was left out of the analysis. The number of porpoises observed from January to June 2005 have been divided by two as a data correction, because surveys were carried out twice a month in this period. Also a significant difference was found between the number of harbour porpoises observed per month: in February, March and April, significantly more porpoises were observed (p=0.009, df=11, Kruskal-Wallis chi-squared=25.0). No significant difference was found in the number of observed porpoises from May until January (p=0.087, df=8, Kruskal-Wallis chi squared=18.3).

Annual patterns

The locations on the Stena Line route where harbour porpoises have been observed have been mapped per year in Figure 5.

The north-south spread of the observations was compared for the different years to detect northward or southward shifts in distribution of the harbour porpoises in the North Sea. No significant difference was found between the spread of the observations from 2007, 2008, 2009 and 2010 ($p=0.117$, $df=4$, Kruskal-Wallis chi-squared=7.38), but the spread of the observations from 2005 and 2006 differed from those of the other years ($p = 0.034$, $df=5$, Kruskal-Wallis chi-squared= 12.0). From 2007 to 2010, harbour porpoises were observed a bit more southern compared to 2005 and 2006 (Fig. 3).

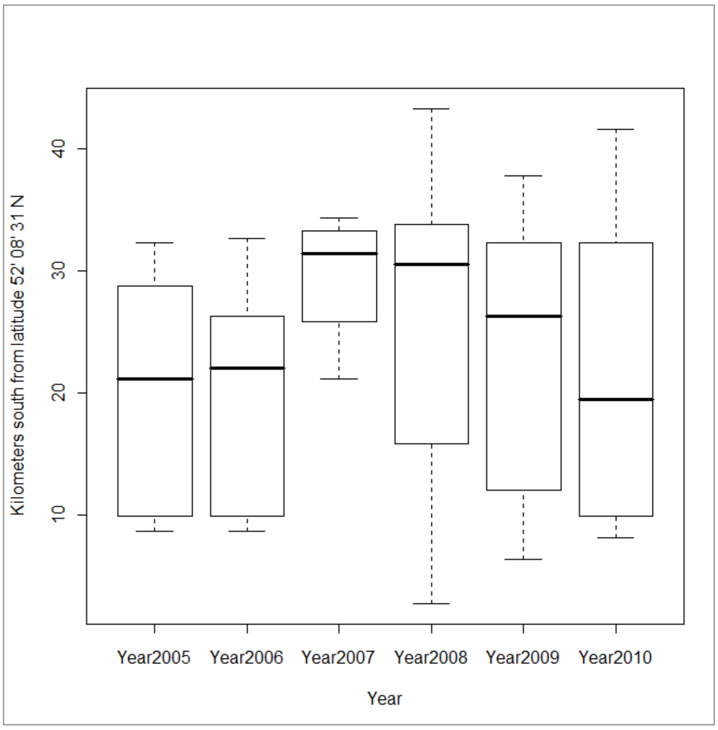

Figure 3: boxplot showing the north-south spread of the sightings per year. N=4 for 2007. In that year, surveys were carried out only from September to December.

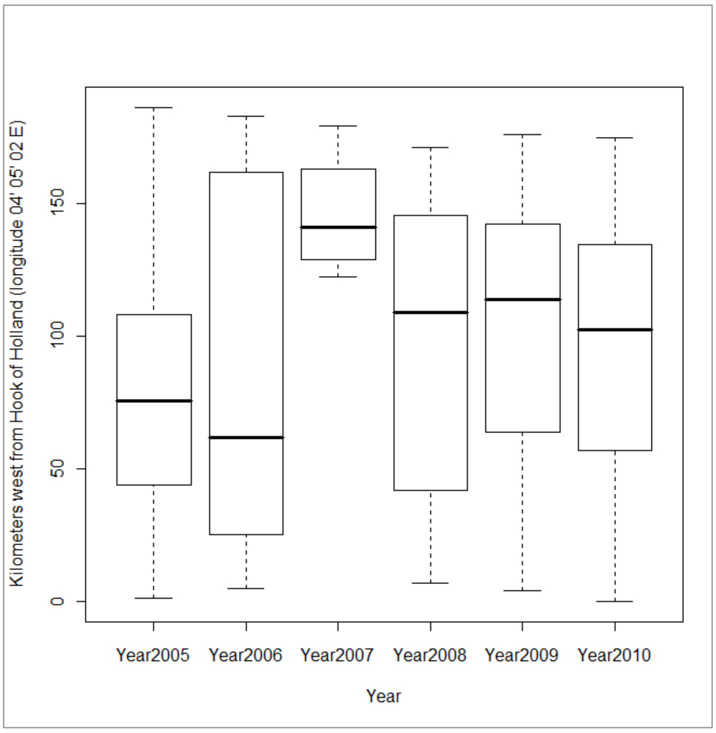

Figure 4: boxplot showing the east-west spread of the sightings per year. N=4 for 2007. In that year, surveys were carried out only from September to December.

The east-west spread of the sightings was compared for the different years to see if east-west or west-east movements have taken place throughout the years. No significant difference was found between the spread of the observations from 2006, 2007, 2008, 2009 and 2010 ($p=0.086$, $df=4$, Kruskal-Wallis chi-squared=5.01) but the data of 2005 differed significantly from the data of the following years ($p=0.011$, $df=5$, Kruskal-Wallis chi-squared= 14.8). The sightings of 2005 are more concentrated offshore compared to the other years, where 50% of the sightings (indicated by the boxes in the boxplot) is more scattered. In 2005, harbour porpoises were observed a bit more on the eastern part of the route compared to the other years (Fig. 4).

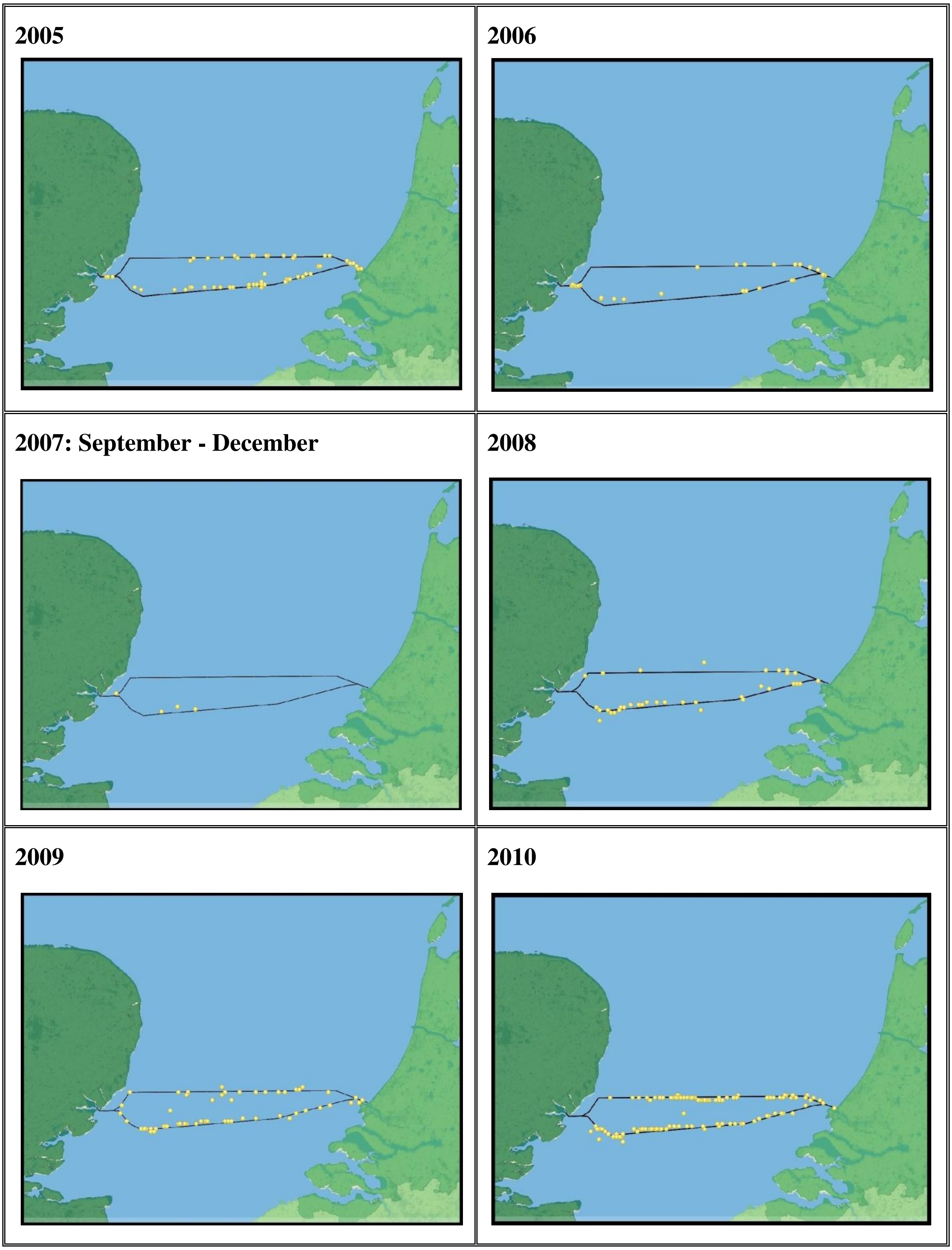

Figure 5: Locations on the Stena Line route where harbour porpoises have been observed. Each dot represents one sighting of one or more harbour porpoises. Data has been grouped per year.

Seasonality

The same analyses as for the annual patterns were done to detect seasonal patterns. The results can be found in Figure 6 and 7. Figure 10a and 10b show the locations of porpoise sightings per month. Figure 6 shows the north-south spread per month. The medians differed significantly between the months (($p<3.07 \cdot 10^{-7}$, df=11, Kruskal-Wallis chi squared=51.7). No significant difference was found between the spread of the data of the months December, January, February and March (p=0.204, df=3, Kruskal-Wallis chi-squared=4.59). The medians of the sightings of April and May did not differ significantly (p=0.861, Wilcoxon rank sum test), but the medians were significantly less kilometres south from the zero point compared to December, January, February and March (p=0.006, df=5, Kruskal-Wallis chi-squared=16.2). The sightings from June, July and August were not used for the analysis, since the sample size was small for these months (N=4 for June, N=1 for July, N=5 for August). Between the spread of the sightings from September, October and November, no significant difference was found (p=0.398, df=2, Kruskal-Wallis chi-squared=1.84). In the boxplots of Figure 6 can be seen that harbour porpoises are observed most southern in September/October and from then on, they are observed gradually more northly. In April and May, the cetaceans are observed most northly compared to the other months. In June, July and August, porpoises were sighted hardly on the Stena Line route.

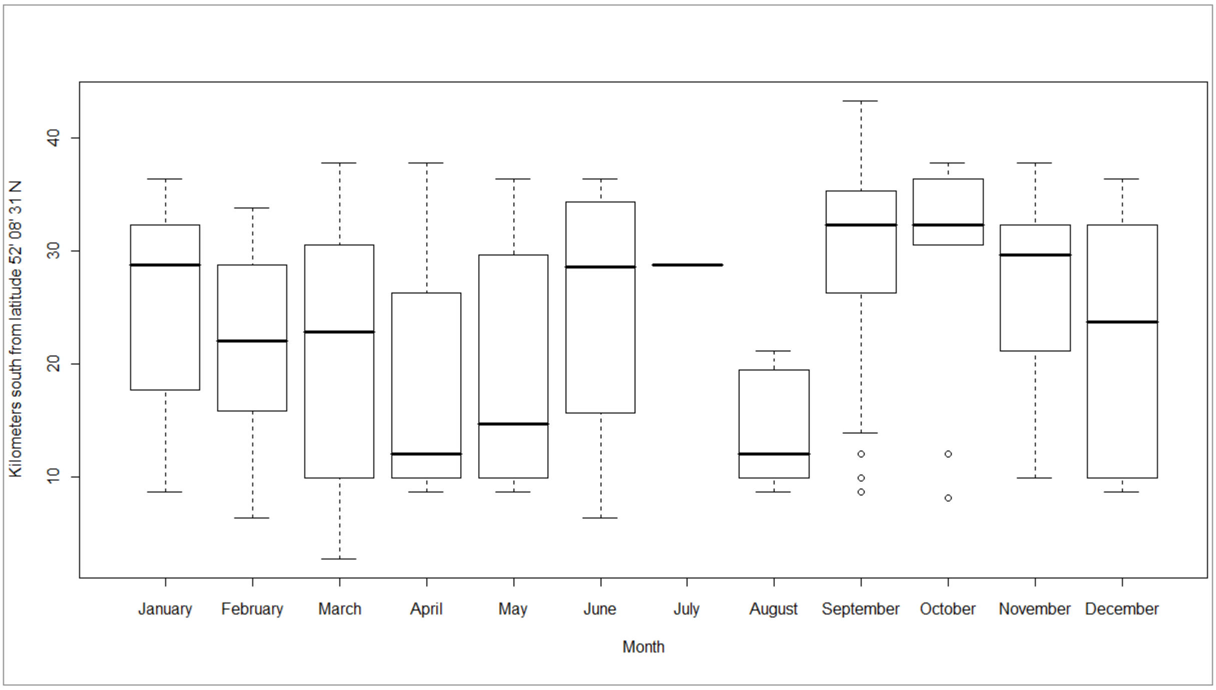

Figure 6: boxplot showing the north-south spread of the sightings per month.

