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Echolocation activity of Harbour Porpoise *Phocoena phocoena* in the Eastern Scheldt estuary (The Netherlands) and the North Sea

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Acknowledgments

I would like to thank and acknowledge Frank Zanderink, coordinator of the Rugvin Foundation, for collecting and providing the data used in this report and for supporting this study. His advices and suggestions were always very valuable and useful. I am grateful to Peter Koppenaal (RWS), captain of the MS Hammen, and his crew, for all their assistance in retrieving and deploying the C-PODs in the Eastern Scheldt. Furthermore, I am very thankful to Lisanne Korpelshoek, Catalina Yunda and Niki Karagkouni, for their readiness and availability to give insights and clarifications every time I had difficulties with the data sets. I am grateful to Els de Jong, Nynke Osinga and Wouter Jan Strietman, for their valuable comments and suggestions that greatly improved this report. I would like to thank WWF Netherlands for financing this study and the work with the C-PODs.

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January 2014

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Abstract

Harbour porpoises (*Phocoena phocoena*) became nearly absent in Dutch coastal waters. However, in the last decades, a remarkable resurgence has been happening. Even in semi-closed coastal waters, such as the Eastern Scheldt (Oosterschelde in Dutch) delta area, harbour porpoise sightings are nowadays common. Due to increasing number of sightings in the last years, it has been confirmed that a resident group of harbour porpoises permanently lives inside the Eastern Scheldt.

The Eastern Scheldt has a storm surge barrier (Oosterscheldekering) that protects the region from flooding if a storm surge occurs. The barrier has tens of gates that allow seawater to flow to and from the sea, depending on the tide. However, the barrier may hinder the activity, behaviour and migrations of harbour porpoises that live or pass nearby. To investigate the activity of porpoises in the vicinity of the storm surge barrier, acoustic data loggers (C-PODs) were deployed on both sides of the barrier, i.e., in the Eastern Scheldt and the North Sea sides. These data loggers use digital waveform characterisation to record and store echolocation trains, with a maximum range of approximately 300 m for porpoise clicks.

We were able to detect the activity and presence of porpoises all year-round inside the Eastern Scheldt, matching with previous recordings and sightings of this resident harbour porpoise group. Furthermore, we found out that porpoises were more frequently active and present during winter and less during spring, suggesting that some individuals might migrate northwards in the North Sea during this season. We also found out that porpoises were present more often near the storm surge barrier during slack tide and hence, when the water level differences were minimal. Harbour porpoises did not show echolocation activity differences according to daily, nocturnal or twilight time intervals.

Our study gives insights on the activity and behaviour of porpoises in the Eastern Scheldt, particularly when near the storm surge barrier. It may help in a better understanding of the relationship between these cetaceans and man-made structures such as the barrier, and hence, help in minimising possible detrimental effects on porpoises. Furthermore, our study can help in devising more informed strategies to conserve the group of harbour porpoises that inhabit the Eastern Scheldt area.

Table of Contents

1. Introduction

In the early 1960s, harbour porpoises became virtually extinct in Dutch coastal waters. Then, the number of sightings started to gradually increase during mid-1980s to early 1990s, followed by a proportional rate of increase of 41% per year until 2004 (Camphuysen 2004). The resurgence of porpoises in Dutch coastal waters was also noticeable in a semi-closed part of the Dutch Delta Area - the Eastern Scheldt (Oosterschelde in Dutch) - triggering the emergence of what is thought to be a resident group living inside the basin (Camphuysen and Heijboer 2008). Two harbour porpoises were observed in 1996 (Witte 2001), ten years after the end of the construction of the storm surge barrier (Oosterscheldekering), which protects the delta area from flooding. On September 2009, in a visual survey done under ideal weather conditions by members of the Rugvin Foundation, 37 porpoises, among which 5 calves, were counted inside the Eastern Scheldt; on May 2010, under less favourable weather conditions, 15 individuals were counted, being calves sighted on June 2010; on June 2011, with very good visibility, 61 individuals were spotted (http://rugvin.wordpress.com/onderzoek/oosterschelde/scans/). The Eastern Scheldt harbour porpoise resident group is estimated to have less than 100 individuals (Zanderink and Osinga 2010). Regular sightings of calves suggest reproductive activities inside the delta area.

Harbour porpoises (*Phocoena phocoena*) are toothed whales and the most abundant cetaceans in North-west European continental shelf waters (Reid et al. 2003). They are among the smallest cetaceans. The adult females reach, on average, 1.6 m in length (60 kg), adult males about 1.5 m (50 kg), and calves between 70 and 75 cm (5 kg) at birth. Harbour porpoises have an average life-span of 8 to 10 years, become sexually mature between at 3 and 4 years of age and have one offspring every 1 or 2 years, with their gestation lasting between 10 to 11 months (Lockyer 2003).

Harbour porpoises have a limited energy storage capacity, reason why they forage constantly throughout the year (Kastelein et al. 1997; Bjørge 2003). Consequently, they need to live nearby their prey (Koopman 1998). Porpoises from cold waters, as the ones from the North Sea and the Eastern Scheldt, need to consume large amounts of food daily. They consume an average of 4 to 9.5% of their body weight per day (Kastelein et al. 1997; Lockyer and Kinze 2003). The main preys of adult porpoises in the Eastern Scheldt are atlantic cod (*Gadus morhua*), whiting (*Merlangius merlangus*) and poor cod (*Trisopterus minutus*) (Korpelshoek 2011;

analysis by Leopold and Jansen). The densities of these prey species vary seasonally and might be responsible for variations in the abundance and activity of harbour porpoises inside the Eastern Scheldt (Korpelshoek 2011). The highest abundance of harbour porpoises along the Dutch coast happens during winter and early spring (Gilles et al. 2009; Haelters and Camphuysen 2009), and during late spring they are seen migrating northwards in the North Sea (Osinga 2005).

Besides prey availability, tidal phases are also known to affect the activity and behaviour of harbour porpoises (Johnston et al. 2005; Skov and Thomsen 2008). Previous research found out that adult porpoises forage more frequently during the ebb tidal phase and against the tidal stream (Pierpoint 2008). This might be related with the higher chance that tidal currents have in carrying prey and funnel them towards awaiting harbour porpoises (Johnston et al. 2005). However, when with calves, female porpoises may avoid strong tidal currents due to the risk of losing their offspring, which might not be able to swim against the water currents (Piermont 2008).

The activity and behaviour of harbour porpoises can also be influenced by light and hence, show diel patterns (Sveegaard 2011). Todd et al. (2009), in a study about the diel echolocation activity of harbour porpoises around North Sea offshore gas installations, found out that the frequency of porpoises presences near the platform was greater by night than by day. They hypothesised that porpoises were feeding near the platform at night and thus, that their diel activity was related and matching with the diel activity of their prey.

Porpoises are known to use echolocation click trains for foraging, orientation, navigation, and communication (Au 1993; Kastelein et al. 1999; Teilmann et al. 2002; DeRuiter et al. 2010), which makes them vulnerable to sound pollution in their environment (Koschinski 2001). The Eastern Scheldt's storm surge barrier (Oosterscheldekering) is a potential source of sound pollution, as the movement of tidal currents against the barrier walls is known to emit noise. Kastelein et al (2005) showed that harbour porpoises are very sensitive to underwater sounds and swim away from noise sources. Near the storm surge barrier, during slack tide, the tidal currents and noise are minimal which may provide opportunities for porpoises to move and/or migrate between the Eastern Scheldt and the North Sea (Korpelshoek 2011).

The distribution and activity of small cetaceans has been estimated mainly through visual surveys (Heide-Jørgensen et al. 1992, 1993; Scheidat et al. 2004). However, these surveys are limited because they can only be done in daylight and under good weather conditions. The use of passive acoustic monitoring tools is becoming more frequent during the last decade (Kyhn et al. 2012). These tools can record porpoise echolocation clicks continuously and under less favourable weather conditions. They have been used to investigate the effect of anthropogenic noise in the activity of harbour porpoises (Carstensen et al. 2006; Tougaard et al. 2009; Scheidat et al. 2011), spatial distribution and migration patterns (Verfuß et al. 2007; Korpelshoek 2011; Yunda and Karagkouni 2012). These acoustic monitoring tools take advantage of the unique acoustic signals that distinguish porpoises from the other cetaceans and other underwater sound sources. Their echolocation clicks are of short duration (ca. 100 µs), with peak frequency around 130 kHz and no energy below 100 kHz (Møhl and Andersen 1973; Villadsgaard et al. 2007).

The aim of this study is to investigate the activity of harbour porpoises near the storm surge barrier, both in the Eastern Scheldt side and in the North Sea side. To achieve this, acoustic data loggers (C-PODs) were deployed in both sides of the storm surge barrier. Our specific objectives are to understand the migration patterns of harbour porpoises and to investigate their activity responses to tidal currents and light. Furthermore, we investigate whether the presence of the storm surge barrier affects harbour porpoises behaviour.

