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Going with the flow: Tidal influence on the occurrence of the harbour porpoise (*Phocoena phocoena*) in the Marsdiep area, The Netherlands

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ABSTRACT

One of the most important factors explaining the distribution and behaviour of coastal marine mammals are tides. Tidal forces drive a large number of primary and secondary processes, such as changes in water depth, salinity, temperature, current velocity and direction. Unravelling which tidal process is the most influential for a certain species is often challenging, due to a lack of observations of all tide related covariates, strong correlation between them, and the elusive nature of most marine organisms which often hampers their detection.

In the Marsdiep area, a tidal inlet between the North Sea and the Dutch Wadden Sea, the presence of harbour porpoises (*Phocoena phocoena*) was studied as a function of tide related covariates. Observations were carried out in early spring from a ferry crossing the inlet on a half hourly basis. Environmental and sightings data were collected by one observer, while an on-board Acoustic Doppler Current Profiler (ADCP) and temperature sensor continuously recorded current velocity profiles and temperature, respectively. Sea surface temperature and salinity were measured at a nearby jetty. Sightings ($n = 134$) were linked to tidal elevation, geographical position, local depth-averaged current velocity, water temperature (with and without trend correction) and salinity.

Variation in sighting rate was best described by salinity, with highest sighting rate at high levels of salinity (>30 g kg^{-1}), indicating that porpoises enter the area in bodies of (more saline) North Sea water. Second best variable was time of day, with the highest sighting rate early morning, and decreasing during the day. However, surveys in the morning happened to coincide more often with high water and hence, the apparent time of day effect could be due to collinearity. Most porpoises were present in the northern part of the Marsdiep, particularly during high tide.

Tide dependent sighting rates confirmed that porpoises reside in the North Sea, and enter the western Wadden Sea during the flood and leave during ebb. This tidal influx is most likely related to prey availability, which corresponds to other recent studies in this area showing higher fish abundance during high tide. Documenting information on tide related patterns could be used in practice, when e.g. planning anthropogenic activities or assessing critical habitats for this species.

1. Introduction

One of the most important factors explaining the distribution and behaviour of coastal marine animals are tides. Many different taxa, such as plankton, crustaceans, fish and cetaceans use the incoming flood tide to enter a tidal zone, and the ebb tide to retreat (Gibson, 2003). In addition to this current-driven up-shore migration, tides cause variations in a number of other environmental conditions, such as salinity, water depth, water temperature, current velocity and inundation time, all of which could contribute to migration patterns of species in an area. Determining which of these factors influence the migration patterns and small-scale spatial preferences of a particular species is challenging. Rarely are measurements of all these tidal variables collected simultaneously, and they are often strongly correlated. The objective of this study is to determine which tidal processes are the most influential on the occurrence of a locally abundant marine mammal: the harbour porpoise (*Phocoena phocoena*).

Harbour porpoises are found in coastal waters and shelf seas of the North Atlantic and the North Pacific oceans (Read, 1999). The North Sea population is estimated to consist of around 250,000 individuals (Hammond et al., 2002), of which up to 85,000 may occur in the Dutch sector of the North Sea (Scheidat et al., 2011; Geelhoed et al., 2013). Within The Netherlands, harbour porpoises are present throughout the year, but are most numerous in late winter to early spring

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(Camphuysen, 2011). They are seen along the entire Dutch coast and in major estuaries such as the main river delta in the south and in the Wadden Sea in the north. Harbour porpoises have historically been abundant in Dutch waters, but were very rare between the early 1960s and 1990s (Camphuysen, 2004; Camphuysen and Siemensma, 2011).

Prior to the disappearance of porpoises from Dutch waters in the 1930s–1950s, detailed studies of harbour porpoises were conducted in the Marsdiep area, a tidal inlet between the mainland of North-Holland and the Wadden Sea island Texel (Verwey, 1975a,b and Fig. 1). Porpoises were abundant in this area and Verwey (1975a,b) suggested that they moved into the Marsdiep area with incoming flood phase of the tide and out again during the ebb phase. In recent years, following the marked increase of porpoise numbers in Dutch coastal waters, the Marsdiep area re-gained significance to this marine mammal. Porpoises are particularly abundant in the Marsdiep area from February to April (with peak abundance in March). In addition to such seasonal variability, also tidal processes seem to drive (short-term) variability in abundance, with most sightings during late flood and early ebb (Boonstra et al., 2013).

Both the historical observations by Verwey (1975a,b) and the more recent studies by Boonstra et al. (2013) were conducted at one or multiple land based observation sites. Hence, information on the occurrence and tide dependence of porpoises in the entire 4.5 km wide channel of the Marsdiep was still incomplete. Furthermore, the sighting rates were only related to variation in tidal stage, while other tide-related covariates were not considered. Tidal currents drive ecosystem dynamics and influences foraging ecology in coastal systems. Prey availability, which is influenced by oceanographic and hydrodynamic drivers, is believed to be the driver of predator's distribution (e.g. Embling et al., 2010, 2012, 2013; Fontaine et al., 2010; Sveegaard et al., 2012). Until now, little research attention is given to small-scale studies linking oceanographic drivers to species densities, as quantitative data required is often lacking (Jones et al., 2014).