In Figure 7 can be seen whether porpoises were observed more often on the western or the eastern part of the Stena Line route. The medians of the observations from September and October did not differ significantly (p=0.367, Wilcoxon rank sum test). In these months, harbour porpoises were observed more on the western part of the route compared to the other months (p=0.001, df=8, Kruskal-Wallis chi-squared=25.9). From November to May, no significant difference was found between the locations of the porpoise sightings (p=0.673, df=6, Kruskal-Wallis chi-squared=4.03). Again, the data from June, July and August were not used for the analysis due to a small sample size.

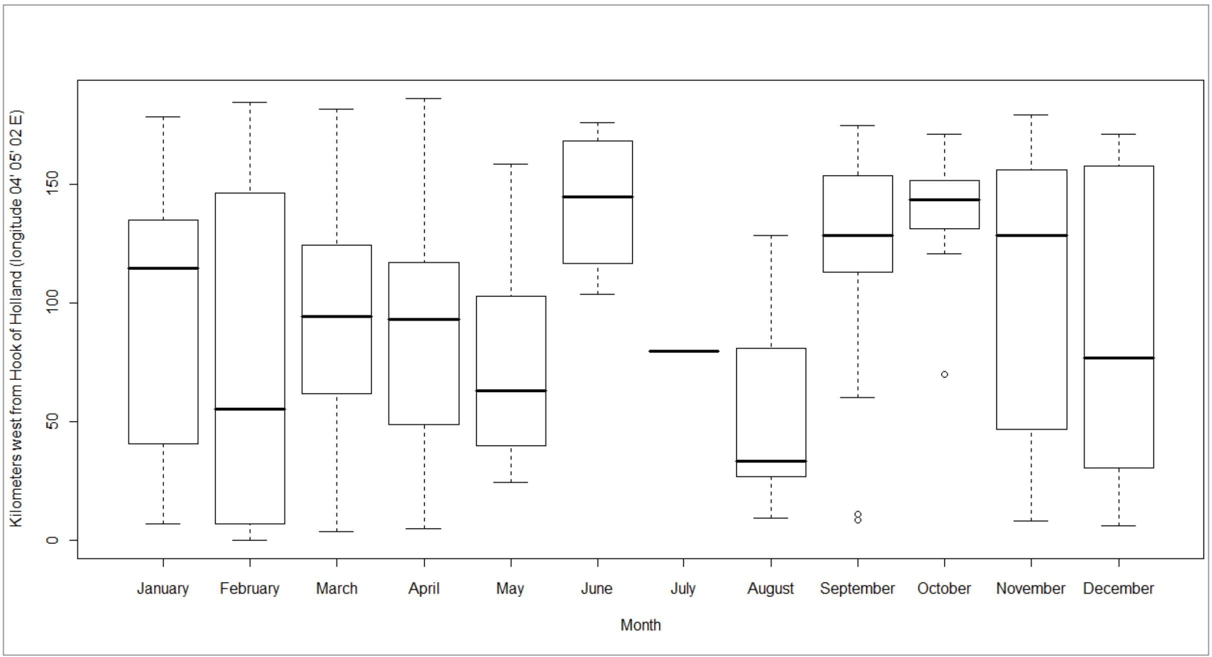

Figure 7: boxplot showing the east-west spread of the sightings per month.

The clicks of harbour porpoises on the North Sea side of the storm surge barrier have been recorded by C-pod 722. These results can be found in Figure 8, grouped per month. The number of intervals in which clicks have been recorded is not equal throughout the year ($p<2.2 \cdot 10^{-16}$, df=11, $\chi^2=585$). Note that no data are available for May and December 2010, because C-pod 722 was defect in those months. On the Stena Line route, porpoises were observed less near the Dutch coast in September and October. By C-pod 722, harbour porpoises were indeed least recorded in September, and also in August and February 2010. But in October, harbour porpoises were not recorded less often compared to March, April, June, July and November of 2010 ($p=0.197$, df=5, proportion test $\chi^2=7.34$). Furthermore, porpoises were not recorded less in summer, when these cetaceans are barely observed on the Stena Line route. This means that at least one harbour porpoise was present at the North Sea side of the storm surge barrier in summer.

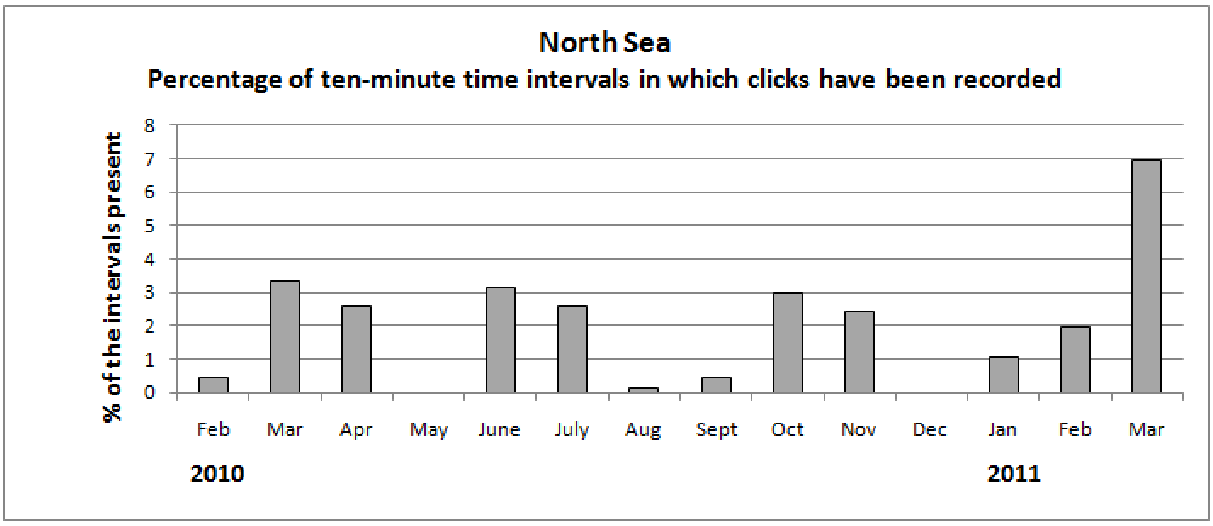

Figure 8: the percentage of the ten-minute time-intervals per month in which harbour porpoise clicks have been recorded by CP722, the C-pod at the North Sea side of the storm surge barrier. No data in May and December due to a defect of CP722.

No significant correlation was found between the percentage of ten-minute time intervals in which harbour porpoise clicks have been recorded on the North Sea side of the storm surge barrier (Fig. 8) and the percentage of positively recorded intervals on the Oosterschelde side (CP720 and CP721, Fig. 11) of the storm surge barrier (Spearman's rank correlation test, rho=0.098, p=0.766).
Also no significant correlation was found between the average number of clicks per month of porpoises on the North Sea side and the Oosterschelde side of the storm surge barrier (Spearman's rank correlation test, rho=0.252, p=0.430).
The number of clicks per ten-minute time interval recorded by CP722 was not the same throughout the year (p=0.005, df=11, Kruskal-Wallis chi-squared=26.8). Less clicks were produced in August, September, January and February (Fig. 9). The time that porpoises spend near the storm surge barrier (North Sea side) is also not equal throughout the year (p=0.0006, df=11, χ^2=32.7). The average time spent near the Oosterschelde barrier was low in the same months as when click production was low, namely January, February, August and September. It is not surprising that these results match since the DPM data and the number of clicks are highly correlated (Spearman's rank correlation test, rho=0.779, $p<2.2\cdot 10^{-16}$).

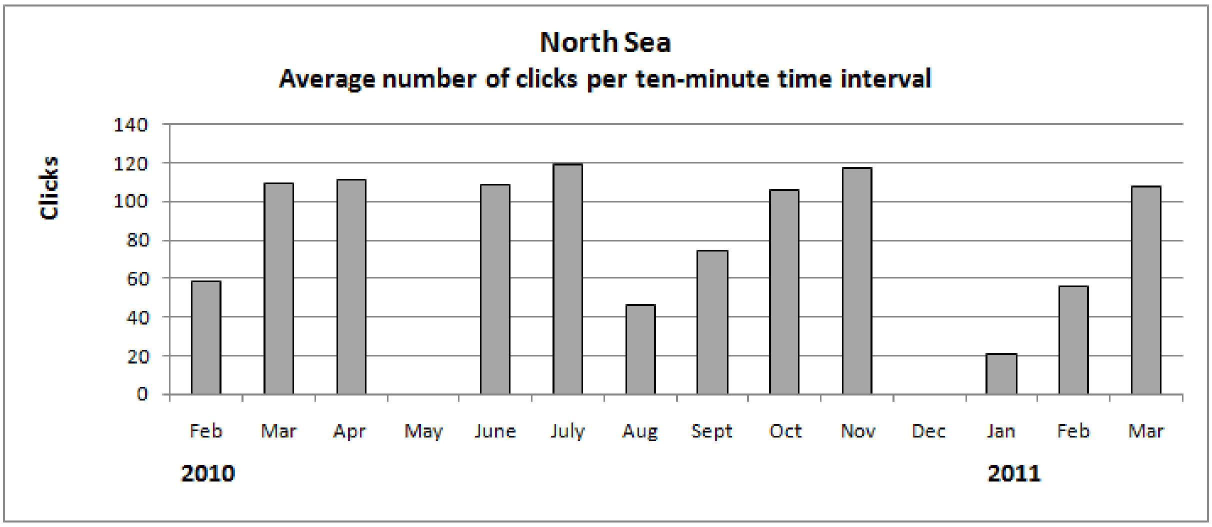

Figure 9: : the average number of clicks per ten-minute time interval per month, recorded by CP722. No data available in May and December, due to a defect of CP722.