2. Methods

2.1. Study Area

We did this study in the Eastern Scheldt delta area, which currently encompasses the largest National Park in the Netherlands, with 37 000 ha (fig. 1A). This is a wetland with a diverse range of habitats, namely the open water mass, the

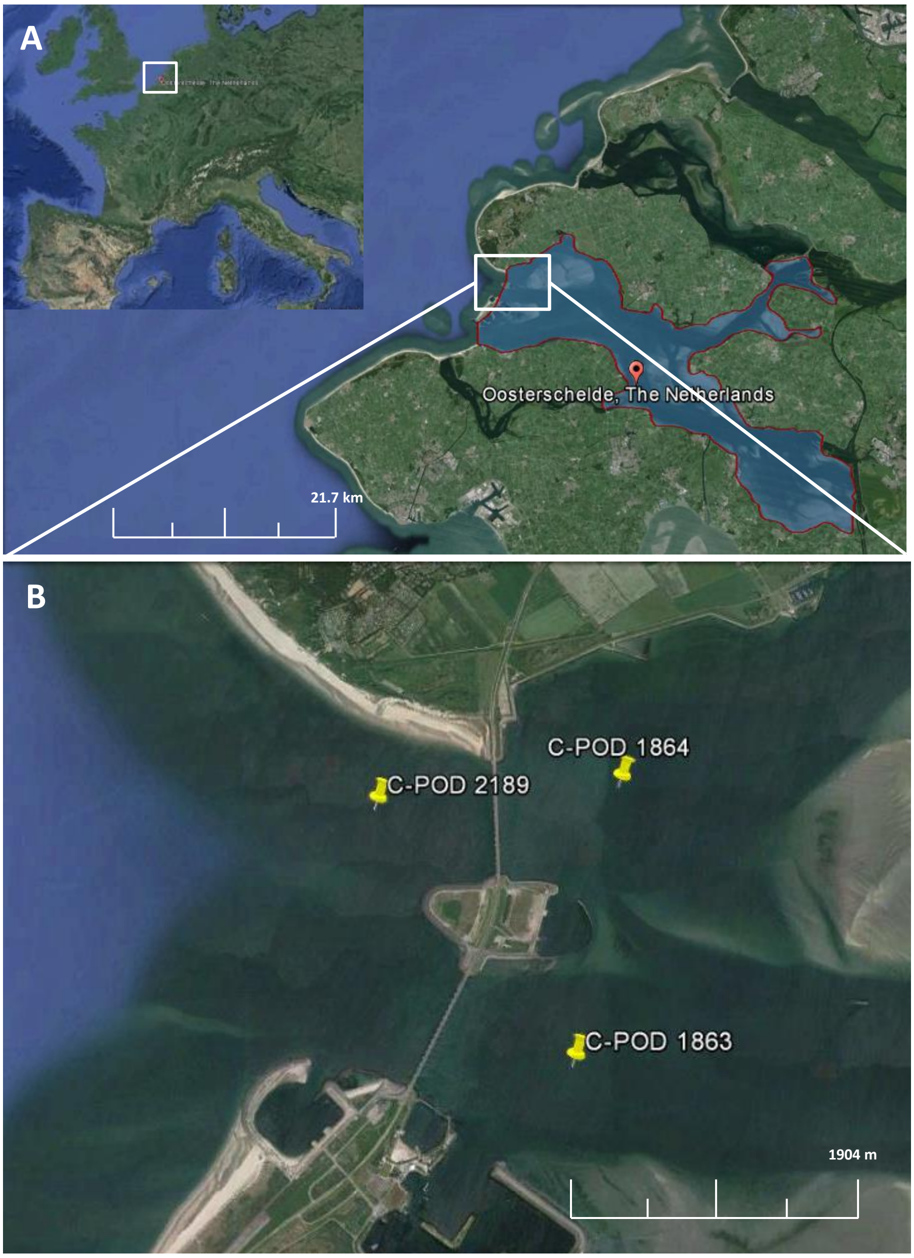

Figure 1 The Eastern Scheldt estuary (Google Earth 2013). **A**: the Eastern Scheldt delta area highlighted. **B**: the C-PODs 1863 and 1864 located in the Eastern Scheldt side of the storm surge barrier and the C-POD 2189 located in the North Sea side.

intertidal sand and mudflats, the supratidal salt marshes, and the artificial hard substrates of seawalls and dikes (Smaal and Nienhuis 1992). These habitats are home, wintering ground, nursery and provisioning area for hundreds of species of fauna and flora (MANFQ 2004). This is an area of particular importance for harbour porpoises since it is the only Dutch sector of the North Sea where a small but increasing resident group is thought to exist (Camphuysen and Siemensma 2011). Besides harbour porpoises, the wetland also supports a diverse range of migratory birds, fish, mussels, oysters, crabs, seals, and halophytes.

In the period between 1979 and 1986, a storm surge barrier (fig. 2) (Oosterscheldekering in Dutch) was built in the mouth of the Eastern Scheldt estuary to protect the human populations and their properties from the storm floods that threaten the area. The barrier is constructed over three channels: the

Figure 2 The storm surge barrier. **A**: an open gate of the barrier. **B**: a harbour porpoise swimming in the Eastern Scheldt with the storm surge barrier in the background.

“Hammen”, the “Schaar van Roggeplaat” and the “Roompot”, with a total length of 3 km (Deltawerken 2013).

The barrier allows tidal movements. When the gates are open, three-quarters of the original tidal movement is maintained (Deltawerken 2013), therefore allowing the exchange of eutrophic water between the wetland and the North Sea, fuelling life inside the Eastern Scheldt (MANFQ 2004).

2.2. Logging the activity of harbour porpoises

We used passive acoustic monitoring instruments called C-PODs Chelonia Ltd, Long Rock, Cornwall, UK) to investigate the presence of harbour porpoises in both sides of the storm surge barrier, and their movement patterns between the Eastern Scheldt and the North Sea. These data loggers use digital waveform characterisation to record cetacean clicks and log the time, centre frequency, sound pressure level, duration and bandwidth of each click (Tregenza 2013). C-PODs have a maximum detection range of approximately 300 m for porpoise clicks.

Three C-PODs were deployed on both sides of the barrier’s safety lines. Specifically, two C-PODs were positioned in the Eastern Scheldt side and one C-POD in the North Sea side (fig. 1B and table 1). All C-PODs were deployed approximately 900 m from the barrier’s gates. C-PODs’ batteries were changed regularly and raw data was collected periodically (figs. 3A to 3D). However, some data was lost due to malfunctions of C-PODs or due to extreme weather, responsible for the loss of one C-POD. The time periods with usable data are displayed in table 1.

The raw data was accessible through the CPOD.exe v2.043 which uses a KERNO classifier to detect and extract coherent click trains in the data (Tregenza 2013). We sorted harbour porpoise click trains by selecting “NBHF cetacean”, meaning that only Narrow Band High Frequency click trains, as the ones from porpoises, were chosen. Furthermore, we only included high and moderate quality click trains and excluded WUTS (Weak Unknown Train Sources).

Figure 3 Handling of C-PODs. **A**: deploying the C-POD. **B**: attaching the C-POD to the safety line and deploying it into the water. **C**: retrieving the C-POD. **D**: Hosing and cleaning the C-POD after retrieval.

Table 1 The location of C-PODs, their GPS coordinates and the time periods from which data was available. The reasons for absent data are also displayed.

C-POD	**1863**	**1864**	**2189**
Location	Eastern Scheldt	Eastern Scheldt	North Sea
GPS Coordinates	51°38′60″ N 03°43′83″ E	51°39′69″ N 03°44′14″ E	51°39′60″ N 03°42′60″ E
Data Timeline			
26.09.2013			C-POD failure
11.09.2013			
22.07.2013			
11.07.2013	C-POD failure	C-POD out of water	
30.06.2013			
16.05.2013		C-POD failure	
25.04.2013			C-POD failure
16.04.2013	C-POD failure		
06.03.2013			
14.02.2013		C-POD loss	C-POD failure
17.12.2012			
11.10.2012			

2.3. Data entry and analysis

After extracting the raw data with CPOD.exe v2.043 and sorting the click trains, we organised the data in Microsoft® Excel 2010 spread sheets and grouped them in three data sets, with intervals of ten minutes, and available as:

- "the number of clicks per ten-minute time interval", which represents the number of porpoise echolocation clicks per interval;
- "DPM" (Detection Positive Minutes), with the amount of minutes per interval (from 0 to 10) in which clicks were recorded;
- "presence of porpoises per ten-minute time interval", a data set created from the previous two data sets, to identify the ten-minute intervals in which porpoises were detected (1 codes for presence and 0 for absence).

We only used intervals with recorded clicks in the analysis of the first two data sets. The data from the C-PODs located in the Eastern Scheldt side of the storm surge barrier (C-PODs 1863 and 1864) was combined by averaging data from coincident time intervals.

We did the statistical analysis with IBM® SPSS® Statistics v. 20.0.0. Firstly, we checked whether the data followed a normal distribution with the Pearson Chi-square test. This test was also used to examine differences between the "presence of porpoises per ten-minute time interval" data set throughout the seasons, and the effect of tide on the activity of porpoises near the storm surge barrier. We used the related-samples Friedman's test to examine differences in the effect of day light. We applied the Kruskal-Wallis test to compare the "the number of clicks per ten-minute time interval" data set, the "DPM" data set, and the effect of tide and day light in the number of clicks per ten-minute time interval. We compared the presence of porpoises between locations (North Sea side and Eastern Scheldt side of the storm surge barrier), and between "the number of clicks per ten-minute time interval" and "DPM", with the Spearman's rank correlation test.

2.4. Migration between the Eastern Scheldt and the North Sea

We considered that porpoises were migrating from the Eastern Scheldt to the North Sea if they were detected by C-PODs in the Eastern Scheldt side of the barrier, and then detected again in the next time interval by the C-POD located in the North Sea side. The opposite is valid for migrations from the North Sea to the Eastern Scheldt. The migration patterns are displayed in table 2, where 1 codes for presence of a porpoise in a given time interval, and 0 codes for absence.

Table 2 Migration patterns between the North Sea and the Eastern Scheldt. 1: harbour porpoise presence; 0: harbour porpoise absence.

Migration Pattern		**North Sea**	**Eastern Scheldt**
From the North Sea to the Eastern Scheldt	Time interval x	1	0
	Time interval y	0	1
From the Eastern Scheldt to the North Sea	Time interval x	0	1
	Time interval y	1	0

To assess the statistical significance of our results and, therefore, to test whether the migration patterns were based or not on coincidence, we randomised the migration data set by following the same procedure as Korpelshoek (2011). We used the algorithm Mersenne Twister and randomised the data set 1000 times for each season. We only assume that migration patterns are found more often than random when the chance of finding the pattern, minimally as often as in the original data set, is lower than 0.05.

