4. DIRECTIONAL BREEDING MIGRATION OF HARBOUR SEALS IN THE WADDEN SEA

Sophie M.J.M. Brasseur, Peter J.H. Reijnders, Roger Kirkwood and Geert Aarts

SUMMARY

Migration plays a central role in the spatial dynamics of many mobile species, but it has not been identified in the harbour seal (*Phoca vitulina*), which is generally considered a non-migratory species. However, in the Wadden Sea, extending from the Netherlands to Denmark, there is a regional misbalance between harbour seal pup production and resident population size. This led to the hypothesis that an annual breeding migration might occur.
Harbour seals in the Netherlands were tracked with GPS data-loggers. The movement data were analysed to study whether harbour seals in the Wadden Sea migrate annually between the feeding and breeding areas. We demonstrate that prior to the breeding season a large proportion (30%) of females from Dutch waters where pup production is low relative to the numbers counted during the moult season; migrate towards Germany in the east, where pup production is higher. Also, the majority of animals tracked after the breeding season, including 78% of adult females, moved in the opposite direction, to the west, suggesting a return migration.

The existence of large individual variation in seal movement might explain why such migrations have not been noticed previously. Historic management regimes that afforded greater protection to breeding seals in Germany, then natal philopatry and breeding site-fidelity are the most likely cause of this migration. This suggests that miss-balances in pup-production across the ranges of harbour seal populations may persist for decades.
Potentially, further study of the movements of these highly individual animals might provide insight into more fundamental questions on migration and ecological questions related to, for example, population development and population genetics.

INTRODUCTION

Migration occurs in all major animal groups, including birds, mammals, fish, reptiles, amphibians, insects, and crustaceans. This behaviour is thought to play a central role in the spatial dynamics of many mobile populations, and is distinct in both form and function from within-population mixing arising from postnatal dispersal and other inter-patch movements (Dingle & Drake 2007). Amongst several pinniped species, long-distance migrations are known. For example, elephant seals (*Mirounga spp.*) spend much of the winter foraging in open waters and migrate back to land each spring to breed (Le Boeuf *et al.* 2000, Hindell & McMahon 2000). Many otariids also disperse from breeding sites outside of their breeding period, often leaving them completely vacant, and migrate back to breed (Beauplet *et al.* 2004, Patterson *et al.* 2016). Harbour seals (*Phoca vitulina*), however, are generally considered a non-migratory species, moving only several tens of kilometres between haul-out sites (Thompson *et al.* 1996, Thompson *et al.* 1998, Tollit *et al.* 1998, Härkönen & Heide-Jørgensen 1990, Härkönen *et al.* 1999, Scheffer & Slipp 1944, Cordes & Thompson 2015).
Harbour seals have a circumpolar distribution and all five subspecies occur in the coastal regions of temperate oceans in the Northern Hemisphere (Reijnders *et al.* 1993). Harbour seals become sexually mature at 3-4 years in females and 4-5 years in males (Härkönen & Heide-Jørgensen 1990). All breed in spring or early summer (May-July), giving birth to a single pup that can swim within hours after birth (Härkönen & Heide-Jørgensen 1990, Bowen *et al.* 1992, Hind & Gurney 1998, Cottrell *et al.* 2002, Muelbert & Bowen 1993). Lactation duration may vary between 15 and 28 days, with a median before 21 days (Sauvé *et al.* 2014, Cordes & Thompson 2013, Thompson & Wheeler 2008, Wieren 1981). After a post weaning fast of up to one month, pups move to haul-outs near feeding sites, which can be near to or distant from the birth sites (Small *et al.* 2005, Bjørge *et al.* 2002, Härkönen & Harding 2001, Blanchet *et al.* 2014). Like all seal species, adult harbour seals spend most of their time at sea, but haul-out on land to rest, breed, and moult (Sjöberg *et al.* 2000, Krieber & C. 1984). They are considered central place foragers, traveling throughout the year from haul-outs to feeding grounds at sea and back (Bailey *et al.* 2014, Bjørge *et al.* 2002, Härkönen *et al.* 2006b, Russell *et al.* 2015, Thompson *et al.* 1998, Womble *et al.* 2014, Sharples *et al.* 2009). Recent tracking studies show that some individuals may move considerable distances away from capture sites (Lesage *et al.* 2004, Peterson *et al.* 2012, Womble & Gende 2013, Bajzak *et al.* 2013, Blanchet *et al.* 2016, Blanchet *et al.* 2014). However, individual variability in these movements is marked, and observations lack the appearance of a collective migration in a specific

direction. So, despite some long-distance movements, observations of migration as such has not been described for this species. In the Wadden Sea, however, analysis of aerial surveys revealed a regional misbalance in the pup production compared with resident population sizes, leading to the hypothesis that an annual migration to and from specific breeding areas in the Wadden Sea could occur (Brasseur *et al.* submitted 2017).

Population estimates of harbour seals are usually based on counts of pups during the breeding period and population counts during annual moult, when a predictably large proportion of the seals is on land (Brasseur *et al.* 2015, Teilmann *et al.* 2010, Cunningham *et al.* 2010, Bailey *et al.* 2014, Reijnders *et al.* 2010a, Thompson *et al.* 2010, Meesters *et al.* 2007, Brown *et al.* 2005, Thompson & Harwood 1990). In the Wadden Sea, which comprises four geo-political regions (Denmark, two German states and the Netherlands), harbour seal pup production in the two German regions showed a relative surplus throughout 40 years of monitoring, between 1974 and 2014 (Brasseur *et al.* submitted 2017). As there are no evident environmental differences between the four regions, it was hypothesised that a proportion of females that bred in Germany, spent other periods of the year in either the Netherlands or Denmark. The situation potentially arose as a carry-over effect of variations in historical management. Hunting potentially caused a more serious decimation of the breeding grounds in the Netherland and Denmark, than in the German areas (Reijnders 1992, Reijnders 1983, Joensen *et al.* 1976, Hoffmeyer 1962). Natal philopatry and fidelity of the seals to breeding areas in Germany could fuel seasonal

	2007		2009	2010	2011	2013			2014			2015			
	Texel	Delta	Ems	Ems	Ems	Ameland	Delta	Texel	Ameland	Delta	Texel	Ameland	Delta	Texel	
March			21^{3}	24	24		6	6^{1}	10	10	10		6	6	123^{4}
F			11	13	14		3	2	4	3	5		3	1	59
a			9^{1}	10	12		1		4	2	3		2	1	44
sa			2	3	2		2	2		1	2		1		15
M			10^{2}	11	10		3	4^{1}	6	7	5		3	5	64
a			9^{2}	10	9		1	3	6	7	4		2	4	55
sa			1	1	1		2	1^{1}			1		1	1	9
September	6^{2}	4^{1}	24^{2}		24	10						10^{1}			78^{6}
F	1		13^{1}		14	4						3			35
a	1		11		12	2						2			28
sa			2^{1}		2	2						1			7
M	5^{2}	4^{1}	11^{1}		10	6						7			43
a	3^{2}	4^{1}	9^{1}		5	3						5^{1}			
sa	2		2		5	3						2			16
November				24											24
F				13											13
a				11											11
sa				2											2
M				11											11
a				9											9
sa				2											2
Total	6^{2}	4^{1}	45^{5}	48	48	10	6	6^{1}	10	10	10	10^{1}	6	6	225^{10}

TABLE 1. SUMMARY OF HARBOUR SEALS EQUIPPED WITH SATELLITE OR GPS/GSM TRANSMITTERS IN THE NETHERLANDS. TRACKERS THAT FUNCTIONED 20 DAYS OR LESS (N=10) ARE INDICATED IN SUPERSCRIPT (SEX: F= FEMALE, M=MALE; AGE ESTIMATED BASED ON LENGTH: A= ADULT, SA= SUB-ADULT).

migrations to and from these areas, and consequently the observed longstanding regional differences in the ratio of pup production versus number of seals observed during the moult might persist for decades.

