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Grey and harbour seals in France: distribution at sea, connectivity and trends in abundance at haulout sites

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Abstract

Grey (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) are sympatric seal species, but they display distinct strategies of habitat use and connectivity between haulout sites. The distribution patterns and variations in relative abundance of both species were investigated along the French coast of the English Channel, at the southern limit of their range where seal numbers are increasing. Regular censuses conducted at all main haulout sites in mainland France showed significant seasonal variations at most sites, with more harbour seals counted during summer (breeding and moulting seasons), and more grey seals during summer only in the eastern English Channel. Trends in maximum haulout numbers at haulout sites showed a significant increase over the last five years, ranging from 9.7 to 30.9% per year for harbour seals, and from 5.8% (in the western English Channel) to 49.2% (in the eastern English Channel) per year for grey seals. These rates of increase in grey seal numbers are not linked to local pup production and most probably result from seal movements from the southwest British Isles and the North Sea, respectively. Aerial surveys conducted across the English Channel showed that most seal observations at sea were concentrated in the north-eastern English Channel. Telemetry showed that the 28 harbour seals tracked remained highly coastal, within a radius of 100km from their haulout sites, and did not move to other known colonies. Grey seals moved much greater distances, reaching up to 1200 km from their capture site. More than half of the 45 grey seals tracked crossed the English Channel, especially during the breeding season, moving to known colonies in the southwest British Isles and the North Sea. Combining individual tracks and long-term surveys of the seal populations allowed a better understanding of the dynamics of these populations and their connectivity at a larger regional scale. The findings provide direct information for the management of grey and harbour seals within the frame of the Marine Strategy Framework Directive, and highlight focus areas where potential interactions between the two species should be monitored.

Keywords: tracking; telemetry; density; census; management units; English Channel; MSFD; OSPAR

1. Introduction

Grey (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) are sympatric seal species with overlapping ranges in Europe and particularly around the British Isles (Jones et al. 2015). As central place foragers, their habitat preferences are constrained by the alternative use of the marine environment, particularly for foraging, and terrestrial haulout sites, for breeding, moulting and resting. During the breeding and moulting seasons, both species spend more time hauled out, while they spend comparatively more time at sea the rest of the year, in order to replenish their body reserves. In the northeast Atlantic, harbour seals breed in June-July and moult in August, while grey seals breed from September to December and moult between February and April. Harbour seals are slightly smaller than grey seals, and are usually reported to forage in shallower waters (Bajzak et al. 2012). They also tend to move shorter distances from their haulout sites, and a number of studies have suggested that distinct haulout groups can be considered as discrete populations (Thompson et al. 1996; Huber et al. 2012; Dietz et al. 2013). On the other hand, both juvenile and adult grey seals can exhibit long distance movements (Sjöberg et al. 1995, McConnell et al. 1999, Oksanen et al.

2014), and a number of studies have shown that they can alternatively use different haulout sites during their annual cycle (Thompson et al. 1996; Russel et al. 2013; Jones et al. 2015). Despite these differences in distribution patterns, the two species overlap both at haulout sites and in their marine habitat use, and this raises questions about the ecological interactions between the two species (Frungillo et al. 2014).

In recent years, the two species showed distinct trends in abundance, particularly in the core of their distribution range around the British Isles. Harbour seal numbers were increasing around the UK until the 2000's, then a number of colonies showed sharp declines in seal counts (up to -93% between 2000-2009) while others remained stable, and some continued increasing (SCOS 2015). Differences in observed trends were attributed to high site philopatry in harbour seals, and therefore limited connectivity between different regions (Sharples et al. 2012). The most recent abundance estimate gives a total number of 36,500 (95% CI 29,900-49,700) harbour seals in the UK (SCOS 2014). This figure is close to the estimated 39,100 harbour seal abundance in the Wadden Sea in 2014 (ICES 2015). In Ireland, the most recent estimate of 4,153 harbour seals dates back from 2003 (Cronin et al. 2003)

Grey seal counts around UK have also shown contrasting trends according to regions in recent years, but they were either stable or increasing (Lonergan et al. 2011;SCOS 2014). In 2013, a total population size of 111,600 (95% CI 92,000-137,900) grey seals were estimated around the UK (SCOS 2014). In Ireland, the grey seal breeding population estimate was 4,409-7,083 individuals in 2005 (Cronin et al. 2014). The species recolonized the Wadden Sea in the early 1990s after centuries of absence: a maximum of 3,062 grey seals were counted during the moulting season in 2012, with a pup production of 412 pups in 2013/2014 (Brasseur et al. 2010).

Grey and harbour seals in France are at the southern limit of their range in the eastern Atlantic (Vincent et al. 2005, Härkönen et al. 2007a, Hassani et al. 2010). This paper focuses on the seals' distribution in mainland France, i.e. not including grey and harbour seals in Saint-Pierre & Miquelon (French overseas territory), in the western Atlantic. Until the early 2000s, there was a rather distinct distribution pattern between grey seals and harbour seals. The two principal grey seal haulout sites are located in Brittany, in the western part of the English Channel: the *Molene archipelago* (MOL) and the *Sept Iles archipelago* (SEP, Figure 1), while the three harbour seal colonies are located in the middle and eastern parts of the English Channel: *baie du Mont-Saint-Michel* (BSM), *baie des Veys* (BDV), and *baie de Somme* (BDS, Figure 1). More recently, grey seals have been increasingly observed at haulout sites in the eastern English Channel, including BDS, *baie d'Authie* (BDA) and *Walde* (WAL). Other haulout sites in Brittany and the eastern English Channel are used by increasing numbers of seals, although not exceeding tens of individuals, and therefore have not been included in this study (Figure 1, 'minor sites'). During these last 15 years, a number of site-based telemetry studies were conducted in order to document the habitat use, movement patterns and activity rhythms of grey and harbour seals from several of these haulout sites along the French coasts (MOL, BSM, BDV and BDS; Vincent et al. 2005, Vincent et al. 2010, Huon et al. 2015). The results from these studies are all presented in this paper, in order to document the seals' habitat use and connectivity at a large scale.

We aimed to provide relevant information on the distribution and trends in abundance of grey and harbour seals in mainland France to local and national managers. Both seal species are protected at the national and European levels - all marine mammals are protected in France, while grey and

harbour seals are listed in Appendix II of the Habitat Directive (1992/43/EC). 'Abundance and distribution of harbour and grey seals' (OSPAR Descriptor M-3) and 'grey seal pup production' (OSPAR Descriptor M-5) are also to be reported by European member states for the assessment of the Good Environmental Status (GES) within the Marine Strategy Framework Directive (MSFD, 2008/56/EC). The objectives of this study were to describe seasonal patterns and inter-annual trends in seal relative abundance at the main haulout sites, at-sea distributions of grey and harbour seals at the southern limit of their range in the Northeast Atlantic, and their connectivity with other colonies. By combining information on movements at sea and trends in seal numbers at haulout sites, we aim to better describe the population dynamics of both species in French waters, and their links with other colonies. Data presented here were obtained from regular censuses conducted by NGOs, Nature Reserves, MPAs and local authorities on seal haulout sites along the French coast of the English Channel, telemetry studies (including limited previously published data and new unpublished data on both species), and aerial surveys conducted on the marine megafauna in the English Channel in 2012 and 2014. Outcomes from this work will provide managers with updated information on MSFD indicators and ecological processes that may affect these indicators in coming years.

2. Material and Methods

2.1 Censuses of seals at haulout sites

Census methods varied among study sites and species, and included visual observation from land, boat and aerial surveys over the haulout sites (Hassani et al. 2010; Vincent et al. 2005). In most cases, haulout sites are available to seals only at low tide. Timing of censuses (with respect to tidal conditions and time of the day) was adapted at each site to count seals during their peak haulout abundance. At all sites, censuses were scheduled at least once a month year-round, depending on weather. At some sites, especially in the northern part of the English Channel, censuses were more frequent, with up to one per day during the breeding season. During the breeding season, pups were counted separately. Given the low numbers of pups born (for both species at all sites), pup production was assumed to be accurately estimated from the number of pups counted during the censuses. For some study sites, censuses started in 1990, while for others they started only a few years ago. Counts of grey seals were classified into sex and age categories, however this was not possible for harbour seals.. Numbers reported here therefore include all sex and age classes for each species. Only haulout sites with counts > 50 during at least one quarter of the year were included in these analyses.