2.5. The effect of tide on the activity of harbour porpoises

We compared the water level differences of the sites *Roompot binnen* (inside the Eastern Scheldt) and *Roompot buiten* (outside the Eastern Scheldt) to investigate the effect of tide on harbour porpoises activity (Rijkswaterstaat 2013). We subtracted the water level of *Roompot binnen* from the water level of *Roompot buiten*. If the difference is positive, the water is flowing from the North Sea into the Eastern Scheldt, whereas a negative difference indicates that the water is flowing from the Eastern Scheldt to the North Sea. We grouped the water level differences in eleven classes (table 3) and tested them with the data set of the number of clicks per ten-minute time interval, and with the data set of the presence of porpoises per interval. All water levels are referent to NAP (*Normaal Amsterdams Peil* or Amsterdam Ordnance Datum) per 10 minutes, GMT+1.

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

Table 3 Water level classes representing the water level differences between *Roompot buiten* (outside the Eastern Scheldt) and *Roompot binnen* (inside the Eastern Scheldt).

2.6. The effect of light on the activity of harbour porpoises

To investigate the influence of light on porpoises, we used the exact time (GMT+1) of sunrise, sunset and astronomical twilight. Since the time points of the study area were not available, we used the ones from Belgium (Royal Observatory of Belgium 2013) due to its proximity to Zeeland/Eastern Scheldt. We split the time points into classes, according to day, night, and twilight. The class "day" includes all time points from sunrise to sunset. The class "night" comprises all time points from the start of astronomical twilight to the end of astronomical twilight. Astronomical twilight begins when the centre of the sun is geometrically 18 degrees below the horizon. The class "twilight" contains all time points between the end of astronomical twilight and sunrise plus all time points between the start of astronomical twilight and sunset. This classification assures that all time periods classified as “day” are fully day light, and the ones classified as “night” are completely dark. We tested these classes with the data set of the number of clicks per ten-minute time interval, and with the data set of the presence of porpoises per interval.

3. Results

3.1. The activity of harbour porpoises near the storm surge barrier

Harbour porpoise clicks were recorded, in the Eastern Scheldt side, by C-PODs 1863 and 1864, from which data was combined. The percentage of ten-minute time intervals with recorded clicks is not equally distributed throughout the different seasons ($p = 0.002; df = 3; \chi^2 = 15.2$). Harbour porpoises spent more time near the storm surge barrier during winter months (fig. 4), as this season showed the highest percentage (50.7%) of ten-minute time intervals with recorded clicks. Autumn was the season with the second highest percentage of recorded clicks (41.3%), followed by summer (27.6%). Porpoises spent less time near the storm surge barrier during spring (21.0%). On average, C-PODs recorded porpoise clicks in 35.2% of all ten-minute time intervals, in the Eastern Scheldt side of the barrier.

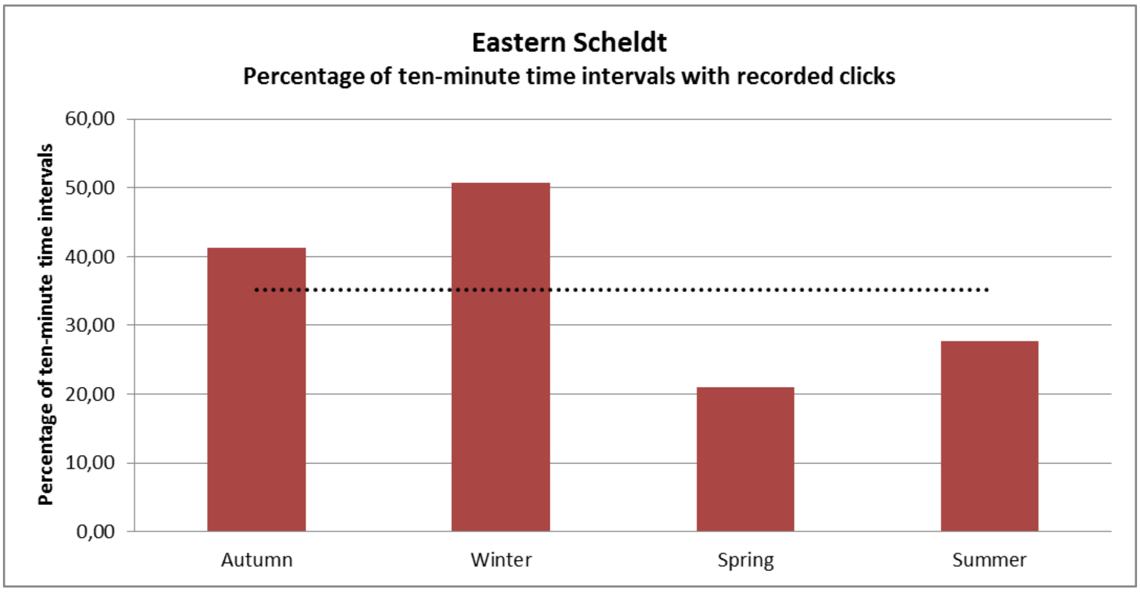

Figure 4 Percentage of ten-minute time intervals with harbour porpoise clicks per season, recorded by C-POD 1863 and C-POD 1864, both located in the Eastern Scheldt. Autumn: 11.10.2012 – 20.12.2012; Winter: 21.12.2012 – 06.03.2013; Spring: 25.04.2013 – 20.06.2013; Summer: 21.06.2013 – 30.06.2013 and 22.07.2013 – 20.09.2013 (data from C-POD 1864 was available only for summer months). The dotted line indicates the average percentage of all intervals with clicks (35.2%).

The Detection Positive Minutes per ten-minute time interval (fig. 5) is not the same during the different seasons ($p = 0.007; df = 3; Kruskal - Wallis\ chi\ square = 12.0$). Porpoises spent, on average, more time (4.9 min per ten-minute time interval) near the barrier during winter months. During the other seasons, they spent, on average, 3.7 min per ten-minute time interval in autumn, 2.4 min in spring, and

1.8 min in summer months. For all seasons, porpoises spent, on average, 3.2 min per ten-minute time interval near the storm surge barrier. Only intervals with observations were included in this analysis.

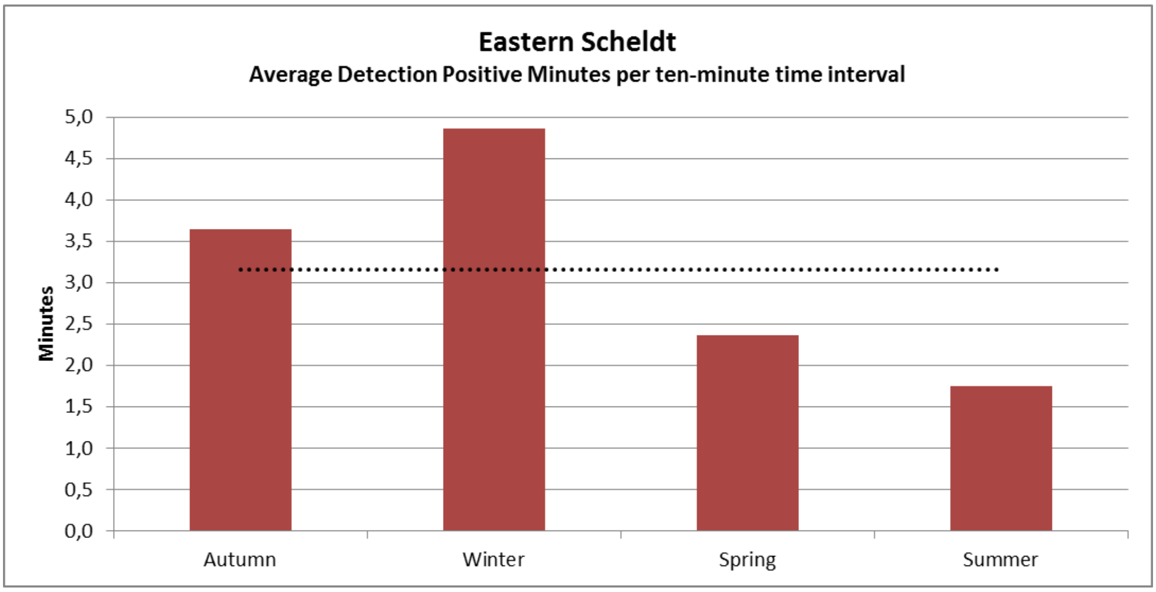

Figure 5 Average Detection Positive Minutes of harbour porpoise clicks per ten-minute time interval per season, recorded by C-POD 1863 and C-POD 1864, both located in the Eastern Scheldt. Autumn: 11.10.2012 – 20.12.2012; Winter: 21.12.2012 – 06.03.2013; Spring: 25.04.2013 – 20.06.2013; Summer: 21.06.2013 – 30.06.2013 and 22.07.2013 – 20.09.2013 (data from C-POD 1864 was available only for for summer months). The dotted line shows the average time of all intervals with clicks (3.2 min).