The aim of this paper is to test the hypothesis of directional breeding migration by harbour seals in the Wadden Sea by analysing individual tracking records obtained from harbour seals caught in Dutch waters.

MATERIAL & METHODS

SEAL TRACKING

Between 2007 and 2016, 225 harbour seals were captured and fitted with tracking devices in the framework of different telemetry projects in the Netherlands (Brasseur *et al.* 2011a, Kirkwood *et al.* 2015, Brasseur *et al.* 2011b, Brasseur & Kirkwood 2016). Catch sites were spread across the Dutch coastal zone, in four areas: the Ems River Estuary in the eastern Wadden Sea, near the island of Ameland in the central Wadden Sea, near the island of Texel in the western Wadden Sea and in the Delta region, in the south-west of the Netherlands (Figure 1; Table 1). Deployment periods were either in early spring (March; n=123), preceding the harbour seals' breeding period, which is in May-July, or in autumn, after the seals' moult (September; n=78, or November; n=24).

All seals were captured by deploying a specifically designed seine-net of approximately 100 m adjacent to a group of seals lying on a haul-out site, typically an intertidal sandbar. Seals fled into the water and became entangled in the net, which was rapidly hauled onto the sandbar. Seals were selected for tracking, aiming for equal numbers of adult females, adult males and sub-adult animals of either sex (Table 1). Unselected seals were immediately released. The selected seals were restrained in specifically-designed cradles for 30–90 min. They were sexed, measured (standard length, nose to tail, in cm) and weighed (±0.5 kg), and assigned to an age-group based on standard length; females >125 cm and males >130 cm were considered to be adult (Härkönen & Heide-Jørgensen 1990).

Each seal was *equi*pped with a GPS-GSM tracking device (Sea Mammal Research Unit, University of St Andrews) with Fastloc GPS hardware (developed by Wildtrack Telemetry Systems Ltd, Leeds, United Kingdom). These devices collect and store location, dive, and haul-out data which are relayed via the GSM mobile phone system (Cronin *et al.* 2010). They were glued to the seal's fur, at the mid-dorsal point immediately above the shoulder blades, using epoxy resin (Permacol). Trackers could stop functioning or fall off any time after deployment, but certainly were lost during the moult in summer (June-August). A total of 10 trackers stopped functioning within 20 days and, were disregarded in this analysis (Table 1).

DATA ANALYSIS

Classification of pregnant females

We interpreted whether female seals pupped based on the data recorded by their trackers. Contrary to most phocid species that remain on land to breed and suckle, harbour seal pups may swim directly after birth so their mothers continue to dive throughout the lactation period (Muelbert & Bowen 1993), albeit being limited by the young pup's swimming ability. As the pup develops it's diving capacity during lactation, the mother may venture deeper with her pup or feed alone for short

periods (Boness *et al.* 1994). In the present study, tracked females were identified as having a pup based when they displayed intensified haul-out behaviour, shallow dives and a lack of great-distance movement during the breeding season. Mostly, they remained in the more sheltered areas of the Wadden Sea, rather than venturing offshore into the North Sea.
More precisely, the following criteria were used to define a female with a pup: 1) intensified haul-out (>30% of each day) for at least 2 weeks, 2) at least 5 consecutive days of shallow dives (<45% of maximum depth during pre-breeding), and 3) a drop in average dive duration to less than 50 sec. Only females that had trackers functioning during the breeding period could be identified to have had a pup.

Quantifying movement of seals between haul-out sites

In this study, we focused on movements between the haul-out sites, disregarding movements to sea which were most likely feeding trips. Haul-out behaviour was detected via a wet/dry sensor in the tracker and locations of these were derived

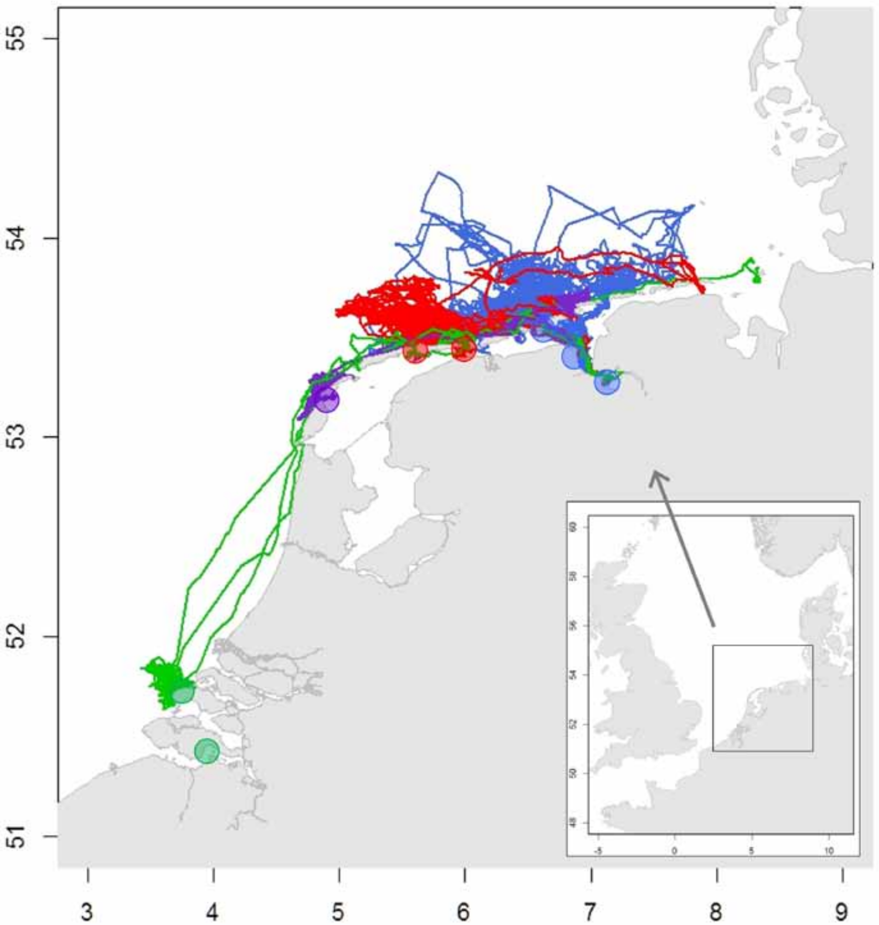


FIGURE 1. TRACKS OF THE FEMALES PRESUMED TO BE BREEDING, INCLUDING CATCH SITES FOR TRACKING STUDIES IN THE NETHERLANDS: BLUE = EMS; RED = AMELAND; PURPLE = TEXEL, AND GREEN = DELTA. INLAY DEMONSTRATES THE LOCATION OF THE STUDY SITE IN THE NORTH SEA AREA

from GPS location data. When there were multiple GPS fixes for different locations during a single haul-out bout, the average location was used. When no GPS fixes were obtained during the haul-out event, the nearest GPS location at sea was used. Data from all years were pooled, as it was assumed that the movement (migration) investigated occurred annually. As we concentrate on movements within the Dutch and German north-facing coastlines of the Wadden Sea, we focussed on longitudinal (east-west) distances of movements, rather than latitudinal (north-south) movements. The movements were compared within and between age and sex groups.
For each seal, the longitudinal movement distance between catching location and each haul-out location was calculated, with positive values representing eastward movements (defined as a positive value), and negative values representing westward movements (defined as negative value). Individual seals were categorised in two groups: those seals that remained within 10 km of the catching site (the residents) and those that moved beyond 10 km of the catching site (the migrants). A test of given proportions ('prop.test' function in R, (Newcombe 1988)) was used to test whether the number of animals moving eastwards significantly differed from the number of animals moving westwards (test probability = 0.5).
To analyse whether the observed movement could be related to breeding-related, migration of seals, we focused on three sub-sets of the tracked seals. Firstly, we identified female breeders and compared the normal spring movements with the movements immediately prior to parturition. Secondly, we compared movements of the breeding females with the movements of other seals in spring. Thirdly, we looked at movements of seals post-breeding/post-moult, to investigate if a 'return migration' was evident.

