Feeding behaviour of harbour porpoises (*Phocoena phocoena*) in the Ems estuary

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Abstract: Passive acoustic monitoring (PAM) was used to study the occurrence and distribution of feeding behaviour of harbour porpoises (*Phocoena phocoena*) in the Ems estuary, on the border between the Netherlands and Germany. Occurrence was expressed as detection positive hours (DPH) per month or station, and feeding behaviour was described as feeding buzz ratio (FBR). Three types of analyses were undertaken: 1. A year-round analysis of FBR and DPH for one PAM station close to the Ems harbour; 2. An analysis of FBR and DPH for 10 PAM stations in the Ems estuary in March and September 2010; and 3. A comparison of porpoise clicks and fish density in the area for September/October of 2010. The year-round analysis results showed a variable seasonal pattern of porpoise occurrence, with in general lower values in April–July, and higher values in August–December. FBR and DPH per station differed between March and September 2010. The March data shows an increase of DPH when moving from the Wadden Sea into the estuary, with at the same time an increase in FBR. In September 2010, DPH decreased from outside to inside the Ems estuary, coinciding with an increase in feeding behaviour. Fish density was analysed for 5 potential prey taxa (smelt, whiting, goby, flounder and herring) at sampling stations in 4 areas along the estuary. Flounder and smelt increased in occurrence towards the inner estuarine waters. Smelt is an anadromous fish that is a known prey species for porpoise. The results of this study suggest that while feeding activity and occurrence of porpoises is observed all along the estuary and throughout the whole year, the presence of a preferred prey might be the reason for porpoises to move far into the Ems estuary at specific times. The Ems is highly used by humans and some activities, such as construction work and intense shipping, could have potential harmful consequences to the locally occurring porpoises. As this study has only covered a short time frame, the results should be considered preliminary. Future studies on the investigation of fish and porpoise occurrence in this area would allow a more in-depth understanding of this relationship and would be of high relevance for conservation and management actions.

Keywords: harbour porpoise, *Phocoena phocoena*, C-POD, feeding buzzes, behaviour, Ems estuary, smelt, anadromous fish.

Introduction

Ranking amongst the smallest of cetaceans in the world, harbour porpoises (*Phocoena phocoena*) are usually found in coastal seas and estuaries in temperate northern climes (Perrin et al. 2002). With a short nursing period (usually less than a year) and reaching sexually maturity at three years, the resting period between pregnancies is brief (Santos & Pierce 2003). The consequence of this feature, plus their small size, is that they cannot store much energy, which makes them highly dependent on year-round food availability (Brodie 2001).

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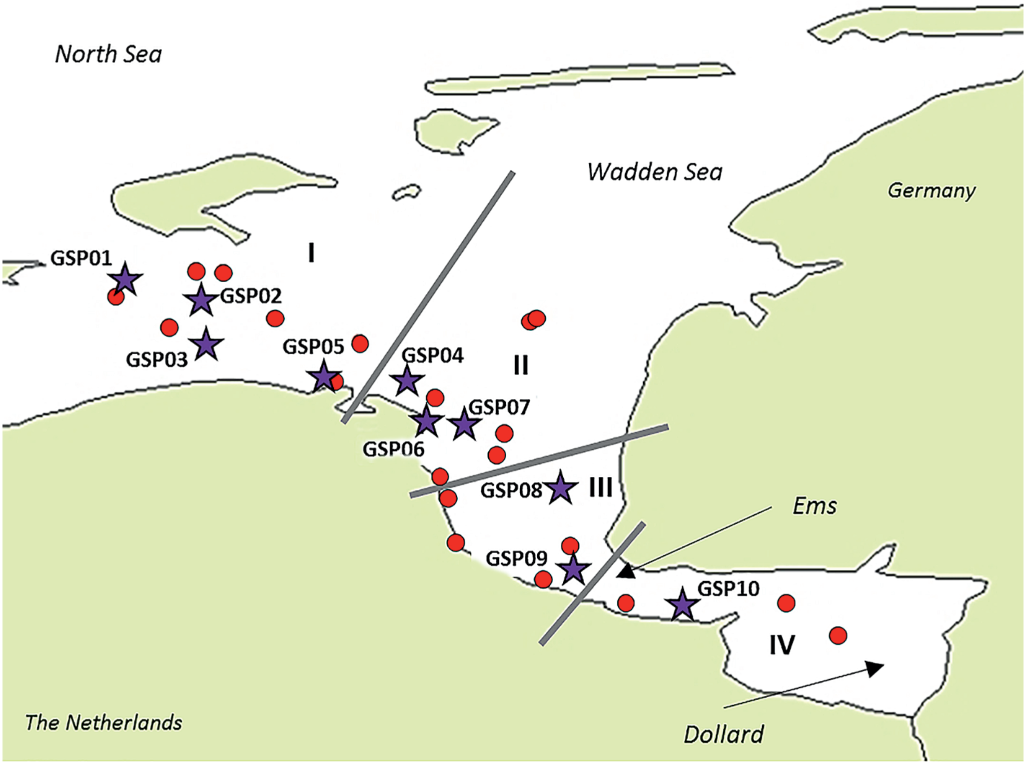

Figure 1. Location of C-PODs (stars; GSP01 to GSP10) in the study area in the Ems-Dollard estuary. The fish sampling stations are represented as dots. The roman numbers (I-IV), indicate the areas used for comparing acoustic and fish sampling data.