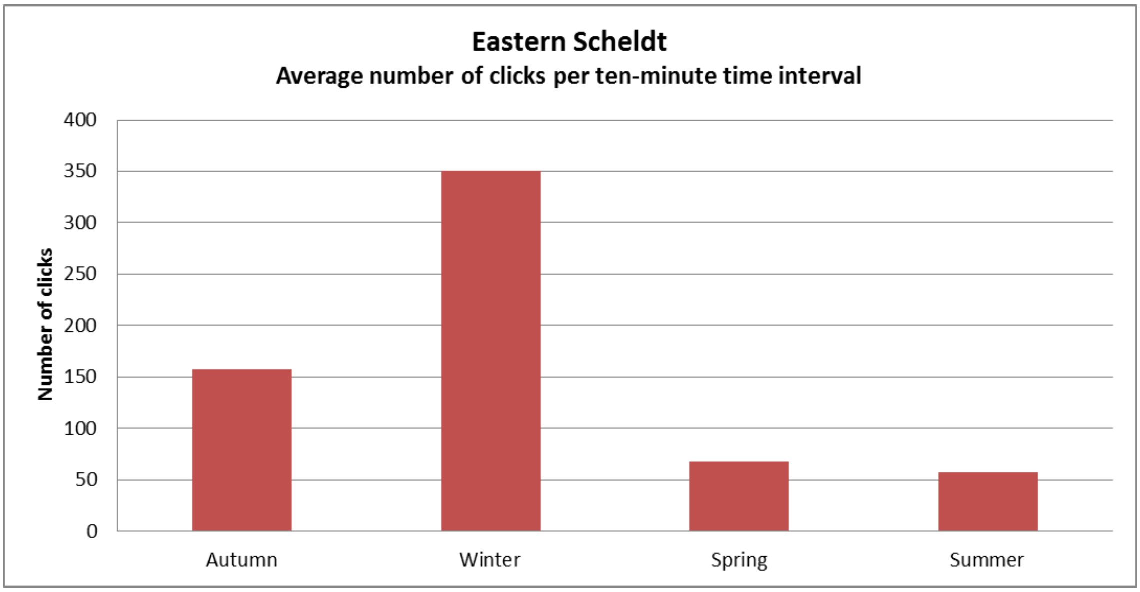

Figure 6 Average number of harbour porpoise clicks per ten-minute time interval per season, recorded by C-POD 1863 and C-POD 1864, both located in the Eastern Scheldt. Autumn: 11.10.2012 – 20.12.2012; Winter: 21.12.2012 – 06.03.2013; Spring: 25.04.2013 – 20.06.2013; Summer: 21.06.2013 – 30.06.2013 and

22.07.2013 – 20.09.2013 (data from C-POD 1864 was available only for summer months).

The average number of clicks (fig. 6), recorded by C-PODs located in the Eastern Scheldt, is not equal during the different seasons ($p < 0.001; df = 3; Kruskal - Wallis\ chi\ square = 632.0$). Porpoises vocalised an average of 350 clicks per interval during winter, 158 clicks during autumn, and 68 clicks during spring months. Summer months had the lowest average echolocation clicks per interval, i.e., 57 clicks. Intervals without clicks were excluded.

The average number of clicks follows the same seasonal pattern as the Detection Positive Minutes. This is expected because they are highly correlated ($p < 0.001; Spearman's\ rank\ correlation\ test, \rho = 0.876$).

On the North Sea side of the storm surge barrier, porpoise clicks were recorded by C-POD 2189 and are not equally distributed throughout the different seasons ($p < 0.001; df = 2; \chi^2 = 20.2$). Figure 7 shows the percentage of ten-minute time intervals with recorded clicks. This percentage is the highest during winter (22.8%), followed by spring (11.9%). During summer (1.4%) and autumn (0.4%) there are fewer intervals with porpoise clicks. The average percentage of positive ten-minute time intervals, for all seasons, is 9.1%.

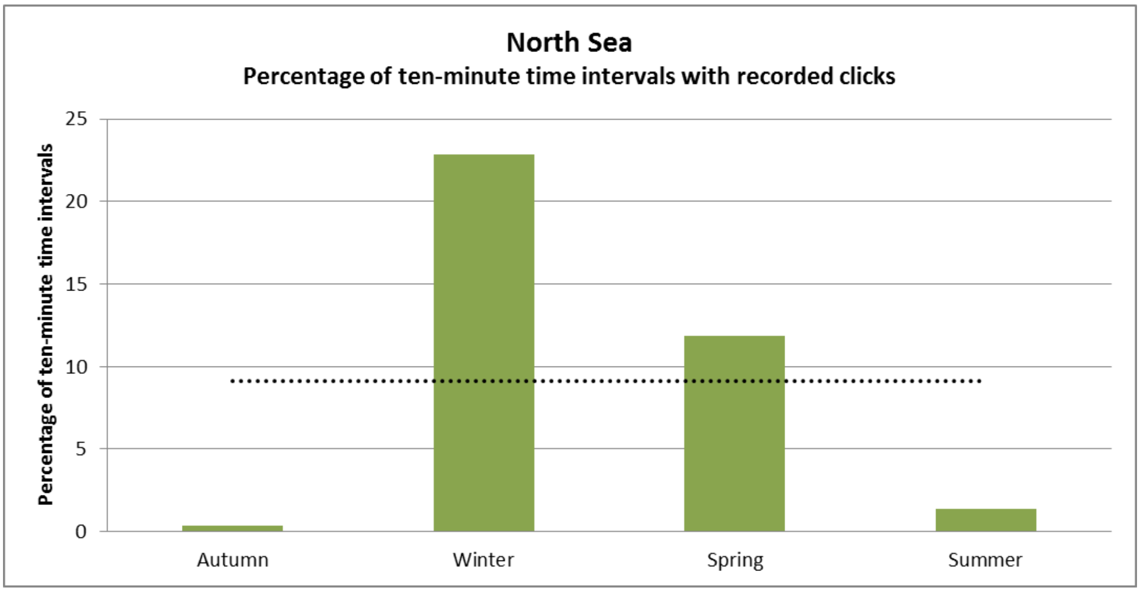

Figure 7 Percentage of ten-minute time intervals with harbour porpoise clicks per season, recorded by C-POD 2189, located in the North Sea. Autumn: 11.10.2012 – 17.12.2012; Winter: 14.02.2013 – 20.03.2013; Spring: 21.03.2013 – 16.04.2013 and 16.05.2013 – 20.06.2013; Summer: 21.06.2013 – 15.08.2013 and 16.08.2013 – 11.09.2013. The dotted line shows the average percentage of all recorded clicks (9.1%).

The Detection Positive Minutes per ten-minute time interval on the North Sea side of the storm surge barrier (fig. 8) is not the same throughout the different seasons ($p = 0.019; df = 3; Kruskal - Wallis\ chi\ square = 10.0$). Harbour porpoises spent, on average, 2.7 min near the barrier in all recorded intervals. They spent more time during winter (4.0 min), followed by spring (3.2 min), summer (1.8 min), and autumn months (1.7 min). Although porpoises spent relatively less time in the North Sea side (2.7 min) of the barrier than in the Eastern Scheldt side (3.2 min), a similar seasonal pattern is noticeable for both sides of the barrier. Only positively recorded intervals were included.

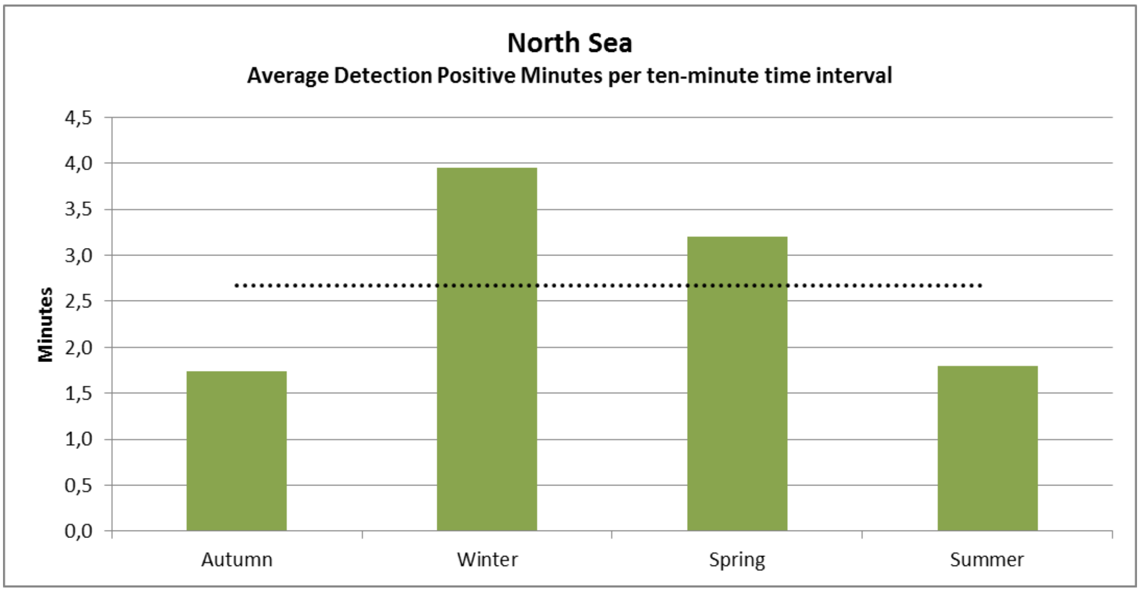

Figure 8 Average Detection Positive Minutes of harbour porpoise clicks per ten-minute time interval per season, recorded by C-POD 2189, located in the North Sea. Autumn: 11.10.2012 – 17.12.2012; Winter: 14.02.2013 – 20.03.2013; Spring: 21.03.2013 – 16.04.2013 and 16.05.2013 – 20.06.2013; Summer: 21.06.2013 – 15.08.2013 and 16.08.2013 – 11.09.2013. The dotted line shows the average time of all intervals with clicks (2.7 min).

The average number of echolocation clicks per ten-minute time interval (fig. 9) is not equal during the different seasons ($p < 0.001; df = 3; Kruskal - Wallis\ chi\ square = 533.0$). During winter months porpoises vocalised, on average, 246 clicks per ten-minute time interval. On spring 190 clicks were recorded per interval, followed by autumn, with an average of 62 clicks, and summer with 36 clicks on average. Intervals without clicks are not considered.