Estimating migration based on aerial population surveys

Between 1974 and 2014, internationally coordinated efforts were made to annually survey harbour seal numbers in all four regions of the Wadden Sea: Denmark, the two German states of Schleswig Holstein and Lower Saxony (including Hamburg), and the Netherlands. All harbour seal haul-outs were surveyed three times during the pupping season (June) and twice during the moult (August). Details of the aerial surveys can be found in (Brasseur *et al.* submitted 2017). In this study, we used the maximum annual pup counts and the maximum count during the moult, from each of the four regions.
Most pregnant females produce one pup a year, so each regional count of pups (p_i) would be proportional to the number of pregnant females in that region. If the regional pup count was proportional to the number of seals present during the moult (n_i), the expected regional pup count ($\hat{p}_i$) would be similar in each region, and equal to:

$$\hat{p}_i = P\frac{n_i}{N}$$

where P is the maximum total pup count in the entire Wadden Sea, and N the maximum total number of seals counted in the entire Wadden Sea during the moulting season. Hence, the "surplus" of breeding females in a region, *i.e.* those present in one region during moult but expected to breed elsewhere, is equal to:

$$\Delta p_i = p_i - P\frac{n_i}{N}$$

or alternatively, if expressed as a percentage of pups observed in each region:

$$\Delta p_i / p_i = \frac{p_i - P \frac{n_i}{N}}{p_i} = 1 - \frac{n_i / N}{p_i / P}$$

Higher percentages (*i.e.* $\Delta p_i / p_i \cdot 100\%$) suggested either higher fecundity or an influx of breeding females during the breeding period (Brasseur *et al.* submitted 2017). The percentage per year was averaged over years within three distinct periods based on the two PDV epizootics: 1974 to 1987 pre-epizootic, 1989 to 2001 between epizootics, and 2003 to 2014 post epizootics. The epizootics, in 1988 and 2002, killed approximately 50% of the population and affected different age groups differently in the four regions (Härkönen *et al.* 2006b). Tracking data for the present study (from 2007 to 2015) coincided with the third period (2003 to 2014).

ACQUIRED PERMITS

Seal handling and aerial surveys were conducted under appropriate permits. These included a permit under the Dutch Nature Protection Act (*Natuurbeschermingswet*) given by national or provincial authorities, a permit under the Flora and Fauna Act (*Flora en Fauna Wet*) given by the Dutch government, and protocols approved by the animal ethics committee (*Dier Ethische Commissie, DEC*) of the Royal Netherlands Academy of Science (*Koninklijke Nederlandse Academie voor Wetenschappen, KNAW*).

RESULTS

TRACKING RESULTS

During our studies, 20,766 days of harbour seal tracking data were collected, and 16,314 haul-out events were recorded. The data covered both sexes approximately equally (10,478 d for females, 10,288 d for males), though sub-adult animals were under-represented (2136 d for females and 2032 d for males). Seal movement was recorded in all months except for August, due to the seals having moulted by this month (Supplement Table 1). Most data (53%) were available from spring (March) deployments. Tracking efforts were biased geographically with 64% of the seals being caught in the Ems region, 13% around Ameland, 12% near Texel and 11% in the southern Delta region.

The periods that individuals were tracked ranged up to 273 d, with the mean duration (following exclusion of those tracked for <20 d) being 96 d (Supplement Table 2). Adult females tended to retain their trackers longer into the moult period than did other seals. Most seals shed their trackers around the end of May, but a number of adult females retained theirs until end of June and some did so into July (Supplement Table 1).

IDENTIFICATION OF BREEDING FEMALES

All autumn-deployed trackers were lost before June, when pup births commence (Reijnders *et al.* 2010a). Out of the 63 females (adults and sub-adults) fitted with trackers in spring, 43 were still functioning in June, and 27 (two of which had been classified as a sub-adult) were identified to have given birth and supported a pup

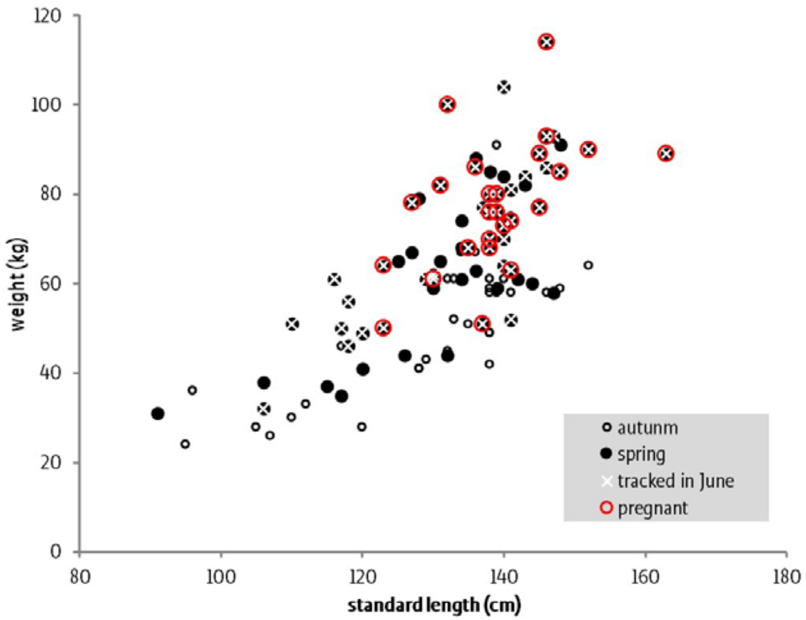


FIGURE 2. LENGTH-WEIGHT RELATIONSHIP IN FEMALES CAPTURED. IN GREY: SEALS CAUGHT IN AUTUMN, BLACK: SEALS CAUGHT IN SPRING (WHITE CROSS INDICATES THE TRACKER WAS STILL FUNCTIONING IN JUNE) RED CIRCLE: SEALS ASSUMED TO GIVE BIRTH DURING TRACKING.

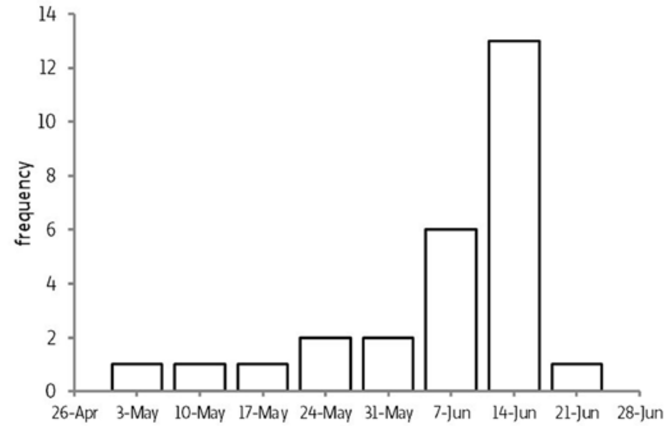


FIGURE 3. FREQUENCY DISTRIBUTION OF THE PRESUMED DATE OF PARTURITION CLASSIFIED PER WEEK FOR THE 27 FEMALES IDENTIFIED AS BREEDING.