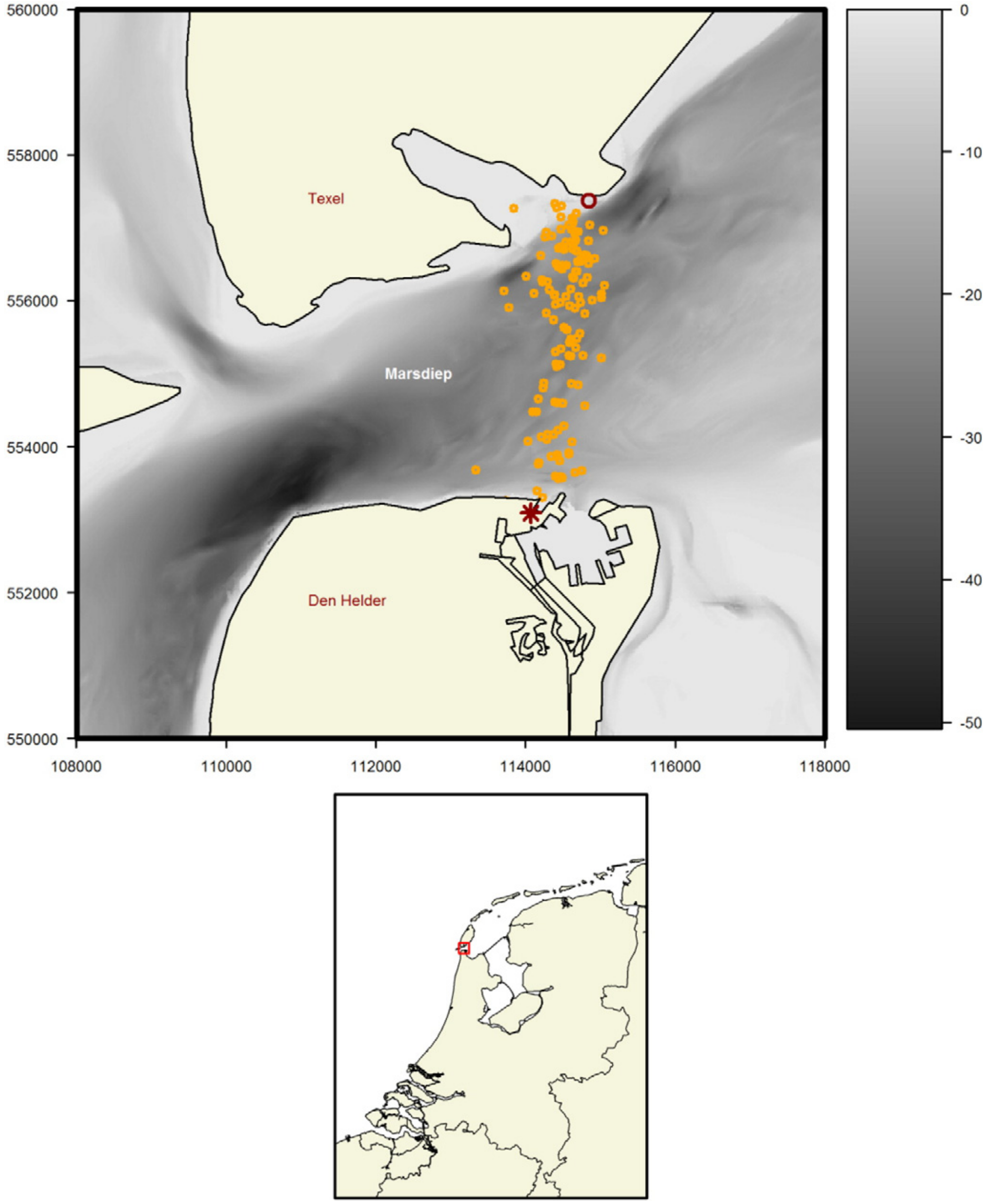

Fig. 1. Harbour porpoise sightings in the study area (orange dots). Of the total of 134 sightings, 89 were located on the north side of the study area (nearer to Texel). The grey coloured bar on the right side indicates the depths (in m) of the area, while the axes indicate the coordinates in the Dutch National Grid (i.e. “Rijksdriehoek” in m) projection. Sightings are scattered around the ferry transect. The red star indicates the location where the SLH measurements were made, and the red circle indicates the location of the NIOZ jetty (in front of the NIOZ), where temperature and salinity were measured continuously.

By collecting effort-corrected data on harbour porpoise presence from a regular ferry crossing the Marsdiep inlet, and linking these to local measurements of current velocity, sea surface salinity, water height, and sea surface temperature, this study attempts to understand when, how and why harbour porpoises use the area, and how tidal processes determine their small-scale spatial preferences. Understanding the mechanisms underlying the tide dependent distribution of porpoises, contributes to identifying critical habitats for this species.

2. Methods

2.1. Study area

The Marsdiep area is an inlet connecting the North Sea with the shallower basin of the Wadden Sea (Fig. 1). It is 4.5 km wide, has a mean depth of 4.5 m and a maximum depth of 53 m. Tidal currents keep the inlet open (Buijsman and Ridderinkhof, 2007). A regular ferry service between the mainland and the island of Texel is operated by TESO ('Texels Eigen Stoomboot Onderneming', Texels Own Steamship Company). Along the ferry transect, the maximum depth is 27 m. Tidal currents are strongest in the southern part of the inlet, and the average tidal range at Den Helder is approximately 1.4 m. In the western Wadden Sea, the rise of the water level is faster than its descent due to tidal asymmetry. This results in relatively strong flood currents, whereas the ebb duration is longer (Buijsman and Ridderinkhof, 2007). The Marsdiep is one of the better studied areas in the Wadden Sea, due to the presence of the Royal Netherlands Institute of Sea Research (NIOZ) located along its shore (Fig. 1).

2.2. Visual observations

Observations in the study area were carried out on board of the roll-on–roll-off ferry 'Dokter Wagemaker', crossing the inlet between the island Texel and the mainland every half hour. The total ship time was 156.5 h spread over 21 days of fieldwork between 20 February and 2 April 2013. The ferry is 130 m long, 23 m wide, has a draught of 4.4 m, and travels at an average speed of about 10 knots (Buijsman and Ridderinkhof, 2007). A single observer was located on the bridge wing at an observation height of c. 17.5 m above the sea surface. Of all fieldwork hours 82 h were spent on-effort within the inlet between the two harbours.