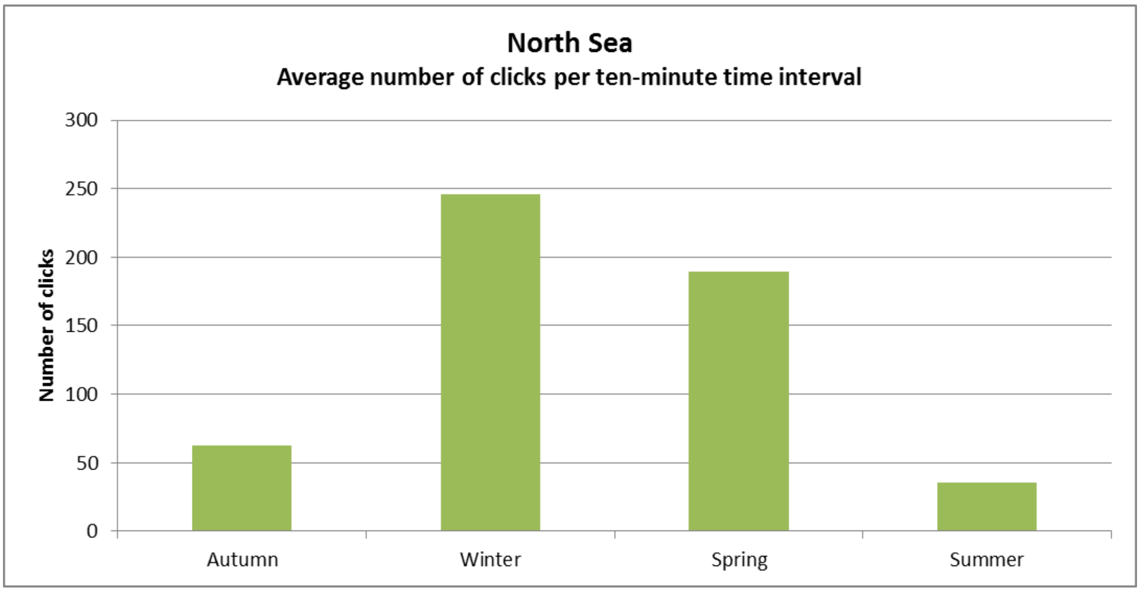

Figure 9 Average number of harbour porpoise clicks per ten-minute time interval per season, recorded by C-POD 2189, located in the North Sea. Autumn: 11.10.2012 – 17.12.2012; Winter: 14.02.2013 – 20.03.2013; Spring: 21.03.2013 – 16.04.2013 and 16.05.2013 – 20.06.2013; Summer: 21.06.2013 – 15.08.2013 and 16.08.2013 – 11.09.2013.

3.2. Migration between the Eastern Scheldt and the North Sea

The pattern representing migration was found in all seasons tested, both from the Eastern Scheldt to the North Sea and from the North Sea to the Eastern Scheldt (table 4). However, after randomizing the migration data 1000 times, we found out that all values were not statistical significant, i.e., the probability of finding the migration pattern, as minimally as often as in the original migration data, was higher than 0.05, in all seasons. This means that there is a high chance that the migration patterns are based on coincidence.

However, we did find a significant correlation ($p < 0.001; Spearman's\ rank\ correlation\ test, \rho = 0.113$) between the percentage of positive ten-minute time intervals on both sides of the storm surge barrier. This correlation indicates that as more porpoise clicks are recorded in the Eastern Scheldt side the barrier, more clicks are recorded in the North Sea side as well. This correlation suggests that harbour porpoises are actively crossing the storm surge barrier.

Table 4 The number of times the pattern representing migration of harbour porpoises through the storm surge barrier was recorded, in the different seasons. **In**: from the North Sea to the Eastern Scheldt. **Out**: from the Eastern Scheldt to the North Sea. The p value represents the probability of migration patterns are based on coincidence. There is statistical significance when $p < 0.05$.

Season	In	Out
Autumn	**2** p = 0.703	**1** p = 0.906
Winter	**9** p = 0.748	**12** p = 0.408
Spring	**18** p = 0.352	**22** p = 0.082
Summer	**8** p = 0.459	**6** p = 0.754

3.3. The effect of tide on the activity of harbour porpoises

We analysed the effect of tide on the activity of porpoises, near the storm surge barrier, by splitting water level differences in several classes, and relating them to our acoustic data sets. Positive water levels represent rising tide inside the Eastern Scheldt, i.e., the direction of the water currents is from the North Sea to the Eastern Scheldt. Negative water levels represent the opposite direction of the water currents, meaning that the tide is falling inside the Eastern Scheldt. When the water level is approximately zero (NAP) the water currents are minimal, whereas for higher water level differences the currents are stronger. Figure 10 shows the percentage of ten-minute time intervals with recorded clicks per tidal class in the Eastern Scheldt side of the storm surge barrier. Positive intervals were recorded in all tidal classes and are not equally distributed among the different classes ($p < 0.001; df = 9; \chi^2 = 41.1$). The highest percentages of positive intervals (between 15% and 20%) were recorded between the [-60 cm; -41 cm] and [20 cm; 39 cm] tidal classes. This indicates that porpoises are present more often near the barrier during periods of “middle range” tidal currents strength, and both during falling and rising tides inside the Eastern Scheldt. Fewer positive intervals were recorded during extreme water level differences.

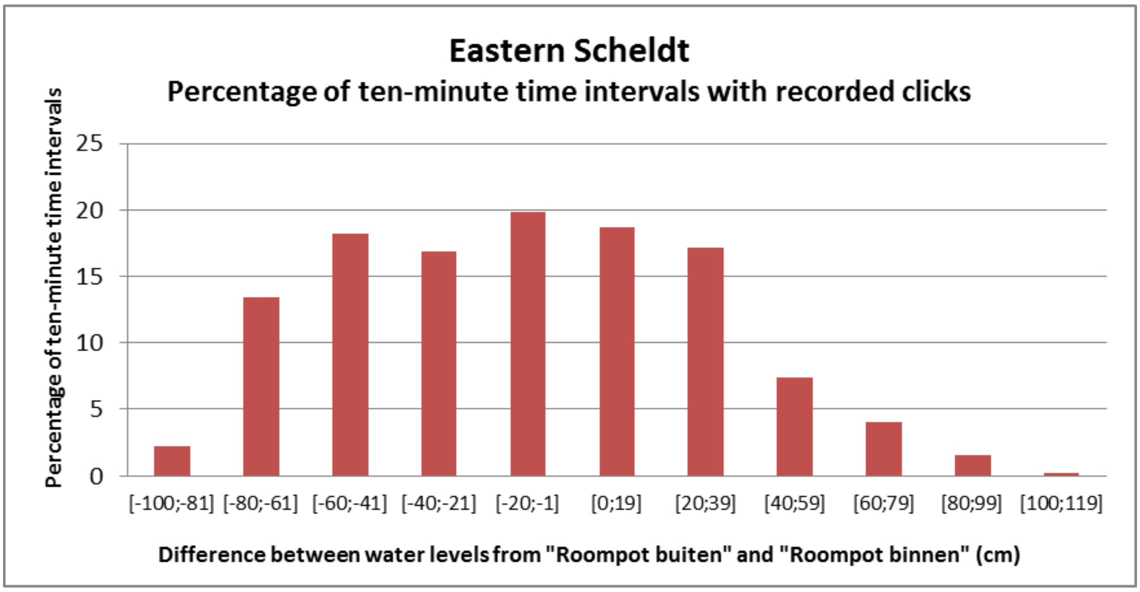

Figure 10 Percentage of ten-minute time intervals with harbour porpoise clicks per water level class, recorded by C-POD 1863 and C-POD 1864, both located in the Eastern Scheldt (data from C-POD 1864 was available only for the time period between 22.07.2013 – 20.09.2013). Water level classes represent the water level differences between *Roompot buiten* (outside the Eastern Scheldt) and *Roompot binnen* (inside the Eastern Scheldt).

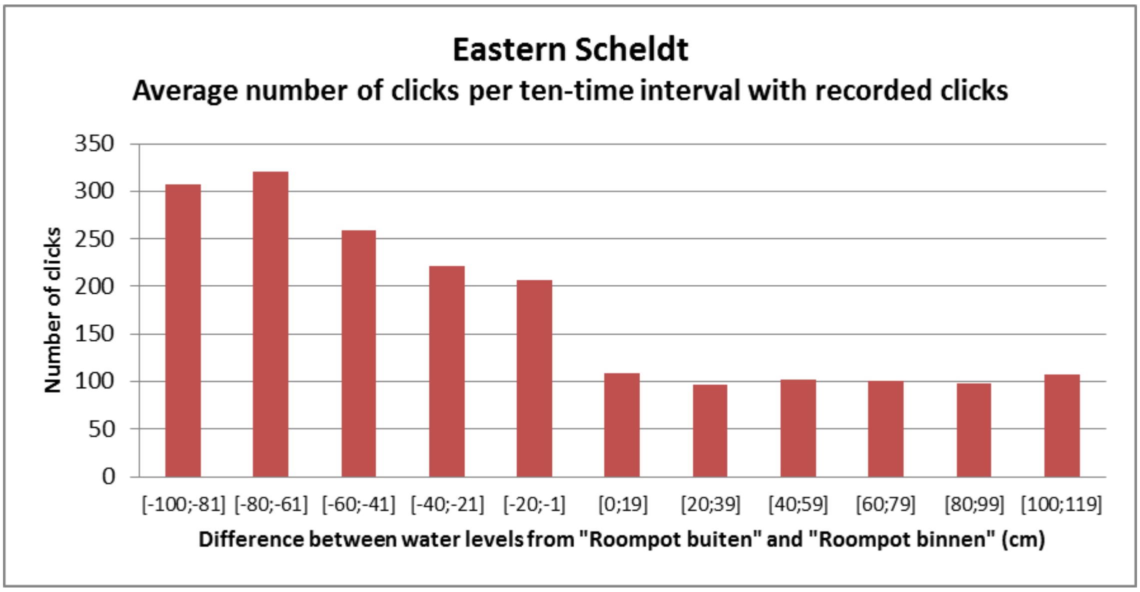

Figure 11 Average number of harbour porpoise clicks per water level class, recorded by C-POD 1863 and C-POD 1864, both located in the Eastern Scheldt (data from C-POD 1864 was available only for the time period between 22.07.2013 – 20.09.2013). Water level classes represent the water level differences between *Roompot buiten* (outside the Eastern Scheldt) and *Roompot binne*n (inside the Eastern Scheldt).