Seasonal variations were assessed for each haulout site by fitting Generalized Linear Mixed-effects Models (GLMM) to the census data. Two models of seal counts were compared, one only including year of the census as a random effect and another one including both year of census and quarter of the year as random effects. We considered Quarter 1 (January-March, corresponding to the moulting season of grey seals), Quarter 2 (April-June, post-moult for grey seals and pre-reproduction for harbour seals), Quarter 3 (July-September, moulting and breeding seasons for harbour seals) and Quarter 4 (October-December, breeding season of grey seals). When more than one census per month was available, the maximum seal number for the month was selected. The two models were fitted in R and compared with a Poisson ANOVA ('lme4' package, R, version 3.2.4, 2016).

Long-term trends in seal abundance at haulout sites were reported from 1990 (for the earliest available) to 2015. A Generalized Linear Model (GLM) was fitted to the yearly maximum seal count at each haulout site, and the rate of increase was assessed from the outputs of the model.

2.2 Aerial surveys at sea

SAMM (*Suivi Aérien de la Mégafaune Marine, Aerial Census of Marine Megafauna*) aerial surveys were conducted during winter 2012, summer 2012 and winter 2014. Visual observations were recorded for the main taxa of marine megafauna, i.e. marine mammals, seabirds, sea turtles, large fish and elasmobranchs. Sampling design was a zigzag pattern to optimize searching effort and to cover the different marine habitats of the English Channel. Survey platforms were high-wing aircrafts, equipped with bubble windows ; transects were flown at a target altitude of 180 m (600 feet) and a ground speed of 170 km/h (90 knots). Survey flights were only conducted during good weather conditions. For marine mammals, data were collected following a *distance sampling protocol* (Buckland et al., 2001). It is difficult to distinguish between harbour and grey seals when observed at sea.. Consequently, these two species were grouped as 'seals' for data analysis.

A density map was drawn from the distribution of seal observations within a grid encompassing the whole English Channel area. Grid cells were 0.1 degree wide. Observations were weighted by the number of transects crossing each cell to take account of the difference in sampling effort. Only cells with sampling effort were indicated on the map.

2.3 Telemetry tracking of seals

A total of 45 grey seals (34 from MOL and 11 from BDS) and 28 harbour seals (6 from BSM, 12 from BDV and 10 from BDS) were tracked for more than a month between 1999 and 2014 (Table 1). In 1999, 2002 and 2003, 15 grey seals fitted with Satellite Relay Data Loggers (SRDLs[1]), while from 2006 all other seals were fitted with Fastloc GPS/GSM tags[2] (all provided by Sea Mammal Research Unit, UK). SRDLs transmit data via Argos (Fedak *et al*., 2002) while GPS/GSM tags record Fastloc GPS locations (Wildtrack Telemetry Systems) and transmit them with behavioural data through the mobile phone network (McConnell *et al*., 2004). Seals were captured at their haulout sites with hoopnets, or in the water surrounding haulout sites using tangle nets. They were weighed to the nearest kilogram and anaesthetised with Zoletil (Virbac, France) at an intramuscular dose rate of approximately 0.8 mg kg^{-1} body weight (Baker et al., 1990).Tags were glued to the fur using quick-setting epoxy glue. Field work was conducted between April and July for grey seals (after their moulting period in March-April; Figure 1S, Supplementary data) and in October for harbour seals (moulting in August; Figure 2S, Supplementary data).

All locations were filtered following the methods of McConnell et al. (1992). For density maps, 20-minute interval locations were interpolated from the real data to avoid over-estimation of coastal locations, since seals spend less time underwater at these locations and can therefore record

[1] http://www.smru.st-and.ac.uk/Instrumentation/Downloads/ (SRDL overview)
[2] http://www.smru.st-and.ac.uk/Instrumentation/GPSPhoneTag/

a GPS location or send an Argos transmission more frequently. Density maps were drawn from the distribution of at-sea, interpolated locations within a 0.1 degree grid encompassing the whole English Channel area as well as the southern Celtic Sea. Locations were weighted by capture site (separately for grey and harbour seals) in order to take into account the number of days x seals of tracking available for each study site. This weighting did not involve the size of the haulouts however (estimated from the onshore counts).

Haulout data were obtained from the wet-dry sensor of the tags (Photopoulou et al. 2015) and used to identify clear changes in activity rhythm of the seals during the breeding season. When a seal was located at a known breeding colony where it spent more than half of its time hauled out (i.e., no deep diving during several weeks), it was considered as engaged in reproduction. An example of such behavioural change is illustrated in Figures 3S and 4S (Supplementary data). On three occasions, visual observation confirmed that the seal was indeed breeding on the identified colony.

3. Results

3.1 Seasonal variations in abundance at haulout sites.

Seasonal variations in seal numbers were significant for all harbour seal counts except those in BDV, while BDS and BDA showed significant seasonal variation (Table 2). Those seasonal variations in counts are illustrated in Figures 2 and 3 for grey and harbour seals respectively, by pooling counts from the last three years only (because of the global trends in seal numbers, see 3.2).

Although not statistically significant, seasonal variation in grey seal counts (from 2013 to 2015) were similar between the two western Channel study sites, which differed from all eastern Channel sites (Figure 2). In MOL and SEP, counts at haulout sites peaked during the first quarter of the year, and showed their minimum during the breeding season. In BDS and BDA, seasonal differences in seal counts were significant with the highest counts during the third quarter (Figure 2, $p<0.0001$, Table 2).

In BSM, BDV, BDS and BDA, the maximum relative abundance of harbour seals appeared from July to September (Figure 3). In BSM, BDS and BDA seasonal patterns in haulout counts were similar, with lower figures in the fourth and first quarters, intermediate in the second and maximum in the third quarter (Figure 3). The largest harbour seal colony in mainland France is located in BDS, where over 470 seals were counted in the summer 2015 with a pup production of 87. The second most important colony is at BDV, with a maximum of nearly 200 harbour seals hauling out in the bay during the same period, and 40 pups born. Both the BDA and BSM had a peak of 80 harbour seals in the summer 2015, with 1 and 23 pups respectively.

3.2 Inter-annual trends in seal counts at haulout sites

Inter-annual trends in seal counts at haulout sites were examined using the seasonal maximum counts, *i.e.* censuses performed during quarter 3 for all harbour seal haulout sites, and for eastern Channel grey seal (BDS and BDA; censuses in WAL were too recent to be included), and

during quarter 1 for MOL and SEP (cf. Section 3.1). Harbour seal numbers have increased at the four main colonies along the French coast since regular censuses began in the early 1990s (Figure 4). The rates of increase are close to +10%/year in BSM, +15%/year in BDV and BDS, and exceed +30%/year in BDA (Table 2). Grey seal numbers increased exponentially at all studied haulout areas (Figure 5). In Brittany (western English Channel) grey seal numbers increased by +5.8%/year and +8.3%/year (in MOL and SEP respectively, Table 2), but the rates of increase were much higher in the eastern English Channel with +21.4%, +49.2% and +49.0% per year in BDS, BDA and WAL respectively (Table 2). In addition to maximum seasonal counts (reported in Figure 5), an exceptional count of 642 grey seals was made in *Walde* (WAL) in February 2014, when a strong storm passed over southeast England. This number is not reported here as it was counted outside the season of usual maximum relative abundance.

3.3 Distribution at sea

Density maps based on telemetry data highlighted the coastal movements of harbour seals, and the high usage of estuaries in proximity to haulout sites (Figure 6). At BSM and BDV, most at-sea locations were obtained close to sandbanks with limited movements along the coasts, while harbour seals from BDS travelled along the coasts, away from the bay. Grey seals locations were also concentrated around haulout sites, both at MOL and BDS (Figure 7). However, the density map highlighted high density of at-sea locations around Goodwin Sands. To a lesser extent, coastal areas located around the Isles of Scilly, Cornwall (England) or Bay of Seine (France) were also used, although the latter was not being used as a haulout. Almost all grid cells in the western and eastern English Channel were visited by at least one of the 45 grey seals included in the study, while about half of the cells located in central Channel were not visited.