Observations were made in front of and to one side of the ferry (90° angle). The optimal observation side of the vessel was chosen based on the wind or sun conditions. Materials used were a voice recorder, an angle board, a GPS and a measuring stick to estimate the distance to the sighting. Porpoises were detected with the naked eye and sighting details were recorded on the voice recorder. Binoculars (10 × 40) were used in some cases to confirm the identification.

For determining site preferences, the centre location of the study area was determined (coordinates: 52° 59′07.33 N, 4° 46′56.66E). Porpoise sightings could be linked to either the northern (N) or the southern (S) side of the area, by determining their position relative to these coordinates.

The data were collected following the SCANS-II protocol for shipboard surveys. However, since the main aim of this study was not to estimate variations in relative abundance, not absolute abundance, no double platform or distance sampling techniques were used (Buckland et al., 2004) and hence no estimates of g0 (i.e. the probability of being at the surface) were made. Instead this study relied on a single observer, to minimize variation in sighting rate which occurs between observers (van der Meer and Camphuysen, 1996). For every sighting, a waypoint was taken using the GPS. The angle of the sighting relative to the ship was measured using the angle board. Next, the distance of the observed porpoise from the observer's point of view was estimated using a measuring stick and divided into six classes: A: 0–50 m, B: 51–100 m, C: 101–200 m, D: 201–300 m, E: 301–500 m and F: >501 m. Directions of movement were recorded with a compass. Behaviour recordings were based on Camphuysen and Garthe (2004), and recorded behaviours included the following: "wheeling or swimming slowly", "escape from ship (rooster tail)", "swimming fast; not avoiding ship", "basking; afloat" and "approaching ship".

2.3. Environmental data

Environmental conditions were recorded at the start of a track and at 5, 10, and 15 min after departure. The environmental data collection protocol was based on SCANS II for shipboard surveys (2008) and included sea state (0–5), glare (0–4), visibility (0–3), cloud cover (1–8), precipitation and wind (speed and direction). Observations were only conducted when the sea was fairly calm (sea state <4 Bft; flat, ripples or occasional white crests) and when the visibility was >500 m.

An Acoustic Doppler Current Profiler (ADCP) has been installed under the ferry since 1998 (Buijsman and Ridderinkhof, 2007; Nauw et al., 2014) to monitor current velocity continuously during each crossing. Also sea surface temperature (SST) was constantly measured with the ADCP. For each passage, the depth-averaged velocity and SST were calculated for the entire transect, as well as for the S and N part separately following the processing steps in Nauw et al. (2014). However, instead of gridding the data onto a regular grid, the data were integrated along the original path (Duran-Matute et al., 2014) and subsequently divided over the total area to obtain the transect averaged velocity. SST was also integrated along the path providing an average temperature. The temperature was detrended by subtracting the 2-day running mean from each temperature measurement. The detrended temperature (T_{trend}) relates to the relative amount of North Sea water in a given water mass. Since the Wadden Sea is relative cold in late winter (Feb–Mar) compared to the North Sea, high values of T_{trend} indicate a relative high amount of North Sea water (van Aken, 2008b).

Salinity and temperature measured at the jetty of the NIOZ, located in the northern part of the Marsdiep inlet (53°00′06.45 N, 4° 47′20.59E, Dutch reference grid: X: 114845 m, Y: 557370 m), were also used (van Aken, 2008a,b). An AANDERAA temperature/salinity sensor 3210 (D) was used to collect the data every 12 s. The measurements were taken at a frequency of 12 Hz at about 1 m below low-water level. The temperature was measured using a Testo 110 thermometer with a precision of 0.1 °C, just below the sea surface. Salinity of a filtered sample of 200 ml taken just below the sea surface was measured using a Guildline Autosal 8400B in the laboratory. Regularly, water samples were analysed for salinity in order to calibrate the electronic sensors. Additional sea surface salinity measurements obtained from Rijkswaterstaat at location 'Marsdiep Noord' (live.waterbase.nl) were also used for the calibration of the electronic sensors.

In short, the calibration procedure is as follows: first, a running median filter (with a 1 min window) was applied to the raw 12 s data to remove outliers. Subsequently, the average of each 1 min was calculated and the value at every half hour was used for further analysis. The difference between the calibration measurements of temperature and salinity and the filtered data was determined, leading to $T_{trend\ 1}$ and $S_{Jetty\ 1}$. Half hour data was interpolated to the exact time of the calibration measurement and again the difference between the calibration measurement and the interpolated value was taken, leading to $T_{trend\ 2}$ and $S_{Jetty\ 2}$. The yearly average of $T_{trend} = (T_{trend\ 1} + T_{trend\ 2})\ /\ 2$ was used to correct the temperature measurement and the $S_{Jetty} = (S_{Jetty\ 1} + S_{Jetty\ 2})\ /\ 2$ was linearly interpolated between calibration measurements. During the calibration measurements, the salinity sensor was cleaned, causing a step in the electronic salinity recordings.

Sea level height (SLH, in cm) relative to Amsterdam Ordnance Datum (NAP or "Normaal Amsterdams Peil") were obtained from Rijkswaterstaat, and measured on the Den Helder side of the Marsdiep area (52°57′ 47.77 N, 4°46′40.96E, Dutch reference grid: X: 114070 m, Y: 553090 m in "RijksDriehoeks" coordinates).