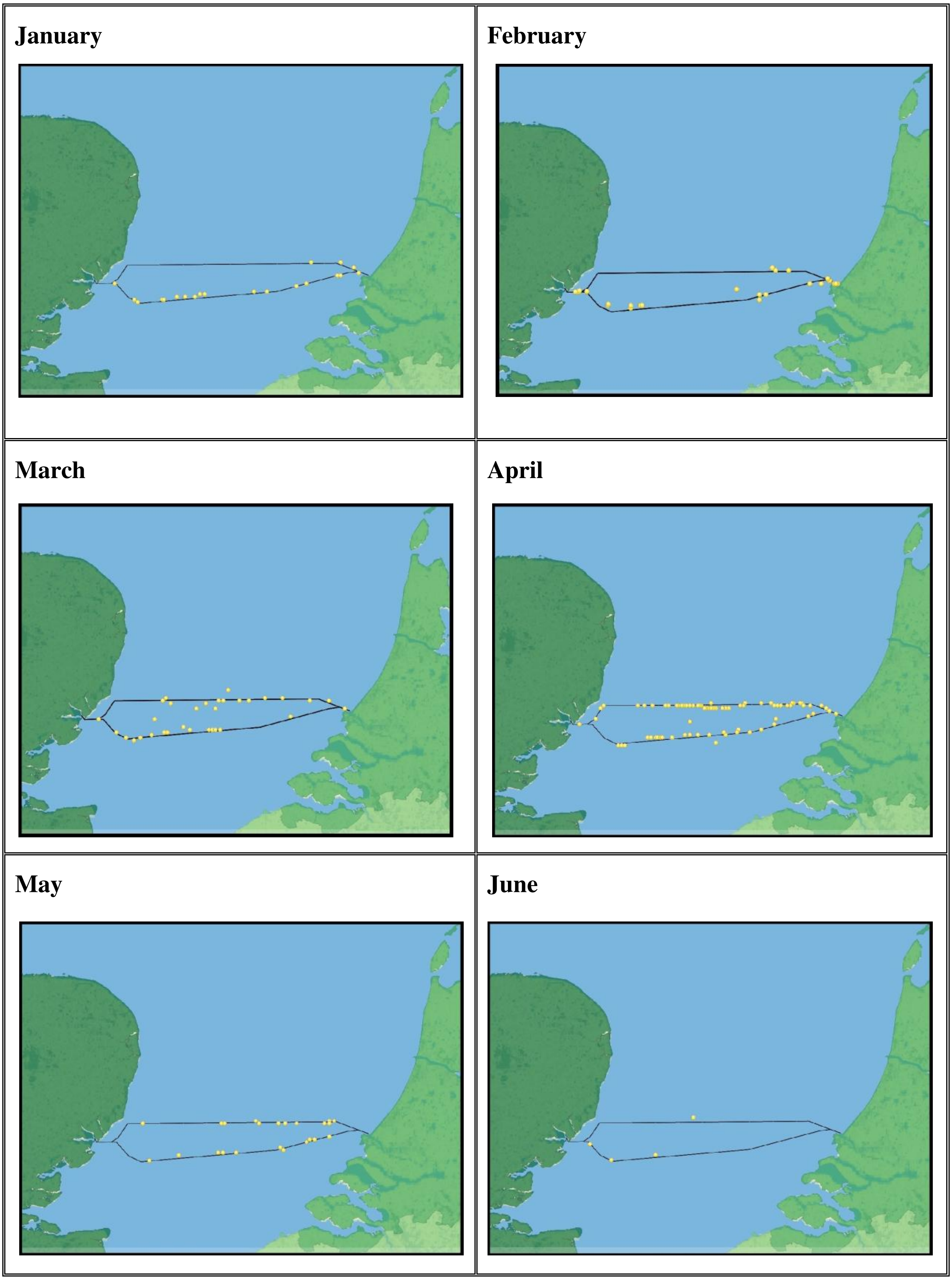

Figure 10a: : Locations on the Stena Line route where harbour porpoises have been observed. Each dot represents one sighting of one or more harbour porpoises. Data has been grouped per month (January – June).

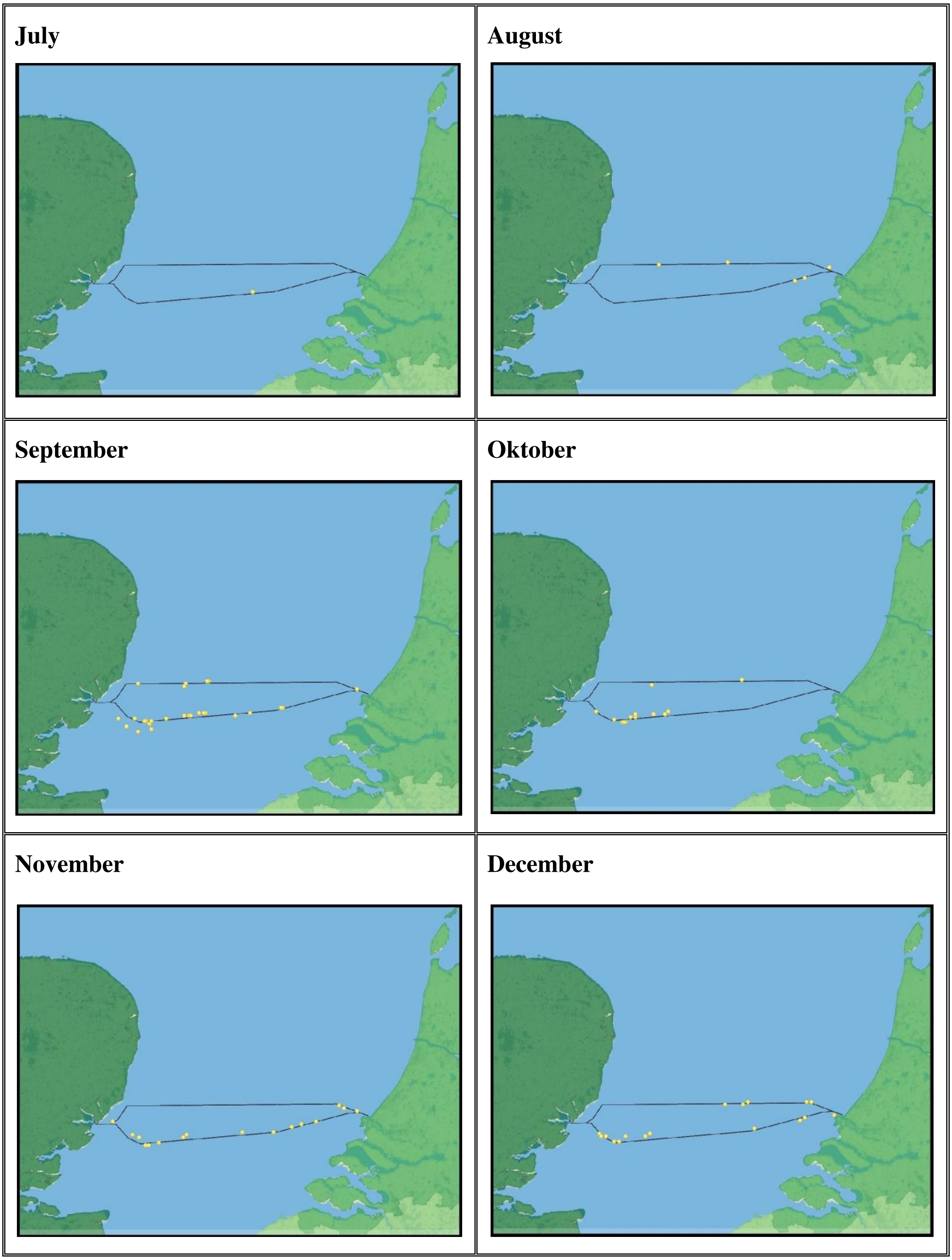

Figure 10b: : Locations on the Stena Line route where harbour porpoises have been observed. Each dot represents one sighting of one or more harbour porpoises. Data has been grouped per month (July – December).

3.1.2 Acoustic research in the Oosterschelde

The clicks of harbour porpoises have been recorded by CP720 and CP721 (both located at the Oosterschelde side of the storm surge barrier) all year (Fig. 11). However, the percentage of intervals in which porpoises were observed was not equally distributed throughout the year ($p<2.2\cdot10^{-16}$, df=13, χ^2=1793.8). On average, clicks were recorded near the storm surge barrier in 20.6% of all ten-minute time intervals. The highest peak can be seen in March 2011, whereas lowest values can be found in November and December of 2010. Figure 12 and Figure 13 show respectively the Detection Positive Minutes and the average click production per ten-minute time interval (time intervals without observations excluded). Porpoises spent on average 2.6 minutes per ten-minute time interval near the storm surge barrier (Fig. 12), but this was not equal throughout the year ($p<2.2\cdot10^{-16}$, df=13, χ^2=1130.862). After a high peak in April with a mean of 3.5 minutes per interval, the average time spent at the storm surge barrier decreases, with a small peak in September. In December 2010, the average DTP is minimal (mean is 1.7 minutes).

The number of clicks recorded by the C-pods in the Oosterschelde is also not equal in every month ($p<2.2\cdot10^{-16}$, df=13, Kruskal-Wallis chi-squared = 727.1). When only time intervals with observations are taken into account, April shows the maximum of on average 278 clicks per interval and December the minimum of on average 54 clicks per ten minutes. Thereafter, the number of clicks per interval starts to increase again, just like in Figure 12. In summer, a small peak can be found in September.

Figure 12 and 13 are very similar in shape: the number of clicks and the detection positive minutes per time interval are significantly correlated (CP720: rho=0.81298, $p<2.2\cdot10^{-16}$, Spearman's rank correlation test, CP721: rho=0.81332, $p<2.2\cdot10^{-16}$, Spearman's rank correlation test).

3.2 Migration between the North Sea and the Oosterschelde

3.2.1 Migration from the North Sea to the Oosterschelde

The pattern representing migration from the North Sea to the Oosterschelde (Table 2) was found in all months tested (from February 2010 to March 2011, with missing data in May and December 2010). After randomizing the data 1000 times for each month, the chance to find the pattern minimally as often as in the original dataset was lower than 0.05 for March 2010 and January 2011. In March 2010, the pattern representing migration was found ten times in the original dataset. Only in 27 out of 1000 randomization runs, the pattern was found ten times or more, so the chance that the findings in the original dataset are based on coincidence is 0.027. In January 2011, the migration pattern was found three times, whereas the chance to find the pattern at least three times is 0.042.

3.2.2 Migration from the Oosterschelde to the North Sea

The pattern representing migration from the Oosterschelde to the North Sea (Table 2) was found in all tested months. Only in September 2010, the chance that the findings were based on coincidence was lower than 0.05. The migration pattern was observed five times in that month. The chance to find the concerning pattern five times or more is 0.026.

In October 2010, the pattern was found five times, which is less often than random: the chance on finding maximally (instead of minimally) five migration patterns appeared to be 0.005.

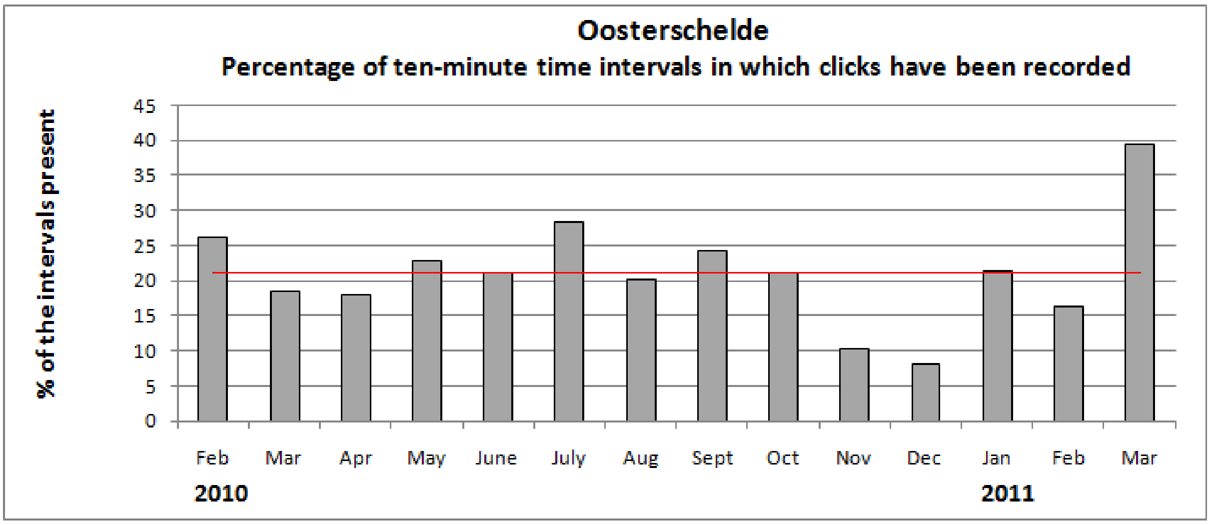

Figure 11: the percentage of the ten-minute time-intervals per month in which harbour porpoise clicks have been recorded by CP720 and/or CP721. De red line indicates the mean of 20.613%.

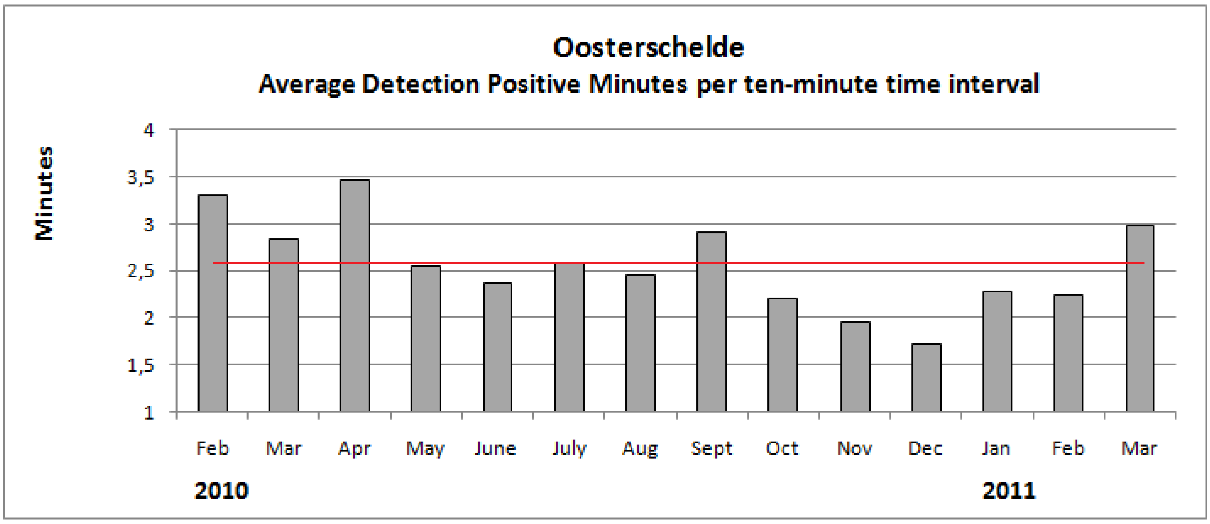

Figure 12: the average Detection Positive Minutes per ten-minute time interval per month, recorded by CP720 and/or CP721. The red line indicates the mean of 2.596 minutes per interval.