According to Brodie (2001), the distribution of this species may strongly reflect the distribution and energy density of their prey.

Harbour porpoise is also the most abundant cetacean species found in Dutch North Sea waters (Hammond et al. 2002, 2013, Geelhoed et al. 2013). Aerial surveys conducted on the Dutch Continental Shelf in 2010 and 2011 showed distinct differences in abundance and distribution between seasons (Geelhoed et al. 2013). Highest densities were found in March, with almost threefold higher values than during summer and autumn (Geelhoed et al. 2013). This observed pattern fits the general seasonal occurrence seen along the Dutch coast during systematic land-based observation (Camphuysen 2011, Camphuysen & Siemensma 2011). Surveys in the Dutch Continental Shelf conducted from 2012-2017, however, suggest that the numbers in summer can be much higher than in spring (Geelhoed & Scheidat 2018).

Harbour porpoises consume a wide variety of fish and cephalopods, and their main prey items appear to vary regionally and seasonally as well as between individuals (Leopold 2015). Several years ago, Santos & Pierce (2003) found the main food source of porpoises in the Netherlands to be whiting (*Merlangius merlangus*), making up around 34% of the total reconstructed prey weight. More recent studies have shown that whiting is still important in the diet of porpoises along the Dutch coast and that herring (*Clupea harengus*), cod (*Gadus morhua*), sprat (*Sprattus sprattus*), gobies (Gobiidae) and lesser sand eel (*Ammodytes* sp.) (Jansen et al. 2013, Leopold 2015) are further key prey.

From mid-2009 to 2014, the effect of construction activities in and around the Ems estuary on harbour porpoise occurrence was studied (Brasseur et al. 2010, Lucke et al. 2011, 2012, Kirkwood et al. 2014). Acoustic data loggers were used to investigate their relative abundance on both temporal and spatial scales (Brasseur et al. 2010, 2011, Lucke et al. 2012). For this paper, we have re-analysed this dataset to specifically investigate acoustically detectable behaviour associated with foraging in the Ems estuary. We explore whether there is a seasonal pattern and geographic variation in feeding behaviour and if any observed patterns can be explained by fish distribution.

Material and Methods

Study site

The Ems-Dollard area is one of the two last open, natural estuaries in the Netherlands (figure 1). It is defined as the semi-enclosed body of water that stretches from the island of Borkum to the end of the range of tidal influence at the flood defence weir in Herbrum (Talke et al. 2006, Bos et al. 2012). The prevailing physical forces that affect the estuary are the tides, wind (both waves and shear), and the freshwater inflow from both the Ems River and the Westerwoldse Aa (Talke et al. 2006, Baptist 2017).

Acoustic monitoring

Harbour porpoises produce distinctive signals, lasting about 50–150 microseconds, with the main part at around 132 kHz within a narrow band between 120–150 kHz (e.g. Au et al. 1999, Teilmann et al. 2002, Madsen et al. 2010). This makes them ideal for automatic detection as most other sounds in the sea, barring some boat sonars, are broadband or lower energy frequencies and can thus be filtered out during post-processing of data (Tregenza 2012). Porpoise click trains are recognisable by a gradual change of click intervals and amplitudes throughout a click sequence, whereas boat sonars and echo sounders have highly consistent inter-click intervals (Tregenza 2012).

C-PODs (Continuous-Porpoise Detectors, Chelonia Ltd., Mousehole, UK) are acoustic data loggers widely used to study porpoises and other odontocetes that are producing high frequency clicks (e.g. Brasseur et al. 2010, Scheidat et al. 2006, 2012, Tougaard et al. 2006, 2009, Castellote et al. 2012). They consist of a polypropylene casing with hydrophone housing at one end, and a removable lid on the other. Contained within the housing is an amplifier, a digital waveform analyser, a data-logger that continuously logs echolocation click-activity and 10 D-cell batteries. A summary of click features is logged, such as time, duration, dominant frequency, bandwidth and amplitude, and stored on a secure digital flash card (SD).

Ten C-POD locations were chosen between the island of Borkum and Dollard (Brasseur et al. 2010, 2011; see figure 1). The water depth at the C-POD locations ranged from 8 to 15 metres (Brasseur et al. 2010). The devices were anchored to a weight and attached to a light buoy equipped with an alarm, the C-POD itself positioned about a metre above the bottom. Every 8–10 weeks, the C-PODs were retrieved to offload the data, replace batteries and for general maintenance (Brasseur et al. 2010). Data were collected from April 2009 until January 2011. Because of icy conditions, and the related risk of damage and loosening of the buoys attached to the C-PODs, the buoys and associated C-PODs GSP 07, GSP 08 and GSP 09 were retrieved on 23 December 2010; the GSP 10 C-POD was lost (Brasseur et al. 2011).