2.4. Data analysis

First we studied how the sighting rate (number of porpoises per hour of observation) varied as a function of tide related variables. Here the number of sightings was defined as the response variable and the log of the observation duration of each segment (in h) was included as the offset. This essentially amounts to modelling the number of porpoises p/h, however it takes into account differences in sampling effort (Scheidat et al., 2011). The response variable was assumed to follow a Negative binomial distribution with log link. This distribution allows for over-dispersion (i.e. many zeros and occasional high counts). Several explanatory variables were included in the analysis: sea state, time relative to high tide, SLH, side (N or S), current velocity, temperature, trend-corrected temperature and salinity.

Sighting rate was modelled as smooth functions of these explanatory variables using generalized additive models (Wood, 2006). The smooth functions were defined as cubic regression splines with a maximum of 4 degrees of freedom, to prevent overly complex models.

To select the best model, *k*-fold likelihood-based cross validation was used (Horne and Garton, 2006; Aarts et al., 2013). Here, a model was fitted to data from all but one day. Next the summed log-likelihood values for the holdout data (with parameters set to values estimated from the model data) was used as a goodness-of-fit measure (Horne and Garton, 2006). This was repeated for all *k* days. The motivation for using likelihood-based CV was that it prevents overly-complex models resulting from serial correlation on short time-scales (i.e. within days). Also the Akaike's Information Criterion (AIC) was used. AIC is a measure of the goodness of fit, but penalizes for the number of parameters included in the model; the lower the AIC the better the model (Burnham and Anderson, 2002). To test whether a particular variable explains variations in the sighting rate significantly, a likelihood ratio test based on the 'Chi-square' statistics was used. The outcome of these tests were considered significant when the p-value was <0.05. The covariates used in the models are shown in Table 1.

At first, only the explanatory power and significance of single covariates were investigated. Subsequently, we explored the effect of additional covariates on the variation in porpoise sighting rate.

3. Results

3.1. Survey effort and conditions

Most survey effort took place during sea state 2 (36%), followed by sea state 1 (28%) and 3 (26%). Less survey effort was carried out at sea state 0 (5%), and sea state 4 (5%). Glare was mostly absent (83%). Visibility was good most of the time: usually more than 4 km, which is approximately the distance between Texel and Den Helder. The average cloud cover during all fieldwork days was 5.4/8 and there was no precipitation during the observation period.

As mentioned earlier, the Marsdiep area is characterized by a relative longer flood than ebb phases. In addition, the strong easterly winds during the fieldwork period led to a shorter survey period of low and rising tide. Therefore observation effort during high tide was 24.75 h, during descending tide 29.33 h, during low tide 15.45 h, and during rising tide 12.12 h. Due to these predominately eastern winds, most sighting effort was on the western side of the ferry. The Wadden Sea on the eastern side of the ferry transect was observed for 34% of time; the North Sea on the western side for 66% of time.

Current velocities (m/s) during the study period ranged from -0.83 (i.e. a current directed westward or in the ebb direction) to 0.95 m/s (eastward, or in the flood direction) with a standard deviation of 0.56. In the Marsdiep area the maximum flood velocities occur about 2 h before high tide. Slack water occurs about 2 h after high tide, and the maximum ebb velocities about 4 h after high tide (Fig. 2).

Water temperature (T_{ferry}) during all survey days ranged from 1.25 °C to 4.47 °C. The monthly mean water temperature in March is 4.5 ± 1.6 °C (van Aken, 2008b), however, March 2013 was anomalously cold with a monthly mean air temperature of 2.5 °C, much lower compared with a normal temperature of 6.2 °C (source: Royal Netherlands Meteorological Institute, KNMI). These anomalously low temperatures were associated with frequent easterly winds; where winds in this area are normally predominantly from a south-westerly direction. These low air temperatures led to seawater with a monthly mean temperature of 2.6 °C (based on the 8 AM values as was done in van Aken, 2008b).

3.2. Porpoise sightings

During the observation effort a total of 134 harbour porpoise sightings were recorded (Fig. 1). Group sizes varied from one to three animals per sighting, with a mean group size of 1.3 and in most cases (72%) solitary porpoises observed. In total 14 sightings were made during sea state 0; 58 sightings during sea state 1; 32 sightings during sea state 2; 25 sightings during sea state 3; and 5 sightings were made during sea state 4.

Observation distances ranged from 20 to 700 m. The average observation distance of porpoises was 190 m (SD = 121), with the majority of porpoise sightings between 100 and 200 m. Wheeling (or swimming slowly) was the most commonly observed behaviour (81%). During 13% of the sightings, porpoises were observed swimming fast without any sign of avoiding the ferry. Escaping from the ship and basking were observed for 3 and 5 sightings, respectively.

3.3. The effect of tidal variables on porpoise occurrence

Several tide-related covariates are correlated, which complicates the designation of the most influential covariate on porpoise occurrence (Fig. 3). Particularly the temperature-related covariates were highly

Table 1
Overview of covariates used to explain the difference in sighting rate (1–10) and side selection (1–12).