During aerial surveys of the English Channel, observations of seals at the sea surface were generally scarce. A total of 61 seals were observed during the 24,608 km of effort conducted under good observation conditions. Cumulative encounter rates were similar between summer and winter with a total of 0.16 and 0.20 sightings per 100 km respectively. In the western part of the English Channel, only few observations occurred around MOL and off BSM in the vicinity of known haulout sites (Figure 8). By contrast, a higher density of seals was recorded in the southern part of the North Sea where seals, probably mostly grey seals, were regularly observed swimming or resting at the sea surface in the Strait of Dover (particularly around Goodwin Sands) between the French and English coasts.

3.4 Individual movements and connectivity

Tag deployments provided 149±55 days (n=45) of tracking per grey seal and 127±47 days (n=28) of tracking per harbour seal (Figures 1S and 2S, Supplementary data), excluding the six seals that were tracked for less than a month. Harbour seal tracks terminated prior to the breeding season, except for one adult male in BSM (Figure 2S). Most grey seal tracks however covered the end of the breeding season or beginning of the moulting season, from October to January (Figure 1S).

Harbour seal telemetry data revealed no connectivity between colonies (Figure 9). In BSM, seals were tracked for 95±45 days (n=6) and they all remained in the tidal range of the bay. In BDV, the average track duration was higher (138±40 days; n=12) than at BSM, seals remained in the vicinity of their capture site, moving either north of the Bay (especially towards the St Marcouf islands) or along the coast, up to 30-70 km west or east (Figure 9). One seal did cross the English Channel and reached the English coast, but its tracking duration was shorter than a month and was not included in this study. Harbour seals from BDS were tracked for 134±53 days (n=10) and also showed coastal movements, up to a hundred km from the Bay south- or northwardly. Trips at sea did not exceed 15-20 km from the shore (Figure 9).

Almost all the harbour seals in this study hauled out exclusively in the bays where they were captured, only one captured in BDS used another haulout site during the tracking period, located in BDA (15 km from BDS).

Grey seals moved over much greater distances than harbour seals (Figure 10). The duration of grey seal tracking was 146±56 (n=34) and 161±50 (n=12) days on average from MOL and BDS, respectively. Tags deployed in western Brittany (MOL) showed regular movements to colonies in the southwest British Isles, especially the Isles of Scilly (200 km from MOL), Cornwall and western Ireland (500 to 800 km from their capture site). Some seals also moved to Wales (n=2), and to eastern Scotland (n=1; 1200 km from MOL). Seals hauled out at established grey seal colonies along these coasts. Fewer trips occurred eastwards in the English Channel, only four seals hauled out or passed close to SEP, two other seals spent some time around the Channel Islands. Only one animal tagged in Brittany visited the eastern English Channel, a young female that made a long exploratory trip to the Thames estuary (Figure 10). Among the 34 grey seals tagged at MOL, 35% remained within 50 km of MOL for the whole tracking duration, while the remainder crossed the English Channel and/or the Celtic Sea, with six seals hauling out in both Southwest UK and Ireland. Most of these movements occurred close to the breeding season. Breeding colonies used by the seals tracked from MOL included Islay (Scotland), Inishark and the Blasket islands (Ireland), the Isles of Scilly (England), and SEP and MOL (France) (Figure 10; breeding behaviour assessed from Figures 3S and 4S). Only one adult female tracked during the breeding period gave birth to a pup in SEP (confirmed by visual observation). Grey seals tagged at BDS (n=11) also showed long-range movements. In addition to using alternative haulout sites along the French coasts, seven of twelve seals regularly visited Goodwin Sands (Figure 10). Other haulout sites included those along the coasts of England (Norfolk) and Scotland (Scottish Borders), up to 750 km from BDS, and along the coast of the Dutch Wadden Sea, 600 km from BDS. Many of these colonies (in southern Scotland, Norfolk and the islands of the Wadden Sea) were visited during the breeding season (Figure 10). Only two seals (tracked for 111 and 157 days) did not show movement away from the French coast.

4. Discussion

4.1 Seasonal and inter-annual trends in counts at haulout sites

Over the last three years, harbour seal counts at haulout sites along the French coast were usually highest during the third quarter of the year, *i.e.* the breeding and moulting season. This was expected, as a higher proportion of seals haul out during these periods (*e.g*. Cunningham et al. 2010).

In other areas however the maximum number of harbour seals hauled out has been reported later in the year (*e.g*. mid October after the moult, Cronin et al. 2009).

In this study, long term trends in harbour seal haulout counts showed a consistent increase. Trends were very similar at BDS and BDV over the last 20 years, with rates of increase close to +15% per year. At BSM the rate of increase is lower (close to +10% per year currently) while it was much higher at BDA (+31% per year). Geographically, BDA is much closer to BDS than BDV, and some seals tracked from BDS hauled out at BDA. The very high rate of increase at BDA might therefore not result from local production but rather from frequent movements between BDA and BDS, with an increasing use of this haulout site potentially reflecting an expansion of the nearby haulout group of BDS.

Grey seal haulout counts also increased over the study period. At MOL and SEP, the rate of increase reached +6%/year and +8%/year respectively. Haulout counts were highly variable however, and the maximum number of seals was not always counted during the moulting season. Difficult weather conditions during winter precluded a number of censuses over the years, so that data were unavailable for the first quarter in some years at these two sites. A maximum abundance at haulout sites during the moulting season is expected in grey seals, and has also been observed at the Isles of Scilly (Leeney et al. 2010). Lower abundance during the breeding season is less expected though, as adult seals spend a larger proportion of time hauled out during reproduction than the rest of the year. At MOL, low counts at haulout sites are in accordance with observed movements to British or Irish grey seal colonies during the breeding season, as well as the very low pup production (potentially a few pups a year). At SEP, counts were the lowest during the fourth quarter, while 32 pups were counted at this site during the breeding season 2014. This suggests that, as in MOL, a significant proportion of the seals counted at this haulout site during the year breed elsewhere. In the eastern English Channel, grey seals have not reproduced successfully at any of the known haulout sites (although a few dead newborn pups were found in February in recent years) and the maximum number of seals hauled out was recorded during the third quarter, *i.e*. outside the breeding and moulting seasons. This maximum abundance during summer has already been reported at other sites in the North Sea (i.e. Thompson et al. 1996) and supports the hypothesis that these seals belong to a larger population, using a number of haulout sites during their annual cycle. The rates of increase of grey seals at BDS and BDA are much higher than in Brittany, with +21%/year at BDS and +49%/year at BDA and WAL. WAL is the closest site to the nearby Goodwin Sands (Kent, England), where many grey seals tracked from BDS hauled out. One striking example of this is the observation of 642 grey seals at WAL in February 2014, while a storm was hitting the coasts of Kent: it is suggested that a large proportion of the seals counted during the aerial surveys might not necessarily use the haulout sites censused along the French coast, but might instead use haulout sites located along the nearby English coast. Overall, given the observed connectivity with sites in the North Sea, increased haulout numbers of grey seals in the eastern English Channel are in accordance with the increasing grey seal numbers (and pup production) along the English and Dutch coasts of the North Sea (Brasseur et al. 2014, SCOS 2014).

At at least two sites (BDS and BDA), both species are now regularly observed together, whereas only harbour seals were present 10 to 15 years ago. The differences in rates of increase, the larger size of the grey seals and their wider distribution pattern, raise the question of potential inter-specific interaction. In the eastern English Channel as in other parts of their range, the two species' ranges overlap (Thompson et al. 1996, Jones et al. 2015). Ecological interactions between the two species have been documented by a number of studies (Bowen et al. 2003, Skeate et al. 2012,

Frungillo 2014). Harbour seals are also known to be more susceptible to high mortalities during Phocine Distemper Virus (PDV) outbreaks (Hall et al. 2006, Härkönen et al. 2007b). Svensson (2012) estimated that under moderate or strong inter-species competition, rates of increase in the Baltic grey seal population would be a direct function of the prevalence of PDV, as it would reduce the competitive strength of harbour seals. Monitoring the abundance of these two species is recommended to evaluate the degree of inter-species competition.