Feeding behaviour

Harbour porpoise use their narrowband high frequency echolocation clicks to communi-

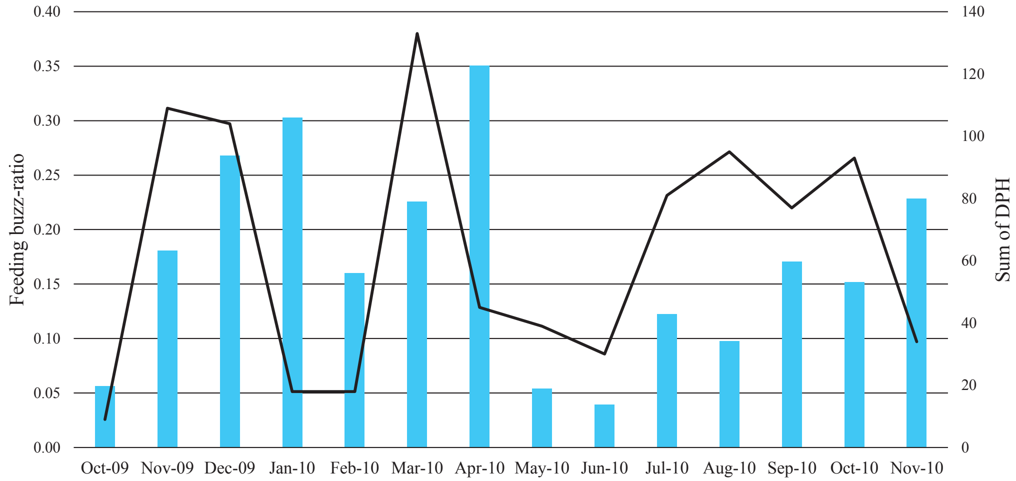

Figure 2. Feeding buzz-ratios (FBR) per month (blue bars) versus acoustic activity expressed as the summation of detection positive hours (DPH) per month (black line) for C-POD location GSP03.

cate, navigate and hunt (Verboom & Kastelein 1995, 1997, Au et al. 1999, Teilmann et al. 2002, Madsen et al. 2010). To find their prey, they emit high-powered, directional clicks and subsequently receive and process the returning echoes (Madsen et al. 2010). A number of studies have investigated how the varying interclick interval (ICI) between clicks may be used to distinguish different acoustic behaviours (Koschinski et al. 2008, Verfuss et al. 2009, Miller et al. 2010). During foraging, after a stable ICI of 50–60 ms (the initial part of the approach phase), the interval decreases progressively (Miller et al. 2010). When closing in on prey, the ICI drops sharply from roughly 50 ms to below 20 ms. Within the last one metre, the click train ends with a "buzz", with an ICI below 2 ms, indicating prey capture (Carlström 2005, Verfuss et al. 2009, Miller et al. 2010, Nurminen 2010). These click trains are often referred to as feeding buzzes (Nurminen 2010) and have been used as an indicator of feeding activity (e.g. Weel 2016). These buzzes have been seen to continue beyond the first contact with the fish, often extending after the fish has been caught (De Ruiter et al. 2009).

The minimum or maximum ICI per train is the shortest or respectively longest recorded period between two successive clicks within a train (Carlström 2005). Click sequences with a minimum ICI below 10 ms have been used as an indicator for foraging activity for porpoise (Carlström 2005, Todd et al. 2009, Verfuß et al. 2009, Linnenschmidt et al. 2013, Nuuttila et al. 2013). Pirotta et al. (2014) used C-POD data to calculate the inter-click intervals (ICIs). Each ICI was classified as either a regular ICI (regular clicking for navigation and prey searching), a buzz ICI (buzzes associated with attempted prey captures or social communication), or an inter-train ICI (pauses between click trains). They found changes in buzz occurrence related to seismic activity. Schaffeld et al. (2016) found that foraging sequences of harbour porpoises can show extreme variations in ICI before a sudden decrease to below 10 ms. They analysed the data by using those sequences that showed a sudden decrease in ICI, of at least 5 clicks with an ICI <10 ms and with clicks at an ICI level between 40 and 70 ms before the decrease. Their results indicate that the most stereotypical part of foraging sequences is the sudden decrease in ICIs, and that using this value instead of the ICIs below 10ms is providing a conservative, but likely more accurate, indicator than only using the ICI.

At sea, a correlation between buzz activity and feeding success should not be assumed *a priori* without experimental evidence, since a higher buzz rate could just mean that more effort is put into capturing the same amount of prey (Todd et al. 2009). A proxy of potential feeding activity could be inferred, however, by investigating the relative incidence of rising click rates, emitted during range locking echolocation behaviour, and the accompanying decrease of ICI (Verfuss et al. 2002, Carlström 2005, Johnson et al. 2006, Todd et al. 2009, Leeney et al. 2011).

For this study, we used the feeding-buzz ratio (FBR) as an indicator of likely porpoise feeding activity (Todd et al. 2009, Leeney et al. 2011). The term feeding-buzz ratio was borrowed from bat literature (e.g. Vaughan et al. 1996, Turner 2002). Using the feeding-buzz ratio will help obtain a relatively continuous value of activity. In their study on porpoises, Todd et al. (2009) generated these ratios by dividing the number of trains with a minimum ICI (MICI) of <10 ms by those with MICIs of >10 ms for each diel phase. A similar approach was used by Leeney et al. (2011) in their study on Heaviside's dolphins (*Cephalorhynchus heavisidii*), but instead of minimum ICI, they used the mean ICI. This method allows for a ratio of fast, possibly feeding associated, click trains, to all other trains (Todd et al. 2009). A value greater than one would indicate that a greater proportion of porpoise click trains have ICIs <10 ms, indicative of potential feeding, and *vice versa* (Todd et al. 2009). A value of one would mean a near 50/50 share of clicks more or less than 10 ms. A higher ratio suggests more time spent producing buzz trains, and therefore possible feeding behaviour (Leeney et al. 2011). They base their description of a minimum ICI per train on Carlström (2005) and Philpott et al. (2007), and use 10 ms as a proxy indication of porpoise feeding activity (Todd et al. 2009).