ID	Notation	Unit	Explanation	Measurement gained from
1	v	m/s	Average current velocity	Ferry ADCP
2	T_{ferry}	°C	Water temperature	Ferry temperature sensor
3	S_{Jetty}		Salinity	NIOZ Jetty salinity sensor
4	T_{Jetty}	°C	Temperature	NIOZ Jetty temperature sensor
5	$T_{de\text{-}trend}$	°C	Difference in temperature between the measured temperature and temporal trend in temperature	Ferry temperature sensor
6	T_{trend}	°C	Temporal trend in temperature	Ferry temperature sensor
7	SLH	cm	Sea level height (SLH) relative to the NAP (in cm)	SLH sensor of "Rijkswaterstaat" located in Den Helder
8	$t_{to\ high\ water}$	h	The time to highest SLH (in h). Negative values indicate the time preceding the high tide	SLH sensor of "Rijkswaterstaat" located in Den Helder
9	$t_{day\ of\ year}$	days	Number of days since 1-1-2013	–
10	Sea state	Bft (Beaufort scale)	Sea state	Observer
11	$t_{of\ day}$	h	Time of day (in h)	–

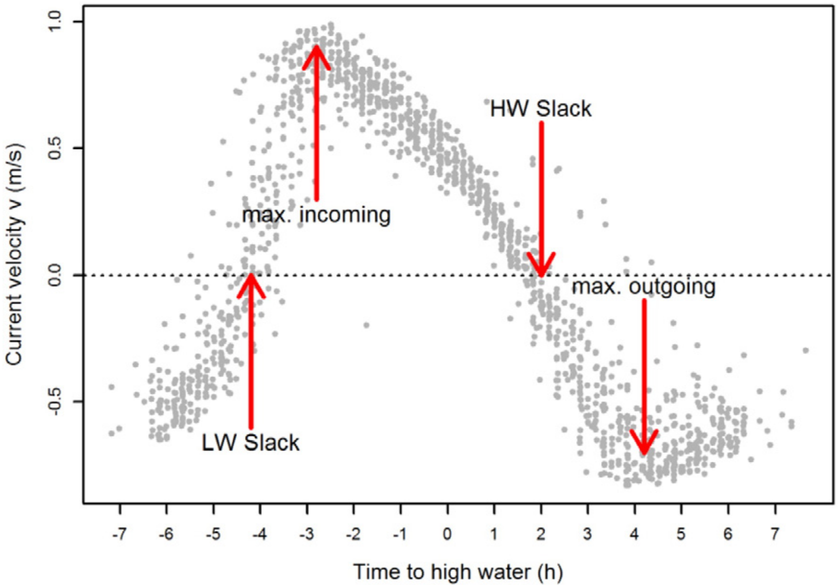

Fig. 2. Tide dependent current velocity (ferry observations) as a function of time to high water (Den Helder ferry terminal). LW slack and HW slack are slack waters around low water and high water, respectively. During high water (i.e. time to high water = 0), the tidal currents are still incoming and only 1–2 h later, the currents reverse.

correlated (Fig. SF1). E.g. the correlation between temperature measured by the ferry and the jetty was 0.96, showing there is little difference between the two, and that measurements at the jetty represent conditions observed elsewhere in the Marsdiep. Other strongly correlated covariates are water velocity and current velocity (Pearson correlation = 0.75), and salinity and day of the year (Pearson correlation = 0.66).

All tidal variables significantly influenced the observed variation in porpoise sighting rate (Table 2).

Salinity (measured at the jetty) was the best single explanatory variable explaining the variation in porpoise sighting rate (AIC = 721.5). Porpoise sighting rate was highest at high levels of salinity (>30 g kg^{-1}, Fig. 4a). Model diagnostics are shown in Fig. SF2. The second best single covariate is SLH (AIC = 730.1) (Fig. 4b), with more porpoises being present at high tide. SLH and salinity are correlated (Pearson correlation $\rho = 0.359$, $t = 12.8$, $p < 0.001$), however the AIC of the model containing salinity is much lower than the model with SLH (Table 2), suggesting that salinity is the main covariate explaining porpoise occurrence. Day of year, was the third most important single covariate, with the highest sighting rate near the end of the survey period (Fig. 4g). Time to high water ($t_{to\ high\ water}$) was the fourth best explanatory variable (Fig. 4d), and the detrended temperature the fifth ($T_{de\text{-}trend}$ = temperature − 2 day running mean temperature). Porpoise sighting rate was highest at high detrended temperature values (Fig. 4e). The remaining tidal covariates were temperature measured at the jetty, day of year, time of day and sea state (Fig. 4c, f–i). Porpoise sighting rate was highest around high tide, at relative high temperatures and intermediate current velocities, i.e. slack water.

When retaining the smooth of salinity, and continuing the forward model selection procedure (see Table ST1), adding a smooth of time of day leads to the lowest CV log-likelihood (i.e. −355.79). This term suggests that porpoise sighting rate is highest in the morning, and decreases during the day. The second best term is the smooth of SLH, with a CV log-likelihood of −357.99. This variable is (negatively) correlated with time of day (Fig. 2, Pearson correlation = −0.50); on average survey effort during high water occurred more often in the morning. Therefore, there is a risk that the effect of time of day is confounded by SLH. Indeed when we would retain the smooth of SLH (instead of time of day), time of day is not retained in the subsequent model selection steps (Table ST2). From this we conclude one cannot distinguish between time of day and the effect of SLH.

In the following model selection steps, the other covariates included were the location (i.e. N or S of the Marsdiep), revealing a higher sighting rate on the Texel side. From the total of 134 sightings, 89 sightings (63%) were observed at the N side and 45 sightings (32%) at the S side (nearer to Den Helder). Finally, a smooth function of sea state was significant, showing that sighting rate decreased with increasing sea state. The effect of the covariates on the sighting rate for the full final model is shown in Fig. SF4. No other tide related variables were retained in the forward model selection procedure.

4. Discussion

The best single explanatory variable explaining the variation in harbour porpoise sighting rate is salinity, with higher sighting rates at increased salinity levels. The effect of salinity suggests that porpoises enter the area in bodies of (more saline, >30 g kg^{-1}) North Sea water (Fig. 5). The second best variable is time of day, with the highest sighting rate early morning, and decreasing during the day. However, on average most survey effort in the morning took place around high water, and hence this may be an artefact resulting from collinearity. Although all tidal covariates are at least to some extent correlated, the goodness-of-fit of salinity is substantially higher than the other (tidal) covariates, providing support for this tide-related covariate explaining the occurrence of harbour porpoises in the Marsdiep tidal inlet.