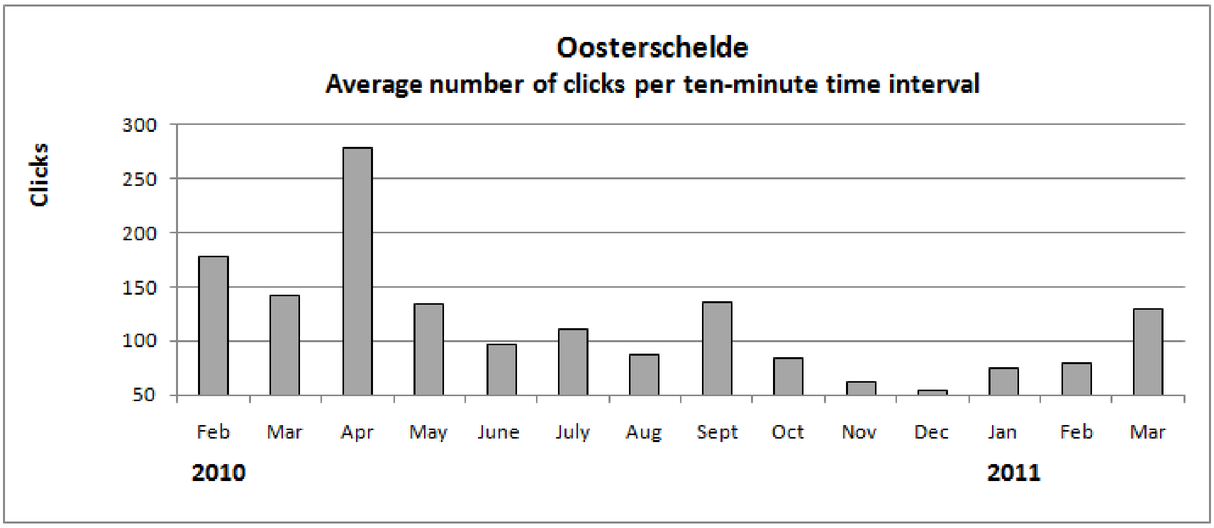

Figure 13: the average number of clicks per ten-minute interval per month, recorded by CP720 and/or CP721.

3.3 Daily movement patterns

3.3.1 The effect of tide on harbour porpoises in the Oosterschelde

The effect of tide on the daily movements has been investigated for harbour porpoises in the Oosterschelde as well as for harbour porpoises in the North Sea. Figure 14 below shows the percentage of intervals in which clicks have been recorded in the Oosterschelde near the storm surge barrier in different tidal stages. When the water level difference is negative, the direction of the water currents is from the Oosterschelde to the North Sea (falling tide in the Oosterschelde). A positive water level difference means that the water is flowing into the Oosterschelde (rising tide in the Oosterschelde). During slack tide, the water level difference is around zero, which means that the water current is minimal. Tidal currents are the strongest when the water level differences are the highest.

Clicks of harbour porpoises are recorded in all classes of water level differences, but the percentage of the ten-minute time intervals in which clicks have been recorded was not equal ($p<2.2\cdot 10^{-16}$, df=10, χ^2=1013). The bell-shaped histogram indicates that clicks are less recorded when the difference in water level is large. Moreover, the peak can be found when the water level of 'Roompot buiten' is 20 to 39 centimetres higher than the water level of 'Roompot binnen', so when the water currents are flowing into the Oosterschelde.

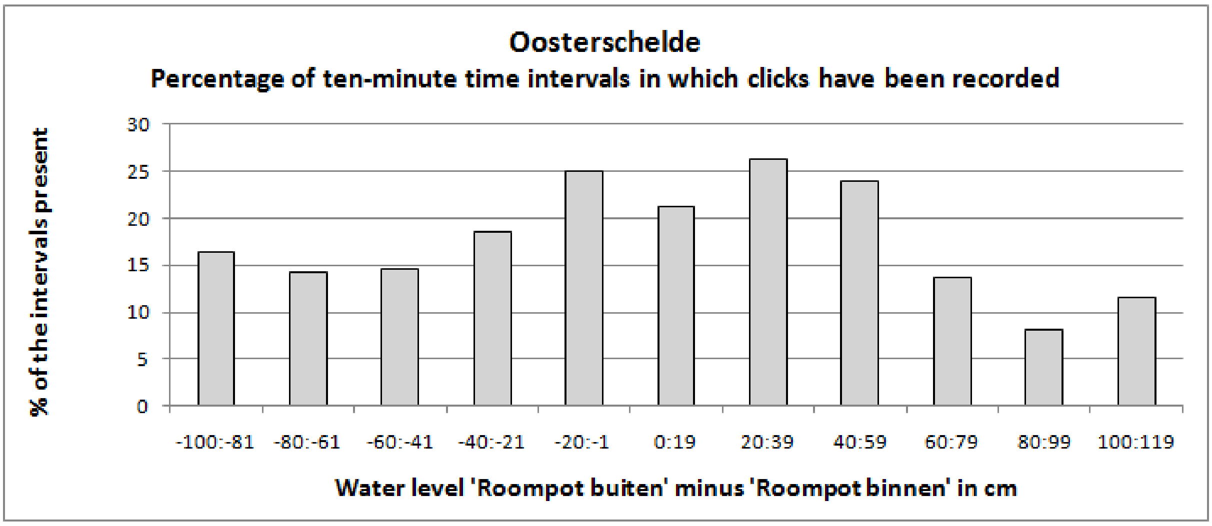

Figure 14: the percentage of the ten-minute time intervals per class of water level difference that harbour porpoise clicks have been recorded by CP720 and/or CP721.

However, when only the positively recorded intervals are analyzed, the production of echolocation clicks does not seem to follow this pattern (Fig. 15). The number of clicks per time interval is also not the same in the different classes ($p=2.19\cdot 10^{-8}$, df=10, Kruskal-Wallis chi-squared = 55.9), but the peak of the bell-shaped histogram is more on the left side of the x-axis, which is in contradiction with Figure 14. Harbour porpoises seem to be less active in sound production when the water level differences are the highest, but the peaks can be found during falling tide, when the direction of water currents is from the Oosterschelde to the North Sea. The average number of clicks is decreasing with rising tide. The faster tide is rising, the lower the average number of clicks.

Since the number of clicks and the detection positive minutes per time interval were already shown to be highly correlated, the average DTP per time interval is also not equal in the different classes ($p<2.2\cdot 10^{-16}$, df=10, χ^2=102.4).

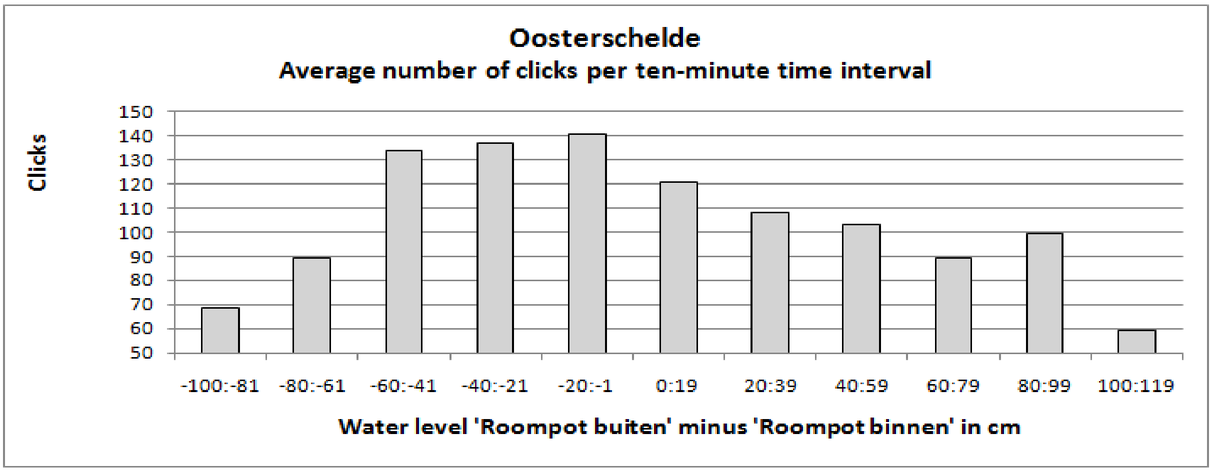

Figure 15: the average number of clicks per ten-minute interval at different tidal stages in the Oosterschelde.

3.3.2 The effect of day light on harbour porpoises in the Oosterschelde

Figure 16 shows the percentage of time intervals during day, twilight and night that harbour porpoises were present near the storm surge barrier. A significant difference ($p<0.05$, Wilcoxon rank sum test) was found in the percentage of intervals in which clicks had been recorded between day, twilight and night for all months. In February and March of 2010, harbour porpoises were more often recorded by CP720 and CP721 at night. In April 2010, clicks were recorded significantly more frequently during twilight and night compared to day. From May 2010 on, the percentage of the time intervals that harbour porpoises were present was significantly higher during day, with the exception of December. In that month, the percentage of positively tested time intervals was higher at night.

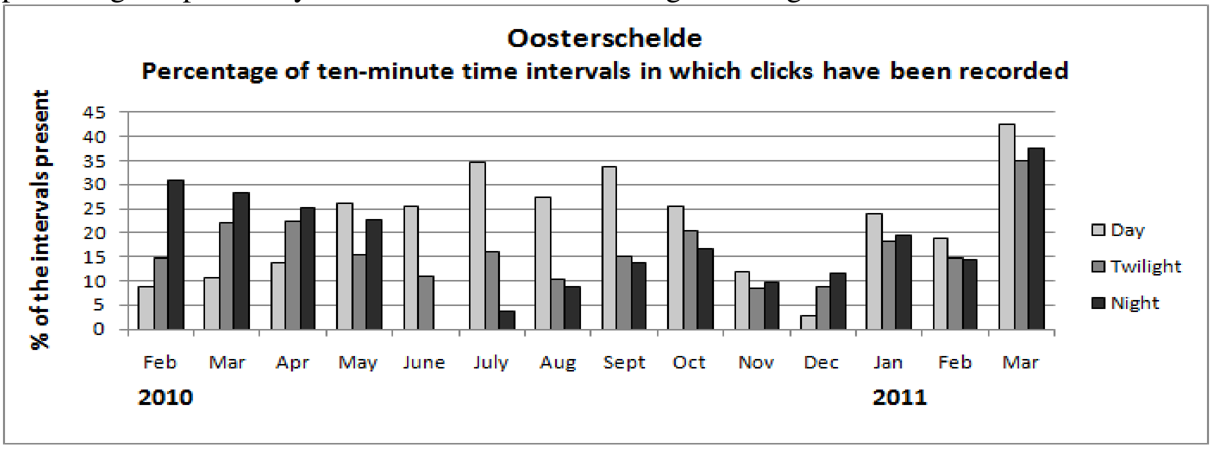

Figure 16: the percentage of the ten-minute time intervals per day/twilight/night that harbour porpoise clicks have been recorded by CP720 and/or CP721.

When comparing relative presence at day throughout the year (so not compared to twilight and night), it can be concluded that the percentage of intervals in which porpoise clicks have been recorded, is not the same throughout the year ($p<2.2\cdot10^{-16}$, df=13, proportion test χ^2= 2390.099). During summer months, harbour porpoise clicks have been recorded in relatively more time intervals at day time than during winter months, except for March 2011, when presence is high anyway. The difference in relative presence at day compared to twilight and night is also better visible in summer. At night and during twilight, presence is also not equal throughout the year (respectively $p<2.2\cdot10^{-16}$, df=12, proportion test χ^2=1112.649; $p<2.2\cdot10^{-16}$, df=13, proportion test χ^2= 434.3443). There must be noticed that there is no astronomic darkness in June, so only day and twilight were used. The percentage of positively tested intervals at night is lower in summer months and higher in winter months.