One unresolved issue is that when animals move their heads side to side while searching for prey, click trains are recorded only partially. In addition to this, the actual number of click trains is influenced by the algorithm in the CPOD.exe program, which splits trains more often when the ICI is long. An assessment to what degree the number of trains created is consistent under different scenarios would therefore be very helpful for future analyses.

For our analyses, we followed Carlström (2005) and used the minimum ICI for the analyses. Whilst Carlström (2005) used the older model T-PODs, this approach was deemed useful to describe potential feeding activity for the newer C-PODs as well. To increase the chance of obtaining actual feeding click trains and in lieu of more recent studies (e.g. Koschinski et al. 2008, Verfuss et al. 2009, Nurminen 2010), an MICI of 3 ms was used in Weel (2016), instead of 10 ms. Buzz ratios were recorded on nearly all days, except for 21-31 October 2009 and 1-12 November 2010. More details on the performance of the feeding-buzz ratio in comparison to the visual detection of feeding buzzes can be found in Weel (2016).

Fish monitoring

The Demersal Fish Survey (DFS), an annual beam trawl survey, run by Wageningen Marine Research, is carried out in coastal waters from the southern border of the Netherlands to Esbjerg, Denmark (down to 25 m depth) (van Beek et al. 1989, Tulp et al. 2017). The survey also covers the Wadden Sea and the outer part of the Ems-Dollard estuary, and occurs during the period September-October (van Beek et al. 1989). The survey is stratified by regions, demarcated according to tidal basins or other geographic features (Boddeke et al. 1972).

Within the Wadden Sea and Ems estuary, sampling was carried out with a 3 m beam trawl (Tulp et al. 2017). The beam trawls were equipped with one tickler chain, a bobbin rope, and a fine-meshed cod-end (20 mm). Both gears were rigged in the same way; only the size of the beams varied. Fishing was limited to the tidal channels and gullies deeper than 2 m because of the draught of the research vessel. The combination of low fishing speed (2-3 knots) and finer mesh size results in the selection of smaller fish species and younger year classes (Tulp et al. 2017).

To study the possible links between porpoise and fish presence, data on the abundance of five potential fish prey species (smelt (*Osmerus eperlanus*), gobies, flounder (*Platichthys flesus*), herring and whiting) were used from the DFS. The study area was divided into four sub-areas and the average density of the five potential fish prey species was calculated for each area. As shown in figure 1, the C-PODs positioned in the Wadden Sea (GSP 01, 02, 03 and 05) were designated to area I; those near the outer part of the Ems (GSP 04, 06 and 07) to area II; those midway the Ems (GSP 08 and 09) to area III and POD GSP 10, positioned near Dollard, to area IV. For comparison with the fish data, the C-PODs were analysed for the period of 1-23 September 2010 for each of the sub-areas.

Data analysis

The C-POD data were analysed with the software from the manufacturer (CPOD.exe version V2.044, Chelonia Ltd). The default settings were used, for instance 'all cetacean species', unmodified 'train values', and 'click filters' (for more details see Brasseur et al. 2010, 2011). Only 'Hi' and 'Mod' trains were analysed, which is the designation CPOD.exe uses for trains most likely to have been produced by the target species. All automatic detections, and how their click train type is classified, were manually checked. Manual analysis also permitted exclusion of multiple false detections caused by noise, which are relatively easy to recognise by their broad frequency coverage, lack of coherence in temporal scale, pulse bandwidth, number of cycles and envelope (Castellote et al. 2015). Checking for false detections was only done for the one-year overview analysis and was not quantified.

Average counts of feeding buzzes as defined for this study were obtained for each day of every month and location where possible (similar to the study of Nurminen 2010). Next, the click activity data were aggregated into daily values of minutes in which porpoise clicks were detected. The parameter used was detection positive 10 minutes per day (DP10M/day), as the number of detections was usually low, and this measure minimises potential differences in sensitivity between C-PODs (Haelters et al. 2011). In addition, for this study, detection positive hours (DPH) were summed per day to obtain DPH/day, and further aggregated to DPH/month. The DPH value provides a proxy for porpoise occurrence. As mentioned above, min ICIs values were extracted from the data for the feeding-buzz ratio determination. More details on the data collection methodology can be found in Brasseur et al. 2010.

For the C-POD location GSP 03 (see figure 1), data have been logged for several years (Brasseur et al. 2010, 2011, Lucke et al. 2011). We chose GSP 03, as this location provided more than one continuous year of complete data. The dataset comprised 389 days of continuous recordings from 20 October 2009 to 12 November 2010.