4.2 Distribution and connectivity

Harbour seals remained very coastal during the study period, staying within 20 km from the shoreline at the three study areas (BSM, BDV and BDS). Along the coast, their movements did not exceed 100 km from the haulout site where they were caught. Such coastal movements have been described in the eastern (McClintock et al. 2013, Blanchet et al. 2014, Jones et al. 2015) and western Atlantic (Bajzak et al. 2012). Distances covered by the seals from their haulout sites in this study (a few tens to a hundred kilometres) are similar to those reported elsewhere (Thompson et al. 1996, Härkönen et al. 2001, Cunningham et al. 2009, Bailey et al. 2014). However harbour seals, and especially juveniles, are known to cover greater distances in some areas, reaching several hundred or even thousand kilometres (*e.g*. Lowry et al. 2001, Björge et al. 2002, Dietz et al. 2013, Womble & Gende 2013). In this study the at-sea distribution was based on sub-adult and adult individuals.

Compared with harbour seals, grey seals showed a much wider distribution in the English Channel. Movements observed in the western English Channel were mostly transitional between MOL and other haulout sites located in the Southwest British Isles. In contrast, the majority of movements observed in the eastern English Channel represented central place foraging behaviour with long return-trips at haulout sites in BDS or Goodwin Sands. Grey seals around Ireland or the UK use offshore areas more so than harbour seals, with corridors between alternative haulout sites (Cronin et al. 2014; Jones et al. 2015). Offshore movements of grey seals have also been described in other parts of the species' range (Harvey et al. 2008, Austin et al. 2004; Breed et al. 2006). Although our results showed a lower density of seal locations in the middle part of the English Channel, no telemetry was conducted from the Sept Iles archipelago (SEP) nor from the Channel islands, where grey seals are known to haul out (Vincent *et al*., 2005). This gap in distribution may simply reflect the absence of tracking effort in this area. Because of the heavily biased ratio of males in our sample, we could not explore gender-based differences in distribution patterns, although such differences are known to occur in this species, potentially reducing intra-specific competition (Breed et al. 2006). Most adult females are known to leave MOL during the breeding season (Gerondeau et al., 2007), which is consistent with the very low pup production. While the number of tracked adult females from MOL was too low in our study to identify their breeding sites, one grey seal female photographed at MOL during summers 1998 to 2000 was previously photo-identified while breeding in the Blasket islands, western Ireland, in mid November 1996 (O. O'Cadhla & L. Hiby, pers. comm.).

Aerial surveys conducted in the English Channel in 2012 and 2014 did not detect a large number of seals in the middle or western part of the English Channel, but highlighted higher seal densities in the eastern English Channel/southern North Sea. Seals at sea can be cryptic because they spend the majority of their time diving, however aerial surveys provide a unique method for

monitoring the at-sea distribution of the population (Herr et al. 2009), while telemetry only allows short-term tracking of a limited number of individuals. The higher number of seals observed in the eastern English Channel could be due to the proximity of the largest harbour seal colony in BDS, but it is rather suggested, given the high densities recorded further north and/or further offshore, that most of these seal observations were grey seals. This also concurs with the large size of the seals reported by the observers.

Connectivity between haulout sites was very different for the two species. No movement between the three harbour seal haulouts in France was observed, and only one movement to the UK suggested by an incomplete track of a seal captured in BSM (not shown). Movements between distinct harbour seal haulout sites have been reported in the Kattegat (Dietz et al. 2013), the western British Isles and the North Sea, including between the Wash (eastern England) and BDS (Sharples et al. 2012). Local site fidelity is considered high however, and connectivity between harbour seal haulout sites low (Sharples et al. 2012).

The present study showed connectivity between grey seal haulout sites within the study area and outside, both during and out of the breeding season. More than half of the tracked grey seals moved across the English Channel. In the western Channel, connectivity was high between MOL and the Isles of Scilly/Cornwall as well as western Ireland, and to a lesser extent with Wales and southwest Scotland. In the eastern English Channel, the main connections were between BDS and southeast England and the Wadden Sea, and less frequently to southeast Scotland and the Dutch coast. All of the haulout sites where tracked seals were assumed to be engaged in reproduction are known breeding grey seal colonies (e.g. Isles of Scilly and Cornwall, Leeney et al. 2010; Horsey, Blakeney Point and Fast Castle, SCOS 2013; Blasket Islands and Inishark, Kiely & Myers, 1998, Cronin et al. 2014).

Strong breeding site fidelity in adult grey seals would explain genetic differentiation between colonies, despite extensive movements of individuals outside the breeding season (Allen et al. 1995). Although philopatry would be the general rule for female and male grey seals (Pomeroy et al. 1994, Twiss et al. 1994, Pomeroy et al. 2000), immigration from colonies in the UK outside the breeding season was suggested to explain the rapid increase in grey seal numbers in Germany (Abt et al. 2002). Density-dependent effects may lead to the establishment of new breeding colonies, as observed in the North Sea (Gaggiotti et al. 2002). Long range movements of grey seals shown here both during and outside the breeding season are therefore consistent with what was already known in this species in the core area of its range (Hammond et al. 1993, McConnell et al. 1999). Russell et al. (2013) showed that between 21% and 58% of breeding females around the British Isles used different regions for breeding and foraging. In our study such long distance movements between distinct haulout sites were not observed in all tracked grey seals, with twelve of thirty-four individuals tracked from MOL remaining within 50 km of their capture site during the whole tracking period, often including the breeding season. This highlights the large variability in individual movement patterns (Thompson et al. 1993) as well as the high degree of site fidelity, at least seasonally (Abt et al. 2002, Karlsson et al. 2005, Oksanen et al. 2012).

4.3 Implications for management units

The monitoring of distribution and abundance of grey and harbour seals by EU member states is now expected under the Marine Strategy Framework Directive (MSFD). Two seal indicators were set up by OSPAR, indicator M-3 ('Abundance and distribution of harbour and grey seals') and M-5 ('grey seal pup production'), to coordinate reporting at a large regional scale, deemed more suitable than national levels for mobile species, such as grey seals. It was suggested that grey seals around the British Isles should be considered as a single population (Hammond et al. 1993), hence indicator M-3 is calculated for a unique management unit for this species in Europe (ICES, 2016). Connectivity levels as well as frequencies of individual movements of grey seals tracked from the French haulout sites fully support the suggestion that seals in these areas belong to a larger population, centered around the British Isles. There seems however to be two very distinctive patterns of connectivity for the grey seal between the western and eastern part of the English Channel. The tagged animals showed frequent movements towards the southwest British Isles from MOL and the North Sea from BDS, whereas almost no exchange existed along the Channel itself suggesting that grey seals at the two extremities of the Channel belonged to distinct entities. Consistently, they also displayed very different seasonal patterns of abundance and long term trends in relative abundance. Grey seals observed at MOL clearly belong to a larger entity occupying the Irish and Celtic Seas, potentially reaching western Scotland, while grey seals of the eastern Channel belong to another entity widely ranging in the North Sea. As no such clear separation seems to exist in the northern British Isles (Hammond et al., 1993), this suggests that grey seal distribution around the British Isles follows a horse-shoe pattern, with extremities at the western and eastern English Channel, separated by a few hundred kilometres (Figure 11). This schematic view could be refined further when more data are available from the Irish Sea and the Channel Islands. However it illustrates the contrasting population dynamics and movement patterns observed from both ends of the Channel from the French coasts that suggest very limited connectivity. This situation is probably a consequence of the southern recolonization of the Northeast Atlantic grey seal population during the second half of the twentieth century (Duguy 1980, this study), following two avenues along the western seaboard of the British Isles and through the North Sea, respectively. Genetic studies could confirm this hypothesis and quantify the differentiation of breeding colonies at both ends of this horse-shoe distribution (Gaggiotti et al. 2002, Wood et al. 2011). In terms of management units, while keeping one management unit for grey seals in the Northeast Atlantic (outside the Baltic) makes sense at the international level, the current situation of the species in France would justify managing haulout sites from both sides of the Channel as distinct units. It is expected that numbers of grey seals in the eastern Channel would continue to increase rapidly and that the distribution of the species at sea would gradually expand throughout the Channel, given the continuous increase in grey seal numbers reported in the southern North Sea (Brasseur et al. 2014, SCOS 2014, ICES 2015).

