6. GREY SEAL TRACKING REVEALS DIFFERENT BEHAVIOURS OF RESIDENT AND TRANSIENT POPULATION COMPONENTS

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SUMMARY

Grey seals recently recolonised the Dutch coasts. The exponential population growth is fuelled by immigrating grey seals from the UK, who subsequently breed in the Netherlands. In addition, population survey data suggested that a number of grey seals use the Dutch area to forage, but return to the UK to breed. Although such population surveys can provide insight into discrepancies and regional imbalances in the number of seals observed on land, the data are insufficient to measure the actual underlying migration processes. Using an extensive data set on individually tracked grey seals, we study the movement of grey seals in relation to where they forage and breed.
The tracked seals of different age and sex classes were recognised to be either resident or transient based on where they went during and outside the breeding season. The grey seals breeding in the Netherlands also only haul-out in the Netherlands throughout the period between the moult and next breeding season. Only animals that bred elsewhere (respectively 50% of the adult females and 67% of the adult males tracked in this study) visited regions other than Dutch waters during the rest of the year. Some however, remained in Dutch waters continuously between the breeding trips to other countries. The tracking data suggest a higher number of grey seals might be visiting the Dutch waters than was estimated in a population analysis based on aerial surveys. These results might also have consequences for the population modelling used to estimate the grey seal population size in the UK.
As eastern Atlantic grey seals in the North Sea are a mixed meta-population, coordinated, international collaborations are needed to assess their status and trends. Since transient seals might be driven by intraspecific competition, ecological studies on for example, the role of grey seals as a top predator, need to consider the entire North Sea grey seal population.

INTRODUCTION

From the 11th century onwards the grey seals of the eastern Atlantic were confined to the northern United Kingdom but, since the mid-1900s, have greatly expanded their range and population size (Brasseur *et al.* 2015, Svensson *et al.* 2011, Lonergan *et al.* 2011, Abt & Engler 2009, Bowen *et al.* 2007). Though many individuals appear to remain in local areas, the expansion in range is potentially stimulated by the long-distance movements of some individuals (Austin *et al.* 2004). In the Netherlands, the range expansion by grey seals saw the first pup born in 1985 (Reijnders *et al.* 1995). By 2015, there were 657 pups born and, in March-April 2016, a total of 3,696 grey seals were counted on Dutch sandbanks (Brasseur *et al.* 2016). The population counts suggested that the local breeding population appeared to be boosted each year by young seals, but also by temporary visitors that were present only for part of the year, outside the breeding season (Brasseur *et al.* 2015). When and where seals allocate their foraging and breeding time, is largely unknown, but has relevance to managing the grey seal population (Russell *et al.* 2013), as well as relevance for understanding how any pinniped species colonises new areas (Gaggiotti *et al.* 2002).

Grey seals are the largest pinnipeds in the temperate waters of the North Atlantic Ocean. Based on distribution, size, behavioural and genetic differences, they are

divided into three distinct populations: the Baltic, the western Atlantic, and the eastern Atlantic (Klimova *et al.* 2014, Bonner 1972). North Sea grey seals are part of the eastern Atlantic population (Reijnders *et al.* 1993). Though most populations are presently thriving (Brasseur *et al.* 2015, Svensson *et al.* 2011, Lonergan *et al.* 2011, Abt & Engler 2009, Bowen *et al.* 2007), the general perception that grey seals were rare persisted until the second half of the 20th century (Bonner 1989). From the Middle Ages through to the 1900s, the eastern Atlantic population was subjected to ongoing hunting, causing severe restrictions in their range (Härkönen *et al.* 2007a). Grey seal remains were common in early findings along the Dutch coast, but disappeared in the late Middle Ages, with only occasional vagrants recorded through to the mid-1900s (Reijnders *et al.* 1995). After protection of the grey seals in the UK during the mid-1900s (Lambert 2002), the species slowly recolonised the British North Sea coasts, which eventually facilitated the emigration of animals towards mainland Europe (Abt *et al.* 2002, Hall *et al.* 2001, Reijnders *et al.* 1995, Brasseur *et al.* 2015, Härkönen *et al.* 2007a, Dupuis 2011).

In the Netherlands, grey seals breed between the end of November and early January, with the peak in the first weeks of December; they moult in March-April (Schop *et al.* 2017, Brasseur *et al.* 2015). Aerial surveys conducted between 1985 and 2014, were used to demonstrate the local breeding population grew at an average rate of 19% annually (Brasseur *et al.* 2015). This was beyond the intrinsic growth rate and, therefore, was likely fuelled by a constant influx of new animals. Also, there was a surplus of seals observed in surveys during the moult and the feeding season not participating in the local breeding population. Based on the numbers in the neighbouring countries, immigrating animals most likely came from the eastern North Sea coast of the UK, where the population was much larger and also growing in numbers (SCOS 2010). Potentially, grey seals that are dependent on resources in Dutch waters (i.e. resting sites and prey) comprise both those breeding locally and those breeding elsewhere, most likely the UK. Though the aerial surveys do provide a strong suggestion for these permanent and temporary visitors, they are not adequate to determine the actual movements.