Results

Seasonal and spatial pattern

The C-POD location GSP 03 showed that FBR varies greatly over time, with the highest feeding buzz ratio found in April 2010 and the lowest in June 2010 (figure 2). Porpoise occurrence (expressed as DPH per month) seems to show a more regular pattern with the high-

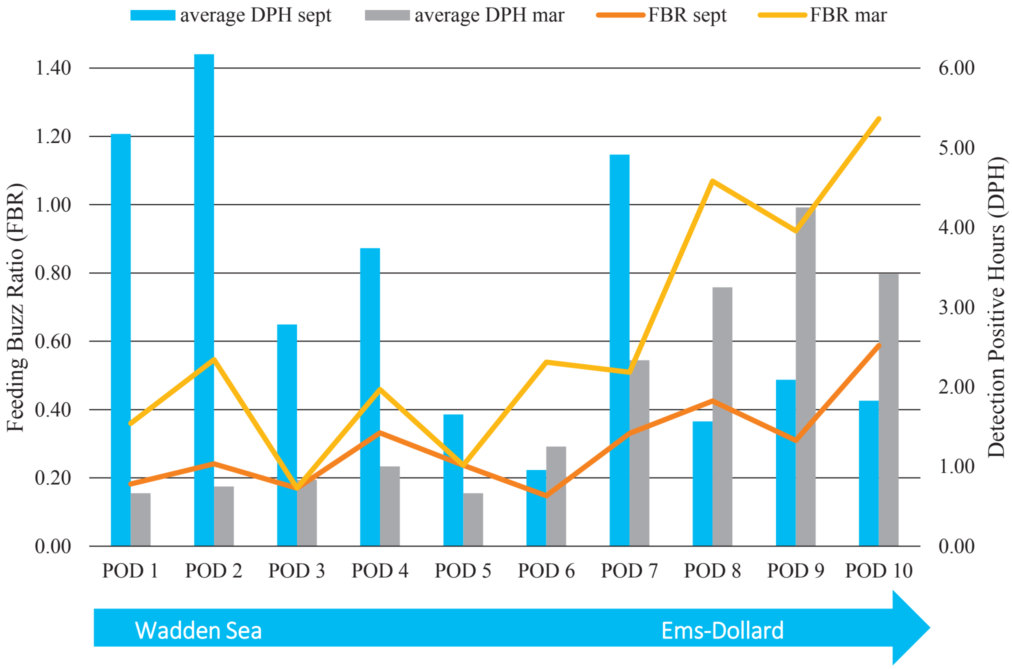

Figure 3. Feeding buzz ratio (FBR) determined for all C-PODs during 1-21 September (orange line) and 17-28 March (yellow line) in 2010 and detection positive hours (DPH) determined for all C-PODs during 1-21 September (blue bar) and 17-28 March 2010 (grey bar).

est click activity recorded from November to April, a strong decrease in May, and a gradual increase again in the late summer. In some months both FBR and DPH are high, which is to be expected as more animals clicking should lead to more feeding buzzes occurring. However, this is not always the case as some months show a reverse pattern. For example, in January 2010, porpoise occurrence is low while the FBR is high, while in August 2010, feeding buzz-ratio is low and DPH values are high.

DPH and feeding buzz-ratios showed no clear linear relationship and no significant correlation (Pearson's correlation coefficient -0.392, *P*-value 0.166; Spearman correlation coefficient -0.213, *P*-value 0.463).

The highest FBR is seen in POD stations 8, 9 and 10 in March 2010, and the highest FBR for POD 10 in September (figure 3). This suggests feeding activity was highest in March near POD stations 8, 9 and 10, and highest in September around POD 10. POD 3 and 5 showed low FBRs in March. FBR increased from outside the estuary upstream both in March and in September. DPH for both periods is also shown, the highest found during September for POD 1, the lowest found in March for POD 5. There is a generally lower number of DPH during March for most PODs, except at the inner estuary for PODs 8, 9 and 10.

The pattern of average DPH and FBR differed between March and September 2010. In March, both DPH and FBR increase from the Wadden Sea into the Ems-Dollard estuary. By contrast, in September the occurrence of porpoises is lower than in March for the first five POD stations, but higher for the last three. The FBR still increases with distance from the Wadden Sea.

The relationship between average DPH and FBR (figure 4) in March 2010 showed a significant positive correlation (Pearson's correlation coefficient 0.840, *P*-value 0.002; Spear-