The average number of clicks per ten-minute time interval with recordings is also not the same among tidal classes $(p < 0.001; df = 10; Kruskal - Wallis\ chi\ square =$

1928.0). Only intervals with recorded clicks are included. When the number of echolocation clicks is taken into consideration (fig. 11), the pattern is quite different from the previous figure. The emission of echolocation click trains is much more intense when water is flowing from the Eastern Scheldt to the North Sea. Particularly, harbour porpoises vocalise more during very high water level differences ([-100 cm;-81 cm] and [-80 cm;-61 cm]) and vocalise progressively less until slack tide ([0 cm; 19 cm]). When the tide is rising inside the Eastern Scheldt, the emission of echolocation click trains is fairly constant.

In the North Sea side of the storm surge barrier, the percentage of ten-minute intervals with recordings is not equally distributed among the different water level classes $(p < 0.001; df = 8; \chi^2 = 100.0)$. The highest percentages of ten-minute time intervals with echolocation click trains (between 20% and 30%) were recorded in the central tidal classes (fig. 12). Thus, porpoises were present more often near the barrier when the tidal currents were quite weak and minimal. They were almost absent when the water levels were very high, both when water was flowing to and from the Eastern Scheldt. This differs from the activity of porpoises in the Eastern Scheldt side of the barrier, in the fact that much lower percentages of click trains (less than 5%) were recorded when the water was flowing from the North Sea to the Eastern Scheldt ([-60 cm;-41 cm] and [-40 cm;-21 cm]).

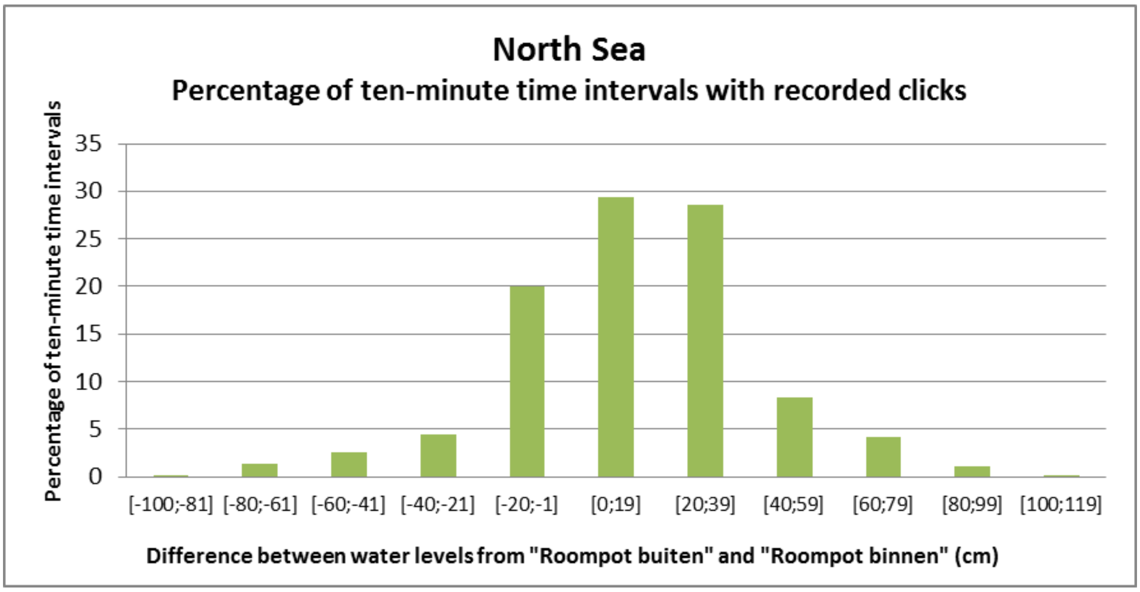

Figure 12 Percentage of ten-minute time intervals with harbour porpoise clicks per water level class, recorded by C-POD 2189, located in the North Sea. Water level classes represent the water level differences between *Roompot buiten* (outside the Eastern Scheldt) and *Roompot binnen* (inside the Eastern Scheldt).

The average number of clicks per ten-minute time interval was not the same in all tidal classes $(p < 0.001; df = 10; Kruskal - Wallis\ chi\ square = 1315.0)$. The peak of porpoises vocalisations was during slack tide ([0 cm;19 cm]). There was also a higher number of recorded clicks when water was flowing from the North Sea to the Eastern Scheldt. Much less echolocation click trains were recorded in the classes representing water flowing from the Eastern Scheldt to the North Sea (from [-100 cm;-81 cm] to [-40 cm;-21 cm]).

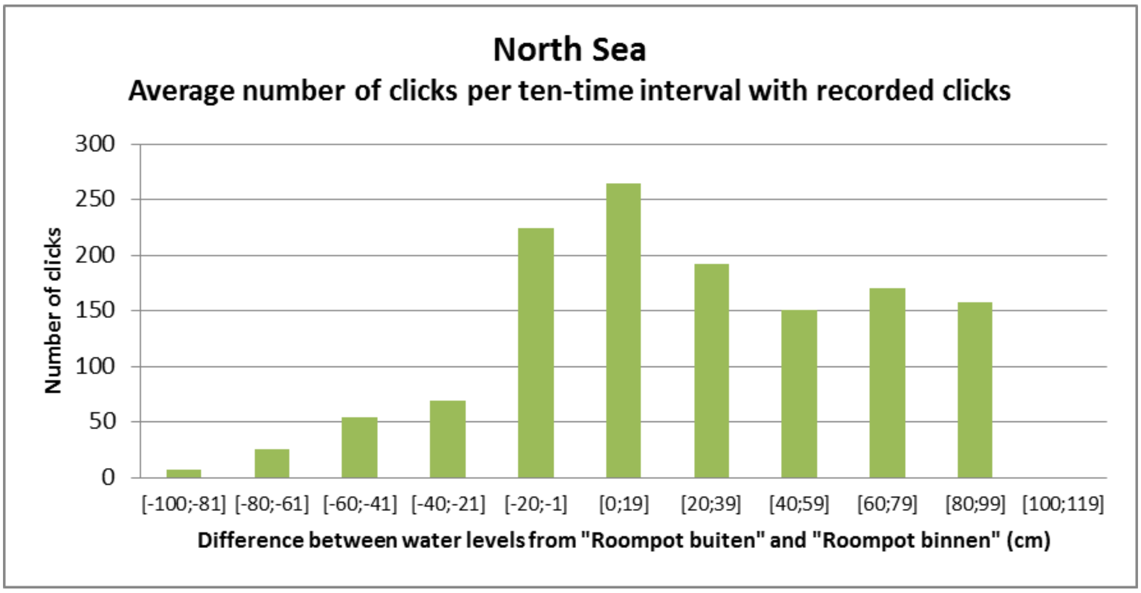

Figure 13 Average number of harbour porpoise clicks per water level class, recorded by C-POD 2189, located in the North Sea. Water level classes represent the water level differences between *Roompot buiten* (outside the Eastern Scheldt) and *Roompot binnen* (inside the Eastern Scheldt).

3.4. The effect of light on the activity of harbour porpoises

We investigated the effect of light on the activity of harbour porpoises near the storm surge barrier in the Eastern Scheldt side (fig. 14). Differences between day, night, and twilight ten-minute time intervals with recordings are not statistically significant $(p = 0.368; df = 2; Related - samples\ Friedman's\ test)$. However, when comparing the different classes independently throughout the seasons, "day" and "night" are statistically different $(p < 0.001; df = 3; \chi^2 = 41.6; p < 0.001; df = 3; \chi^2 = 60.5$; respectively). The "twilight" data does not vary significantly across seasons $(p = 0.998; df = 3; \chi^2 = 0.041)$.

During daily ten-minute time intervals, porpoises are more often present near the storm barrier during spring (73.1%) and summer months (65.3%). Fewer presences were detected during autumn (30.1%) and winter (20.7%). Regarding nocturnal intervals, we detected an opposite pattern. There are more presences near the barrier during winter (61.4%) and autumn months (51.6%), and fewer during summer (16.5%) and spring months (7.5%). It should be noted that there are not astronomical twilight periods during June, so there are not nocturnal click recordings during this month.

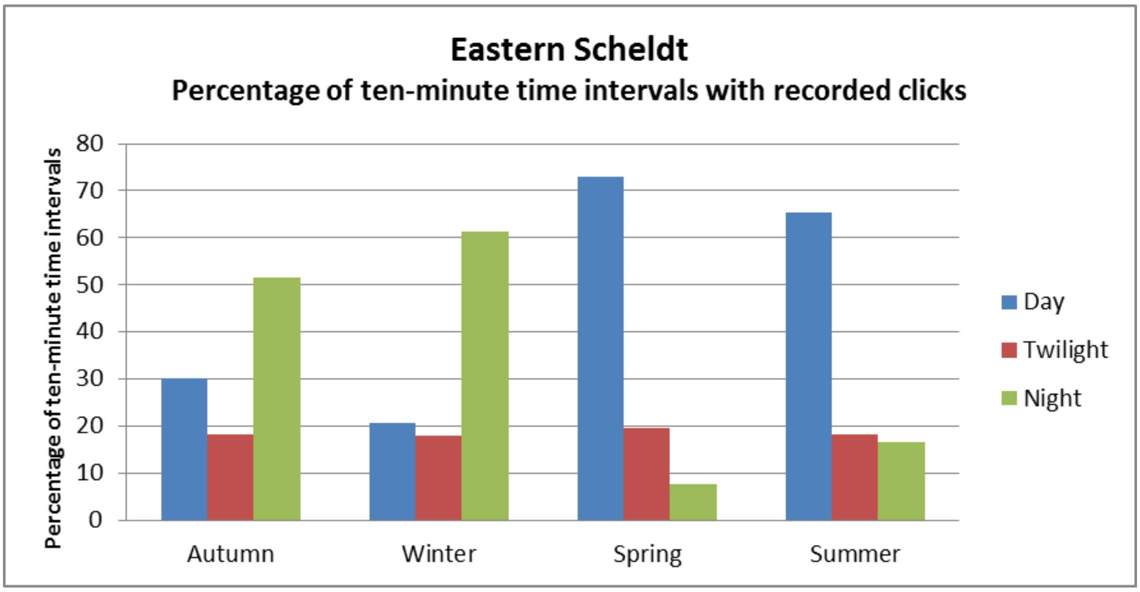

Figure 14 Percentage of ten-minute time intervals with harbour porpoise clicks per day/night/twilight per season, recorded by C-POD 1863 and C-POD 1864, both located in the Eastern Scheldt. Autumn: 11.10.2012 – 20.12.2012; Winter: 21.12.2012 – 06.03.2013; Spring: 25.04.2013 – 20.06.2013; Summer: 21.06.2013 – 30.06.2013 and 22.07.2013 – 20.09.2013 (data from C-POD 1864 was available only for the last time period). Day: period between sunrise and sunset; Night: period between the start of astronomical twilight and the end of astronomical twilight; Twilight: period between the end of astronomical twilight and sunrise plus the period between sunset and the start of astronomical twilight.