Click production did not differ significantly between day, night and twilight when data of all year were combined and intervals without observations were excluded (p=0.5556, df=2, Kruskal-Wallis chi-squared=1.1756), but when the data were sorted per month, significant differences were found (p<0.05, Kruskal-Wallis test) except for July, August, November and January 2011 (Fig. 17). Porpoises produced more clicks at day than during twilight in June. In April, May, December and February 2011, a higher click production was found at night. In October, the click production was higher during twilight. In February 2010, more clicks were produced during day and night. In March 2010, significantly less clicks were recorded at day compared to twilight and night. In September and March 2011, the number of clicks per ten-minute time interval was higher at day and during twilight. Again, there must be noticed that there is no astronomic darkness in June, so only day and twilight were compared. In July, clicks were recorded in only three time intervals, so the 'night' data from July were not taken into account for the analysis.

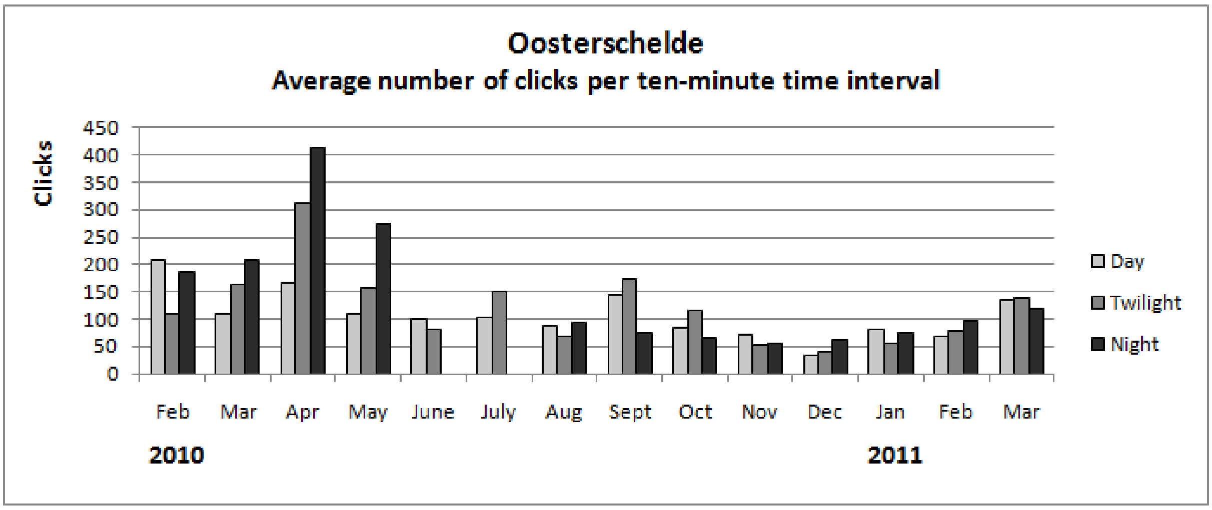

Figure 17: the average number of clicks per ten-minute time intervals per day/twilight/night, recorded by CP720 and/or CP721.

3.3.3 The effect of tide on harbour porpoises in the North Sea

Harbour porpoises were always observed swimming in a southern or northern direction; never in a eastern or western direction. In 27.78% of all observations, the water currents were not directed northwards or southwards. These observations excluded, no significant difference was found in the proportion of porpoises swimming upstream or downstream (p=0.8155, df=1, proportion test χ^2=0.0544): 48.98% was swimming downstream, whereas 51.02% was swimming upstream.

3.4 Diet and spatial usage of the habitat

3.4.1 Diet of harbour porpoises in the Oosterschelde

The results of the stomach content analysis, performed by M. Leopold and O. Jansen, can be found in Figure 18. The diet of adult harbour porpoises stranded in the Oosterschelde consists mainly of Atlantic cod (*Gadus morhua*, 46.93%), whiting (*Merlangius merlangus*, 30.23%) and poor cod (*Trisopterus minutes*, 17.16%). The diet of juveniles differed from that of the adults: more than 70% of the stomach contents was sand goby (*Pomatoschistus minutus*). Furthermore, the stomach content analysis revealed that 14.06% was whiting (*Merlangius merlangus*). Other species that contributed to the diet, however to a lesser extent, can also be found in Figure 18.

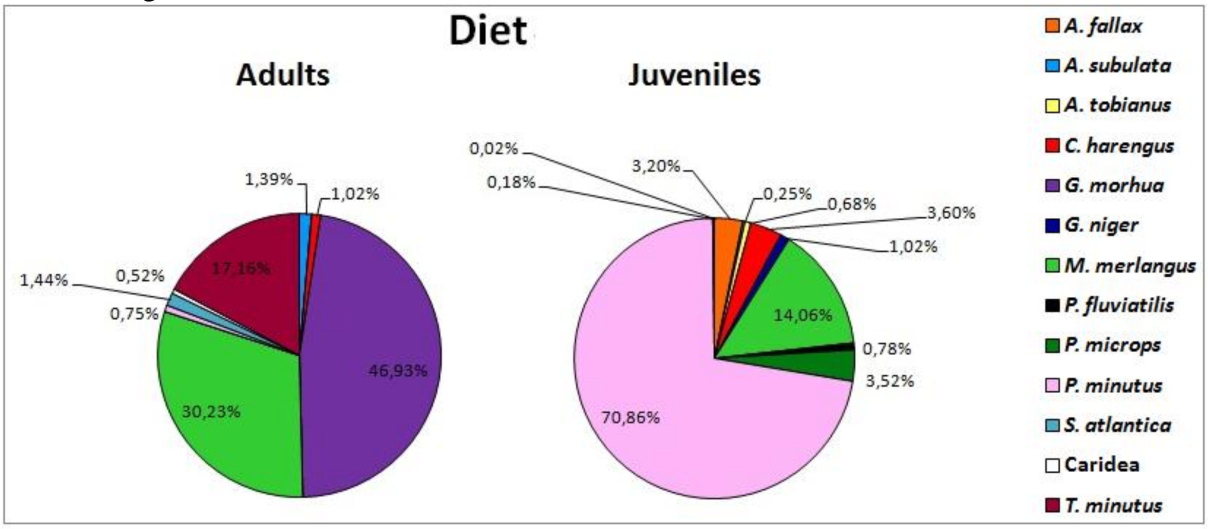

Figure 18: stomach contents of twelve harbour porpoises stranded in the Oosterschelde (M. Leopold & O. Jansen, personal communication).

3.4.2 Spatial usage of the Oosterschelde by harbour porpoises

During the Oosterschelde survey in September 2009, 37 harbour porpoises were observed, among which five calves (Fig. 19). In May 2010, 15 individuals were counted (Fig. 20). During this survey, no calves were observed. The latest scan in June 2011 resulted in 61 observed harbour porpoises, among which at least four mother-calf pairs (Fig. 21). The locations of the sightings of 2010 and 2011 correspond to the locations where harbour porpoises have been observed during the first survey in 2009. Comparing this to the depth chart of the Oosterschelde (Fig. 22), it can be seen that harbour porpoises have been observed in the deeper parts of the Oosterschelde.

Figure 19: Locations of harbour porpoise observations during the Oosterschelde survey in September 2009. Each dot represents one sighting of one or more harbour porpoises.

Figure 20: Locations of harbour porpoise observations during the Oosterschelde survey in May 2010. Each dot represents one sighting of one or more harbour porpoises.

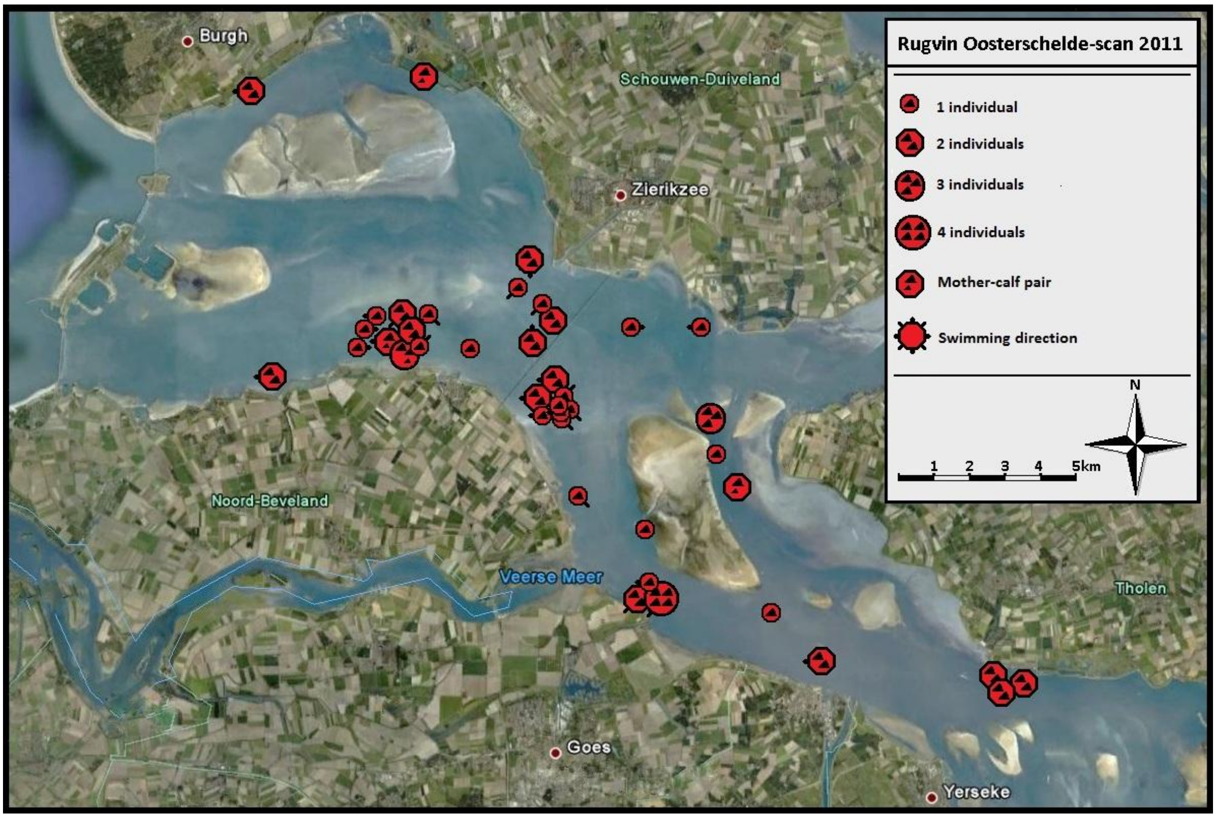

Figure 21: Locations of harbour porpoise observations during the Oosterschelde survey in June 2011. Each dot represents one sighting of one or more harbour porpoises.