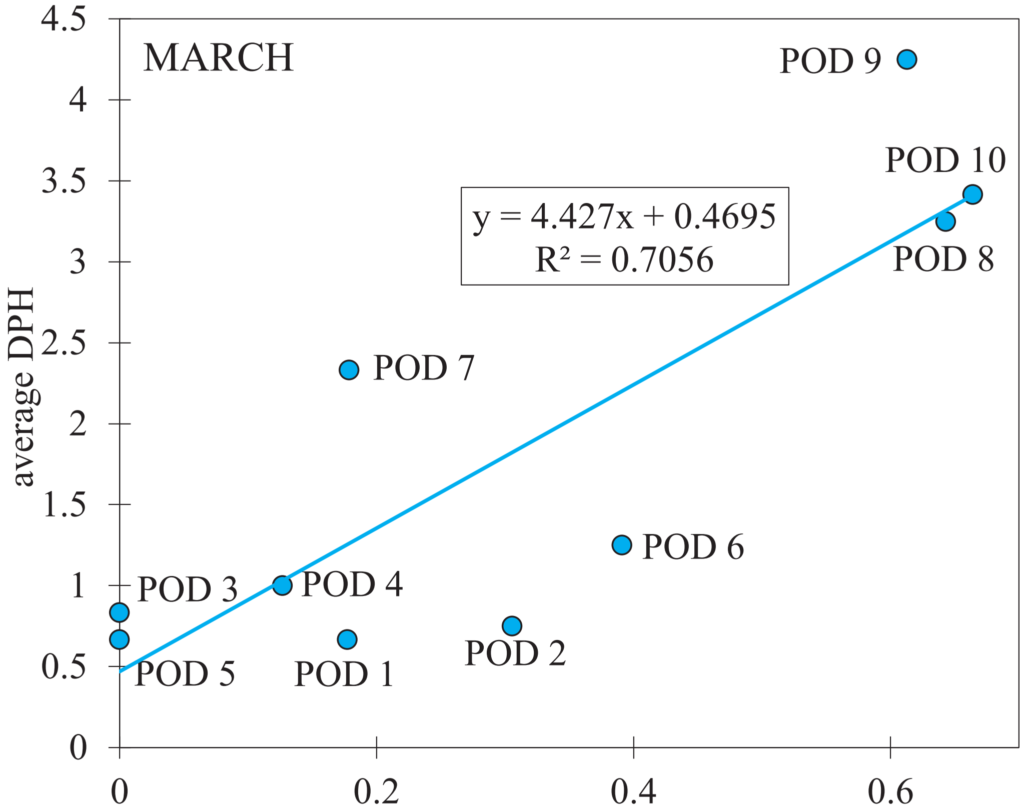

Figure 4. Scatter plot showing average detection positive hours (DPH) and feeding buzz ratio (FBR) per C-POD station (POD 1 to POD 10) for March 2010.

man correlation coefficient 0.777, *P*-value 0.012) whereas average DPH and FBR in September 2010 showed no significant correlation (Pearson's correlation coefficient – 0.212, *P*-value 0.557; Spearman correlation coefficient – 0.006, *P*-value 1).

Relation to fish occurrence

To investigate the relation between harbour porpoise and fish occurrence in the Ems we analysed a sub-sample of the C-POD dataset for the period from 1-23 September 2010. The fish sampling took place in September and October at the sampling stations shown in figure 1. To compare fish density with acoustic activity, the study area was sectioned into four areas (figure 1). The selection of the C-POD data time period was driven by the availability of complete data sets from all stations which allowed a direct comparison of the results.

Figure 5 shows the average fish density (per species) for all stations per area, in relation to the average DPH and FBR recorded on the C-PODs per area. The results show that acoustic activity of porpoises halved from area I towards area IV. At the same time, the feeding buzz ratio approximately triples from area I to area IV.

The occurrence of the five fish taxa in the Ems differs between the sample areas. Both smelt and flounder density increase upstream, while gobies, whiting and herring decrease (figure 5).

The data indicate that an overall increase in

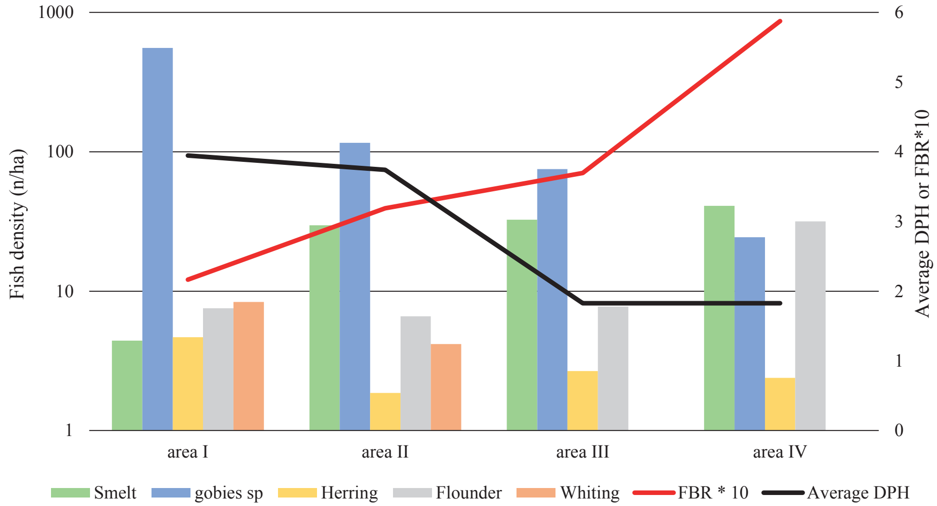

Figure 5. Average fish density for five taxa for all stations per area (expressed as n/ha on a logarithmic scale) and average DPH per area (black line) and FBR (red line, shown as FBR*10) for the period 1-23 September 2010.

fish abundance is not necessarily an indicator of an increase in foraging behaviour by harbour porpoises. Only for smelt and flounder is there an increase in fish abundance and FBR. For the other species, gobies, whiting and herring, this pattern is reversed (figure 5).