(Figure 2). Most of the females identified to have given birth were heavier (mean 77 kg) when weighed at capture in March than the females that did not give birth (mean 66 kg). However, as the trackers may fall off in the course of the breeding period, some females assumed not to have given birth, might have done so after their tracker stopped.

Parturition date varied greatly between females and started earlier than expected, ranging from the beginning of May to the end of June, though the distribution was skewed and the peak in this sample occurred in the week centred around 14th of June (Figure 3). This distribution could be biased towards the early parturition date,

since later parturition was less likely to be recorded, as many tags were shed by then.
When synchronised based on the presumed parturition date, the females clearly altered their dive behaviour during breeding. The mean percentage of time spent hauled-out rose from approximately 20% to over 50% during the first days of breeding, then decreased continuously until weaning. A mirrored pattern was evident in dive-depth and dive-duration as the females presumably stayed with their pup near the surface when not hauled out (Figure 4).

PRE-BREEDING LONGITUDINAL MOVEMENTS OF BREEDING FEMALES

Tracked females assumed to have given birth were separated into those that bred near their capture site (<10 km, n=12, 44%) and those that moved to another site (>10 km, n=15, 56%) (Figure 5 and 6).

The latter group, travelled significantly further eastwards (p-value = 0.007, based on probability test), with an average movement distance of 40 km (se = 15.3). Of these

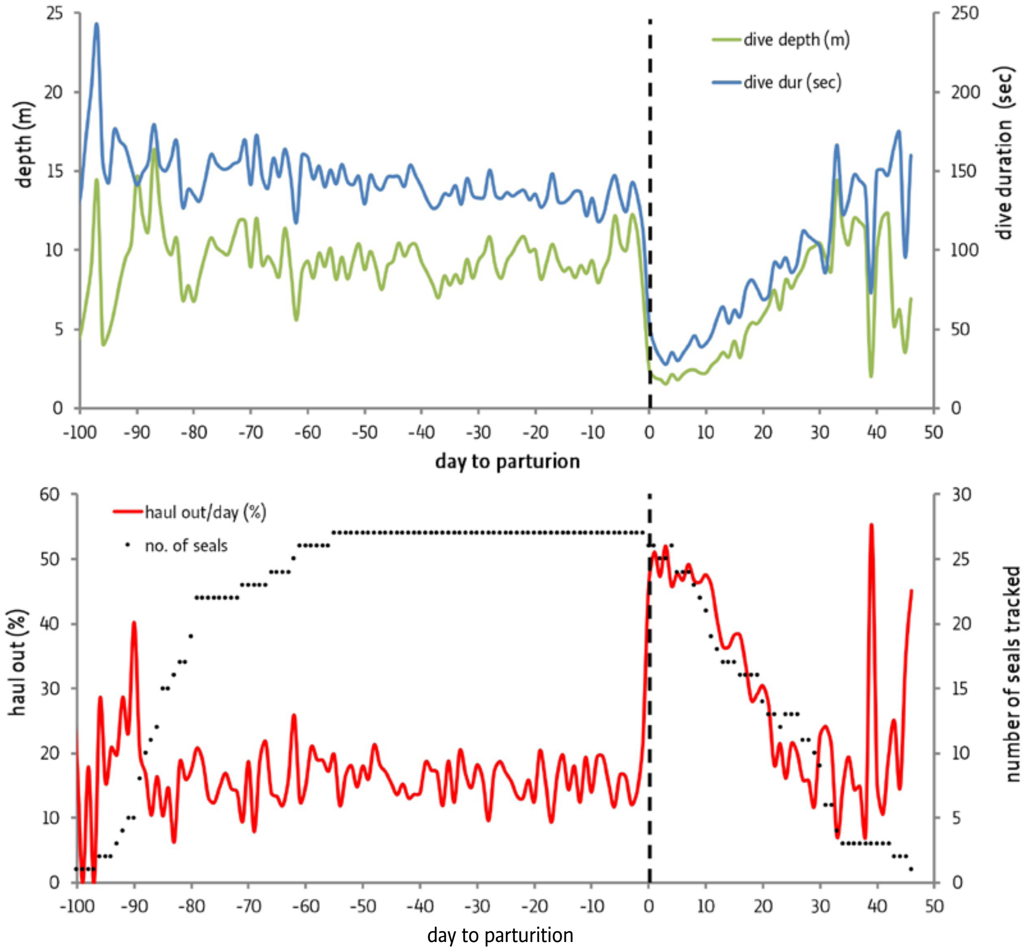


FIGURE 4. FEMALE HARBOUR SEAL BEHAVIOUR IN RELATION TO PRESUMED BIRTH DATE (DASHED BLACK LINE). BOTTOM: AVERAGE HAUL-OUT PERCENTAGE PER DAY (RED) AND NUMBER OF FEMALES PRESUMED BREEDING (BLACK). TOP: AVERAGE MAXIMUM DIVE DEPTH (GREEN) AND MAXIMUM DIVE DURATION (BLUE).

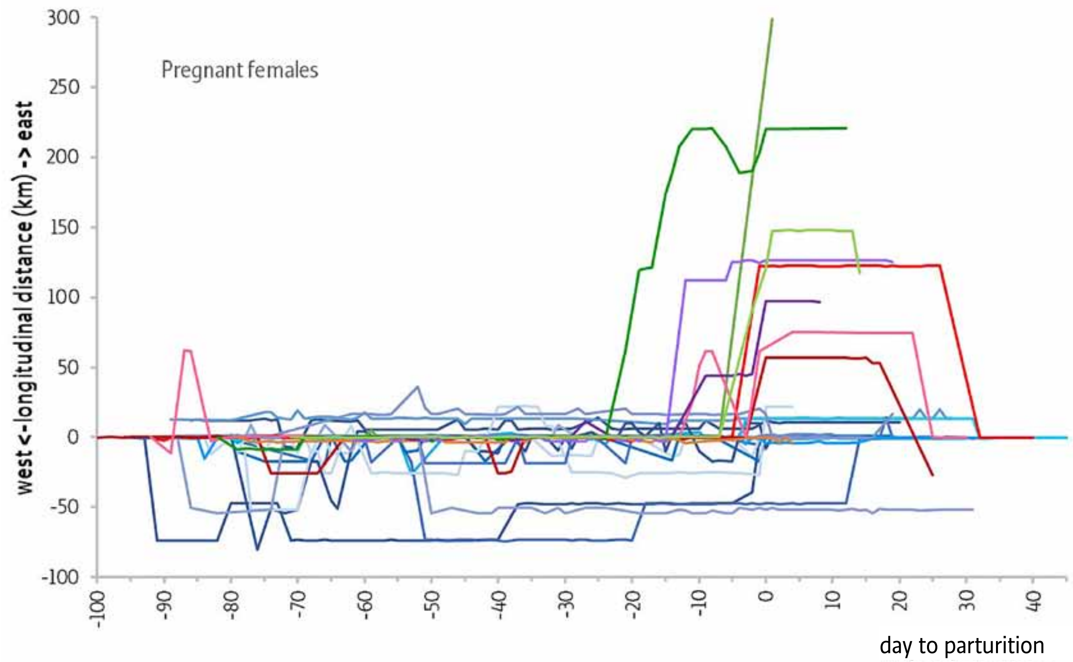
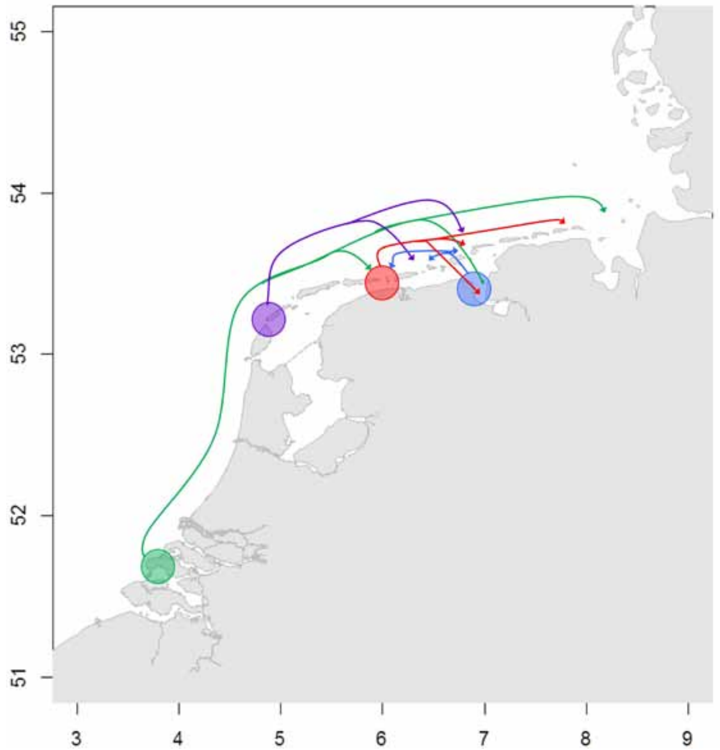