The movements of seals are expected to vary between age and sex classes. Female grey seals show a high fidelity to the pupping sites where they return to after the feeding season between the moult and breeding (Pomeroy *et al.* 2000b, Pomeroy *et al.* 2001, Pomeroy *et al.* 2005). However, a variable proportion of females may use different regions for feeding and breeding (Russell *et al.* 2013, Vincent *et al.* 2005, Gerondeau *et al.* 2007). Females used different feeding areas than males, especially immediately following moult and in the months before parturition (Beck *et al.* 2003b, Breed *et al.* 2006). Young seals near Sable Island (Nova Scotia) tend to avoid feeding areas of the adult females, which is most likely driven by intraspecific competition in this densely populated area (Breed *et al.* 2013). As the breeding colonies on the UK coasts in the southern North Sea have grown explosively in recent decades (SCOS 2016) there is a high probability of young grey seals, possibly also adult animals traversing towards haul-out sites in the Netherlands and foraging from them. The use of the Dutch waters and haul-outs by transient seals of different age and sex classes likely results in a seasonal change in representation of the different age and sex classes.
To better understand relationships and differences between the resident and the temporary visiting individuals in the Netherlands, grey seals were tracked during

non-breeding and breeding periods of the year. Tracked seals were recognised to be either resident or transient based on where individuals went during the foraging and breeding season.

MATERIALS & METHODS

GREY SEAL TRACKING

Between 2007 and 2015, 84 grey seals were captured and fitted with tracking devices in the framework of different telemetry projects in the Netherlands (Brasseur & Kirkwood 2016, Kirkwood *et al.* 2015, Brasseur & Kirkwood 2015, Kirkwood *et al.* 2014, Brasseur *et al.* 2010). Catch sites were spread across the Dutch coastal zone: Ameland in the central Wadden Sea, Texel in the western Wadden Sea and coastal sandbars in the southern Delta region (Figure 1). Deployment periods were either in late winter/ early spring (March-May; n=58), following the grey seals' moulting period, or in late summer/ autumn (September; n=26), preceding the seals' breeding season (Nov-Jan). All seals were captured by rapidly setting a specifically designed seine-net of approximately 100 m length in front of a group of seals lying on a haul-out site, typically an intertidal sandbar. Seals fled into the water and became ensnared in the net, which was hauled onto the sandbar. Seals for tracking were selected, aiming for equal numbers of adult females, adult males and sub-adult animals of either sex. Unselected seals were immediately released. The selected seals were restrained in specifically-designed cradles to be processed. They were sexed, measured (standard -nose to tail- and total length in cm) and weighed (±0.5 kg). All seals were released within 90 min after the net had been set. Females were defined as adult when they were larger than 135 cm, males when they were larger than 150 cm.

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 timing data, which were relayed via the GSM mobile phone system to data storage facilities (Cronin *et al.* 2010). The trackers 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 spring (March-April).

DATA PROCESSING

For this study summary data were used, summarising the seals behaviour, at either 2- or 4-hour interval. These summaries included the percentage of time spent diving, hauled out and surfing but also maximum and average dive depth. Summary data were linked to the GPS location nearest in time. Each summary record with at least 80% haul-out was subsequently linked to the closest known haul-out site along the North Sea coast. Each summary record was allocated to one of the three periods: the foraging period prior to breeding (March to November), breeding (November to December) and post-breeding (December-February). As the aim was