Discussion

Harbour porpoise distribution in the North Sea has shifted over the last two decades from the northern and central North Sea to the central and southern North Sea (Hammond et al. 2002, 2013, 2017). This is most likely the reason for the increase in porpoise occurrence in Dutch North Sea waters since the late 1990s (Camphuysen 2004). There are indications that the driving factors for this change could be linked to a change in prey availability (Camphuysen 2004, MacLeod et al. 2007), although the evidence is mostly circumstantial. Harbour porpoise occurrence in the Dutch sector of the North Sea shows a strong seasonal pattern, with highest densities in the early spring and lowest numbers in the summer (Geelhoed et al. 2013), although with an increase in summer densities this seasonal difference has been less distinct in the last few years (Geelhoed & Scheidat 2018).

There has been a number of studies showing that click frequency, and in particular the metrics of detection positive hours, can be used as a reliable proxy for the density of porpoises (e.g. Williamson et al. 2016, Anonymous 2016). Based on this premise, the C-POD monitoring study in the Ems shows that although there are seasonal changes with lowest density of porpoises in the winter (Brasseur et al. 2010), porpoises occur in the estuary year-round. The seasonal comparison specifically for station GSP03 showed that the lowest numbers of porpoises occurred in May and June. The comparison of all C-POD sampling stations between March and September shows a more complex pattern, indicating that in September porpoises are present throughout the estuary, with more animals occurring downstream, whilst in March this pattern notably changes, with more activity upstream. Interestingly, the feeding buzz ratio in both cases is showing a clear increase from the outer C-POD stations to the inner C-POD stations, indicating a relatively high occurrence of foraging behaviour in that area for both these months.

Harbour porpoises have a large body surface to volume ratio, and they require relatively large amounts of food (Kastelein 1998, Leopold 2015). Recent work using high-resolution sound and movement tags on porpoises have shown porpoises may hunt up to 550 small fish prey per hour with a >90% capture success rate (Wisniewska et al. 2016). Prey with high energy density, if available, is generally preferred (Leopold 2015). Harbour porpoises have been found to take small schooling fish with a high lipid content (Jansen et al. 2013, Leopold 2015). For example, animals feeding in the Western Scheldt showed the highest average energy density of prey of all sampled Dutch porpoises due to the smelt being eaten here (Leopold 2015). However, the costs of the hunt and the skills needed to catch certain prey probably also determine which prey is taken. Leaner prey species, such as gobies, dominate the prey of young porpoises (Leopold 2015). Specific needs, as well as foraging skills, probably vary amongst individual porpoises and with age, body condition, as well as reproductive status (Leopold 2015). Environmental factors (such as season, tidal state, sea temperature, time of day) further impact porpoises as well as their prey, thus driving the observed pattern. The local variation in fish occurrence adds to the complexity of the situation.

Our study indicates that porpoises in the inner waters of the Ems show a higher feeding buzz ratio in comparison to the area closer to the Wadden Sea. As the Ems estuary waters are turbid, with an increase from the outer to the inner estuary, one could hypothesise that this might have an impact on the echolocation of porpoises and affect the results for FBR as well. Several studies have shown that porpoises tend to use stable mean inter click intervals when navigating, as well as during the search and approach phases for prey (e.g. Teilmann et al. 2002, de Ruiter et al. 2009). These ICIs are all at least an order of magnitude larger than those for feeding buzzes (de Ruiter et al. 2009). Thus, one would expect that if porpoises need to intensify their echolocation to find prey or to navigate, that they would increase the overall click frequency. In contrast, our results point to an increase in FBR, which means a higher occurrence of feeding buzzes with very short ICIs of 3 ms or lower.

One hypothesis that could explain the apparent increase of feeding buzzes in the inner Ems estuary is that porpoises encounter prey here, such as the European smelt. Smelt is an anadromous fish that occurs in the estuary and migrates upstream from February to May. Its abundance has increased over the last decades in the Eastern Wadden Sea as well as in the Ems Dollard estuary (Tulp et al. 2017). Smelt swim upstream to spawn in February-March when the water temperature reaches 5°C (de Groot 2002). As the exact start of the smelt migration is dependent on water temperature, it is likely that there is an inter-annual variance in the onset of migration for smelt. At spawning, smelt form aggregations that may provide good feeding opportunities for porpoises. During our study, the time period in which our data on the overlap of fish occurrence and porpoise acoustic behaviour is fairly short. Also, the sample stations for fish and porpoises are not exactly in the same locations, and by pooling the data into larger areas, potential small-scale variation between stations is not considered. To appropriately determine how fish, and in particular smelt occurrence influences the behaviour of porpoise in the Ems estuary, a designated multi-year study of fish and porpoise occurrence, as well as feeding behaviour, would be needed.

A study on porpoises in the river Weser (Wenger & Koschinski 2012) confirmed that porpoises move up into the river and that this is a comparatively recent phenomenon. Porpoises have also increased in the Elbe River in Germany (Wenger & Koschinski 2012, Wenger et al. 2016) and in the Western Scheldt in the Netherlands (Leopold 2015). For all three cases, the observed occurrence was linked to the presence of anadromous fish.