FIGURE 5. SPRING LONGITUDINAL DISTANCE OF HAUL-OUT SITE LOCATIONS COMPARED TO THE CATCHING SITE FOR BREEDING FEMALE SEALS: BLUE = EMS; RED = AMELAND; PURPLE = TEXEL, AND GREEN = DELTA.

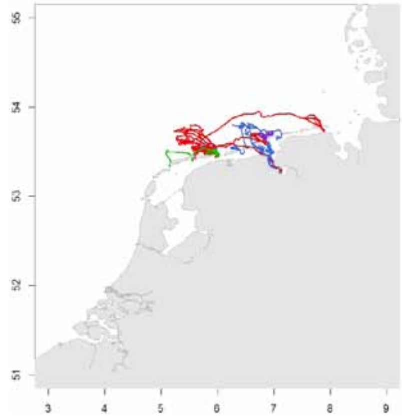
15 individuals, only two females moved to the west (47 and 52 km) of the catching site. The 13 remaining females (48% of those breeding) moved east (10-220 km), seven of which (26% of all breeding females) moved over 50 km east before breeding. While the two seals that moved westwards had done so almost 50 days prior to the assumed parturition date in March and April, most females that moved east, did so within five days of pupping (in May and June, depending on the pupping date). Eight of them moved more than 20 km east within two days prior to the presumed parturition day. Out of the 27 breeding females, eight (30%) bred on haul-outs in German waters.
Six females that had a pup were tracked long enough to observe behavioural changes which indicated the termination of lactation and post-breeding movements (Figure 6). Changes in the longitude of the haul-out locations of the seals occurred 13, 14, 19, 22, 31 and 32 days after parturition. Five of these moved to the west, *i.e.* back into the Dutch Wadden Sea.

OTHER FEMALES DURING THE PRE-BREEDING PERIOD

As many trackers fell off during the pre-breeding period, not all females could be tested for actual breeding. Therefore, females that were classified as 'non-breeding' were probably a mixture of both breeding and non-breeding (adult) females, and sub-adults. Of the 18 adult 'non-breeding' females, 12 transmitters were still active at the end of June, and only two (17%) moved beyond 10 km from there capture site (Figure 7). Of the 12 sub-adult females, eight trackers were still active at the end of June, and four (50%) moved beyond 10 km from the capture site. Although most of these seals moved eastwards prior to the breeding period, there was no significant evidence for an eastward migration (p=0.16 for adults, and p=0.32 for sub-adult non-breeding females), probably due a low sample size.



A. SCHEMATICS OF MOVEMENTS FROM 10D PRIOR TO PUPPING UNTIL PUPPING DATE



B. FROM 10D POST-PARTURITION TO TAG LOSS

FIGURE 6. TRACKS OF THE FEMALES PRESUMED TO BE BREEDING. DIFFERENT MAPS REPRESENT DIFFERENT PERIODS IN RELATION TO PARTURITION. TRACKS ARE COLOUR CODED BASED ON CATCHING SITE: EMS (YELLOW), AMELAND (BLUE), TEXEL (RED) DELTA (GREEN)

MALE PRE-BREEDING BEHAVIOUR

In total, 53 adult males were tagged in March, and 42 of these were still operational in June. Only 15 animals (36%) had moved beyond 10 km from the catching site by June, of which seven to the east, three of which extended further than 100 km (Figure 8). Although these few animals made large eastward movement, on average, there was no evidence for directional pre-breeding migration in males (p=0.80). In May, one animal moved over 230 km west to the Wash in the UK and lost his tracker in mid-June after visiting a haul-out site in the UK that was 135 km west of the catching site. Most movements of the sub-adult males were not clearly related to the breeding period. None of the nine sub-adult males tracked in the pre-breeding period between March and July, showed a clear tendency to move east in relation to the breeding period. The only sub adult male that had moved to the east, had lost its tracker in May.

FEMALES AUTUMN (POST-MOULT) MOVEMENTS

Out of the 27 adult females carrying operational trackers in December, 16 (59%) moved more than 10 km away from their capture site (Figure 9). Out of these, 14 (81%) adult females relocated to haul-out sites more than 10 km to the west during this post-breeding period. Only two animals moved eastwards. The average movement of the migrating animals was 80 km to the west, and six animals relocated to haul-out sites more than 100 km westwards (Figure 9). On average, during

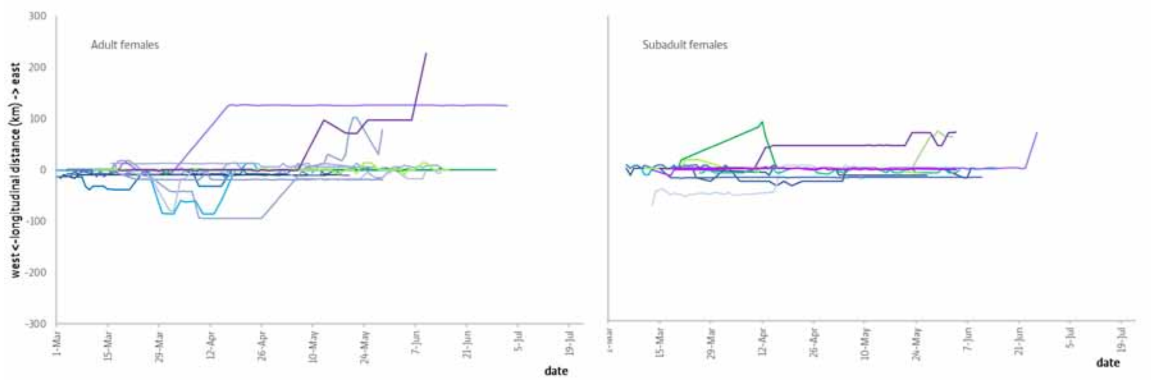


FIGURE 7. SPRING LONGITUDINAL DISTANCE OF HAUL-OUT SITE LOCATIONS COMPARED TO THE CATCHING SITE FOR NON-BREEDING FEMALE SEALS. LEFT: ADULT FEMALES; RIGHT: SUB-ADULT FEMALES. COLOUR INDICATES THE DIFFERENT CATCHING SITES: BLUE = EMS; RED = AMELAND; PURPLE = TEXEL AND GREEN = DELTA.