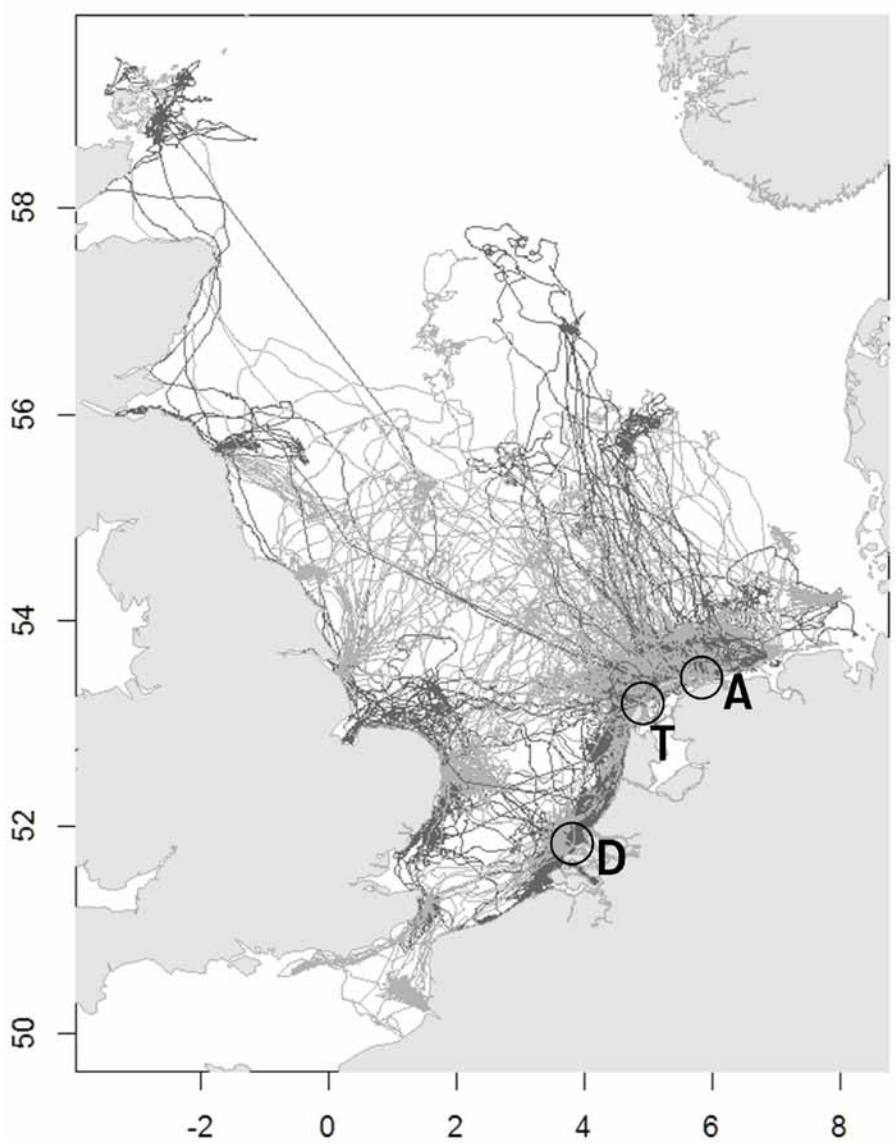

FIGURE 1. TRACKS OF ALL GREY SEALS CAPTURED IN THE DUTCH WATERS 2007-2015. MALES ARE INDICATED IN LIGHT GREY FEMALES IN DARK GREY CAPTURE AREAS ARE INDICATED WITH A BLACK CIRCLE (A=AMELAND, T=TEXEL AND D= DELTA REGION).

to link seals to potential breeding areas, only seals with trackers functioning until the early December were considered in this study. Grey seals in the North Sea may commence breeding in November in the UK, or December in the Netherlands. Within this group, breeding seals were identified based on their movement. Breeders were assumed to be those that attended known breeding sites during the breeding period and remained there sufficiently long to participate in breeding. Persistent presence (at least 5 days) near these sites was used as the primary criterion to define breeding animals. Adult males could hold territories for several weeks or, if unable to hold territories, may reside on land or in the water for just a few days while attempting to mate with departing females. Adult females had to remain at a breeding colony for at least several days to have a pup and approximately 19 days to

raise a pup to weaning (Pomeroy *et al.* 1999). As males do not remain with the pup, which is initially a poor swimmer, they may dive more often than females during the breeding season (Lidgard *et al.* 2003). Movements between haul–out sites of both breeding and non-breeding seals were investigated.

RESULTS

Tracking data up to and including December were obtained for 34 seals (Table 1); 21 females and 13 males (Table 1). The majority (28) of the 34 seals had been captured at the Wadden Sea sites, with six coming from the Delta.

Out of the selected seals, all adults (16 females and six males) were identified to have participated in breeding based on their restricted movement. During the identified breeding period, these seals spent more time hauled-out, less time diving and, when diving, attained shallower depths than during the pre-breeding period (Table 2).

For the seals determined to have participated in breeding, there were distinct changes in behaviour on the day of arrival at their breeding site (Figure 2, Table 2).