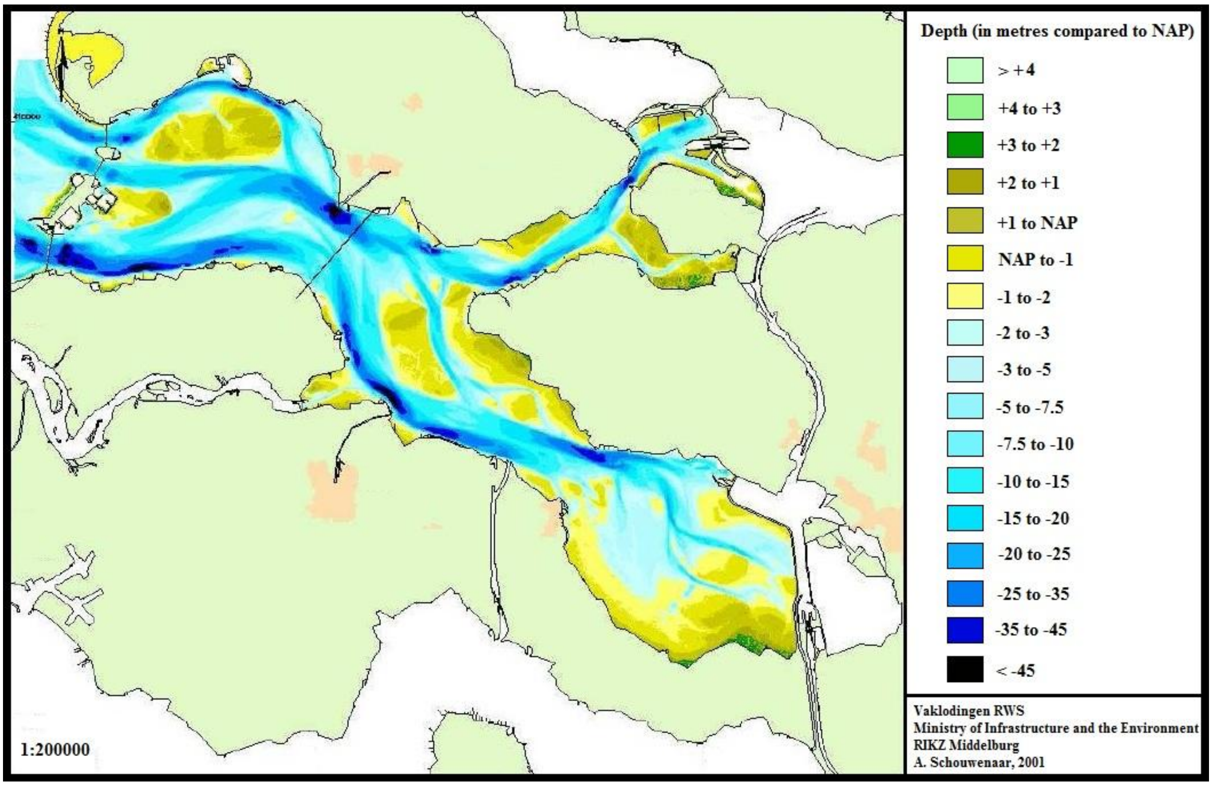

Figure 22: Depth chart of the Oosterschelde. The darker the blue, the deeper the water.

4. Discussion

4.1 Migratory behaviour and exchange

To see how the migratory behaviour of harbour porpoises in the Oosterschelde is related to that of the porpoises in the southern North Sea, data of the acoustic research in the Oosterschelde were compared with the results of the Stena Line monitoring program.

On the Stena Line route, porpoises were hardly observed in summer (Fig. 10a; Fig. 10b), also in the most recent years (Appendix I). Porpoises were observed more southern on the route in September and October (Fig. 6) and from then on a northward movement can be observed. From December to March, porpoises are observed more northerly than in September and October. Earlier research report that a peak in coastal number is reached in winter and early spring (Gilles *et al.,* 2009; Haelters & Camphuysen, 2009; Jak *et al.,* 2010), but this could not be concluded from the Stena Line data (Fig. 7). More sightings were made in April, but no evidence for a more coastal movement was found for this period. Only in February, a movement towards the coast could be observed, but the locations of sightings were not significantly closer to the shore than in other months. In March and April, when most porpoises were seen, harbour porpoises are observed most northerly on the route compared to the rest of the year. Because in the following months barely any porpoises are observed, this suggest that porpoises indeed still migrate northwards during spring.

The spread of the locations where porpoises have been observed from the Stena Line ferries does not differ significantly between the years, which suggests that no major changes have occurred recently concerning the distribution of harbour porpoises in this area. Compared to 2005 and 2006, porpoises are observed somewhat more southern on the route in the more recent years (Fig. 3). Figure 4 shows that the data of 2005 are less scattered than the other years, but that might be caused by the fact that observations were done twice a month in the first half of that year. Although no major changes in the spread were found, the data suggest that the number of porpoises in the southern North Sea is increasing (Table 4; Fig. 5). In 2010, up to 403 porpoises were counted, whereas in previous years, the number of observed porpoises has never been higher than 100 (Table 4). Indeed, in 2009 and 2010, significantly more harbour porpoises had been observed on the route. The trend that porpoises leave the southern part of the North Sea in spring remains the same, since harbour porpoises were also barely observed in summer in 2010 (Table 4; Appendix I).

In the Oosterschelde, porpoise classified click trains have been recorded in all months (Fig. 11; Fig. 12; Fig. 13). A decrease in the percentage of time intervals in which porpoise clicks have been recorded can be found in November in December (Fig. 11). However, this does not necessarily mean that porpoises are less present in this period. Figure 12 and 13 show that porpoises produce less clicks in November and December anyway (intervals without observations have been excluded from these analyses and figures). Harbour porpoises might still be present, but it is possible that they do not produce clicks all the time, which may lead to some time intervals to be scored as negative. In April 2010, a peak can be seen in the average number of clicks per ten minutes (Fig. 13). However, the percentage of intervals in which clicks have been recorded (Fig. 11) shows no peak in April. So although more clicks are produced per ten minutes, clicks have not been recorded in relatively more time intervals. This suggests that the number of clicks per ten minutes does not reflect the presence of porpoises well. Even though the percentage of time intervals in which click trains have been recorded also will turn out lower by non-active harbour porpoises, this method will give a better indication of the presence of harbour porpoises than the number of clicks, since one classified porpoise click train is enough to score the time interval as porpoise-positive.

It remains unclear why the echolocation activity of porpoises is so much higher in April compared to the rest of the year (Fig. 13). Porpoises use echolocation for spatial orientation and the localization of prey (Verfuβ *et al.,* 2005), so it might have something to do with fish species that migrate into the Oosterschelde in that period, but little information is available about different seasons and fish migration between the North Sea and the Oosterschelde.

When comparing the Stena Line results to the data of the acoustic research in the Oosterschelde, it becomes clear that porpoises are present in the Oosterschelde all year, since clicks have been recorded in every month (Fig. 11; Fig. 12; Fig. 13). Because evidence was found for migration between the North Sea and the Oosterschelde in both ways (see paragraph 3.2), it is unclear whether the same individuals are present year-round or whether new members join the Oosterschelde population and other individuals leave the group. Since the pattern representing migration (from the North Sea to the Oosterschelde) was found significantly more often than random in March 2010 and January 2011, it is assumed that migration has occurred from the North Sea to the Oosterschelde in those months.

Porpoise presence at the North Sea side of the storm surge barrier was not the highest in those months (Fig. 8; Fig. 9). Earlier research however shows that the highest abundance of harbour porpoises along the Dutch coast is reached in winter and early spring (Gilles *et al.,* 2009; Jak *et al.,* 2010). The chance on encountering the storm surge barrier and potentially swimming through it would then be higher. Nevertheless, there must be noticed that a lack of evidence for migration during the rest of the year does not mean that migration does not occur. Furthermore, migration to the North Sea has been found to have occurred in September 2010, followed by a decline in presence (in the Oosterschelde) in October and especially in November and December. The presence of porpoises at the North Sea side of the barrier increases in October and November. It is possible that one or more porpoises swam to the North Sea and stayed there, which resulted in recordings of that individual in the following months. It is also possible that one or more porpoises left the area, and that the increase in porpoise presence at the North Sea side of the barrier in October and November is caused by other porpoises. However, since porpoises are shown to be less active in the production of echolocation click trains in November and December (Fig. 13), it is not afforded to conclude that porpoises are less present in those months.

Because it was not possible to identify individuals, no conclusions can be drawn about behavior of particular individuals before and after crossing the storm surge barrier. Since evidence for migration is only found in three months, it is suggested that visits from the Oosterschelde to the North Sea are not occurring daily.

It can be concluded that not all harbour porpoises migrate northwards during spring, because echolocation clicks are still recorded in summer and autumn and porpoises were also visually observed. Since migration to the North Sea only was observed in September 2010, it is not likely that individuals from the Oosterschelde show a northward migration. It is possible that in late winter or early spring, porpoises swim to the Oosterschelde instead of migrating northwards. The migrating porpoises normally return in the southern North Sea in September. Because in this month evidence for migration to the North Sea has been found, it is possible that some porpoises stay in the Oosterschelde in summer and return to the North Sea in September. After prolongation of this study for a couple of years, together with visual surveys, it will be possible to detect trends in periods of migration between the Oosterschelde and the North Sea.

One remarkable result was found concerning migration to the North Sea: in October 2010, migration was found less often than random. This indicates a negative relation between porpoise clicks on the Oosterschelde side and clicks on the North Sea side in subsequent time intervals. This phenomenon was found only for October and it remains unclear what caused this result.

Echolocation click trains were also recorded by the C-pod in the North Sea in summer months. It is unclear whether this is caused by North Sea porpoises that do not migrate, or whether Oosterschelde porpoises have crossed the storm surge barrier and stay in the surroundings. Research in the German part of the North Sea resulted in most observations during summer, with the maximum of sightings occurring in July (Siebert *et al.,* 2006). The majority of sightings was made around the islands of Sylt and Amrun. Calves were reported here in July, August and September. Since the pattern of observations is exactly in contrast with the pattern of observations in the southern North Sea, it is suggested that porpoises migrate between these areas. Calves were also observed near Aberdeenshire in summer (Weir *et al.,* 2007), so it is also possible that a part of the porpoise population migrates to the Scottish part of the North Sea. Since porpoise calves have been observed in the Oosterschelde in summer, it is suggested that these calves were not born in the surroundings of neither Sylt nor Scotland. Research in Swedish coastal waters has shown that mother-calf pairs can travel a distance of only 100 kilometers (Teilmann *et al.*, 1997 in: Witte, 2001), so it is likely that the observed calves were born either in the Oosterschelde or in the Belgian or Dutch part of the North Sea, nearby the Oosterschelde. Future research with visual observations could reveal whether calves are born in the Oosterschelde or whether a new calving ground has formed near the Dutch Delta Area.

4.2 Daily movement patterns

4.2.1 The effect of tide on harbour porpoises

The effect of tidal currents on the movements of harbour porpoises was investigated for porpoises in both the Oosterschelde and the North Sea. In the North Sea, no significant effect was found of the direction of tidal currents on the swimming direction of porpoises, but in the Oosterschelde, tidal state did have an effect on the activity of porpoises. Figure 14 and 15 respectively show the percentage of time intervals in which clicks have been recorded by the C-pods in the Oosterschelde and the average number of clicks per time interval, separated per class of water level difference. The bell-shaped graph in Figure 14 indicates that clicks are recorded in relatively more time intervals when the water level difference between the North Sea and the Oosterschelde is low. This confirms the ‘negative effect’ hypothesis. Besides, the peak can be found when the water level of ‘Roompot buiten’ is 20 to 39 centimetres higher than the water level of ‘Roompot binnen’, so when the water currents are flowing into the Oosterschelde. This suggests that porpoises are more often present when the direction of the water currents is from the North Sea to the Oosterschelde. However, the average number of clicks is significantly higher when the direction of the water currents is from the Oosterschelde to the North Sea. Again, this proves that the number of clicks per interval is not a good indication of the presence of harbour porpoises. So harbour porpoises are more often present during rising tide (incoming water currents), but they have a significantly higher click production during falling tide (outgoing water currents). This is in contradiction with the hypothesis that porpoises use rising tide to feed on incoming fishes. It is already known that porpoises use strong tidal currents during foraging, because aggregations of prey are funnelled towards porpoises (Watts & Gaskin, 1985; Johnston *et al.,* 2005), but in this research porpoises use their echolocation more often when water currents (possibly together with prey) are flowing out the Oosterschelde. Pierpoint (2008) found that considered foraging porpoises were often surfacing against the stream. Maybe porpoises have to produce less clicks when fishes come into the Oosterschelde during rising tide, because it is easier to catch a prey. During falling tide, it is expected that fishes flow out the Oosterschelde and that harbour porpoises have to try harder to catch fish, and therefore need to produce more echolocation click trains to localize and catch the prey.

A negative effect of tidal state on the Oosterschelde porpoises was found, which confirms the hypothesis that porpoises are affected by the noise or the strong tidal currents of the storm surge barrier, when the water level difference is high. However, it does not seem to be impossible for harbour porpoises to cross the storm surge barrier when the water level difference is high. Porpoises are namely still present when water level difference is maximal. Furthermore, the result that porpoises were observed in more intervals when the water was flowing into the Oosterschelde, suggest that they indeed use the tidal stream to wait for incoming fishes.