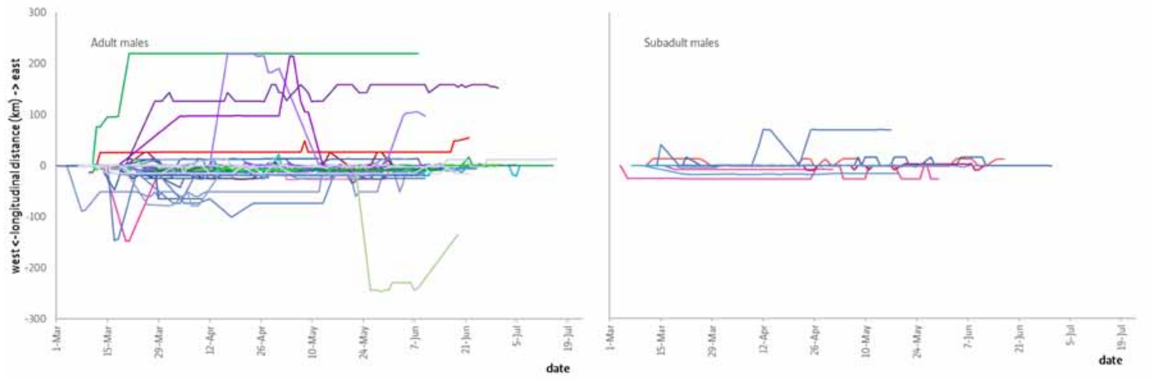


FIGURE 8. SPRING LONGITUDINAL DISTANCE OF HAUL-OUT SITE LOCATIONS COMPARED TO THE CATCHING SITE FOR ADULT MALE SEALS (LEFT) SUB-ADULT MALE SEALS (RIGHT). COLOUR INDICATES THE DIFFERENT CATCHING SITES: BLUE = EMS; RED = AMELAND; PURPLE = TEXEL AND GREEN = DELTA.

post-moult period (from September to December) adult females relocated to more westerly haul-out sites (p<0.0027). Contrary to the pre-breeding movement (eastwards), these post-moult movements were less synchronised and occurred throughout the period September-March.

Post moulting movements of sub-adult females were similar to those of the adult females, but less animals were tracked (n=6). In December, four sub-adult females (67%) relocated to haul-outs more than 10 km west (*i.e.* 71, 83, 61 & 57 km) from where they were tagged. The remaining two were found within 1 km of their capture site at the end of the tagging period.

MALE AUTUMN (POST-MOULTING) MOVEMENTS

In this period, more males were found near (<10 km) their catching site compared to females. Of the 21 adult males with operational trackers in December, only eight (38%) moved beyond 10 km of their catching site (Figure 10). Two animals moved to the east, and the remaining six moved westwards. These six males all relocated more than 50 km west, and four extended their trip to over 100 km west, but there was no evidence for significant directional migration (p=0.16), most likely due to

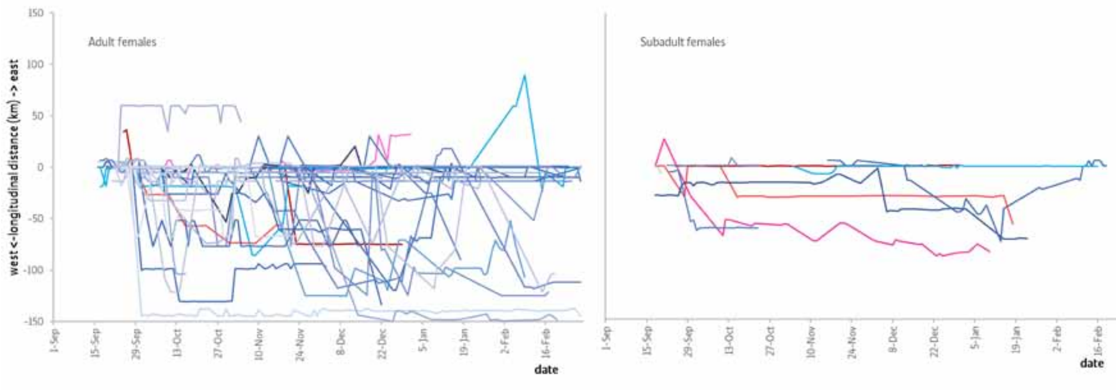


FIGURE 9. LONGITUDINAL MOVEMENTS BETWEEN SEPTEMBER AND MARCH OF ADULT FEMALES (LEFT) AND SUB-ADULT FEMALES (RIGHT). COLOUR INDICATES THE DIFFERENT CATCHING SITES: BLUE = EMS; RED = AMELAND.

the small sample of migrating animals. The average longitudinal distance of the migrating animals based on their location in December, was 66 km. In March, only nine adult males caught in September, had trackers that were still functioning. The 6 moving beyond 10 km of their catching site, all had moved eastwards, which does suggest directional movement (p-value = 0.014).
For sub-adults, four out of the seven functioning trackers (57%) were found near (<10 km) their catching site, of the remaining 3, one (14%) had gone east.

ESTIMATED ANNUAL MOVEMENT BETWEEN WADDEN SEA REGIONS BASED ON POPULATION COUNT DATA

Based on the percentage of pups born in a region relative to total seals recorded there during the moult, the annual net movement of pregnant females (*i.e.* $\Delta p_i / p_i \cdot 100\%$) between regions of the Wadden Sea was estimated (Table 2; negative results imply a net out-flux of females). The extent of the estimated movement between regions varied substantially over time. During post-epizootic years

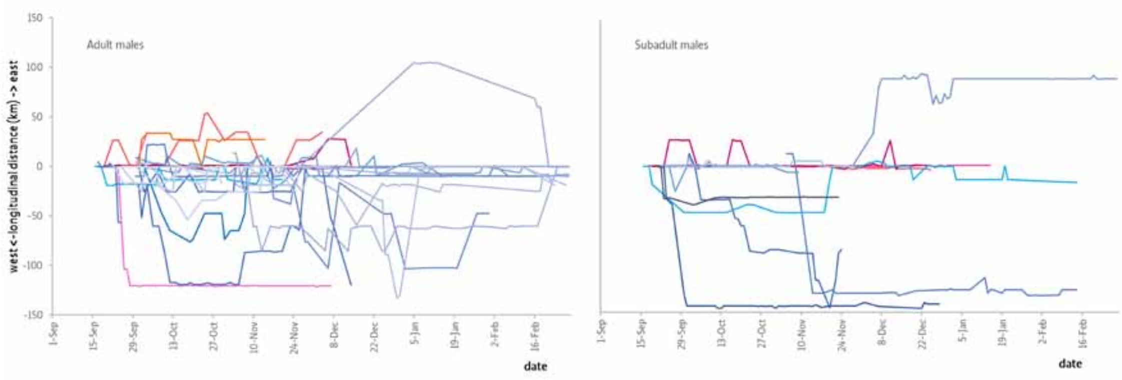


FIGURE 10. LONGITUDINAL MOVEMENTS BETWEEN SEPTEMBER AND MARCH OF ADULT MALES (LEFT) AND SUB-ADULT MALES (RIGHT). COLOUR INDICATES THE DIFFERENT CATCHING SITES: BLUE = EMS; RED = AMELAND.