Out of the 16 females, two females did not remain at breeding sites sufficiently long to have raised a pup to weaning. Both animals left the breeding site and were diving for more than 80% of their time after 6 days. Three other females spent some time diving during the period they were presumably suckling a pup. The other 11 seals

Catch location	Catch period	Fa	Fsa		Ma	Msa		total
Delta	spring	4		4	1	1	2	6
Texel (east Wadden)	spring	7	1	8	3		3	11
	autumn		1	1		1	1	2
Ameland (central Wadden)	autumn	6	2	8	2	5	7	15
Grand Total		16	5	21	6	7	13	34

TABLE 1. OVERVIEW OF SEALS THAT RETAINED THEIR TRACKER UNTIL THE BREEDING SEASON

	Males		Females	
	breeding	prior to breeding	breeding	prior to breeding
Haul-out %	>30%	~26%	>40%	~24%
Dive%	<20%	~48%	<10%	~50%
Dive depth (avg.)	<5m	~15%	<5m	~12m

TABLE 2. COMPARISON OF BREEDING AND NONBREEDING BEHAVIOUR

remained on land for at least 16 days. All the six males presumed to breed spent some days diving during the period they were attending a breeding site. Interestingly, two out of the six males moved between several breeding sites during the breeding season.

In the months of March to November, i.e. prior to the breeding period, 14 of 21 females (67%) only hauled out in the Netherlands. These comprised nine adult and six sub-adult females (Figure 3), and included just one of the four females (all were adult) tracked from the Delta area. The remaining seven females all visited the UK in this period prior to breeding. Out of 13 males, eight (62%; three adults, five sub-adults) used only Dutch haul-out sites prior to breeding. One adult male did