We did find out statistically significant differences ($p = 0.018; df = 2; Related - samples\ Friedman's\ test$) in the average number of echolocation click trains per ten-minute interval between day, night, and twilight, throughout the different seasons (fig. 15). Only positive intervals are included. We found out the same pattern for all seasons - porpoises vocalised always more frequently during twilight, followed by night, and fewer times during daily time intervals.

We compared each class independently and all of them showed statistically significant differences throughout the seasons (day: $p < 0.001; df = 3; Kruskal - Wallis\ chi\ square = 499.0$; night: $p < 0.001; df = 3; Kruskal - Wallis\ chi\ square = 655.0$; twilight: $p < 0.001; df = 3; Kruskal - Wallis\ chi\ square = 789.0$). Porpoises emitted more echolocation click trains during winter, followed by autumn, spring, and less click trains during summer months. This is valid for all the classes, i.e., day, night, and twilight.

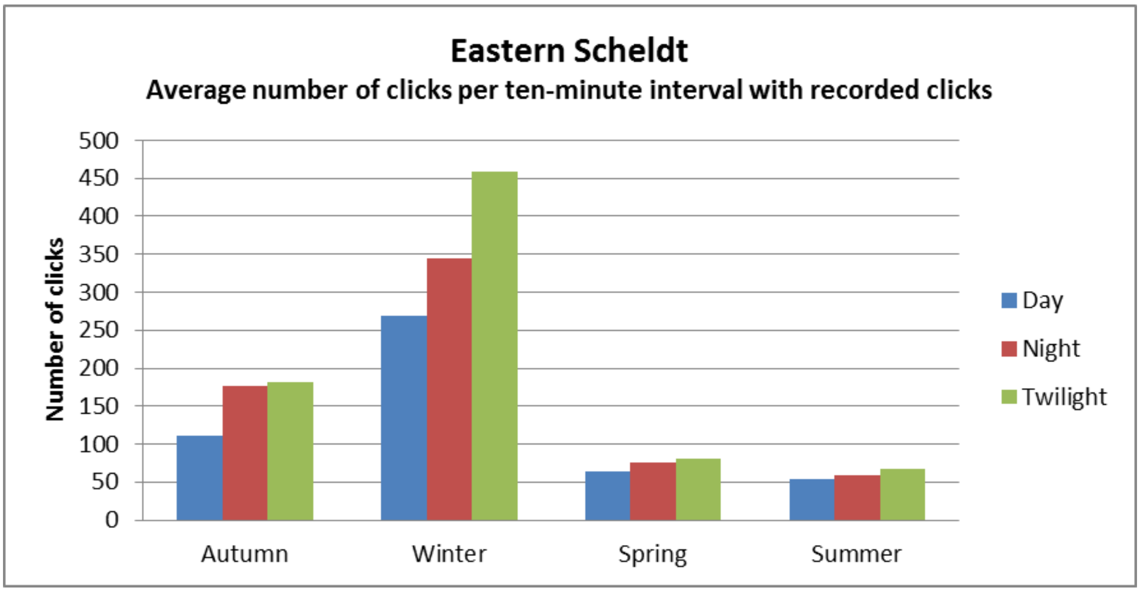

Figure 15 Average number of harbour porpoise clicks per day/night/twilight per season, recorded by C-POD 1863 and C-POD 1864, both located in the Eastern Scheldt. Autumn: 11.10.2012 – 20.12.2012; Winter: 21.12.2012 – 06.03.2013; Spring: 25.04.2013 – 20.06.2013; Summer: 21.06.2013 – 30.06.2013 and 22.07.2013 – 20.09.2013 (data from C-POD 1864 was available only for the last time period). Day: period between sunrise and sunset; Night: period between the start of astronomical twilight and the end of astronomical twilight; Twilight: period between the end of astronomical twilight and sunrise plus the period between sunset and the start of astronomical twilight.

The different classes of ten-minute time intervals with porpoise echolocation click trains in the North Sea side of the storm surge barrier (fig. 16) are not statistically different throughout the seasons ($p = 0.105; df = 2; Related - samples\ Friedman's\ test$). Nevertheless, when sorting the classes independently, the "day" and "night" classes are statistically different across seasons, while the class "twilight" is not (day: $p = 0.002; df = 3; \chi^2 = 15.3$; night: $p < 0.001; df = 3; \chi^2 = 38.6$; twilight: $p = 0.619; df = 3; \chi^2 = 1.78$). The percentage of daily ten-minute time intervals with porpoises presences near the storm surge barrier is highest during summer (75.5%), followed by spring (52.8%), autumn (44.7%) and winter months (36.9%). On the contrary, for nocturnal ten-minute time intervals, the highest percentage of positive intervals is during winter (46.7%) and the lowest during summer months (2.5%).

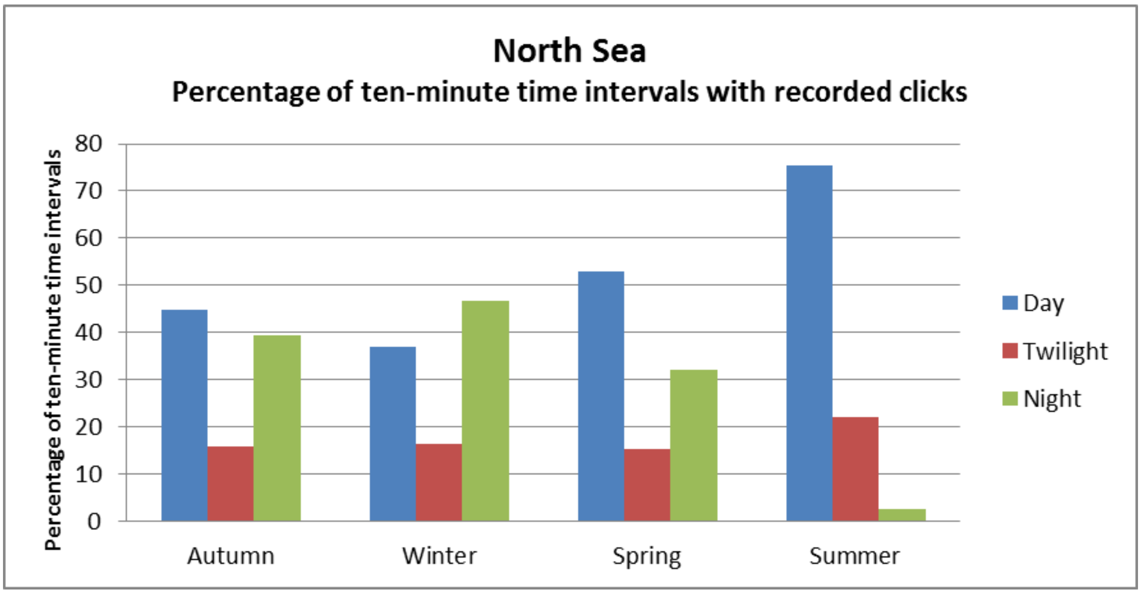

Figure 16 Percentage of ten-minute time intervals with harbour porpoise clicks per day/night/twilight per season, recorded by C-POD 2189, located in the North Sea. Autumn: 11.10.2012 – 17.12.2012; Winter: 14.02.2013 – 20.03.2013; Spring: 21.03.2013 – 16.04.2013 and 16.05.2013 – 20.06.2013; Summer: 21.06.2013 – 15.08.2013 and 16.08.2013 – 11.09.2013. Day: period between sunrise and sunset; Night: period between the start of astronomical twilight and the end of astronomical twilight; Twilight: period between the end of astronomical twilight and sunrise plus the period between sunset and the start of astronomical twilight.

We did not find differences in the average echolocation click trains production per ten-minute time intervals in the North Sea side of the barrier for the different classes (day, night, and twilight) across the seasons ($p = 1.0; df = 2; Related - samples\ Friedman's\ test$). Likewise, we did not find statistical differences when comparing the classes independently ($p = 0.392; df = 3; Kruskal - Wallis\ chi\ square = 3.0$, for all classes).

4. Discussion

4.1. The activity of harbour porpoises near the storm surge barrier and migration between the Eastern Scheldt and the North Sea

Harbour porpoises spent more time and were present more frequently near the storm surge barrier during winter months, both in the Eastern Scheldt and in the North Sea sides (figs. 4, 5, 7, and 8). Fewer ten-minute intervals had porpoise recordings during spring and summer months. These results may indicate that some individuals leave the Eastern Scheldt area and move northwards during spring and summer, and that some porpoises may enter and/or return to the estuary in autumn and winter, as an increase in click recordings is again noticeable during this period (fig. 4). Previous research corroborates these assumptions. Several studies indicate that a peak in the number of porpoises near coastal areas is reached in winter (Gilles et al. 2009; Haelters and Camphuysen 2009). Korpelshoek (2011), resorting to visual surveys, suggests that harbour porpoises migrate northwards in the North Sea during spring, and are found in more southern North Sea areas in the months of September and October, i.e., during autumn. Considering that porpoises spend more time near Dutch coastal areas during autumn and winter, the probability of finding the storm surge barrier and enter inside the Eastern Scheldt is higher during these periods.