Region	Average percentage of pups relative to total population count			Estimated net movement of number of pregnant females (ΔP)		
	1974-1987	1989-2001	2003-2014	1974-1987	1989-2001	2003-2014
Denmark	17.5%	17.8%	19.2%	-10.3%	-19.5%	-30.5%
the Netherlands	13.1%	19.9%	21.7%	-32.8%	-5.8%	-21.6%
Lower Saxony and Hamburg	17.8%	23.5%	27.0%	-9.0%	11.5%	-2.4%
Schleswig Holstein	22.9%	21.7%	36.0%	17.3%	3.2%	30.4%
Total Wadden Sea	**19.6%**	**21.1%**	**27.6%**			

TABLE 2. OVERVIEW OF THE AVERAGE PUP VS MOULT COUNT RATIOS FOR THE DIFFERENT REGIONS OF THE WADDEN SEA (BRASSEUR ET AL. SUBMITTED 2017) AND ESTIMATED NET MOVEMENT OF NUMBER OF PREGNANT FEMALES PER REGION I.E. FEMALES PRESENT DURING MOULT THAT WERE NOT IN THAT REGION DURING THE BREEDING PERIOD (NEGATIVE RESULTS IMPLY MORE FEMALES PRESENT DURING MOULT THAN INDICATED BY PUPS BORN).

(2003-2014), coinciding with the movement study, approximately 21.6% of the adult females in the Netherlands during moult, likely had their pups elsewhere. On the other hand, 30.4% of the females breeding in the Schleswig-Holstein region are likely to come from other regions in the Wadden Sea (*i.e.* a negative value).

DISCUSSION

In many species, migrations are perceived as a mass event, with large groups of animals moving in one (general) direction or towards one goal. Good examples are autumn and winter breeding migrations of large whales (*e.g.* grey and humpback whales, (Claphamp 1996, Nerini 1984)), autumn bird migrations from the Northern Hemisphere to southern wintering grounds, or crab and even frog migration to or from breeding ponds (Adamczewska & Morris 2001, Hahn *et al.* 2009, Fahrig *et al.* 1995). Clearly, this is not the case in harbour seals. The results of this study demonstrate, however, a strong tendency of a large proportion of female harbour seals that are assumed to be breeding, to migrate from Dutch waters eastwards prior to their breeding season. Out of 27 apparently breeding females that were tracked through to pupping, 13 (44%) pupped east of where they were caught. Seven (26%) had moved more than 50 km east only days prior to parturition. Moreover, eight females (30%) pupped in Germany, where pup production relative to numbers of seals present during the moult is higher than in other Wadden Sea areas. Also, the majority of adult females and, though to a lesser extent, other seals tracked post-breeding, moved to the west, possibly indicating a return migration, presumably to the haul-outs from which they spend much of the year prior to commuting to their feeding areas.

DIRECTIONAL MIGRATION AS A RESULT OF BREEDING SITE FIDELITY

The observed migration in this study is presumably the result of breeding site fidelity amongst female harbour seals , demonstrated in earlier studies (Schaeff *et al.* 1999). Branded females from the Kattegat-Skagerrak area were observed to return to their breeding grounds for over ten years (Härkönen *et al.* 1999). Also, pups have been tracked back to, or observed to return to, their breeding grounds (Small *et al.* 2005, Härkönen & Harding 2001). This fidelity to breeding sites is recently supported by genetic studies (Olsen *et al.* 2014) which showed fine-scale population structuring in the Scandinavian harbour seal population. Furthermore, there are indications of individual preference, if not fidelity, to certain feeding areas outside the breeding season (Cordes *et al.* 2011).

The trips observed in this study could be similar to the trips seen in, for example, a study by (Womble & Gende 2013) of individual female harbour seal movements in Alaska, that demonstrated seals that travelled extensively during the post moult period (Sept-May) and returned to the initial catching area approaching the breeding period. Similarly, male harbour seals were described to return to breeding sites after spending time in other areas (Bajzak *et al.* 2013, Blundell *et al.* 2011, Lesage *et al.* 2004, Peterson *et al.* 2012). In all harbour seal tracking studies, as with our study, there seemed to be great variation between individuals in timing and distance moved. In the other studies, however, movements of harbour seals between feeding and breeding grounds are without clear shared direction and not considered in terms of being a migration. The breeding migration by harbour seals in the Wadden Sea may be exceptional in that sense.

In general, harbour seal pups are weaned after approximately 24 days after birth and are expected to scatter after approximately a month of post weaning fast (Small *et al.* 2005). When they reach adulthood, many seals could return to their birth site, while a proportion might choose to settle in a new area. Hence, all populations of harbour seals likely exhibit some form of breeding season migration to natal grounds. Since from a very young age the seals are not supported by the guidance of their elders or socialised in a group, as many other mammalian species do, the direction of the movements is expected to be subject to large individual variation.

In the Wadden Sea, the observed breeding migration towards the east by a portion of the seals, especially breeding females, could have been initiated by disparate former hunting or management regimes. When hunting stopped, females extant at the time might have continued to return to their breeding grounds, which were best protected in German waters, and their offspring might continue to perform this breeding season movement. The larger number of females that survived in the German regions produced many more pups than did the remnant, post-hunt, populations in the Dutch and Danish regions. The low pup production in Dutch waters was further hampered by high pollutant levels which reduced female fecundity (Reijnders 1981, Reijnders 1986). Despite recovery of the breeding areas in the Netherlands, where currently approximately 20% of all pups in the Wadden Sea are born, the easterly migration by a proportion of the population still occurs.

The present study is the first to document a coordinated, breeding-related, annual migration within a harbour seal population. It will be interesting to observe for how long the directional, seasonal migration persists. Potentially, after sufficient time for the population to recover, through dispersal, from the disparity between regions in birth rates, the directional, Dutch to German breeding season migration will

become obscured.

Based on these findings, one would expect to observe similar directional breeding migration of harbour seals where suitable breeding areas are distant from feeding grounds and the seals are forced to migrate. This might be the case for the southern Dutch Delta area where approximately 600 seals were counted during the moult in 2013, and average growth is over 20% per year, despite the relatively small areas suitable for breeding and low pup numbers: in 2013 less than 50 pups were born (Arts *et al.* 2015). Tracking results showing adult females moving to the Wadden Sea for the breeding season corroborate this supposition (Brasseur & Reijnders 2001a, Brasseur & Reijnders 2001b, Reijnders *et al.* 2000). This latter case might be similar to, for example, the elephant seals which are also weaned at an early age (thus not taught by their parents) but are known to migrate to and from their feeding grounds back to their breeding areas, often thousands of kilometres away (Hindell *et al.* 2016). Alternatively, it could also reflect the Dutch-German migration within the Wadden Sea, of a step toward colonisation which is being partially retarded, or distantly supported, by fidelity to a safe and distant breeding ground.

EXTENT OF MIGRATION BETWEEN REGIONS

Change through time in the distribution of pups across the different regions of the Wadden Sea (Table 2) could simply reflect variation in the surveys as a result of timing, or environmental conditions during the surveys. More likely, or additionally, it reflects selective survival and recovery of seals from a range of influences. These include historic hunting or the PDV epizootics, which affected various sections of the population differently, depending on the time of breeding when the disease successively reached the different regions (Härkönen *et al.* 2006b). It could also reflect more local factors, such as pollution levels in some Dutch waters in the 1980's. Further coordinated monitoring of pup production, population levels and movements of seals well help elucidate the driving factors influencing balanced harbour seal pup production in the Wadden Sea.