Management units of harbour seals in Europe are much smaller than for the grey seal, based on the more limited movement patterns shown by the species (ICES 2014). One unit covers all haulout sites located along the French coasts of the English Channel. Most of these haulout sites seem to show similar trends in relative abundance, although some local disparity does exist. Genetic studies could be conducted in order to assess the degree of differentiation between the breeding colonies. Goodman (1998) identified six different units in European harbour seals, including one in eastern England, and showed that genetic differentiation increased with geographic distance. Huber et al. (2012) also showed that breeding harbour seal populations could be genetically distinct even when separated by distances similar to those between haulout sites along the French coast.

For both grey and harbour seals, most haulouts were located in Nature Reserves or Special Areas of Conservation (SACs), either in France or in the UK, Ireland and the Netherlands (Table 3). Virtually all harbour seal haulout locations were located in such protected areas (100% in BSM and BDS, 98% in BDV), all along the French coast. Grey seals tracked from MOL hauled out more in SACs than those tracked from BDS (93% and 66% respectively), and haulouts recorded in SACs outside France accounted for 16% and 21% respectively (Table 3).The time spent at sea (percentage of interpolated at-sea locations obtained from telemetry) lying within SACs and other Marine Protected Areas (such as marine National Parks and Offshore SACs) ranged from 51% to 77% for grey seals (BDS and MOL respectively) and 74% to 99% for harbour seals (BDS and BSM respectively, Table 3).These results highlight the relevance of the Natura 2000/MPA networks for the conservation of mobile species, and should encourage local and national conservation strategies from France, Ireland, the UK and the Netherlands to develop an international approach to the management of the grey seals in those protected areas. To our knowledge, this is the first time that these percentages of time spent in MPAs are estimated. While these figures could be expected for the comparatively more sedentary harbour seals, they highlight the relevance of such MPAs for both haulout and marine habitat use for the more mobile grey seals.

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List of Figures

Fig 1: Map of all grey seal (red) and harbour seal (green) haulout sites in metropolitan France. Circles indicate haulout sites where the seasonal maximum number of seals exceeds 50 individuals. Stars indicate smaller haulout sites used by fewer seals, not detailed in this study. Symbols surrounded by thick, black circles show the seal colonies where telemetry was conducted. Marine Protected Areas are also shown, including Special Areas of Conservation and Marine National Parks. Nature Reserves are not visible but also encompass some haulout sites, in SEP, BDS and BDV for instance. Haulout sites are: *Molene archipelago* (MOL), *Sept iles archipelago* (SEP), *baie du Mont-Saint-Michel* (BSM), *baie des Veys* (BDV), *baie de Somme* (BDS), *baie d'Authie* (BDA) and *Walde* (WAL).

Fig 2: Seasonal variations in harbour seal counts at haulout sites, according to quarters of the year. Up to one maximum count per month is included for years 2013, 2014 and 2015 (see Table 1 for the number of counts per site and species). Quarter 1 = January to March; Quarter 2 = April to June; Quarter 3 = July to September; Quarter 4 = October to December.

Fig 3: Seasonal variations in grey seal counts at haulout sites, according to quarters of the year. Up to one maximum count per month is included for years 2013, 2014 and 2015 (see Table 1 for the number of counts per site and species). Quarter 1 = January to March; Quarter 2 = April to June; Quarter 3 = July to September; Quarter 4 = October to December.

Fig 4: Maximum yearly counts (dots) of harbour seals and associated trends (lines) in the four main study sites.

Fig 5: Maximum yearly counts (dots) of grey seals and associated trends (lines) in the four main study sites.

Fig 6: Density of harbour seal locations (per grid cell) obtained by telemetry from 2006 to 2010, from individuals captured in BSM, BDV and BDS.

Fig 7: Density of grey seal locations (per grid cell) obtained by telemetry from 1999 to 2013, from individuals captured in MOL and BDS.

Fig 8: Densities of seal observations (per grid cell) from the aerial surveys conducted in 2012 and 2014: absence of transect is shown by the absence of grid cells while seal densities are given as a number of seals observed in a given grid divided by the number of flight passages per grid cell. The seal species are not detailed in these aerial surveys.

Fig 9: Harbour seal telemetry tracks from BSM (6 individuals tracked in 2006 and 2007, in purple), BDV (12 individuals tracked in 2007 and 2008, in blue) and BDS (10 individuals tracked in 2010, in orange). Red dots indicate haulout locations of the seals. Seals tracked for less than a month are not shown here.

Fig 10: Grey seal telemetry tracks from MOL (15 individuals tracked by Argos tags from 1999 to 2003, in light blue, and 19 individuals tracked by GPS/GSM tags from 2010 to 2013, in dark blue) and BDS (11 individuals tracked in 2012, in green). Red dots indicate haulout locations of the seals. Thick, red circles indicate breeding locations, as suggested from the activity budget of the seals (see Figures 3S and 4S, supplementary data).

Fig 11: Schematic view of the suggested horse-shoe distribution pattern of grey seals around the British Isles. Grey seals' real distribution is wider than the orange shape shown here. Black arrows indicate areas of recent grey seal recolonization and/or high rates of increase in the southern North Sea and eastern Channel.

Table 1: Number of seals tagged by species, sex, location and year, with deployment details (tag type and mean tracking duration) as well as reference when tracking data was previously published.

Year of deployment	Species	Tag type	Number of tags	Sex ratio (M:F)	Mean tag lifespan (days)	Tagging locations		Reference
						Full name	Code	
1999	grey seals	SRDL	5	3:2	89	Molene archipelago	MOL	Vincent et al. (2005)
2002	grey seals	SRDL	8	6:2	119	Molene archipelago	MOL	Vincent et al. (2005)
2003	grey seals	SRDL	2	0:2	128	Molene archipelago	MOL	Vincent et al. (2005)
2006	harbour seals	GPS/GSM	4	2:2	68	Baie du Mont Saint-Michel	BSM	Vincent et al. (2010)
2007	harbour seals	GPS/GSM	2	1:1	148	Baie du Mont Saint-Michel	BSM	Vincent et al. (2010)
2007	harbour seals	GPS/GSM	7	4:3	142	Baie des Veys	BDV	Vincent et al. (2010)
2008	harbour seals	GPS/GSM	5	5:0	132	Baie des Veys	BDV	*unpublished*
2008	harbour seals	GPS/GSM	10	9:1	134	Baie de Somme	BDS	*unpublished*
2010	grey seals	GPS/GSM	2	2:0	57	Molene archipelago	MOL	Huon et al (2015)
2011	grey seals	GPS/GSM	8	6:2	182	Molene archipelago	MOL	Huon et al (2015)
2012	grey seals	GPS/GSM	2	2:0	184	Molene archipelago	MOL	Huon et al (2015)
2012	grey seals	GPS/GSM	11	11:0	161	Baie de Somme	BDS	*unpublished*
2013	grey seals	GPS/GSM	7	6:1	196	Molene archipelago	MOL	Huon et al (2015)

Table 2: Inter-annual trends and seasonal variations in seal numbers obtained from haulout counts. Haulout sites are: *Molene archipelago* (MOL), *Sept iles archipelago* (SEP), *baie du Mont-Saint-Michel* (BSM), *baie des Veys* (BDV), *baie de Somme* (BDS), *baie d'Authie* (BDA) and *Walde* (WAL). The total number (N) of counts included in the GLM or GLMM respectively are indicated, as well as the p-value of the selected models (in bold, significant trends or seasonal variations, respectively).