These results do not mean that all harbour porpoises leave the Eastern Scheldt area because clicks were recorded all year near the storm surge barrier (figs. 4, 5, 6, 7, 8, and 9). This is in line with previous research done in the Eastern Scheldt, under similar conditions, in the years 2010 and 2011 (Korpelshoek 2011). Both studies detect and confirm the presence of porpoises all year-round inside the Eastern Scheldt estuary. Nonetheless, it is not possible to conclude whether the same individuals stay year-round inside the Oosterschelde or whether they cross the barrier sporadically and return to the estuary, or even whether there is a continuous exchange of individuals that leave and enter the estuary.

We indeed found migratory patterns in the ten-minute intervals recorded by C-PODs located in both sides of the storm surge barrier, in all seasons tested (table 4). These results could have aid in unveiling a clearer picture about harbour porpoise migrations from and to the Eastern Scheldt estuary. However, all results turned out to be not statistically significant, meaning that the chance the patterns are based on coincidence is high. This may indicate, on one hand, that migrations were not substantial or, on the other hand, that our data set was not robust enough to draw significant results.

Porpoises are known to use echolocation click trains for spatial orientation and navigation (Verfuß et al. 2005), and for foraging (Verfuß et al. 2008). The densities of atlantic cod (*Gadus morhua*), whiting (*Merlangius merlangus*) and poor cod (*Trisopterus minutus*), the main prey species for porpoises in the Eastern Scheldt (Korpelshoek 2011; analysis by Leopold and Jansen), reach the lowest numbers during winter months (Meijer 2002; ANEMOON 2009; Maandag 1999). These low prey densities may incite porpoises to forage more actively during this period. Considering the average number of porpoise clicks per ten-minute interval, we did find out that porpoises vocalised more during winter months, in both sides of the storm surge barrier (figs. 6 and 9). Moreover, they spent more time near the barrier in the same season (figs. 5 and 8). It should be noted that we only considered intervals with porpoise clicks in the average number of clicks per interval data set and in the DPM data set.

4.2. The effect of tide on the activity of harbour porpoises

Harbour porpoises were present more frequently near the storm surge barrier when the water level differences were not too high, both in the Eastern Scheldt and on the North Sea sides (figs. 10 and 12). The highest percentage of ten-minute time intervals with porpoise clicks in the Eastern Scheldt side corresponded to water level differences of -20 cm to -1 cm, and 0 cm to 19 cm in the North Sea side. These results indicate that porpoises are present near the barrier significantly more often during slack tide, and fewer times when the tide is rising or falling and the currents are strong. Moreover, when in the North Sea side of the storm surge barrier, porpoises vocalised more frequently during slack tide (fig. 13). We should not exclude the possibility that the barrier, by emitting high levels of noise during periods of higher water level differences between both sides, camouflages porpoises clicks recordings by CPODs. However, we could not test this possibility.

It is known that porpoises are sensitive to underwater noise and avoid areas with abnormal noise sources (Koschinski 2001), because it may cause masking of naturally-generated sounds, which imperil interspecific communication and prey detection (Au 1993). In view of this, it is possible that the storm surge barrier influences the presence and activity of harbour porpoises. During slack tide periods, water currents are weaker and generate less noise against the barrier walls, which porpoises may tolerate better than when the currents are very strong and hence, noisier. It also should be noted that female porpoises with dependant calves prefer areas with weaker currents to avoid the risk of separation, as the calves might swim with difficulty against the tidal currents (Pierpoint 2008). This may in part explain the highest percentages of ten-minute time intervals with clicks near the storm surge barrier. However, to confirm this assumption, visual surveys and/or tagging devices are needed.

When only porpoise-positive intervals are taken into account and we consider the average number of clicks per interval (fig. 11), the results suggest that when porpoises are present in the Eastern Scheldt side of the barrier they vocalise significantly more clicks during ebb tide (falling tide) and when the currents are strong, as the peak in click production is reached in the interval -80 cm to -61 cm. Previous research found out that porpoises foraged more frequently during the ebb tidal phase and against the tidal stream (Pierpoint 2008). This suggests that porpoises possibly vocalise more frequently and forage more actively to ambush prey carried in tidal currents, because the chance that prey is funnelled to them is higher (Johnston et al. 2005).

4.3. The effect of light on the activity of harbour porpoises

Harbour Porpoises did not follow diel activity patterns, i.e., preferences for day, night, or twilight time periods, when near both sides of the barrier (figs. 14 and 16). However, when considering day intervals independently, we found out that porpoises were present more often near the barrier during spring and summer months, and fewer times during winter and autumn, in both sides of the barrier. The Eastern Scheldt waters are much busier with tourist and sailing boats during spring and summer months than in the remaining seasons. As the area next to the barrier can be dangerous to boats, there is a possibility that porpoises swim to this area to avoid noisier and busier areas of the estuary.

We found out an opposite pattern for night intervals: porpoises were present more frequently near both sides of the barrier during winter and autumn, and less frequently during spring and summer. These results are expected since, as we mentioned above, we did not find differences between day, night, and twilight time intervals, in what regards porpoise presences, so we can assume that porpoises were present more times in day intervals during summer and spring, because these are the seasons where the period between sunrise and sunset are longer in the year. The same logic applies to the relationship between night intervals and winter and autumn months.

In what regards the emission of echolocation train clicks by porpoises in the Eastern Scheldt side of the barrier, we indeed found differences between day, night, and twilight intervals that were statistically significant (fig. 15). We found the same pattern in all seasons. Porpoises vocalised more often during twilight, i.e., between the sunset and the start of astronomical twilight, and between the end of astronomical twilight and sunrise. Since previous studies point out that harbour porpoises, in controlled environments, emit similar amounts of echolocation clicks in light as well as in darkness (Kastelein et al. 1995; Verfuß et al. 2005), other reasons other than diel porpoise preferences must hold true. Our results may be related with the changes in the vertical distribution and availability of porpoises' prey during different diel periods. The main preys of adult porpoises in the Eastern Scheldt are demersal fish species (Korpelshoek 2011). Research in the Zeeschelde estuary (Maes et al. 1999), an estuary in Belgium with similar conditions as the Eastern Scheldt, showed diel differences in the vertical distribution of demersal fish. They remained hidden in the bottom at day, while at night exploited the water column. The fact that porpoises vocalise more frequently during the transition periods between day and night (twilight) may be related with foraging for these demersal fish species that are leaving the bottom and start to explore the pelagic zone during these diel periods.

In the North Sea side of the barrier, we did not find statistically significant differences in the average number of echolocation train clicks per interval, in the different diel classes. The same was true when considering each class independently across seasons.

5. Conclusion

Our study found out that harbour porpoises were present and active, in both sides of the storm surge barrier, all year-round. This is based on the fact that all deployed C-PODs recorded porpoise echolocation click trains in all seasons. These results support the previous studies that suggested a harbour porpoise resident group living inside the Eastern Scheldt permanently.

We registered seasonal variations in the activity and presence of harbour porpoises in our study area. Porpoises spent more time and were more frequently present, in both sides of the storm surge barrier, during winter months. This may indicate that some individuals enter and/or return to the Eastern Scheldt area during this period of the year, while some may migrate northwards in the North Sea during spring, as fewer time intervals have porpoise echolocation activity during this season. We tried to confirm these assumptions by analysing migration patterns between the Eastern Scheldt and the North Sea. We indeed detected migration patterns but they were not statistically significant. This may mean that migrations were not occurring substantially or that our data set was not robust enough to draw significant conclusions. A future study that combines the migration data used in this report with data from previous Rugvin reports may find significant patterns of migration. In addition, the use of tagging devices in future research has a tremendous potential to clarify this issue.

Our C-PODs recorded a greater amount of echolocation click trains per interval during winter months, meaning that harbour porpoises vocalised more frequently in this period. This may be related with an overall less prey availability during this season, which results in more active foraging by porpoises and thus, in more click train emissions to find their prey. Other hypothesis is the presence of more porpoises inside the Eastern Scheldt area, due to more prey availability than in the North Sea. Nevertheless, a high number of all ten-minute time intervals (35.2%) recorded porpoise activity during winter. Efforts should be made to further understand and protect this apparent higher abundance of porpoises in the Eastern Scheldt during winter months.

Regarding the effect of tide in the activity of porpoises, we found out that they were present more frequently near the barrier during slack tides and hence, when the water level differences were minimal. This might be related with the influence of the storm surge barrier in the presence and activity of harbour porpoises. During slack tide periods, water currents are minimal and do not generate too much noise against the barrier walls, as when the water level differences are higher and the currents stronger. Porpoises may tolerate better weaker water currents than stronger and noisier ones. However, when we considered only time intervals when porpoises were present in the Eastern Scheldt side of the barrier, we found out that they vocalised significantly more clicks during ebb tide (falling tide) and when the currents were strong. This suggests that porpoises, when near the barrier, vocalised more frequently and foraged more actively to ambush prey carried in tidal currents, because the chance that prey is funnelled to them is higher. We did not find solid evidence of a negative influence exerted by the storm surge barrier in harbour porpoise behaviour. Further research is needed to clarify this issue.

We did not find diel activity patterns by harbour porpoises, when near the storm surge barrier. However, when day intervals are taken into consideration independently, we found out that porpoises were more frequently present and active during spring and summer months, and fewer times during winter and autumn, in both sides of the barrier. We found out an opposite pattern in winter and autumn. Porpoises preferred nocturnal intervals in these seasons. These results are expected because, as we did not find differences between day, night, and twilight time intervals, porpoises were present more times in day intervals during summer and spring, because these are the seasons where the period between sunrise and sunset are longer in the year. The same logic applies to the relationship between night intervals and winter and autumn months.

Our study used recordings of the echolocation activity of harbour porpoises to investigate and understand their behaviour in the Eastern Scheldt, particularly when near the storm surge barrier. It may contribute to a better understanding between porpoises and man-made structures, such as the barrier, and thus help in minimising possible detrimental effects that these structures have on porpoises. Furthermore, it may help in devising more informed strategies to conserve the group of harbour porpoises in the Eastern Scheldt area.

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