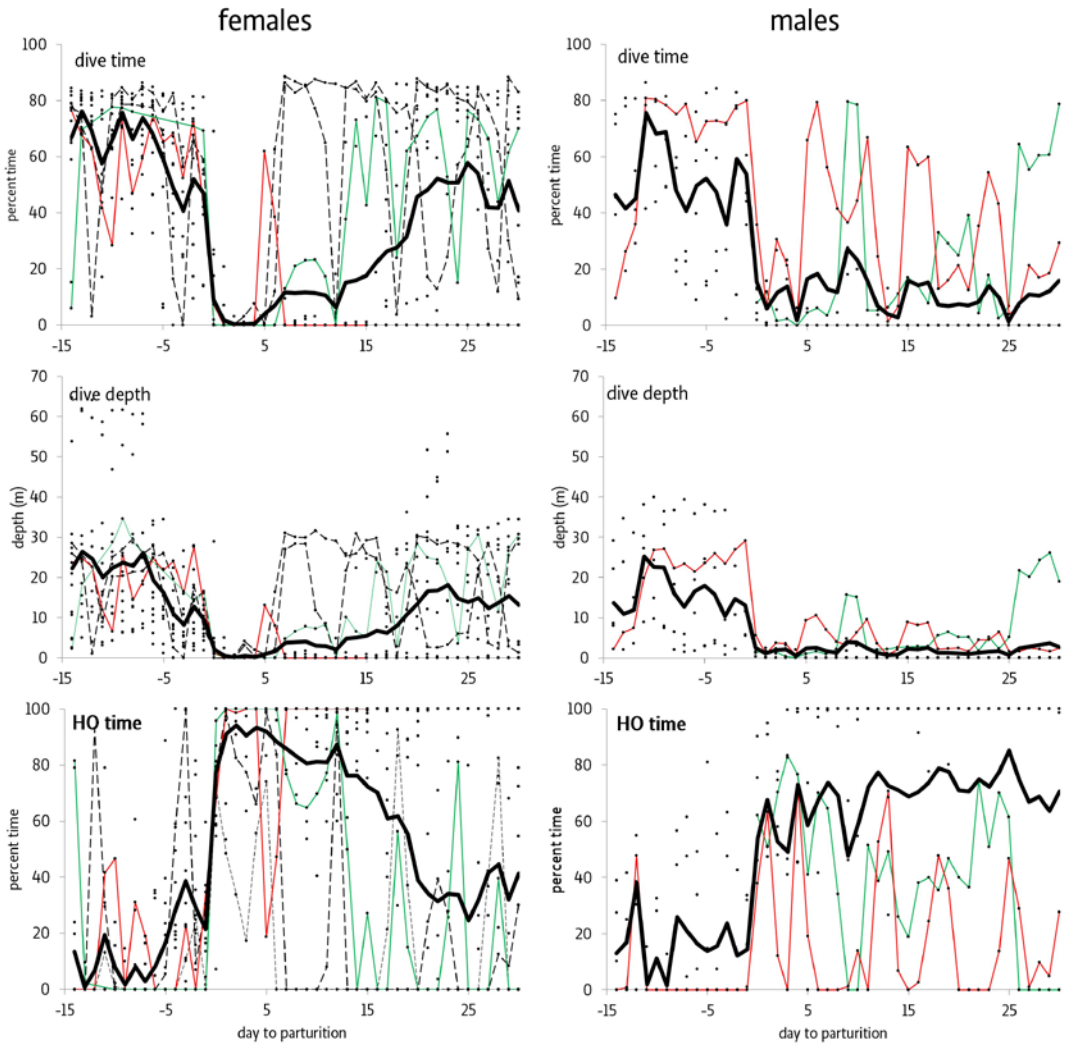

FIGURE 2. THE AVERAGE DIVE DEPTH (TOP ROW) PERCENT OF TIME SPENT DIVING (CENTRE ROW), AND HAULED OUT TIME (BOTTOM ROW) FOR BREEDING FEMALES (LEFT; N=16) AND MALES (RIGHT; N=6). THICK BLACK LINES INDICATE THE AVERAGE, BLACK DOTS INDICATE VALUES FOR THE INDIVIDUAL SEALS. DOTTED LINES INDICATE FEMALES THAT MIGHT NOT HAVE SUCKLED PUPS THROUGH TO WEANING, AND COLOURED LINES INDICATE ANIMALS (MALE AND FEMALE) THAT PERFORM DIVES DURING THE BREEDING PERIODS.

move to the Delta area from the Wadden Sea. The remaining five males visited sites in other countries, one adult male went to the UK, one (adult) hauled out in France and the UK, and three (two adults, one sub-adult) visited Germany, two of which also moved to the UK.

During the breeding period, all of the sub-adult females and eight of the nine adult females which had stayed in the Netherlands prior to breeding, stayed in the Netherlands to pup (Figure 3 and Figure 4). Seven females (44% of the adult females) had their pup in the UK and one (6% of the adult females) moved to Germany to breed. Two (33%) adult males move to German waters and two moved to the UK