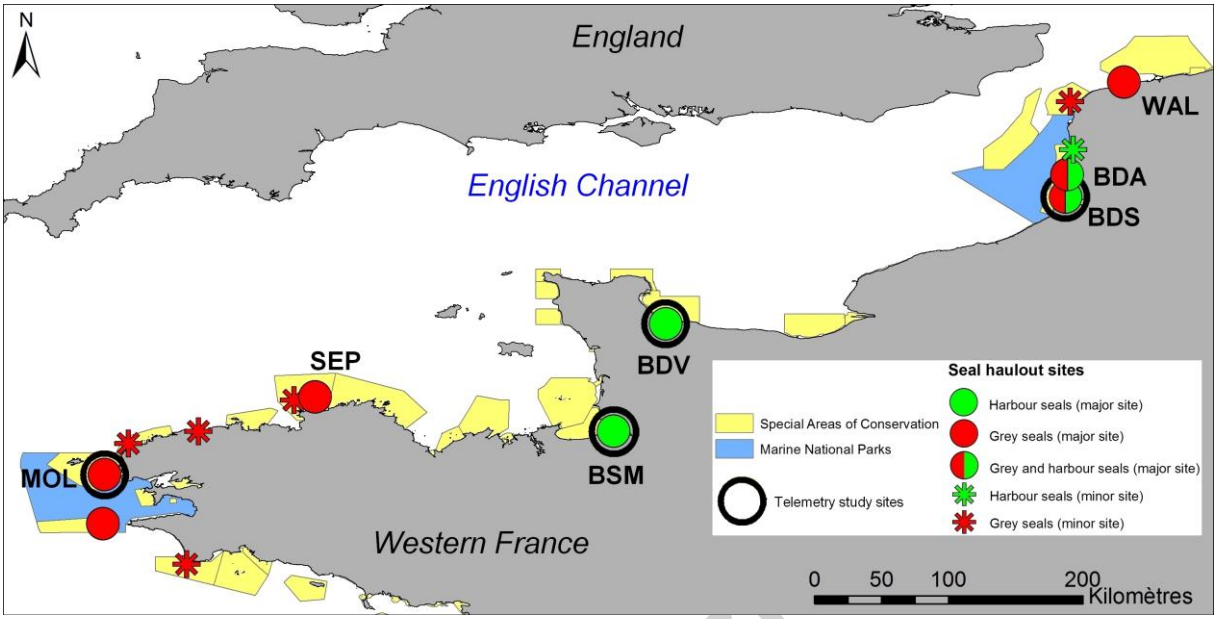
Haulout site	Species	Study period	Inter-annual trends			Seasonal variations	
			N counts	p-value	Rate of increase	N counts	p-value
MOL	Grey seals	1992-2015	17	**p < 0.0001**	+ 5.8% /yr	25	p = 0.421
SEP	Grey seals	1999-2015	15	**p = 0.002**	+ 8.3% /yr	32	p = 0.320
BSM	Harbour seals	1990-2015*	24	**p < 0.0001**	+ 9.7% /yr	32	**p < 0.0001**
BDV	Harbour seals	1990-2015	26	**p < 0.0001**	+ 15.0% /yr	26	p = 0.509
BDS	Harbour seals	1990-2015	26	**p < 0.0001**	+ 14.6% /yr	36	**p < 0.0001**
	Grey seals	1990-2015	26	**p < 0.0001**	+ 21.4% /yr	36	**p < 0.0001**
BDA	Harbour seals	2001-2015	15	**p < 0.0001**	+ 30.9% /yr	36	**p < 0.0001**
	Grey seals	2003-2015	13	**p < 0.0001**	+ 49.2% /yr	33	**p < 0.0001**
WAL	Grey seals	2012-2015	4	**p = 0.030**	+ 49.0% /yr	36	p = 0.145

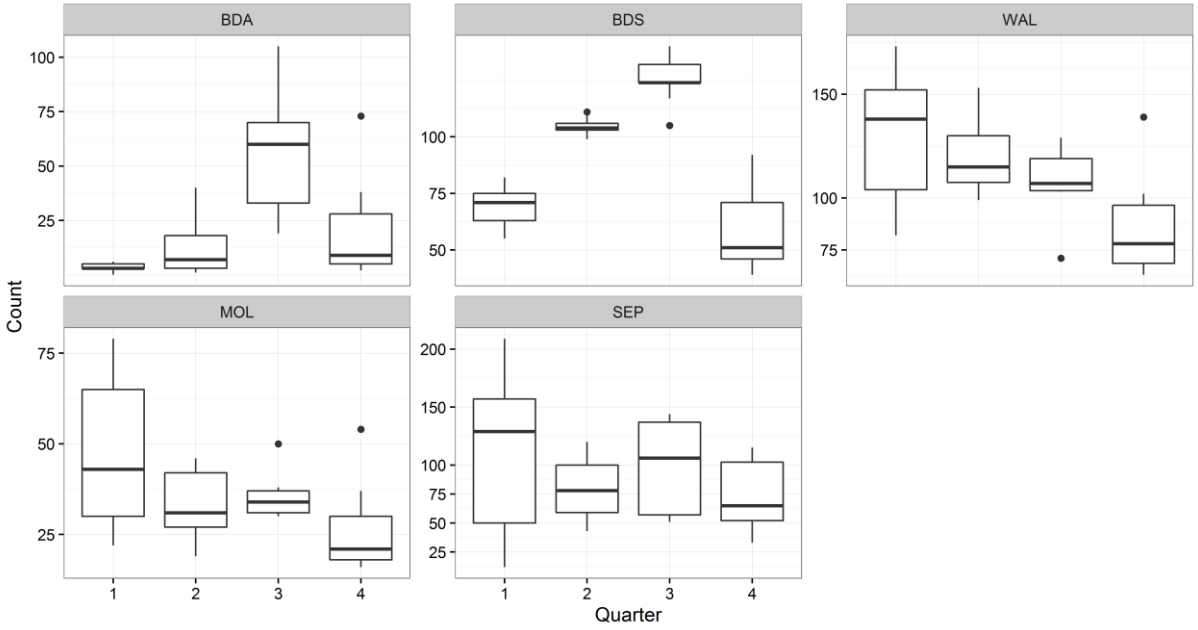
* With two missing years in 2010-2011

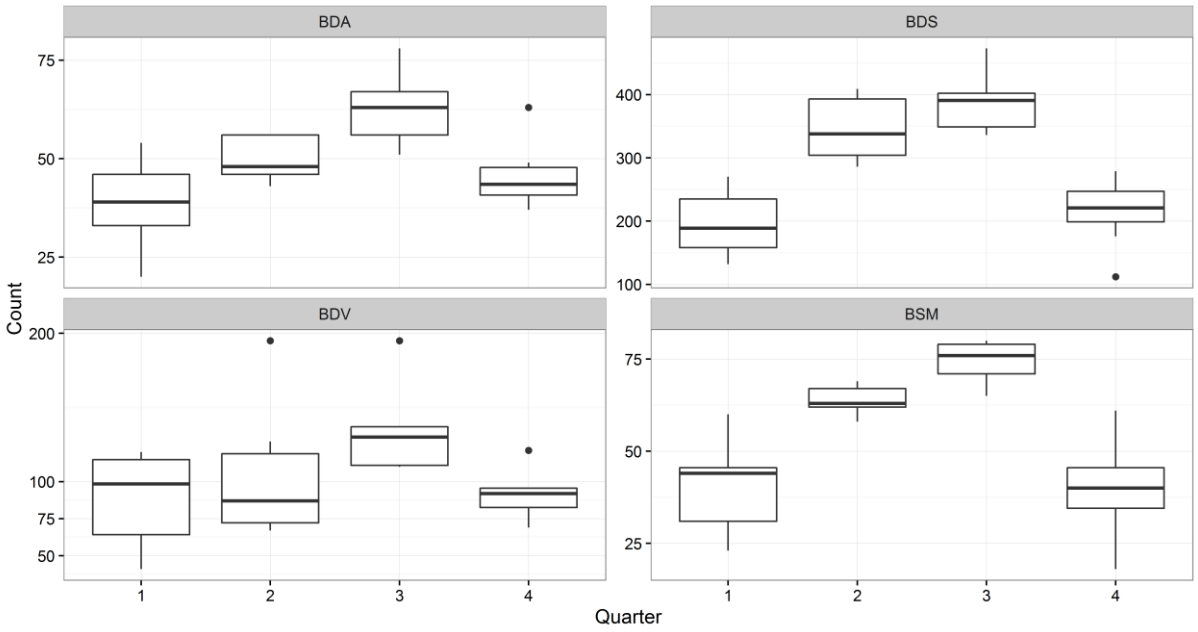
Table 3: Percentage of haulouts and percentage of at-sea (interpolated) locations of the tracked seals of both species located in Special Areas of Conservation (SACs) or other Marine Protected Areas (MPAs, such as marine national parks and offshore SACs) in different European countries.