4.2.2 The effect of day light on harbour porpoises

Research performed by Todd and colleagues (2009) revealed that harbour porpoises around North Sea off-shore gas installations show a nocturnal pattern: the number of visits was greater at night than by day, and also a pronounced diel pattern in echolocation was found. An interpretation of this pattern was that porpoises were feeding below or around the platform at night (Todd *et al.*, 2009). It was suggested that this diel activity pattern is related to the diel activity of their prey. Porpoises in the area of the gas installations feed mainly on sand eels and herring, and both prey species show a diel pattern. Sand eels feed in open water by day and rest at night, by burying themselves into the sand where they are an easy prey for the echolocating porpoises (Kastelein *et al.,* 1997). Herring is a more pelagic species and shows a daily vertical migration: at night this species comes to the surface and swims more slowly than at day, which makes it an easier prey to catch. Soldal *et al.* (2002) found that around a platform in the Norwegian part of the North Sea, demersal fish spread throughout the water column at night. Highest fish densities were found within 10m of the seabed, where porpoises are presumed to feed (Santos & Pierce, 2003). From the research in the Zeeschelde estuary (Maes *et al.,* 1999), it also became clear that the vertical distribution of demersal fish changed at night. Demersal fish remained on the bottom at day, while at least a part of the populations exploited the surface water at night (Maes *et al.,* 1999). It is expected that this is also applicable for the Oosterschelde.

Figure 16 shows the percentage of porpoise-positive intervals per month. The percentage of porpoise-positive intervals during twilight lies between the results of day and night, which implies a gradual transition between day and night. When only looking at the histogram of ‘day’, the percentage is increasing in summer months and decreasing in winter months. In contradiction, the percentage of intervals in which click trains have been recorded during night is decreasing in summer. These results indicate that porpoises are more frequently present near the storm surge barrier at day in summer and at night in winter.

The pattern of echolocation clicks was less clear (Fig. 17). Again, in summer months, click production seemed to be higher at day and twilight, whereas in winter months clicks production was found to be higher at night. However, it is not certain that harbour porpoises use the storm surge barrier as a foraging location. Therefore, results and patterns concerning echolocation clicks near the storm surge barrier may not be generalized for porpoises foraging in the Oosterschelde area.

4.3 Diet and spatial usage of the habitat

Because of seasonal and geographical variation in diet, the harbour porpoise is often considered to be an opportunistic feeder (Martin, 1996; Teilmann & Dietz, 1996), feeding mainly on small shoaling fishes from both demersal and pelagic habitats (Santos & Pierce, 2003). Significant differences between the diet of porpoises from Scotland, Denmark, The Netherlands and northwestern Spain were found by Santos (1998): the Spanish porpoises had a more varied diet than the porpoises of the other three areas. More sandeels were consumed by porpoises from Scotland than by porpoises from Denmark and Holland, whereas porpoises from Denmark and Holland had taken more gobies compared to those of Scotland. The Dutch porpoises had taken smaller gobies in autumn than in winter and spring, which is suggested to be related to the life cycle of this fish species. Also, a relation was found between the size of the harbour porpoise and the size of the prey: adults took bigger gobies and sand eels than juveniles. Furthermore, smaller porpoises took fewer whiting but more gobies than bigger porpoises did (Santos, 1998). Whiting was also considered as one of the main prey species of Dutch harbour porpoises. These results correspond to the later stomach content analyses performed by Leopold and Camphuysen (2006): gobies were the main prey consumed by porpoises stranded along the Dutch coast in 2006. Whiting was still present as prey species, but less abundant. This is suggested to be related to the collapse of cod stocks in the North Sea. Furthermore, sand eels and sprat were frequently found within the stomachs of the Dutch porpoises. In a demersal fish survey along the Dutch coast, carried out by IMARES in 2006, gobies showed the highest relative abundance (defined as the number of fish caught from a species divided by the total catch) compared to other demersal fish species. Combined with the result that gobies were found to be the main prey of Dutch porpoises (Leopold & Camphuysen, 2006) and the abovementioned seasonal and geographical variation in diet, this suggest that harbour porpoises indeed feed on prey species that are available in large numbers. Nevertheless, they can also be selective. Herring found in the stomachs was always mature. Börjesson *et al.* (2003) stated that porpoises feed on adult herring instead of juvenile herring because the fat content of these individuals is much higher. This may explain why sprat was found more often than herring in the stomachs of Dutch porpoises: a lot of juvenile herring is found along the Dutch coast. Sprat however already has a higher fat percentage compared to herring of the same length.

The stomach content analysis performed by M. Leopold and O. Jansen revealed that the diet of adult porpoises in the Oosterschelde consists mainly of Atlantic cod, whiting and poor cod (Fig. 18). Atlantic cod and whiting belong to the very common inhabitants of the Oosterschelde and can be caught throughout the year (Meijer, 2002). Highest densities of both species in this area are reached in summer; in winter, densities have become low (Meijer, 2002; Stichting ANEMOON, 2009; Maandag, 1999). Although over 17% of the diet of adult porpoises consists of poor cod, this species is observed accidentally in the Oosterschelde (Meijer, 2002). However, researchers of Stichting ANEMOON (2009) have observed poor cod frequently, with also highest densities in summer and low densities in February, March and April. The main prey of juveniles appeared to be sand goby, a sedentary fish with high densities throughout the year. Gobies were one of the main prey species of porpoises within the Dutch part of the North Sea, but they make up not even 1% of the diet of adult porpoises in the Oosterschelde. However, the sample size of the stomach content analysis of porpoises in the Oosterschelde was only twelve, so it cannot be concluded that adult porpoises barely eat gobies. It is expected that they prefer bigger prey items such as whiting and cod, but when the densities of these species become low, they will switch to gobies which are present all year. By comparing figure 18, 19 and 20 with figure 21, it becomes clear that porpoises have been observed mostly in the deeper parts of the Oosterschelde. Since harbour porpoises cannot store large amounts of energy, it was suggested that porpoises have to stay close to their prey. Comparing this with the results of STICHTING ANEMOON (2009), the hotspots of the prey species indeed correspond with the locations where porpoises have been observed most (Fig. 22). The hotspots of the prey species, which are chiefly demersal, are also located in the deeper parts of the Oosterschelde (Fig. 14), but there must be noticed that the research of STICHTING ANEMOON (2009) was performed only near-shore. The locations where multiple sightings have been done suit with the largest hotspots of the prey species, encircled in Figure 22. No data were available about prey species for the inner part of the Oosterschelde, so no conclusions can be drawn from the porpoise sightings there.

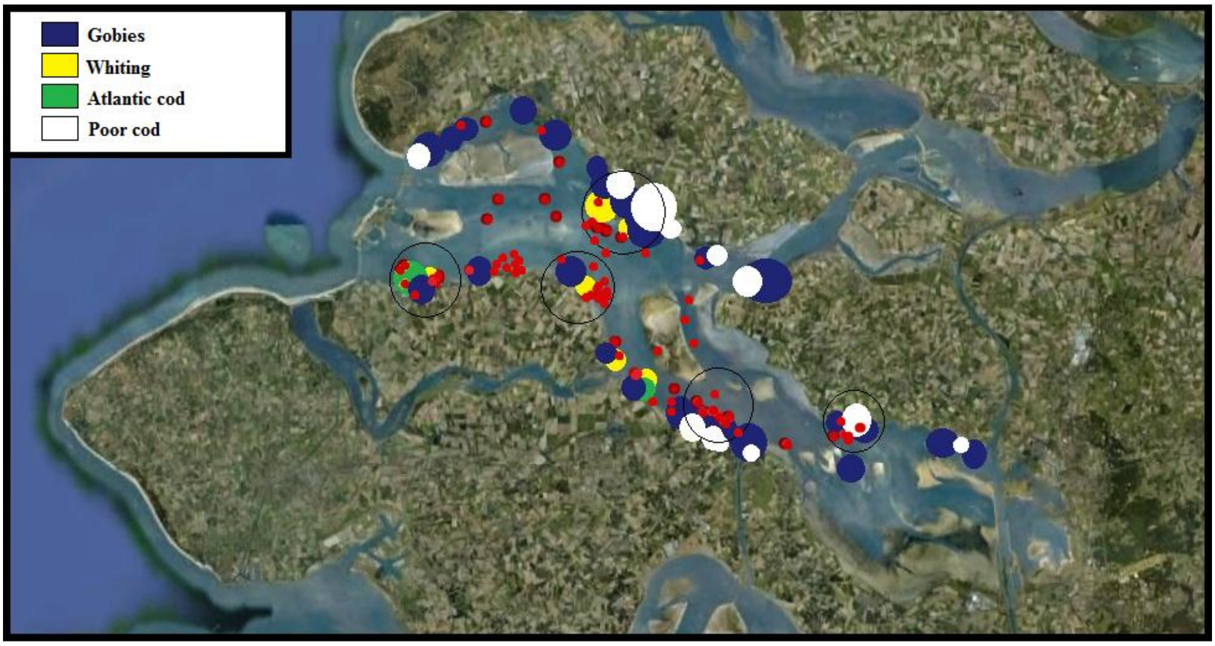

Figure 22: Map showing the locations in the Oosterschelde where porpoises have been observed and the hotspots of their prey species. Each red dot represent one porpoise sighting of one or more individuals. The largest dots coding for prey species indicate the locations with the highest densities of that particular fish species. Note: no data available for the inner part of the Oosterschelde.

4.4 Working with C-pods

Using the C-pods, it was possible to detect migration. However, migration could have been missed when it takes less time than ten minutes, because porpoise clicks would then have been recorded by C-pods on both sides of the Oosterschelde barrier in one time interval. It was not possible to prove this with the analyses done in the current study. Furthermore, data should be carefully interpreted. This study proves that the number of clicks per time interval is not a good indicator for the presence of harbour porpoises, since porpoises are shown to produce more clicks or less clicks in some periods of the year. Scoring the presence or absence of clicks per time interval is a more useful method.

4.5 Future research

The study presented here was performed as a pilot study to gain more information about harbour porpoises in the Oosterschelde related to harbour porpoises in the North Sea. Data of one year were available. A follow-up study will run for the next couple of years and will give the possibility to detect trends and seasonal patterns. Evidence was found for migration of harbour porpoises between the North Sea and the Oosterschelde. Visual observations could give more reliability about the frequency of crossing the storm surge barrier. Because it remains unclear whether some individuals from the Oosterschelde cross the barrier multiple times or whether porpoises from the North Sea visit the Oosterschelde, it would be very useful to perform a DNA analysis for porpoises inside and outside the Oosterschelde. In this way, it is possible to investigate whether the Oosterschelde porpoises already form a separated population or whether new individuals still join the group. Furthermore, little information is available about the calves observed in the Oosterschelde. It is unknown whether they were born in or outside the Oosterschelde. No calving grounds in the southern North sea nor the Oosterschelde are known, so it would be interesting to investigate where the observed calves were born.

5. Conclusion

This research revealed that the harbour porpoises in the southern North Sea still leave this area during spring. However, not all porpoises living in the Oosterschelde show this migration, because porpoise-identified click trains had been recorded in all months. Since evidence was found for migration between the Oosterschelde and the North Sea in both ways, it is not impossible for porpoises to cross the storm surge barrier, but the results suggest that this does not happen very frequently. Evidence for migration from the North Sea to the Oosterschelde was found in March 2010 and January 2011 and evidence for migration back to the North Sea was found in September 2010. Migration is suggested to be prey-related and in summer, prey densities are the highest in the Oosterschelde. It is hypothesized that some North Sea porpoises stay in the Oosterschelde in summer and return to the North Sea in September.

Also the effect of tide and day light on the daily movements of porpoise was investigated. Although the direction of the tidal currents did not have a significant effect on the swimming direction of porpoises in the North Sea, a significant effect was found of the direction of the tidal currents of the storm surge barrier on the click production and presence of harbour porpoises. The bigger the water level difference, the less porpoise clicks had been recorded. Harbour porpoises are affected by (the noise of) the strong tidal currents, but are still present when water level difference is maximal, however to a lesser extent. Harbour porpoises were more often present when water was flowing into the Oosterschelde, which suits with the hypothesis that they use the tidal stream to wait for incoming fishes. Clicks of harbour porpoises were recorded in relatively more time intervals during rising tide, whereas click production was higher during falling tide. A new hypothesis can be: harbour porpoises have to try harder for catching prey during falling tide, when fishes flow out the Oosterschelde with the tidal stream and therefore need to produce more click trains before they can catch the prey. Furthermore, harbour porpoises are more frequently present near the storm surge barrier at night in winter and at day in summer.

The diet of porpoises living in the North Sea and the Oosterschelde corresponded for the greater part: whiting and gobies form the main menu of porpoises occurring along the Dutch coast. These species were also found within the stomachs of porpoises stranded in the Oosterschelde and in addition, also Atlantic cod and poor cod were found. It is hypothesized that prey availability plays an important role in the food choice of the harbour porpoise. In the Oosterschelde, the locations where harbour porpoises have been observed most frequently correspond to the hotspots of their prey species.