Currently, the tendency for adult females to migrate east to breed, as evident in the tracking data, seems to be slightly higher than the population survey results suggest. From the sample of the assumed breeding females in this study, 30% bred in Germany whereas 21.6 % (Table 2) could be expected based on the counts. The tracking sample size is small compared to total seal numbers, however, such that the differences may not be significant. Nonetheless, there are also considerable differences between year and the catch locations, so it is worth speculating on what might cause the disparity. The difference between the observed and expected number of migrators could relate to differences between sampling locations over time. For instance, the largest sample of seals was in the eastern Dutch Wadden Sea, the Ems Estuary, close to the German border, in 2009-2011 (Table 1, Figure 1 & 6). In later years, more seals were tracked from westerly locations (Ameland and Texel) and the outer southern Delta. The females in the later years travelled further east (mean 127 km, range 18 to 299 km, n=9) than did the females caught in the Ems Estuary (mean 2 km west range 51 km west to 21 km east, n=18). Differences in pup production within the Dutch Wadden Sea have been documented in earlier studies, with the Ems area identified as having a relative surplus of pups (Ries *et al.* 1999, Reijnders 1978a). Clearly, further detail on the migrations of harbour seals across the Wadden Sea are yet to be revealed.

CONCLUSION

The results from this study are supportive of the hypothesis (Brasseur *et al.* submitted 2017), that a proportion of females from Dutch waters migrates east into German waters to have their pup, and then back into Dutch waters after breeding. Presumably, this directed migration is a remnant of historic regional differences in pup production that resulted from uneven hunting pressure. Site fidelity of the breeding females and natal philopatry of their pups means that, in this long-lived species, the differences are still apparent even after almost half a century. Such directional migration might not be apparent in other areas, but it is likely that many harbour seal populations exhibit some form of breeding season migration from feeding grounds to breeding grounds. The directionality of the migration will be influenced by past and present variations in survival across the populations' range and could be masked by the strong individual variation observed in the species. Potentially, the study of the movements of these highly individual animals might provide insight into more fundamental questions on migration and ecological questions related to, for example, population development and population genetics.

SUPPLEMENT

	Female adult				Female sub adult				Male adult				Male sub-adult				
deployment	MAR	SEP	NOV		MAR	SEP	NOV		MAR	SEP	NOV		MAR	SEP	NOV		
	43	**29**	**11**	**83**	**13**	**13**	**2**	**28**	**54**	**32**	**9**	**95**	**9**	**15**	**2**	**26**	**232**
15 Sep - 1 Oct		29		**29**		13		**13**		32		**32**		15		**15**	**89**
1 Oct - 15 Oct		29		**29**		12		**12**		29		**29**		15		**15**	**85**
15 Oct - 1 Nov		29		**29**		12		**12**		28		**28**		15		**15**	**84**
1 Nov - 15 Nov		25	11	**36**		10	2	**12**		27	9	**36**		14	2	**16**	**100**
15 Nov - 1 Dec		20	11	**31**		10	2	**12**		24	9	**33**		12	2	**14**	**90**
1 Dec - 15 Dec		17	11	**28**		10	2	**12**		20	9	**29**		7	2	**9**	**78**
15 Dec - 1 Jan		15	11	**26**		10	2	**12**		12	9	**21**		7	2	**9**	**68**
1 Jan - 15 Jan		10	11	**21**		10	2	**12**		8	9	**17**		4	2	**6**	**56**
15 Jan - 01 Feb		8	11	**19**		2	2	**4**		5	9	**14**		2	2	**4**	**41**
01 Feb - 15 Feb		5	11	**16**		1	2	**3**		5	8	**13**		1	2	**3**	**35**
15 Feb - 01 Mrt		5	11	**16**			2	**2**		5	7	**12**		1	2	**3**	**33**
01 Mrt - 15 Mrt		3	9	**12**			1	**1**		3	7	**10**			1	**1**	**24**
15 Mrt - 1 Apr	43	3	7	**53**	13		1	**14**	54	2	6	**62**	9		1	**10**	**139**
1 Apr - 15 Apr	42	2	5	**49**	13		1	**14**	52	2	5	**59**	9			**9**	**131**
15 Apr - 1 May	42	2	4	**48**	12		1	**13**	52	1	4	**57**	9			**9**	**127**
1 May - 15 May	42	2	3	**47**	11		1	**12**	52	1	3	**56**	9			**9**	**124**
15 May - 1 Jun	41	2	3	**46**	10			**10**	48	1	1	**50**	8			**8**	**114**
1 Jun - 15 Jun	35			**35**	8			**8**	44	1	1	**46**	6			**6**	**95**
15 Jun - 1 Jul	27			**27**	3			**3**	22		1	**23**	2			**2**	**55**
1 Jul - 15 Jul	12			**12**	1			**1**	7			**7**	1			**1**	**21**
15 Jul - 1 Aug	4			**4**	1			**1**	2			**2**				**1**	**8**

SUPPLEMENT TABLE 1 BI- WEEKLY OVERVIEW OF NUMBER OF TRACKED SEALS

		AUTUMN			SPRING		
		No. of seals	Average tagging duration (d)	range	No. of seals	Average tagging duration (d)	range
Female		**47**	**106.91**	**25-246**	**57**	**93.84**	**43-135**
adult		**39**	**107.31**	**25-246**	**43**	**97.37**	**53-135**
	2007	1	65.00	65-65			-
	2009	11	128.36	71-246	8	93.50	53-109
	2010	11	140.91	96-198	10	101.80	76-123
	2011	12	67.83	25-157	12	92.92	66-133
	2013	2	73.00	71-75	1	94.00	94-94
	2014			-	9	104.22	72-135
	2015	2	99.00	97-101	3	91.33	87-99
sub-adult		**8**	**105.00**	**34-178**	**14**	**83.00**	**43-123**
	2009	1	138.00	138-138	2	63.50	43-84
	2010	2	142.50	107-178	3	88.00	79-100
	2011	2	34.50	34-35	2	106.50	90-123
	2013	2	121.50	118-125	3	72.33	56-84
	2014			-	3	88.00	73-102
	2015	1	105.00	105-105	1	77.00	77-77
Male		**49**	**96.31**	**32-237**	**62**	**87.40**	**34-122**
adult		**33**	**104.00**	**41-237**	**53**	**88.21**	**34-122**
	2007	4	111.25	44-154			-
	2009	8	100.25	51-196	7	83.43	49-115
	2010	9	154.78	89-237	10	82.40	34-102
	2011	5	54.60	41-78	9	90.22	73-113
	2013	3	76.67	63-84	4	82.25	49-111
	2014			-	17	92.88	76-122
	2015	4	72.25	53-83	6	91.17	68-110
sub-adult		**16**	**80.44**	**32-153**	**9**	**82.67**	**48-104**
	2007	2	49.50	32-67			-
	2009	2	106.00	59-153	1	90.00	90-90
	2010	2	112.50	105-120	1	103.00	103-103
	2011	5	66.00	43-101	1	48.00	48-48
	2013	3	67.67	32-103	3	85.33	66-104
	2014			-	1	88.00	88-88
	2015	2	109.00	99-119	2	79.50	75-84
Total		**96**	**101.50**	**25-246**	**119**	**90.49**	**34-135**

SUPPLEMENT TABLE 2. OVERVIEW OF TRACKING RESULTS FOR HARBOUR SEALS IN THE NETHERLANDS