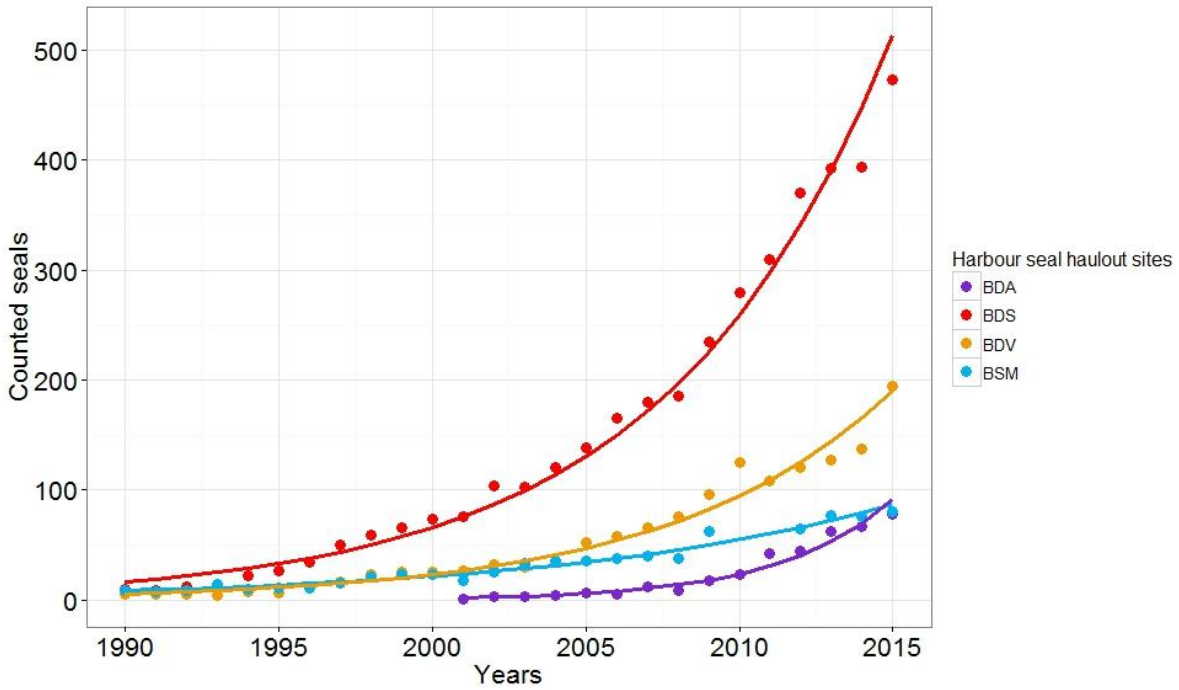
Percentages of tracking locations in SACs and MPAs		Harbour seals			Grey seals	
		BSM	BDV	BDS	MOL	BDS
Haulout events	France	100.0%	98.2%	100.0%	77.4%	45.3%
	UK	-	-	-	3.2%	9.1%
	Ireland	-	-	-	12.5%	-
	Netherlands	-	-	-	-	11.8%
	TOTAL	100.0%	98.2%	100.0%	93.1%	66.2%
At-sea (interpolated) locations	France	98.9%	74.1%	86.3%	72.4%	41.8%
	UK	-	-	-	2.5%	3.6%
	Ireland	-	-	-	2.0%	-

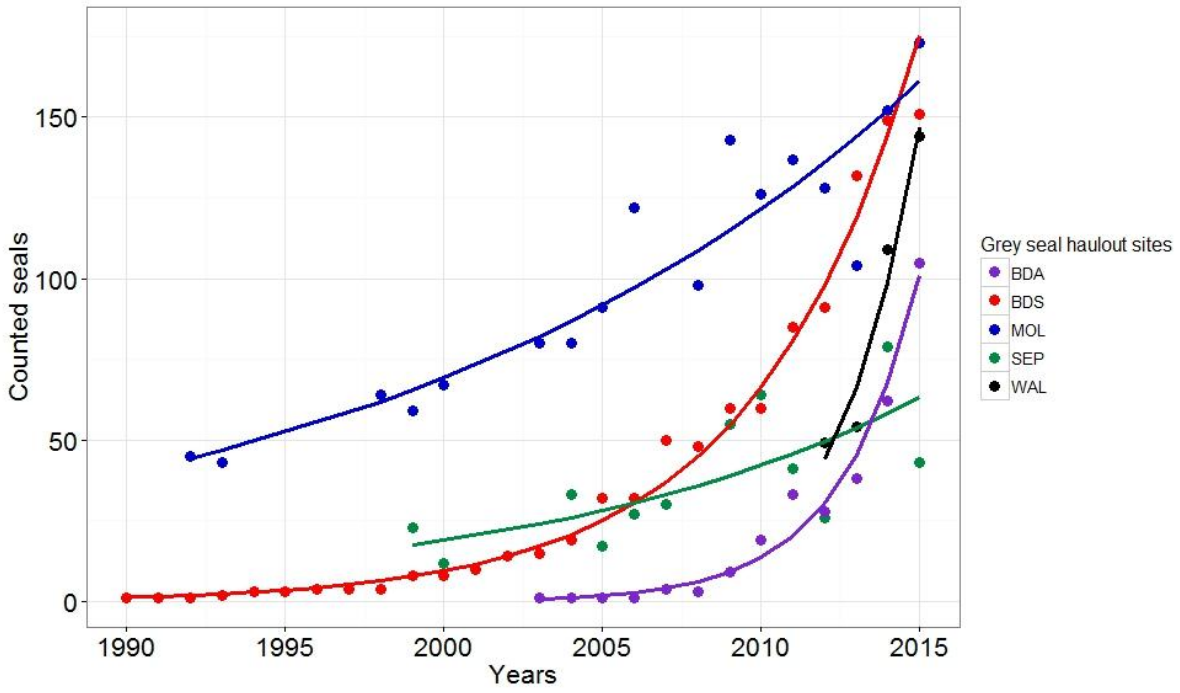
Netherlands	-	-	-	-	5.8%
TOTAL	98.9%	74.1%	86.3%	76.9%	51.2%