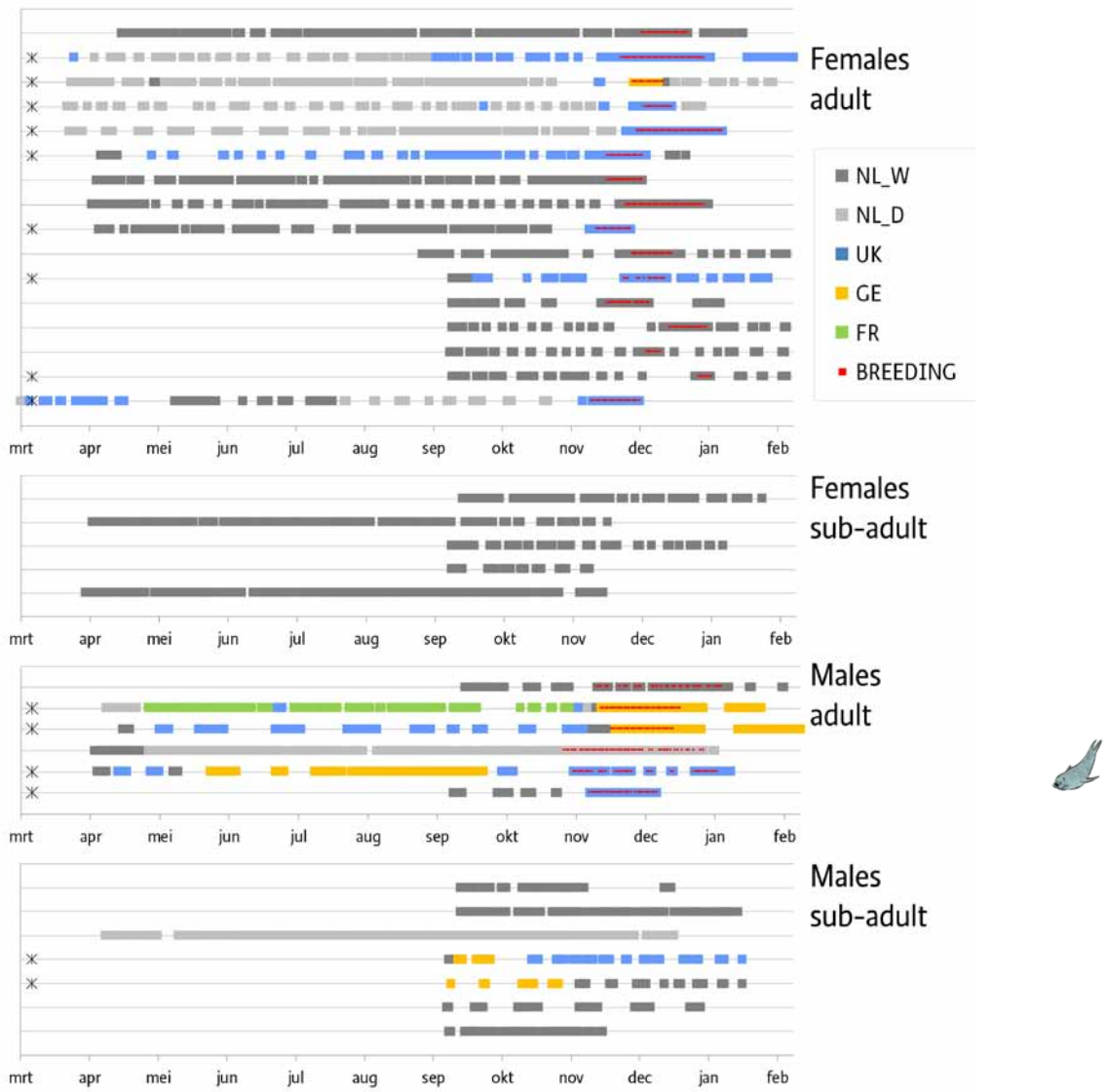

FIGURE 3. HAUL-OUT REGION FOR INDIVIDUAL SEALS DURING THE TRACK PERIOD. INDIVIDUAL SEALS ARE REPRESENTED AS A SINGLE LINE. SQUARES REPRESENT DAYS WITH >80% HAUL-OUT EVENTS, COLOUR CODED DEPENDING ON THE REGION: NL_W=DUTCH WADDEN SEA; NL_D= DUTCH DELTA; UK= UK; GE=GERMANY; FR= FRANCE.* INDICATES TRANSIENT SEALS.

during the breeding period. One sub-adult male also went to the UK. Eight males (six sub-adults, two adults) remained in Dutch waters during breeding. The two remaining sub-adult males spend most of the breeding period in the Netherlands, and then one moved to the UK and the other to Germany.
In the post-breeding period for adults, or after December 31st for sub adults, most seals remained in their breeding region, although three females that pupped elsewhere (two in UK and one in Germany) were tracked back to the Netherlands.

DISCUSSION

This study demonstrates the grey seals' flexibility in choice of haul-out sites during foraging and breeding, which likely assisted their rapid recolonization of North Sea coastlines since protection from hunting in the mid-1900s. Two important results of the study are singled out for discussion here. Firstly, those grey seals breeding in the Netherlands only haul-out in the Netherlands throughout the tagging period between the moult and breeding season (the 'residents'). Only animals that bred elsewhere visited regions other than Dutch waters during the rest of the year (the 'transients'). Some of these, however, remained in Dutch waters continuously until the breeding season elsewhere. Secondly, the tagging data suggests that the number of animals visiting the Dutch waters might be even higher than was estimated in a population analysis that was based on aerial surveys (Brasseur *et al.* 2015).

Also, in other areas of their geographical range, grey seals were observed with similar transient and resident behaviour: In the UK, 42 to 79% of adult female grey