The fact that porpoises are (re-)entering our estuaries and rivers can be considered good news. It is most likely an indicator of an abundance of prey that is highly sought-after due to their high energy content. However, when porpoises enter the Ems estuary, they are also entering an area that is intensively used by humans. Therefore, by following their prey, they are risking negative effects from anthropogenic activities. Even though contamination of the Ems has decreased, concentrations of polychlorinated biphenyls (PCBs) and dichlorodiphenyltrichloroethanes (DDTs) measured in organisms are still considerable high (Bos et al. 2012). The large number of vessels potentially causing risk of ship strike, construction works and other noise sources, most likely lead to an increase in stress for porpoises. However, the benefit of having high quality prey may outweigh the potential negative effects of anthropogenic activities.

Using C-POD data to analyse porpoise behaviour has some caveats, since the data lack full spectrum acoustical information, and the C-POD might not be in the path of the narrow echolocation beam of a foraging animal (Linnenschmidt et al. 2013). For benthic prey, porpoises will direct their search effort, and thus their buzzes, towards the bottom. For pelagic prey, which also tends to be more mobile, buzzes will occur in the water column. Sostres Alonso and Nuuttila (2014) discuss that changing foraging strategies could explain differences in click detection between different deployment depths of C-PODs.

We have described a number of studies that have attempted to improve the analyses of C-POD data to quantify when porpoises are catching prey (Pirotta et al. 2014, Schaffeld et al. 2016, Nuuttila et al. 2018). A thorough comparison to see which of these approaches is best is still lacking. From detailed foraging data collected in captivity (Verfuss et al. 2002), it is clear that C-POD data provide a very limited sample of the actual acoustic behaviour of porpoises. Recent work, using detachable tags recording the acoustic activity of porpoises, has confirmed this by providing in-depth information on foraging behaviour and actual feeding events in the wild (Wisniewska et al. 2016). In future studies, it would be good to use these data sets to allow a better interpretation of C-POD data. An assessment of the most adequate approach, in combination with an automated analysis tool, would allow analyses of the large amount of data that has been collected in the past. This could lead to important insights in the foraging behaviour of porpoises.

Our study explored porpoises in the Ems Dollard estuary, and offers the hypothesis that there is a link between increased feeding behaviour and the seasonal occurrence of prey. To fully test this hypothesis, designated studies would be needed that focus on both porpoise and fish at the same spatial and temporal scale, and that would consider both physical and biological factors that could affect data collection for the two taxa. Future work to obtain an improved understanding on this phenomenon – and how it links to environmental parameters, the presence of certain fish species, and its variation over time – is especially important to ensure adequate conservation action for the Ems harbour porpoise.

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Samenvatting

Foerageergedrag van bruinvissen (*Phocoena phocoena*) in het Eems-estuarium

Om het voorkomen en de verspreiding van foerageergedrag van bruinvissen (*Phocoena phocoena*) in het Eems-estuarium te bestuderen is gebruik gemaakt van Passieve Akoestische Monitoring (PAM). Het voorkomen werd uitgedrukt als 'detection positive hour' (DPH): een uur dat een bruinvis is gedetecteerd. De mate waarin naar verwachting foerageergedrag plaatsvond werd beschreven als 'feeding buzz ratio' (FBR). Hiermee werden drie analyses gedaan: 1. Een jaarrondanalyse van DPH en FBR voor een PAM-station vlakbij de Eemshaven; 2. Een analyse van DPH en FBR voor tien PAM-stations in het Eems-estuarium in maart en september 2010; 3. Een vergelijking van bruinvisactiviteit met visdichtheid in het gebied in september-oktober 2010. De jaarrondanalyse liet een seizoenspatroon in het voorkomen van bruinvissen zien, met over het algemeen lagere waarden in april-juli en hogere waarden in augustus-december. FBR en DPH per station verschilden tussen maart en september 2010. De maartgegevens tonen een landinwaartse toename van zowel DPH als FBR van de Waddenzee naar het estuarium. In september 2010 daalde DPH van buiten naar binnen in het Eems-estuarium, wat samenviel met een toename van het foerageergedrag. Visdichtheid werd bepaald voor vijf potentiele prooisoorten (spiering, wijting, grondel, bot en haring) op bemonsteringsstations in

vier gebieden in het estuarium. Bot en spiering namen toe van de Noordzeekant naar de binnenwateren van het estuarium. Smelt is een anadrome vis die bekend is als prooisoort voor bruinvissen. Deze studie suggereert dat bruinvissen het gehele jaar in het gebied voorkomen, en dat foerageergedrag jaarrond plaatsvindt, maar dat de aanwezigheid van een geprefereerde prooi de reden kan zijn dat bruinvissen op bepaalde tijden ver het Eems-estuarium in zwemmen. In de Eems vinden veel menselijke activiteiten plaats, waarvan sommige, zoals bouwwerkzaamheden en intensieve scheepvaart, mogelijk schadelijke gevolgen kunnen hebben voor de aanwezige bruinvissen. Aangezien deze studie slechts een korte periode beslaat, moeten de resultaten als voorlopig worden beschouwd. Toekomstige studies naar de relatie tussen het voorkomen van prooivissen en bruinvissen in dit gebied kunnen leiden tot een beter begrip van deze relatie en kunnen daarom van groot belang zijn voor beschermings- en beheersmaatregelen.

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