Tide dependent patterns in occurrence of harbour porpoises were also found in many other studies; e.g. in the Bay of Fundy, Canada, a significantly higher density of porpoises during flood than ebb phases was observed (Johnston et al., 2005); in Lee Bay, Southwest Britain, tides resulted in differences in behaviour and group sizes of porpoises present (Goodwin, 2008); in Wales presence of porpoises was restricted to the ebb tidal phase in an high-energy, near-shore area as a result of foraging movements (Pierpoint, 2008); on the west coast of Scotland porpoises avoided areas of high tidal current, but were present in higher numbers during spring and slack tides (Embling et al., 2010); near the offshore island Bardsey, Wales (UK), porpoises were most abundant during low water slack tide and flood tide, particularly a few days following the neap tidal phase (de Boer et al., 2014); and off the coast of southwest Cornwall porpoises occurred in greater numbers during ebbing tidal

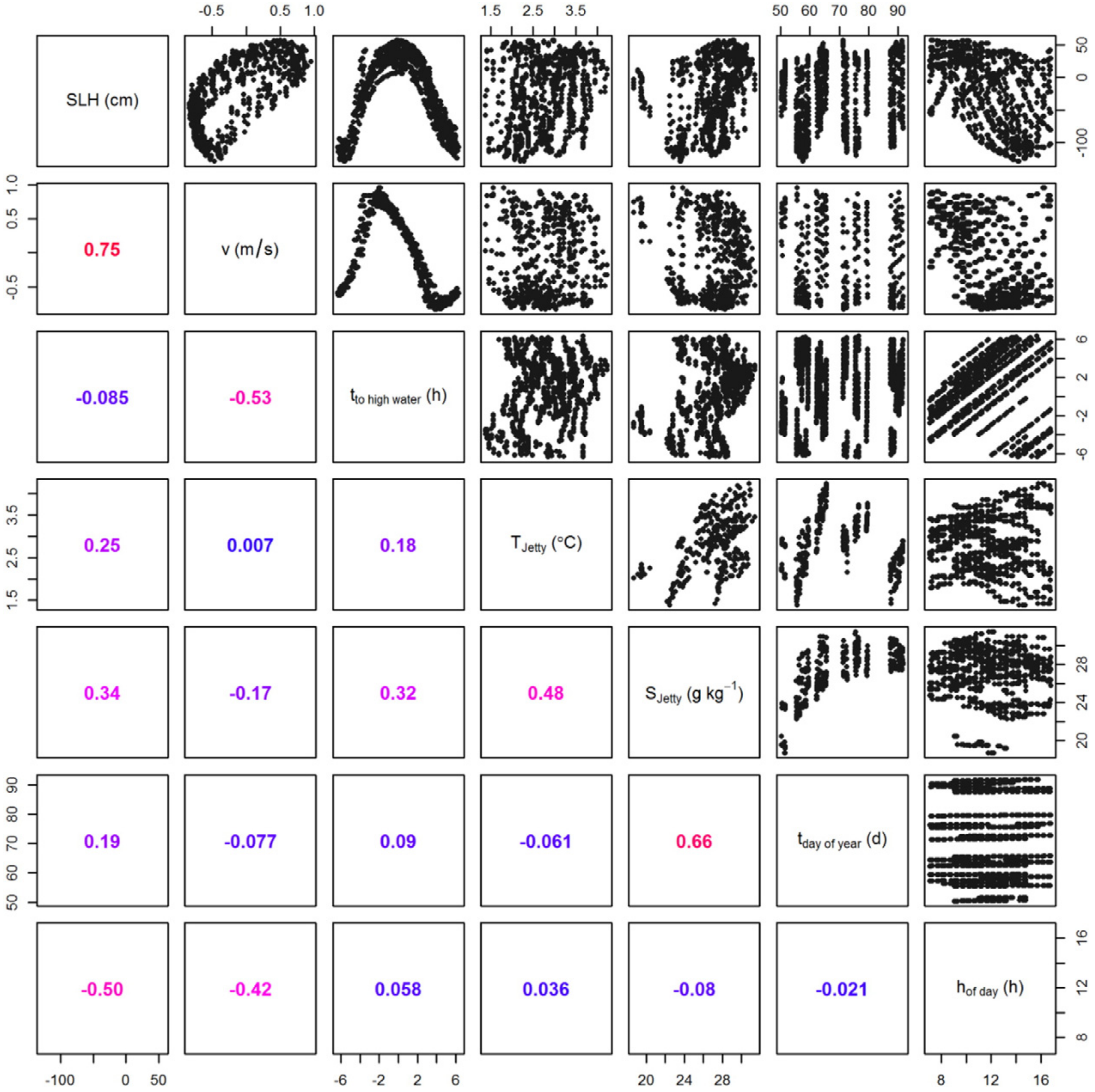

Fig. 3. Pairwise correlation plots of environmental covariates. Values in lower level plot are Pearson correlations, colour-coded by the absolute strength of the correlation (red = strong correlation, blue = weak correlation).
Adapted from Zuur et al. (2009).

Table 2
Explanatory power of each single covariate for explaining harbour porpoise sighting rate. Bold values indicate the model with the highest cross-validation log-likelihood (CV log lik.). The best model containing a single covariate indicates the one with a smooth function of the salinity measured at the jetty. Here, s(x) represents a smooth function of the covariate x, "edf" is the effective degrees of freedom for each smooth, R^2 is the adjusted R^2, "Chi^2-value" and "p-value" relate to the significance of the smooth term. See Table 1 for an explanation of the covariates.