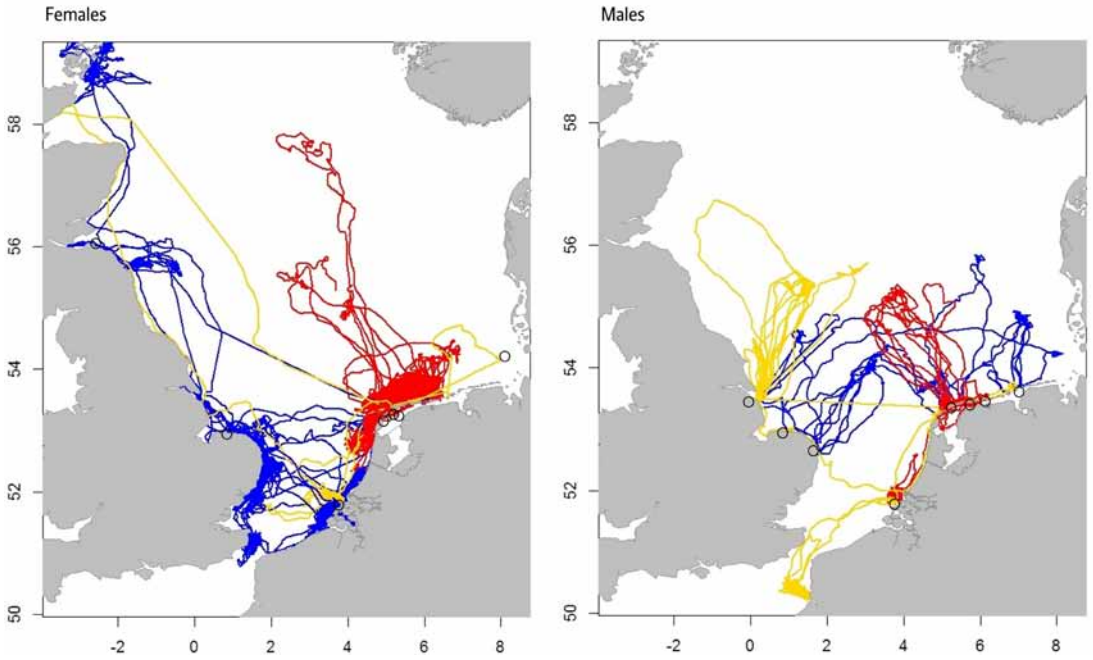

FIGURE 4. MAPS OF THE TRACKS OF THE BREEDING SEALS (LEFT=FEMALES; RIGHT=MALES) COLOUR CODED DEPENDING ON THEIR BREEDING REGION: RED = THE NETHERLANDS; BLUE =UK; YELLOW=GERMANY. BLACK CIRCLES INDICATE THE AREAS WHERE SEALS DISPLAYED BREEDING BEHAVIOUR.

seals used the same regions for breeding and foraging (Russell *et al.* 2013). The proportion of residents and transient grey seals differed substantially between the UK regions. Along the East and South-East coast of the UK, where grey seal numbers have increased exponentially in recent decades (SCOS 2016), both the population survey data and tracking data (n=5), suggested that the majority of grey seals *breeding* there, also foraged in those same regions (residents). In contrast, the majority of animals *foraging* near the East and South-East coast, reproduced elsewhere (transients), mostly in Northern Scotland or Hebrides (Russell *et al.* 2013) . Also at Sable Island, which is the most important breeding site for western Atlantic grey seals, 29% of adults, comprising three of 25 males (12%) and 12 of 27 (44%) females, stayed in the vicinity of the their breeding site to forage (Austin *et al.* 2003). In the Netherlands, all the seals breeding locally continued to use Dutch waters throughout the year to forage. This might be a consequence of the still relatively low numbers of grey seals, as such that the carrying capacity of the region has yet to be reached. Particularly in the Dutch Delta, where despite numbers growing annually (826 grey seals were counted in 2015), records of breeding are still to be made (Brasseur *et al.* 2015, Arts *et al.* 2016). Apparently haul-outs in this region are used as a resting site from which to feed or moult. When breeding, seals move to other areas. This might change in the near future as one of the males recorded in this study remained in this area and tracking data suggests breeding behaviour.
The majority of animals tracked from the Netherlands that reproduce in the UK, do so in the South-East of the UK. This suggests that this region acts as an important source for grey seals in Netherlands. Despite the growing numbers of seals in this UK North Sea region, presumably fuelled by the breeding populations of Northern Scotland (Russell *et al.* 2013, SCOS 2016), a proportion of animals breeding there move to the Dutch region to feed. This suggests that feeding conditions in the South-East of the UK might be more profitable compared to North Scotland, but feeding conditions in the Netherlands might be even better. This could be yet another indication that populations of grey seals in the more northern waters of the North Sea have reached the carrying capacity of the area, causing a southward shift, a process also observed in other top-predators (Hammond *et al.* 2013).
A previous population analysis of the aerial survey data in the Wadden Sea (Brasseur *et al.* 2015) demonstrated that a proportion of grey seals counted in the Netherlands during the moult or post moult (i.e. summer) could be visitors, potentially from the UK. It was estimated a minimum of 150-250 animals were visitors, representing 5 to 8.5% of the total animals observed in the Netherlands, or 1,2% and 0,9% of the UK- North Sea population, excluding pups of the year (Brasseur *et al.* 2015). In the present study, however, 50% of adult females and 67% of adult males tracked from sites in the Netherlands depart from the Netherlands to breed in other regions, most in the UK. Only two sub-adult males, or 17% of all sub-adults, visited other areas. The majority of the seals had spent a considerable amount of time in the Netherlands. Taking into account the estimated age-structure in the population (based on the demographic model presented in Brasseur *et al.* (2015), the proportion of visitors through the year would be more than 30% of the total counts during the post moult and pre breeding season (Table 3).