Although the harbour porpoises in the southern North Sea migrate northwards during spring, the porpoises in the Oosterschelde apparently do not. Tidal currents have an effect on the porpoises living in this area, but evidence was found for migration between the North Sea and the Oosterschelde, which means that it is not impossible for the porpoises to cross the storm surge barrier. Apparently, the conditions are favorable enough to stay here all year and seasonal migration to a northern part of the North Sea is not necessary.

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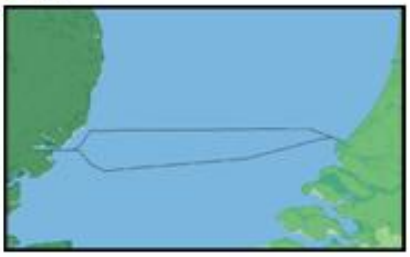
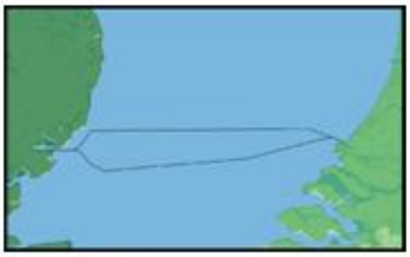
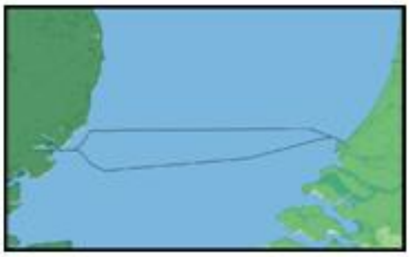
Appendix I: Results of the Stena Line data mapped per month

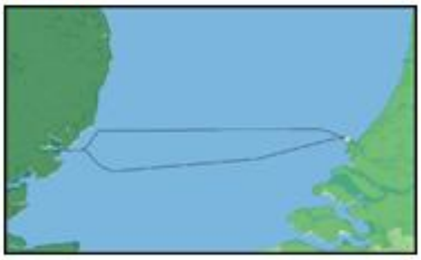
January 2005 	**February 2005** 
March 2005 	**April 2005** 
May 2005 	**June 2005** 
July 2005 	**August 2005** 
September 2005 	**Oktober 2005** 
November 2005 	**December 2005** 

January 2006

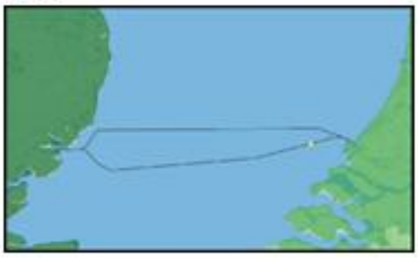
February 2006

March 2006

April 2006

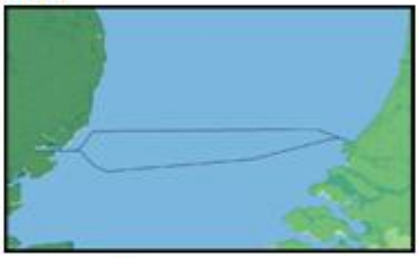


May 2006

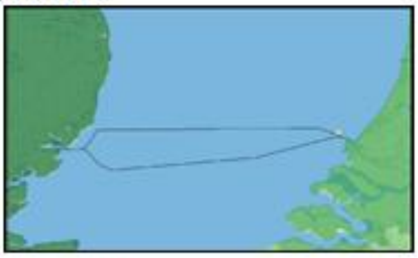


June 2006

July 2006



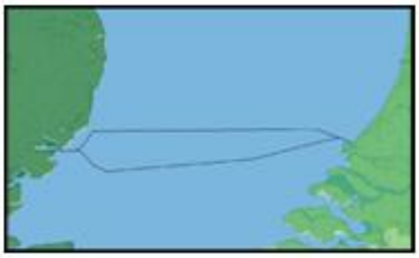
August 2006



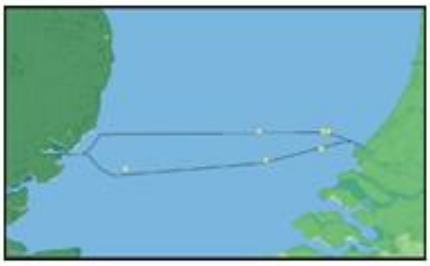
September 2006

Oktober 2006

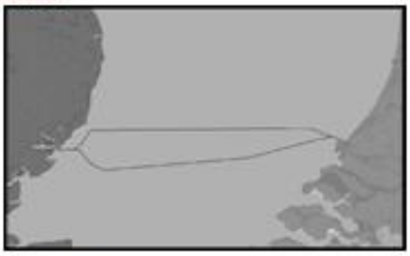
November 2006



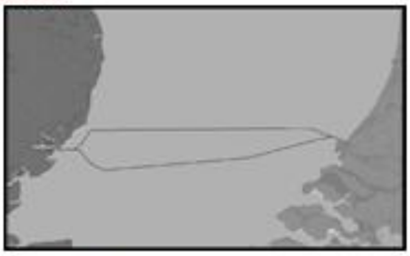
December 2006



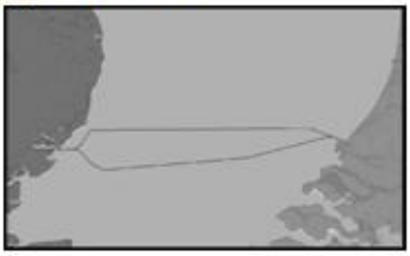
January 2007 - No data



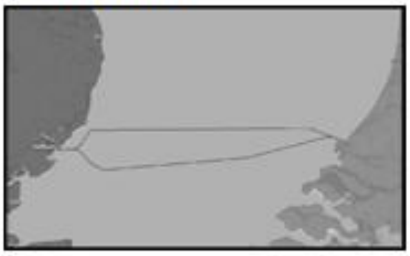
February 2007 - No data



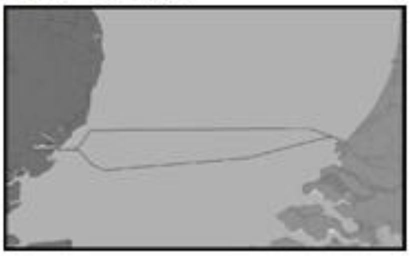
March 2007 - No data



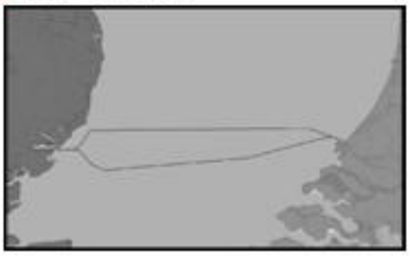
April 2007 - No data



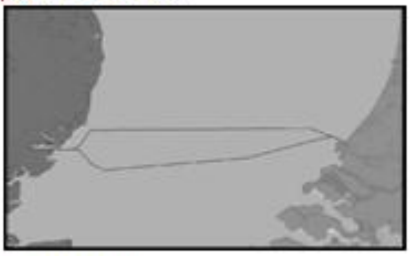
May 2007 - No data



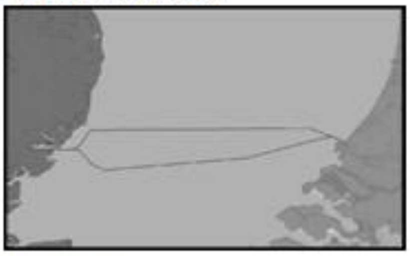
June 2007 - No data



July 2007 - No data



August 2007 - No data

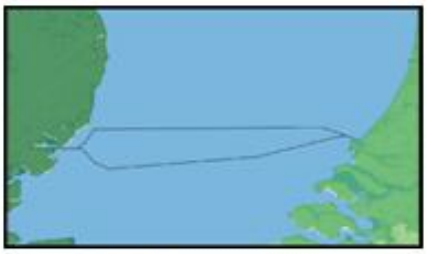


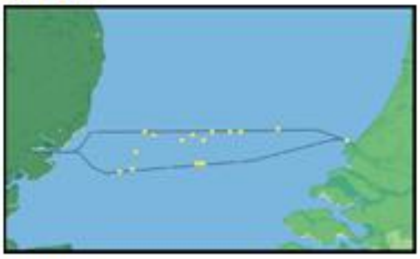
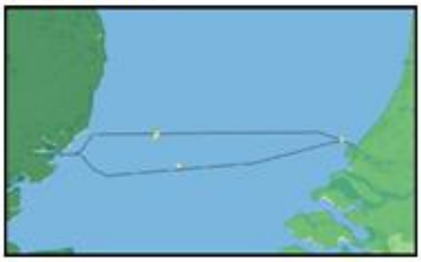
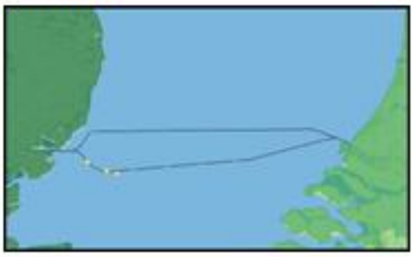
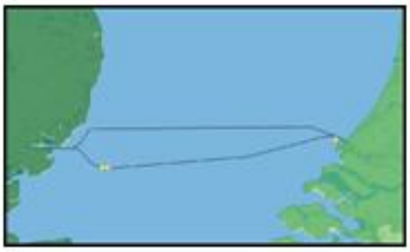
September 2007

Oktober 2007

November 2007

December 2007

January 2008 	**February 2008** 
March 2008 	**April 2008** 
May 2008 	**June 2008** 
July 2008 	**August 2008** 
September 2008 	**Oktober 2008** 
November 2008 	**December 2008** 

January 2009 	**February 2009** 
March 2009 	**April 2009** 
May 2009 	**June 2009** 
July 2009 	**August 2009** 
September 2009 	**Oktober 2009** 
November 2009 	**December 2009** 

January 2010 	February 2010 
March 2010 	April 2010 
May 2010 	June 2010 
July 2010 	August 2010 
September 2010 	Oktober 2010 
November 2010 	December 2010 

Appendix II: Stena Line monitoring program – data forms

FORM CS2: FOR CETACEAN SIGHTINGS MADE DURING EFFORT BASED RECORDING (FORM E1)

ARC
Atlantic Research Coalition

FOR HELP ON FILLING IN THIS FORM REFER TO FORM M1

Please send data to:

DATE (dd / mm / yy)		**NAME OF SHIP**		**OBSERVER NAMES**
POSITION ON SHIP (Bridge or deck no.)		**CONTACT INITIALS & ADDRESS**		1. 2. 3. 4.

TIME		LOCATION		WEATHER		SIGHTING											BEHAVIOUR						
Start	End	Latitude	Longitude	Sea state	Visibility	REF NO.	Angle	Distance	Species	Certainty (tick one)			Number Seen (Record ages if possible)				Type (tick one or more)						
(oo:oo)	(oo:oo)	(deg., min., sec.)	(deg., min., sec.)	(scale 0-9)	(scale 1-6)		(degrees °)	(m)		Def.	Prob.	Poss	TOT.	Ad.	Juv.	Calf	1	2	3	4	5	6	7

SUPPORTING IDENTIFICATION & OTHER NOTES

Sighting Ref. No.

Sighting Ref. No.

Sighting Ref. No.

ASSOCIATED SEABIRDS

Sighting Ref. No.

Sighting Ref. No.

FORM E1: VESSEL-BASED EFFORT RECORDING

FOR HELP ON FILLING IN THIS FORM REFER TO FORM M1

ARC
Atlantic Research Coalition

Please send data to:

DATE (dd / mm / yy)		NAME OF SHIP		OBSERVER NAMES
POSITION ON SHIP (Bridge or deck no.)		CONTACT INITIALS & ADDRESS		1. 2. 3. 4.

IMPORTANT: (1) Record at least every 30 minutes, but preferably every 15 minutes or when ships course changes
(2) * = critical fields required for effort-based analyses

TIME*	LOCATION		SHIPS DETAILS		WEATHER							
	Latitude*	Longitude*	Course*	Speed*	Sea state*	Visibility*	Clouds	Swell Height	Wind Speed	Wind Direction	Precipitation	
(oo:oo)	(deg., min., sec.)	(deg., min., sec.)	(degrees)	(knots)	(Code 0-9)	(Code 1-6)	(Code 0-8)	(Code 1-3)	(Code 0-9)	(N, NNW etc.)	Type	Intensity