Covariate	AIC	edf	Expl. Dev.	R^2	Chi^2-value	p-Value	CV log lik.
s(S_{Jetty})	**721.5**	**2.86**	**9.70**	**0.079**	**29.71**	**<0.001**	**−363.7**
s(SLH)	730.1	1.00	7.04	0.078	26.80	<0.001	−368.4
s($t_{day\ of\ year}$)	736.4	2.03	6.16	0.062	20.41	<0.001	−371.9
s($T_{de\text{-}trend}$)	736.3	2.86	6.55	0.062	10.00	0.018	−373.2
s($t_{to\ high\ water}$)	734.3	2.41	6.74	0.077	24.28	<0.001	−373.5
s($t_{of\ day}$)	738.8	1.93	5.56	0.065	19.79	<0.001	−373.5
s(Sea state)	745.6	1.00	3.64	0.058	15.41	<0.001	−375.9
Side	752.1	1.00	2.18	0.057	3.03	0.002	−378.4
s(T_{Jetty})	751.8	2.03	2.71	0.053	8.36	0.025	−381.8
s(v)	756.0	1.61	1.58	0.048	5.42	0.064	−383.4

flows (Jones et al., 2014). In several studies, and corresponding to our findings, porpoises were most abundant in slack tides (e.g. Embling et al., 2010; de Boer et al., 2014), which suggest they may avoid stronger tidal currents further offshore.

Although marine mammals are well adapted to their hyperosmotic environment, avoiding dehydration by maintaining internal homeostasis is required (Ortiz, 2001). However, it is unlikely that salinity directly impacts porpoises, as they are also observed in much less saline waters such as the Eastern Scheldt (Jansen et al., 2013) and the Scheldt River. Therefore, the relation with salinity is most likely driven by the behaviour and habitat preference of their prey. Prey availability is believed to be the main driver of many predators (e.g. Embling et al., 2010, 2012; Fontaine et al., 2010; Sveegaard et al., 2012). Small cetaceans, like harbour porpoises, have a high metabolism and can therefore gain and lose weight quickly (Kastelein and van Battum, 1990). Their small body size compared to their relatively large surface area could easily result in heat loss, meaning an unfavourable body weight to body ratio (e.g. Kastelein and van Battum, 1990; Koopman, 1998; McLellan et al.,

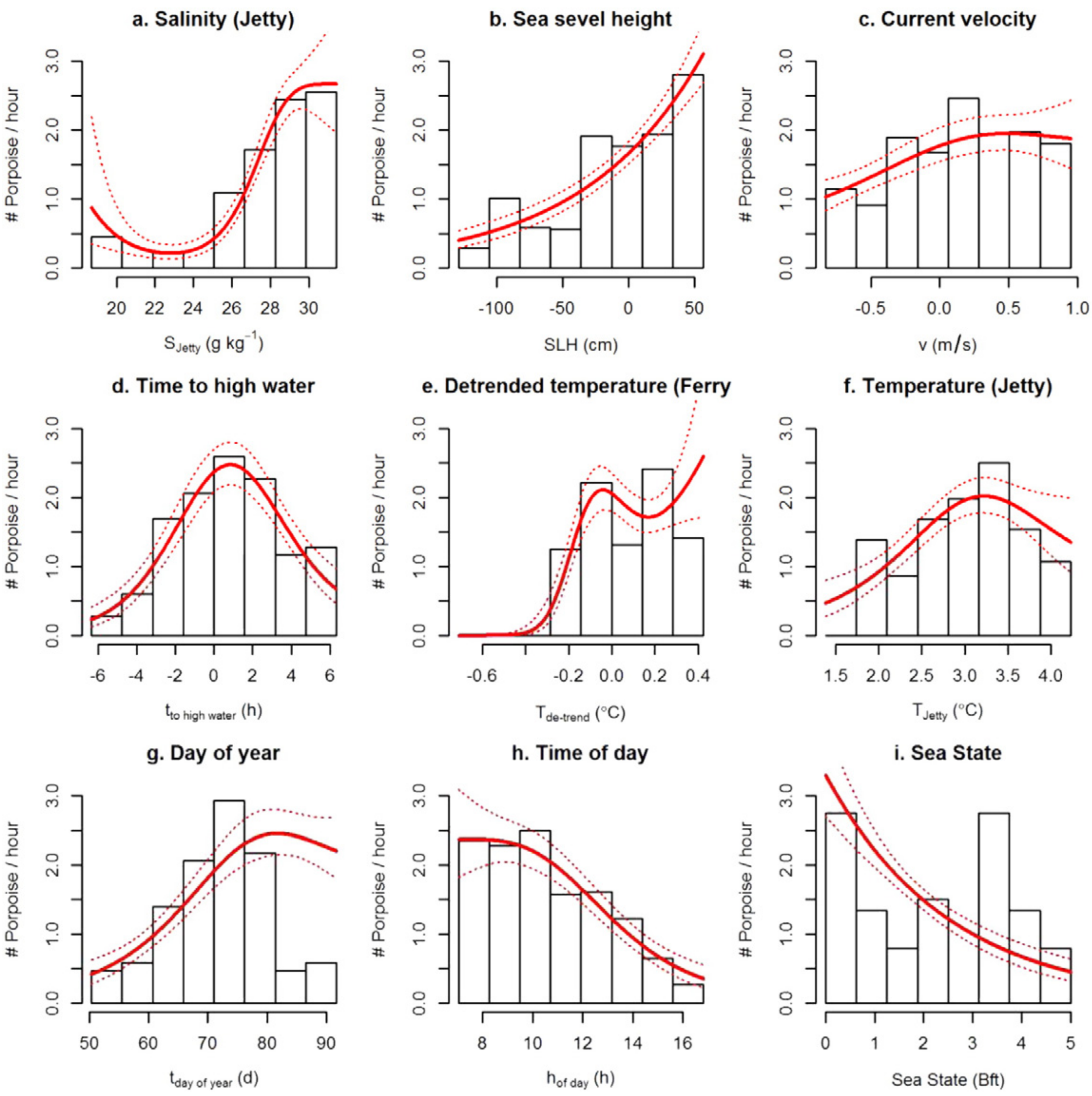

Fig. 4. Porpoise sighting rate as a function of tidal covariates. The height of the bars indicates the average number of porpoises per hour, of the eight bins. The solid red line is the estimated sighting rate based on the GAM. Dotted lines indicate the 95% confidence limits.