Recently, estimates of the UK grey seal population size were scaled downwards, because the counts during the summer months suggested that there were much fewer animals than the model based on the pup counts suggested (SCOS 2016). The present study shows that a large proportion of animals observed in the Dutch

	Pups	Sub-adults	Adult female	Adult male	Total
Estimated demography breeding population in Netherlands (N=1000)	161	505	167	167	1000
Proportion of "visitors" during outside the breeding season	?	17%	50%	67%	>38%
Number of visitors	?	103	167	339	>605
Demography during feeding season	>161 (>10%)	608 (<38%)	334 (<21%)	501 (<31%)	>1605

TABLE 3. ESTIMATED NUMBER OF VISITORS PER 1000 LOCAL BREEDING GREY SEALS IN THE NETHERLANDS, BASED ON THE DEMOGRAPHY DETERMINED IN (BRASSEUR *ET AL.* 2015)

waters breed in the UK. Hence, a portion of the UK breeding population may reside for much of the year in other areas, including the international Wadden Sea, the Dutch Delta, the French coasts and, possibly, the Swedish and Norwegian North Sea coasts. All these regions are well within reach of grey seals breeding in the UK. The fact that eastern Atlantic grey seals in the North Sea exchange between the different countries, highlights the importance of having an internationally coordinated and executed survey program. Such a North Sea wide survey program will provide valuable data to monitor the status and trends of the grey seal colonies in the North Sea, but also provide insight into how the growing human use of the area in search for energy and protein sources might influence the grey seal population development and distribution.

In conclusion, the North Sea grey seal population is likely to comprise resident (local) and transient components, with the transient components, possibly driven by for example intraspecific competition as suggested by Breed *et al.* (2013). Further studies could be aimed at better understanding the motivation of individual seals to remain or leave their breeding area to forage and the consequences for the population. Recently, it was proposed that also harbour seals in some areas could be considered as migratory (Brasseur *et al.* submitted, see chapter 4, this thesis). There, it was demonstrated that a proportion of animals foraged in the Netherlands, but driven by breeding site fidelity and natal philopatry, bred in Germany. Intraspecific competition close to the German breeding areas was proposed as one potential driver for this phenomenon. Ecological studies on, for example, the role of grey seals as a top predator should take account of the transient seals that potentially will have great effect on the predation estimates in an area.

APPENDIX 1, LIST OF SEALS TRACKED USED IN THIS STUDY

SEX/ STATUS	REF	L(CM)	W(KG)	START DATE	END DATE
Females Breeding	hg41-874-13	134	139	18-9-2013	18-2-2014
	hg43LZ-Z024-14	149	82	3-4-2014	30-12-2014
	hg43LT-T040-14	152	97	15-4-2014	25-1-2015
	hg41-862-13	154	114	19-9-2013	1-3-2014
	hg41-911-13	154	130	19-9-2013	29-1-2014
	hg43LT-T003-14	155	74	16-4-2014	9-12-2014
	hg43LT-T875-14	159	108	15-4-2014	12-1-2015
	hg41-897-13	162	117	19-9-2013	19-2-2014
	hg43LZ-Z062-14	165	86	4-4-2014	8-1-2015
	hg43LZ-Z046-14	168	101	4-4-2014	18-1-2015
	hg41-906-13	169	169	19-9-2013	22-1-2014
	hg43LZ-Z006-14	170	121	4-4-2014	15-1-2015
	hg38-T737-13	175	96	12-3-2013	19-11-2013
	hg43G-A074-14	178	166	4-9-2014	1-2-2015
	hg46LT-01-15	178	115	28-4-2015	23-1-2016
	hg43LT-T076-14	179	101	16-4-2014	12-12-2014
Females Non-Breeding	hg21g-804-07	120	40	18-9-2008	22-12-2008
	hg41-901-13	120	41	18-9-2013	19-1-2014
	hg51-121-15	123	41	23-9-2015	2-2-2016
	hg16g-F1-07	129	49	12-4-2007	1-12-2007
	hg43LT-T042-14	136	50	15-4-2014	9-12-2014
Males Breeding	hg43LT-T078-14	158	80	16-4-2014	16-1-2015
	hg43LT-T079-14	172	134	15-4-2014	31-10-2015
	hg46LT-05-15	183	126	28-4-2015	22-12-2015
	hg51-113-15	184	169	23-9-2015	9-2-2016
	hg41-860-13	190	246	18-9-2013	15-12-2000
	hg46LZ-06-15	211	180	21-4-2015	25-12-2015
Males Non-Breeding	hg41-866-13	116	39	17-9-2013	20-1-2014
	hg41-867-13	116	42	17-9-2013	24-1-2014
	hg21g-769-07	134	44	18-9-2008	15-1-2009
	hg51-112-15	134	47	23-9-2015	29-1-2016
	hg51-144-15	135	47	23-9-2015	24-12-2015
	hg46LZ-02-15	137	65	21-4-2015	27-12-2015
	hg41-900-13	147	34	18-9-2013	3-2-2014