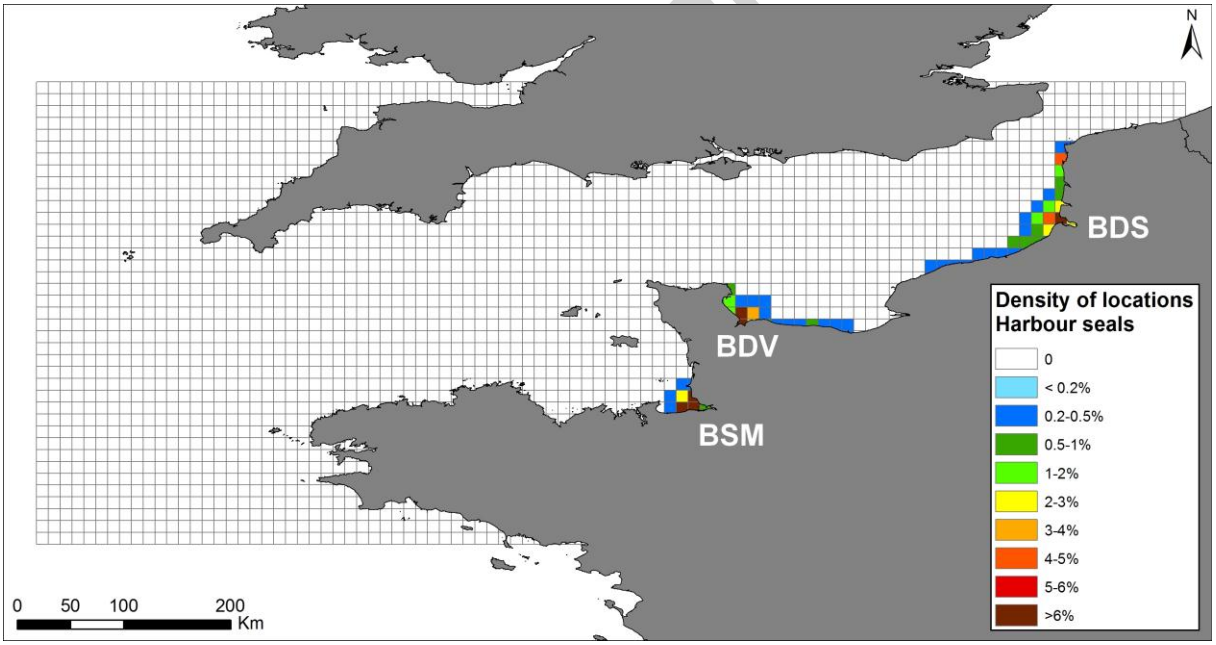


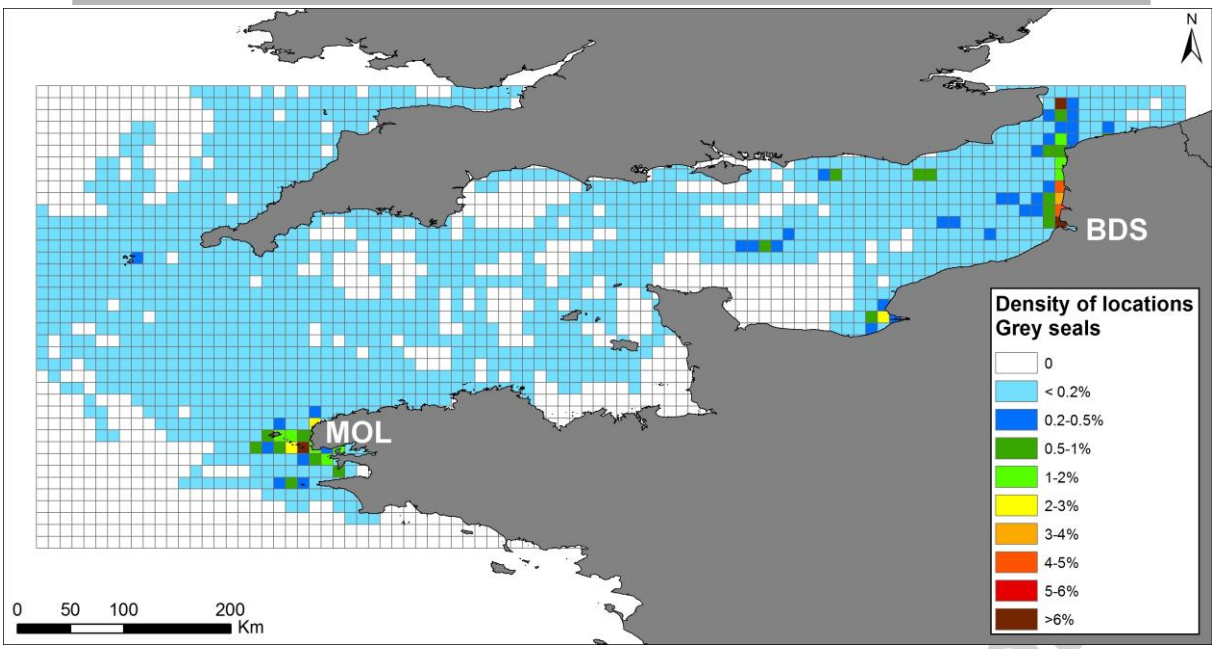


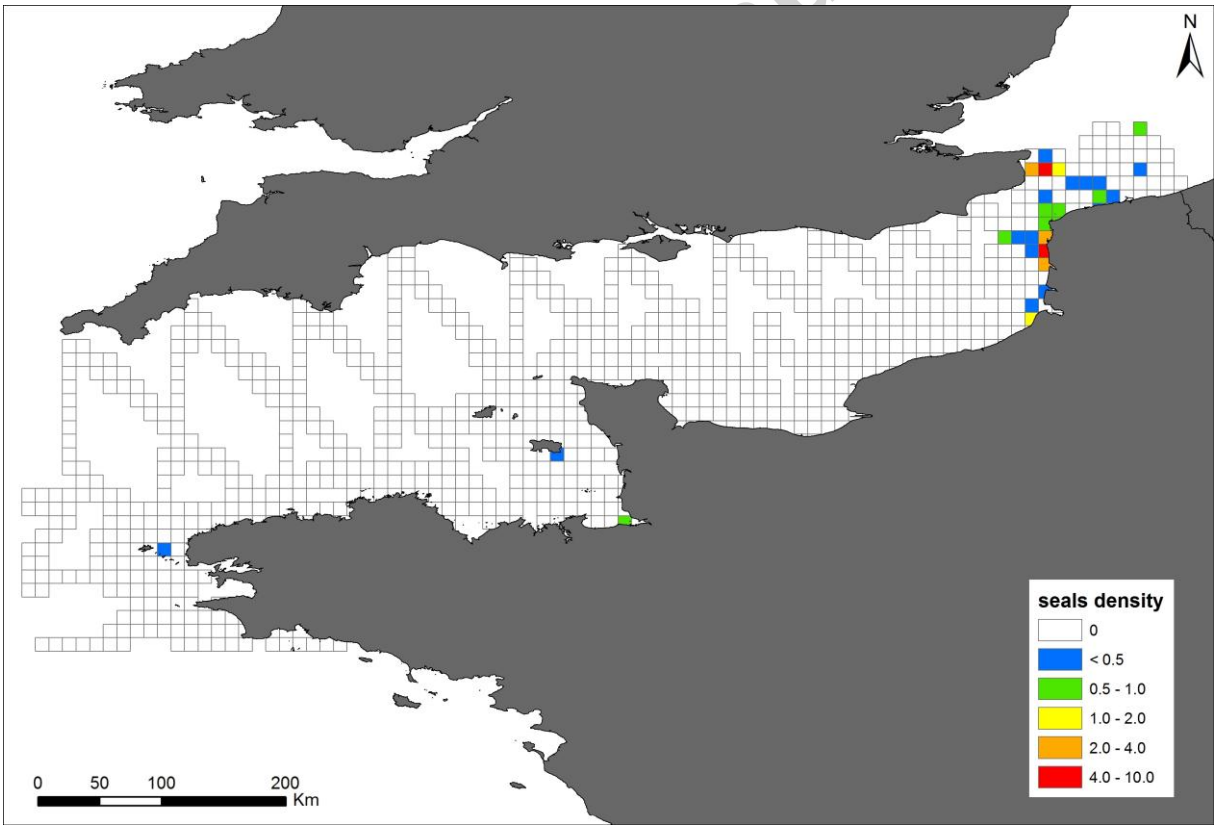

BDA
BDS
BDV
BSM
Count
Quarter
75
50
25
400
300
200
100
1
2
3
4


Counted seals
Years
Harbour seal haulout sites
BDA
BDS
BDV
BSM
500
400
300
200
100
0
1990
1995
2000
2005
2010
2015






N
BDS
MOL
Density of locations
Grey seals
0
< 0.2%
0.2-0.5%
0.5-1%
1-2%
2-3%
3-4%
4-5%
5-6%
>6%
0 50 100 200
Km


N
seals density
0
< 0.5
0.5 - 1.0
1.0 - 2.0
2.0 - 4.0
4.0 - 10.0
0 50 100 200
Km