2002; Santos and Pierce, 2003) making it likely that they remain within close distance of available food sources. Different fish species prefer water masses with certain properties, e.g. they need to adapt to changes in salinity levels through osmoregulation, and there are substantial energetic costs associated with this. In addition, salinity influences food intake and food conversions of fish species, and consequently affects their growth (Bœuf and Payan, 2001). By following the inflow of North Sea water during high tide in the Marsdiep, fish may receive the benefits of increased food availability within tidal estuaries, without the osmoregulation costs. Besides that, recent studies have shown that higher fish abundance occurs in the Marsdiep during high tide (Couperus et al., in preparation).

Another explanation as to why porpoises enter the tidal inlet during high tide and leave during ebb is that the tidal currents push (saline) waters into tidal estuaries, and may passively import both porpoises and fish simultaneously. By following current flows, energy required for translocation is reduced. The second best variable explaining porpoise presence was time of day, with the highest sighting rate early morning with decreasing numbers during the day. Studies on free-ranging tagged harbour porpoises showed differences in day and night patterns in dive and click activity, with most studies showing higher click activity at night in some regions (Carlström, 2005; Todd et al., 2009; Linnenschmidt et al., 2013). The difference in click activity might be linked to foraging behaviour, which is region-specific and related to diel activity and availability of dominant prey (Amano et al., 1998). Several of porpoise main prey species, e.g. herring (*Clupea harengus*), whiting (*Merlangius merlangus*), sandeels (*Ammodytes* sp.) and sprat (*Sprattus sprattus*) become active at night (Santos and Pierce, 2003; Santos et al., 2004; Linnenschmidt et al., 2013). It is therefore possible that porpoise distribution throughout the day differs as an effect of foraging behaviour. However, the effect of time of day should be interpreted with care, because there also exists a correlation between time of day and SLH (Fig. 3 Pearson correlation = −0.50), which may confound the observed daily pattern in sighting rate.

Although salinity was substantially better at explaining variations in porpoise sighting rates, the strong correlation between all tide related covariates complicates the detection of the most influential variable. In this study, data were collected from the end of February until beginning of April (2013). These months were characterized by relative low temperatures compared to previous years (March had a monthly mean air temperature of 2.5 °C, which in other years was 6.2 °C). Therefore the effect of tidal covariates on sighting rate may be different in

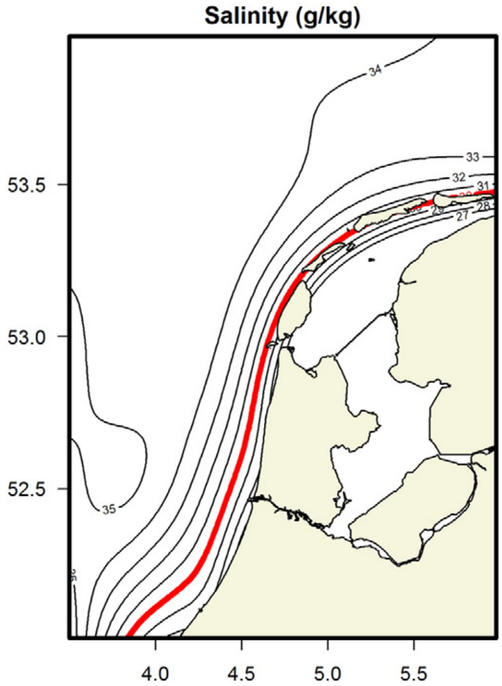

Fig. 5. Map of salinity along the Dutch North sea coast with 30 g kg^{-1} boundary in red. The estimate is based on a generalized additive model (Wood, 2006) with a spatial smooth of *x* and *y*-coordinates, fitted to salinity measurements from the most recent years (1964–2013) collected in Jan–Mar.
Data source: http://ocean.ices.dk/HydChem/.

other years. Observations in other seasons and years should be performed in order to make more solid statements about the underlying mechanism that drives the distribution of this species.

Harbour porpoises inhabit coastal waters, in habitats that are characterized by high diversity and complexity in terms of their bathymetry, substrate and prey (Bjørge, 2003; de Boer et al., 2014). Detailed information on habitat use and diet is still only sparsely available, while this data is the key to our understanding of spatial and temporal patterns in the abundance of porpoises. Understanding the mechanisms underlying the tide dependent distribution of porpoises and/or their spatio-temporal foraging activities, forms the basis of identifying important habitats for this species. The Marsdiep area is a tidal inlet that is of (ecological) significance for a probable high number of harbour porpoises, but only during a fairly short period (late winter and early spring; Verwey, 1975a,b; Camphuysen, 2011; Boonstra et al., 2013), and only under particular environmental and tidal conditions, as described in this paper. Peak abundances were recorded when porpoise move further north, away from the southern North Sea coastline, possibly towards breeding and/or feeding grounds in coastal waters there (Sonntag et al., 1999; Weir et al., 2007; Gilles et al., 2009; Scheidat et al., 2011). Documenting information on these patterns could be used in practice, when for example planning anthropogenic activities and assessing critical habitats for this marine mammal (de Boer et al., 2014).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.seares.2015.07.010.

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